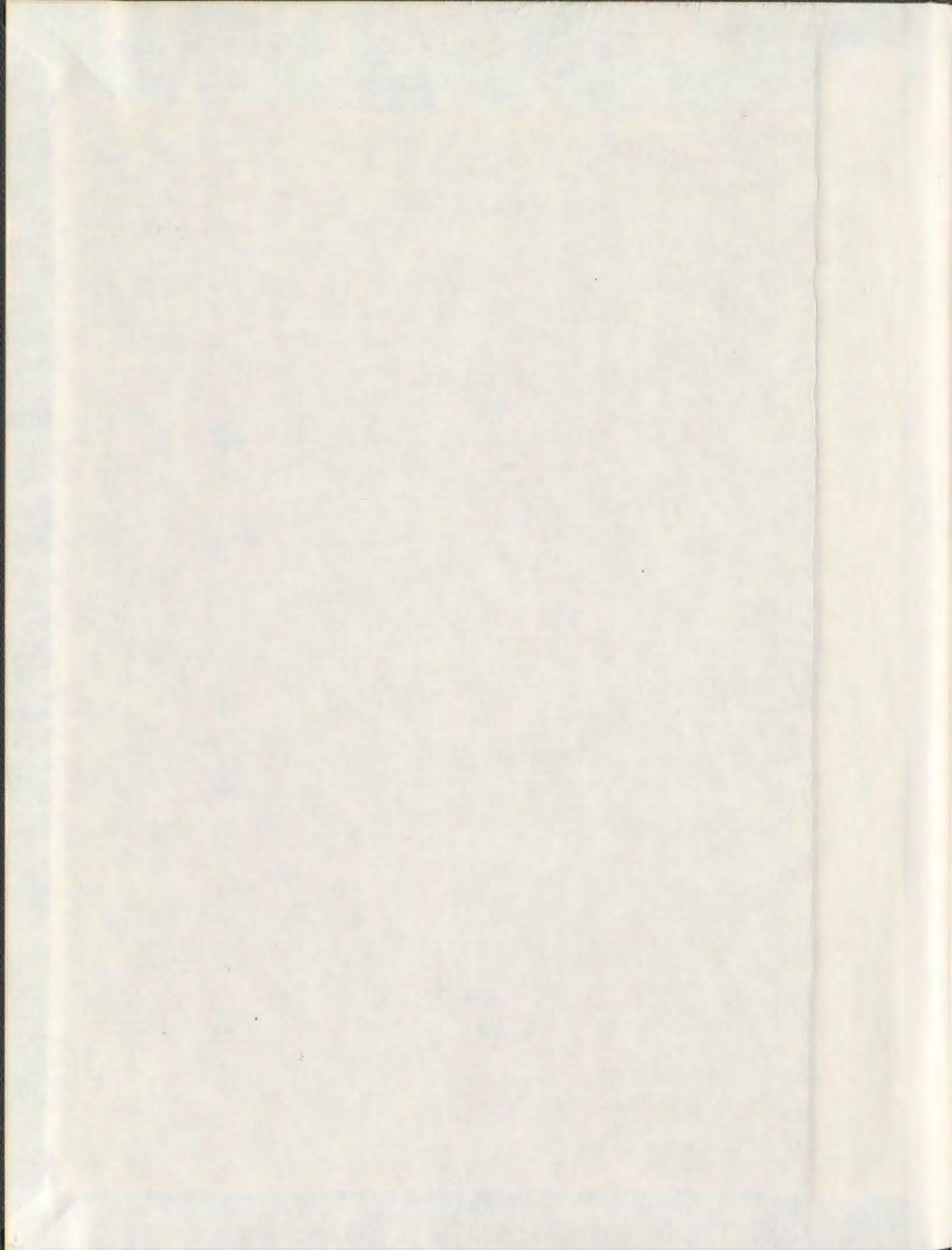


EVOLUTION DYNAMICS OF BIOLOGICAL SYSTEMS  
WITH SPATIAL AND TEMPORAL HETEROGENEITIES

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# Evolution Dynamics of Biological Systems with Spatial and Temporal Heterogeneities

by

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# Abstract

Biological invasion is an important phenomenon in ecology. Mathematical studies of biological invasion involve reaction-diffusion equations which consider continuous reproduction and random movements of species, and integro-differential/difference equations which describe population dispersal via various types of dispersal kernels. The purpose of this thesis is to investigate the spatial dynamics of some reaction-diffusion and integro-differential/difference population models with spatial and temporal heterogeneities.

Introduction and overview of mathematical investigation of biological invasions are presented in Chapter 1.

In Chapter 2, we present some terminologies and theorems which are based on the theories of global attractors, uniform persistence, monotone dynamical systems, asymptotic speeds of spread and traveling waves.

Chapter 3 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 traveling waves for monotone periodic semiflows, we establish the existence of the spreading speed  $c^*$  and the nonexistence of time-periodic traveling wave solutions with the wave speed  $c < c^*$ . In the autonomous case, we further use the method of upper and lower solutions to prove the existence of monotone traveling waves with the wave speed  $c \geq c^*$ , which implies that the spreading speed coincides with the minimal wave speed for monotone traveling waves.

In Chapter 4, we investigate a non-local periodic reaction-diffusion population

model with stage-structure. In the case of unbounded spatial domain, we establish the existence of the asymptotic speed of spread and show that it coincides with the minimal wave speed for monotone time-periodic traveling waves. In the case of bounded spatial domain, we obtain a threshold result on the global attractivity of either zero or a positive periodic solution.

In Chapter 5, we consider a class of discrete-time population models in a periodic lattice habitat. When the recruitment function is monotone, we show that the spreading speeds coincide with the minimal wave speeds for spatially periodic traveling waves in the positive and negative directions, by appealing to the theory of spreading speeds and spatially periodic traveling waves for monotone systems in periodic environments. When the recruitment function is not monotone, we also obtain the existence and formula of the spreading speeds via the comparison method. Moreover, we prove the existence of spatially periodic traveling waves by using the Schauder fixed point theorem.

In Chapter 6, we consider a class of cooperative reaction-diffusion systems, in which one population (or subpopulation) diffuses while the other is sedentary. We use the shooting method to prove the existence of the bistable traveling wave, and then obtain its global attractivity with phase shift and uniqueness (up to translation) via the dynamical system approach. The results are applied to some specific examples of reaction-diffusion population models.

A brief summary of this thesis and some future work are presented in Chapter 7.

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# Chapter 1

## Introduction

Biological invasion happens when an organism or any sort of organism arrives somewhere beyond its previous range [89]. As organisms migrate or disperse by walking, flying, swimming, or being transported by wind or flowing water, biological invasions occur almost everywhere on the surface of the earth that we live on, and are now recognized as one of the most important components of global environment change (e.g., [2, 21, 64, 65, 70, 89]). Although natural invasions occur from minor changes in a small range to major migration across continents, most invasions are due to human induced changes to ecosystems, such as climate change, land-use change, overfishing, chemical pollution, physical destruction of the environment (agriculture, forestry, industrial development and human settlement), fires, the rise in  $CO_2$ , the expansion of human populations, and so on [64]. While human activities are causing more and more invasions, invasions have also been greatly influencing the global environment. They help to establish many aggressive species across the globe, but at the mean time, threaten or cause extinction of native species in some environments, and also increase the spread of infectious diseases (of humans, animals and plants) across the globe. To some extent, biological invasions alter population and community structure of native ecosystems, and their functioning and long-run economic potential as well. The consequences of biological invasions can be clearly seen in New Zealand (e.g., [2, 21, 64]). With no native mammals except bats and seals, New Zealand has been

dramatically altered by the colonization. Lots of native species are extinct and more than hundreds of native species are threatened, while human beings, many animals (e.g., rats, pigs, mice, red deer, and so on) and plants have been introduced and naturalized (e.g., over 25,000 alien plant species being imported during the past 200 years and at least 2,000 of them having been naturalized).

Biological invasions have been attracting increasing attention of biologists, ecologists, mathematicians, and so on. Many mathematical models have been established for the invasion process. The mathematical analysis of these models help determine the level and rate of alien invasions and understand the factors that control invasions and the consequences of invasions for ecosystems. Reaction-diffusion models are the first mathematical models that describe invasions of species. Let  $u(t, x)$  be the density of a population at location  $x \in \Omega$  at time  $t$ , where  $\Omega$  is the habitat. In 1937, Fisher [23] first proposed a one-dimensional equation for population genetics:

$$u_t = u_{xx} + u(1 - u), \quad x \in \mathbb{R}, \quad t \geq 0, \quad (1.1)$$

where  $u(1 - u)$  is the recruitment function and diffusion is only considered along  $x$ -axis. This model describes the process of spatial spread when mutant individuals with higher adaptability appear in a population. Meanwhile, Kolmogorov, Petrovsky and Picoounov [42] considered a similar equation with  $u(1 - u)$  replaced by a function  $f(u)$  having two zeros (e.g.,  $f(0) = 0$ ,  $f(1) = 0$ ), that is,

$$u_t = u_{xx} + f(u), \quad x \in \mathbb{R}, \quad t \geq 0. \quad (1.2)$$

This model has been extended to many higher dimensional models to describe the diffusion for many species and more factors (death of populations, age-structure of a population, competition or cooperation between species, etc) have been considered in the models [4, 5, 6, 12, 13, 14, 19, 20, 22, 23, 31, 32, 35, 39, 51, 42, 57, 65, 67, 70, 71, 72, 75, 78, 82, 90, 91, 92, 94, 97, 98]. By reaction-diffusion equations, the reproduction and diffusion are assumed to occur continuously and the diffusion is subject to random dispersal [40]. Recently, many new models in different mathematical frameworks have been developed to describe more complex features in real-ecosystems, [7, 8, 10, 15,

24, 30, 38, 40, 41, 44, 49, 54, 55, 59, 60, 67, 68, 69, 70, 81, 84, 85, 86, 87, 88, 98]. Among these models, integro-differential/difference equations have been fascinating and using a dispersal kernel to describe the spatial movement of a population is more realistic in cases of long distance dispersal. The simple cases of these models are

$$\frac{\partial u(t, x)}{\partial t} = F(u(t, x)) + \int_{\Omega} k(x, y)u(t, y)dy,$$

and

$$u_{n+1}(x) = \int_{\Omega} k(x, y)F(u_n(y))dy, \quad n \geq 1,$$

where  $F(u)$  is the recruitment function,  $k(x, y)$  is the dispersal kernel that prescribes the proportion of the population leaving from location  $y$  to location  $x$ , and  $u_n(x)$  is the density of the population of the  $n$ -th generation. These models and their improvements have been extensively used to model the disease spreading process and the dispersal process in ecosystems such as streams [24, 38, 40, 41, 44, 49, 55, 59, 60, 67, 68, 81, 87, 88].

A traveling wave is a special solution of the form  $u(t, x) = U(x - ct)$ , where  $c$  is the wave speed. The profile  $U(\cdot)$  travels in the speed  $c$  and it is invariant with respect to translation in space (see Figure 1.1). Fisher [23] showed that for (1.1), the traveling wave solution  $u(t, x) = U(x - ct)$  exists if and only if  $|c| \geq c_{min} = 2$ . Kolmogorov et al. [42] established similar results for (1.2). After their pioneering work, traveling waves have been attracting increasing attention. Extensive investigations of traveling waves for a variety of evolution systems can be found in [5, 6, 19, 38, 47, 52, 53, 59, 69, 78, 88, 90, 94].

A time-periodic traveling wave is a solution of the form  $u(t, x) = U(t, x - ct)$  with  $U(t, \xi) = U(t + T, \xi)$  for some  $T > 0$  and for all  $t \geq 0, \xi \in \mathbb{R}$ . It has been studied for many systems in which some terms are periodic with respect to the time  $t$  [52]. In this thesis, to simplify the notation without any confusion, we call a time-periodic traveling wave "a periodic traveling wave". A spatially periodic traveling wave is a solution of the form  $u(t, x) = W(x, x - ct)$  with  $W(x, s) = W(x + L, s)$  for some  $L > 0$  and for all  $x \in \mathbb{R}, s \in \mathbb{R}$ . This type of special solution always occurs from systems in

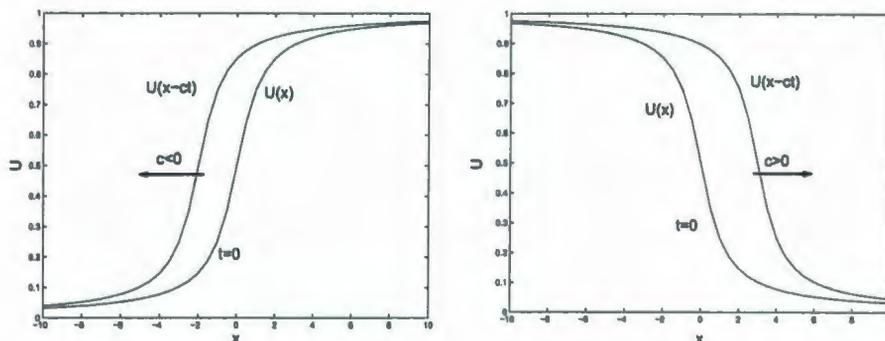


Figure 1.1: Traveling waves for (1.1) ( $|c| > 2$ ).

periodic environments. Weinberger [86] investigated the existence and minimal wave speed of spatially periodic traveling waves for monotone maps in periodic habitats. Berestycki, Hamel and Roques [8] investigated the existence of pulsating traveling waves, which actually correspond to spatially periodic traveling waves, for a type of reaction-diffusion equations in a periodically fragmented environment. Guo and Hamel [30] then studied pulsating traveling waves for discrete periodic monostable equations.

The invasion speed is a fundamental characteristic of biological invasions, since it describes the speed at which the geographic range of the population expands, and in particular, it can help estimate the rapidity of disease spread ([34, 43, 45]) (see Figure 1.2). In mathematical models, we describe the invasion speed by the asymptotic speed of spread (in short, the spreading speed).

The concept of the spreading speed was first introduced by Aronson and Weinberger [5] for reaction-diffusion equations. Aronson and Weinberger [5, 6] studied a class of reaction-diffusion equations and proved the following result.

**Theorem 1.0.1** *Let  $u(t, x)$  be a nonzero solution of (1.2) with  $u(0, x)$  having compact support. Then the following two statements are valid:*

$$(i) \quad \lim_{t \rightarrow \infty, |x| \geq ct} u(t, x) = 0, \quad \forall c > 2;$$

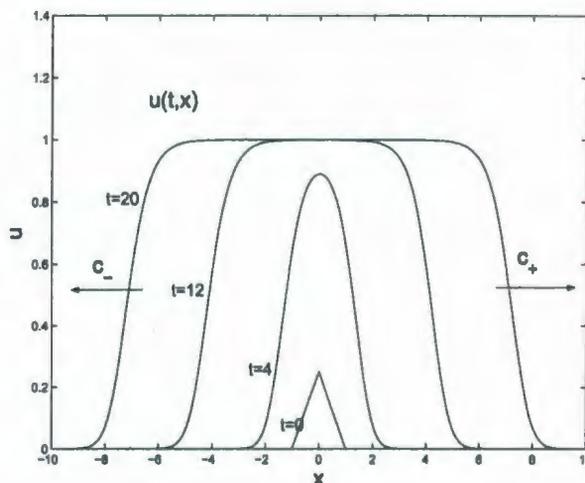


Figure 1.2: Evolution of a solution to (1.1) with initial data having compact support.

$$(ii) \quad \lim_{t \rightarrow \infty, |x| \leq ct} u(t, x) = 1, \quad \forall c \in (0, 2).$$

They call  $c^* = 2$  the asymptotic speed of spread for (1.2). Actually, by Theorem 1.0.1, we can easily have two observations, which can help understand the meaning of the spreading speed. The first observation states that if  $u(t, x)$  satisfies the properties (i) and (ii) above, it then follows that for any  $x_0 \in \mathbb{R}$ , we have

$$(a) \quad \lim_{t \rightarrow \infty} u(t, x_0 \pm ct) = 0, \quad \forall c > 2;$$

$$(b) \quad \lim_{t \rightarrow \infty} u(t, x_0 \pm ct) = 1, \quad \forall c \in (0, 2).$$

We can easily see from this observation that if one leaves  $x_0$  at a speed exceeding  $c^*$ , one will outrun the population, whereas if moving at a speed less than  $c^*$ , the population will overtake the observer [76]. The second observation is that if  $u(t, x)$  satisfies properties (i) and (ii), then for any given  $\rho \in (0, 1)$ , it follows that

$$\lim_{t \rightarrow \infty} \frac{x_{\pm}^{\rho}(t)}{t} = \pm 2,$$

uniformly for  $\rho$  in any compact interval contained in  $(0, 1)$ , where  $x_+^{\rho}(t)$  and  $x_-^{\rho}(t)$  are

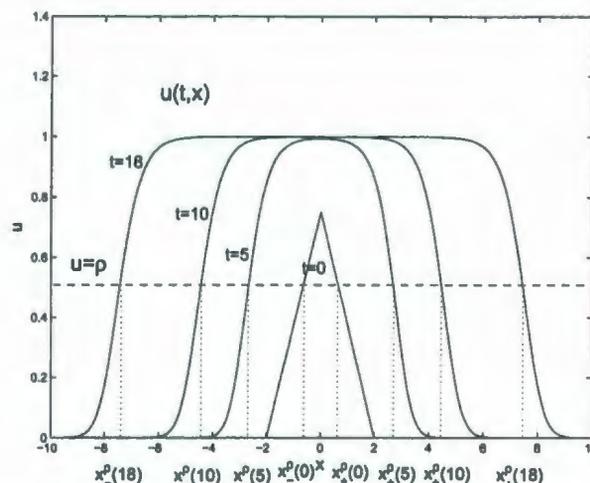


Figure 1.3: Evolution of a solution to (1.1).

the most right and left points with  $u(t, x_{\pm}^{\rho}(t)) = \rho$ , respectively (see Figure 1.3). Thus, if we consider that  $x_{\pm}^{\rho}(t)$  as the distances that the population moves (to the right and left) during the time interval  $[0, t]$ , it is natural to call  $c^* = 2$  as the asymptotic speed of spread. In fact, Aronson and Weinberger [5, 6] also confirmed Fisher's conjecture in [23], which stated that  $c_{min} = 2$  is the asymptotic speed of propagation of the advantageous gene.

After their early works, the spreading speed has been investigated extensively. Weinberger [85, 86] and Lui [54] studied the spreading speeds of monotone maps in homogeneous and periodic habitats. Li, Weinberger and Lewis [50] studied the spreading speed for reaction-diffusion systems with positive diffusion coefficients. Liang and Zhao [53] developed the theory of the spreading speed for discrete and continuous monotone semiflows. Liang, Yi and Zhao [52] further generalized this theory to monotone periodic semiflows. Spreading speeds for non-monotone systems have also been studied in [38, 76, 78]. Many other works about the spreading speeds can also be found in [5, 6, 20, 38, 47, 49, 50, 52, 53, 54, 76, 77, 78, 85, 86, 98].

In this thesis, we study evolutionary dynamics of some reaction-diffusion and

integro-differential/difference models. We mainly study the spreading speeds and the existence and nonexistence of (periodic) traveling waves for four models. In chapter 3, we study spatial dynamics of a class of periodic integro-differential equations, which describe the population dispersal process via a dispersal kernel. We establish the existence of the spreading speed  $c^*$  and the nonexistence of periodic traveling wave solutions with the wave speed  $c < c^*$ . In the autonomous case, we further prove the existence of monotone traveling waves with the wave speed  $c \geq c^*$ , which implies that the spreading speed coincides with the minimal wave speed for monotone traveling waves. In Chapter 4, we investigate a non-local periodic reaction-diffusion population model with stage-structure. We establish the existence of the asymptotic speed of spread and show that it coincides with the minimal wave speed for monotone periodic traveling waves in the case of unbounded spatial domain, and obtain a threshold result on the global attractivity of either zero or a positive periodic solution in the case of bounded spatial domain. In Chapter 5, we consider a class of discrete-time population models in a periodic lattice habitat and show that the spreading speeds coincide with the minimal wave speeds for spatially periodic traveling waves in the positive and negative directions in both cases of monotone and non-monotone recruitment functions. In Chapter 6, we consider a class of cooperative reaction-diffusion systems, in which one population (or subpopulation) diffuses while the other is sedentary, establish the existence of the bistable traveling wave, and then obtain its global attractivity with phase shift and uniqueness (up to translation) via the dynamical system approach. These results are applied to some specific examples of reaction-diffusion population models.

# Chapter 2

## Preliminaries

In this chapter, we present some terminologies and known results which will be used in this thesis. They are involved in global attractors, uniform persistence, monotone dynamical systems, theories of spreading speeds and traveling waves for monotone periodic semiflows and for discrete-time systems in a periodic habitat, and theories of existence of solutions and stability of positive periodic solutions for functional differential equations.

### 2.1 Global attractors and uniform persistence

Let  $X$  be a metric space with metric  $d$  and  $f : X \rightarrow X$  be a continuous map. Let  $X_0 \subset X$  be an open set; define  $\partial X_0 := X \setminus X_0$  and  $M_\partial := \{x \in \partial X_0 : f^n(x) \in \partial X_0, n \geq 0\}$ , which may be empty.

**Definition 2.1.1** *A bounded set  $A$  is said to attract a bounded set  $B$  in  $X$  if*

$$\lim_{n \rightarrow \infty} \sup_{x \in B} \{d(f^n(x), A)\} = 0.$$

*A subset  $A \subseteq X$  is said to be an attractor for  $f$  if  $A$  is nonempty, compact and invariant ( $f(A) = A$ ), and  $A$  attracts some open neighborhood  $U$  of itself. A global attractor for  $f : X \rightarrow X$  is an attractor that attracts every point in  $X$ .*

Recall that the Kuratowski measure of noncompactness,  $\alpha$ , is defined by

$$\alpha(B) = \inf\{r : B \text{ has a finite cover of diameter } < r\},$$

for any bounded set  $B$  of  $X$ . It is not hard to see that  $B$  is precompact if and only if  $\alpha(B) = 0$ .

**Definition 2.1.2** *A continuous mapping  $f : X \rightarrow X$  is said to be point dissipative if there is a bounded set  $B_0$  in  $X$  such that  $B_0$  attracts each point in  $X$ ; compact if  $f$  maps any bounded set to a precompact set in  $X$ ;  $\alpha$ -condensing ( $\alpha$ -contraction of order  $k$ ,  $0 \leq k < 1$ ) if  $f$  takes bounded sets to bounded sets and  $\alpha(f(B)) < \alpha(B)$  ( $\alpha(f(B)) \leq k\alpha(B)$ ) for any nonempty closed bounded set  $B \subset X$  with  $\alpha(B) > 0$ ; asymptotically smooth if for any nonempty closed bounded set  $B \subset X$  for which  $f(B) \subset B$ , there is a compact set  $J \subset B$  such that  $J$  attracts  $B$ .*

**Theorem 2.1.1** ([9, Theorem 3.2]) *If  $f : X \rightarrow X$  is compact and point dissipative, then there is a connected global attractor  $A$  that attracts each bounded set in  $X$ .*

**Definition 2.1.3** *A function  $f : X \rightarrow X$  is said to be uniformly persistent with respect to  $(X_0, \partial X_0)$  if there exists  $\eta > 0$  such that  $\liminf_{n \rightarrow \infty} d(f^n(x), \partial X_0) \geq \eta$  for all  $x \in X_0$ . If "inf" in this inequality is replaced with "sup", then  $f$  is said to be weakly uniformly persistent with respect to  $(X_0, \partial X_0)$ .*

**Theorem 2.1.2** ([97, Theorem 1.3.3]) *Let  $f : X \rightarrow X$  be a continuous map with  $f(X_0) \subset X_0$ . Assume that  $f$  has a global attractor  $A$ . Then weak uniform persistence implies uniform persistence.*

Let  $\{S^n\}_{n=1}^{\infty}$  be the discrete semidynamical system defined by a continuous map  $S : X \rightarrow X$  with  $S(X_0) \subset X_0$ . A point  $x_0 \in X$  is called a coexistence state of  $\{S^n\}_{n=1}^{\infty}$  if  $x_0$  is a fixed point of  $S$  in  $X_0$ , i.e.,  $x_0 \in X_0$  and  $S(x_0) = x_0$ . We have the following result on the existence of coexistence states.

**Theorem 2.1.3** ([95, Theorem 2.3]) *Let  $X$  be a closed subset of a Banach space  $E$ ,  $X_0$  be a convex and relatively open subset in  $X$ , and  $S : X \rightarrow X$  be a continuous map with  $S(X_0) \subset X_0$ . Assume that  $S : X \rightarrow X$  is point dissipative, compact, and uniformly persistent with respect to  $(X_0, \partial X_0)$ . Then there exists a global attractor  $A$  for  $S$  in  $X_0$  and  $S$  has a coexistence state  $x_0 \in A$ .*

## 2.2 Monotone dynamics

Let  $E$  be an ordered Banach space with positive cone  $P$  such that  $\text{int}(P) \neq \emptyset$ . For  $x, y \in E$  we write  $x \geq y$  if  $x - y \in P$ ,  $x > y$  if  $x - y \in P \setminus \{0\}$ , and  $x \gg y$  if  $x - y \in \text{int}(P)$ . If  $a < b$ , we define  $[a, b] := \{x \in E : a \leq x \leq b\}$ .

**Definition 2.2.1** *Let  $U$  be a subset of  $E$  and  $f : U \rightarrow U$  be a continuous map. The map  $f$  is said to be monotone if  $x \geq y$  implies that  $f(x) \geq f(y)$ ; strictly monotone if  $x > y$  implies that  $f(x) > f(y)$ ; strongly monotone if  $x > y$  implies that  $f(x) \gg f(y)$ .*

**Theorem 2.2.1** ([18, Proposition 1]) *Let  $u_1 < u_2$  be fixed points of the strictly monotone continuous mapping  $f : U \rightarrow U$ , let  $I := [u_1, u_2] \subset U$ , and assume that  $f(I)$  is precompact and that  $f$  has no fixed point distinct from  $u_1$  and  $u_2$  in  $I$ . Then either*

- (a) *there exists an entire orbit  $\{x_n\}_{n=-\infty}^{\infty}$  of  $f$  in  $I$  such that  $x_{n+1} > x_n$ ,  $\forall n \in \mathbb{N}$ , and  $\lim_{n \rightarrow -\infty} x_n = u_1$  and  $\lim_{n \rightarrow \infty} x_n = u_2$ , or*
- (b) *there exists an entire orbit  $\{y_n\}_{n=-\infty}^{\infty}$  of  $f$  in  $I$  such that  $y_{n+1} < y_n$ ,  $\forall n \in \mathbb{N}$ , and  $\lim_{n \rightarrow -\infty} y_n = u_2$  and  $\lim_{n \rightarrow \infty} y_n = u_1$ .*

Recall that a linear operator  $L$  on  $E$  is said to be positive if  $L(P) \subset P$ , strongly positive if  $L(P \setminus \{0\}) \subset \text{int}(P)$ . The cone  $P$  is said to be normal if there exists a constant  $M$  such that  $0 \leq x \leq y$  implies that  $\|x\| \leq M\|y\|$ . Denote the Fréchet derivative of  $f$  at  $u = a$  by  $Df(a)$  if it exists, and let  $\tau(Df(a))$  be the spectral radius of the linear operator  $Df(a) : E \rightarrow E$ .

**Theorem 2.2.2** ([99, Theorem 2.1]) *Let the positive cone  $P$  be normal. Assume that*

- (1)  $S : V = a + P \rightarrow V$  is asymptotically smooth and monotone;
- (2)  $S(a) = a$ ,  $DS(a)$  is compact and strongly positive, and  $r(DS(a)) > 1$ .

Then either

- (a) for any  $u > a$ ,  $\lim_{n \rightarrow \infty} \|S^n(u)\| = +\infty$ , or
- (b) there exists  $u^* = S(u^*) \gg a$  such that for any  $a < u \leq u^*$ ,  $\lim_{n \rightarrow \infty} S^n(u) = u^*$ , and there exists a monotone entire orbit connecting  $a$  and  $u^*$ .

Recall that a subset  $K$  of  $E$  is said to be order convex if  $[u, v]_E \subset K$  whenever  $u, v \in E$  satisfy  $u < v$ . A family of mappings  $\{\Phi_t\}_{t \geq 0}$  is said to be a semiflow on a metric space  $(M, d)$  provided that  $\Phi_0 = I$ ,  $\Phi_{t_1}\Phi_{t_2} = \Phi_{t_1+t_2}$ , and  $\Phi_t(v)$  is continuous in  $(t, v) \in \mathbb{R}_+ \times M$ . A point  $e \in M$  is called an equilibrium of  $\{\Phi_t\}_{t \geq 0}$  if  $\Phi_t(e) = e$ ,  $\forall t \geq 0$ .

**Theorem 2.2.3** ([97, Theorem 2.2.4]) *Let  $U$  be a closed and order convex subset of an ordered Banach space  $E$ , and  $\Phi(t) : U \rightarrow U$  be a monotone semiflow. Assume that there exists a monotone homeomorphism  $h$  from  $[0, 1]$  onto a subset of  $U$  such that*

- (1) For each  $s \in [0, 1]$ ,  $h(s)$  is a stable fixed point for  $\Phi(t) : U \rightarrow U$ ;
- (2) Each orbit of  $\Phi(t)$  in  $[h(0), h(1)]_E$  is precompact;
- (3) One of the following two properties holds:
- (3a) If  $\omega(\phi) > h(s_0)$  for some  $s_0 \in [0, 1)$  and  $\phi \in [h(0), h(1)]_E$ , then there exists  $s_1 \in (s_0, 1)$  such that  $\omega(\phi) \geq h(s_1)$ ;
- (3b) If  $\omega(\phi) < h(r_1)$  for some  $r_1 \in (0, 1]$  and  $\phi \in [h(0), h(1)]_E$ , then there exists  $r_0 \in (0, r_1)$  such that  $\omega(\phi) \leq h(r_0)$ .

Then for any precompact orbit  $\gamma^+(\phi_0)$  of  $\Phi(t)$  in  $U$  with  $\omega(\phi_0) \cap [h(0), h(1)]_E \neq \emptyset$ , there exists  $s^* \in [0, 1]$  such that  $\omega(\phi_0) = h(s^*)$ .

**Definition 2.2.2** Let  $U \subset P$  be a nonempty closed and order convex set. A continuous map  $f : U \rightarrow U$  is said to be subhomogeneous if  $f(\lambda x) \geq \lambda f(x)$  for any  $x \in U$  and  $\lambda \in [0, 1]$ ; strictly subhomogeneous if  $f(\lambda x) > \lambda f(x)$  for any  $x \in U$  with  $x \gg 0$  and  $\lambda \in (0, 1)$ ; strongly subhomogeneous if  $f(\lambda x) \gg \lambda f(x)$  for any  $x \in U$  with  $x \gg 0$  and  $\lambda \in (0, 1)$ .

**Theorem 2.2.4** ([96, Lemma 1]) Let either  $V = [0, b]_E$  with  $b \gg 0$  or  $V = P$ . Assume that  $f : V \rightarrow V$  is continuous, strongly monotone and strictly subhomogeneous on  $V$ . Then  $f$  admits at most one positive fixed point in  $V$ .

**Theorem 2.2.5** ([36, Theorem 5.5] and [97, Theorem 2.3.2]) Let  $f : U \rightarrow U$ . Assume that  $f$  is monotone and strongly subhomogeneous or that  $f$  is strongly monotone and strictly subhomogeneous. If  $f$  admits a nonempty compact invariant set  $K \subset \text{int}(P)$ , then  $f$  has a fixed point  $e \gg 0$  such that every nonempty compact invariant set of  $f$  in  $\text{int}(P)$  consists of  $e$ .

**Theorem 2.2.6** ([96, Lemma 1] and [97, Lemma 2.3.2]) Let either  $V = [0, b]$  with  $b \gg 0$  or  $V = P$ . Assume that  $S : V \rightarrow V$  is continuous,  $S(0) = 0$ , and  $DS(0)$  exists. If  $S$  is subhomogeneous, then  $S(u) \leq DS(0)u$ ,  $\forall u \in V$ ; If  $S$  is strictly subhomogeneous, then  $S(u) < DS(0)u$ ,  $\forall u \in V \cap \text{int}(P)$ .

## 2.3 Periodic monostable evolution systems

We equip  $\mathbb{R}^k$  with the norm  $|(u_1, u_2, \dots, u_k)| = \max\{|u_i| : 1 \leq i \leq k\}$  and the positive cone  $\mathbb{R}_+^k$  of  $\mathbb{R}^k$ , such that  $\mathbb{R}^k$  is an ordered Banach space.

Let  $\tau$  be a nonnegative real number and  $C$  be the set of all bounded and continuous functions from  $[-\tau, 0] \times \mathbb{H}$  into  $\mathbb{R}^k$ , where  $\mathbb{H} = \mathbb{R}$  or  $\mathbb{Z}$ . Clearly, any vector in  $\mathbb{R}^k$  and any element in the space  $\mathbb{Y} := C([-\tau, 0], \mathbb{R}^k)$  can be regarded as a function in  $C$ . For  $u = (u_1, u_2, \dots, u_k), v = (v_1, v_2, \dots, v_k) \in C$ , we write  $u \geq v$  ( $u \gg v$ ) provided that  $u_i(\theta, x) \geq v_i(\theta, x)$  ( $u_i(\theta, x) > v_i(\theta, x)$ ),  $\forall i = 1, 2, \dots, k, \theta \in [-\tau, 0], x \in \mathbb{H}$ , and  $u > v$  provided  $u \geq v$  but  $u \neq v$ . For any two vectors  $a, b$  in  $\mathbb{R}^k$  or two functions  $a, b$

in  $\mathbb{Y}$ , we can define  $a \geq b (>, \gg) b$  similarly. For any  $r \in \mathbb{Y}$  with  $r \gg 0$ , we define  $\mathbb{Y}_r = \{\varphi \in \mathbb{Y} : 0 \leq \varphi \leq r\}$  and  $C_r = \{\varphi \in C : 0 \leq \varphi \leq r\}$ . We equip  $\mathbb{Y}$  with the usual supreme norm  $\|\cdot\|_{\mathbb{Y}}$  and  $C$  with the compact open topology, that is,  $u^m \rightarrow u$  in  $C$  means that the sequence of  $u^m(\theta, x)$  converges to  $u(\theta, x)$  as  $m \rightarrow \infty$  uniformly for  $(\theta, x)$  in any compact set on  $[-\tau, 0] \times \mathbb{H}$ . Moreover, we can define the metric function  $d(\cdot, \cdot)$  in  $C$  with respect to this topology by

$$d(u, v) = \sum_{k=1}^{\infty} \frac{\max_{|x| \leq k, \theta \in [-\tau, 0]} |u(\theta, x) - v(\theta, x)|}{2^k}, \quad \forall u, v \in C,$$

where  $|\cdot|$  denotes the usual norm in  $\mathbb{R}^k$ , such that  $(C, d)$  is a metric space.

Let  $X$  be the space of all bounded and continuous functions from  $\mathbb{H}$  into  $\mathbb{R}^k$  equipped with the compact open topology.

Let  $u \in C$ . Define the reflection operator  $\mathcal{R}$  by

$$\mathcal{R}(u)(\theta, x) := u(\theta, -x), \quad \forall \theta \in [-\tau, 0], x \in \mathbb{R}.$$

Given  $y \in \mathbb{R}$ , define the translation operator  $T_y$  by

$$T_y(u)(\theta, x) := u(\theta, x - y), \quad \forall \theta \in [-\tau, 0], x \in \mathbb{R}.$$

Let  $Q : C_{b^*} \rightarrow C_{b^*}$  be a map, where  $b^* \in \mathbb{Y}$  with  $b^* \gg 0$ . Assume that

$$(A1) \quad Q(\mathcal{R}(u)) = \mathcal{R}(Q(u)), \quad T_y(Q(u)) = Q(T_y(u)), \quad \forall y \in \mathbb{R}.$$

(A2)  $Q : C_{b^*} \rightarrow C_{b^*}$  is continuous with respect to the compact open topology.

(A3) One of the following two properties holds:

(a)  $\{Q(u)(\cdot, x) : u \in C_{b^*}, x \in \mathbb{H}\}$  is a precompact subset of  $\mathbb{Y}$ .

(b) The set  $Q(C_{b^*})(0, \cdot)$  is precompact in  $X$ , and there is a positive number  $\varsigma \leq \tau$  such that  $Q(u)(\theta, x) = u(\theta + \varsigma, x)$  for  $-\tau \leq \theta \leq -\varsigma$ , and the operator

$$S(u)(\theta, x) := \begin{cases} u(0, x), & -\tau \leq \theta < -\varsigma, \\ Q(u)(\theta, x), & -\varsigma \leq \theta \leq 0, \end{cases}$$

has the property that  $S(D)(\cdot, 0)$  is precompact in  $\mathbb{Y}$  for any  $T$ -invariant set  $D \subseteq C_{b^*}$  with  $D(0, \cdot)$  is precompact in  $X$ .

(A4)  $Q : C_{b^*} \rightarrow C_{b^*}$  is monotone in the sense that  $Q(u) \geq Q(v)$  whenever  $u \geq v$  in  $C_{b^*}$ .

(A5)  $Q : Y_{b^*} \rightarrow Y_{b^*}$  admits exactly two fixed points 0 and  $b^*$  and for any positive number  $\varepsilon$ , there is an  $\alpha \in Y_{b^*}$  with  $\|\alpha\|_Y < \varepsilon$  such that  $Q(\alpha) \gg \alpha$ .

(A6) One of the following two conditions holds:

(a)  $Q(C_{b^*})$  is precompact in  $C_{b^*}$ .

(b) The set  $Q(C_{b^*})(0, \cdot)$  is precompact in  $X$ , and there is a positive number  $\varsigma \leq \tau$  such that  $Q(u)(\theta, x) = u(\theta + \varsigma, x)$  for  $-\tau \leq \theta \leq -\varsigma$ , the operator

$$S[u](\theta, x) := \begin{cases} u(0, x), & -\tau \leq \theta < -\varsigma, \\ Q[u](\theta, x), & -\varsigma \leq \theta \leq 0, \end{cases}$$

is continuous on  $C_{b^*}$ , and  $S[D](\cdot, 0)$  is precompact in  $Y$  for any  $T$ -invariant set  $D \subseteq C_{b^*}$  with  $D(0, \cdot)$  being precompact in  $X$ . A set  $W \subseteq C_{b^*}$  is said to be  $T$ -invariant if  $T_y W = W$  for all  $y \in \mathbb{R}$ .

**Theorem 2.3.1** ([53, Theorem 2.11, Theorem 2.15, Corollary 2.16] or [52, Theorem A])  
*Suppose that  $Q$  satisfies (A1)-(A5). Let  $u_0 \in C_{b^*}$  and  $u_n = Q(u_{n-1})$  for  $n \geq 1$ . Then there is a real number  $c^*$  such that the following statements are valid:*

(1) *For any  $c > c^*$ , if  $0 \leq u_0 \ll b^*$  and  $u_0(\cdot, x) = 0$  for  $x$  outside a bounded interval, then  $\lim_{n \rightarrow \infty, |x| \geq cn} u_n(\theta, x) = 0$  uniformly for  $\theta \in [-\tau, 0]$ .*

(2) *For any  $c < c^*$  and any  $\sigma \in Y_{b^*}$  with  $\sigma \gg 0$ , there exists  $r_\sigma > 0$  such that if  $u_0(\cdot, x) \geq \sigma(\cdot)$  for  $x$  on an interval of length  $2r_\sigma$ , then  $\lim_{n \rightarrow \infty, |x| \leq cn} u_n(\theta, x) = b^*(\theta)$  uniformly for  $\theta \in [-\tau, 0]$ . If, in addition,  $Q$  is subhomogeneous on  $C_{b^*}$ , then  $r_\sigma$  can be chosen to be independent of  $\sigma \gg 0$ .*

By Theorem 2.3.1, it follows that  $Q$  admits an asymptotic speed of spread  $c^*$  provided that (A1)-(A5) are valid. To estimate  $c^*$ , a linear operator approach was developed in [53]. Let  $M : C \rightarrow C$  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,  $M(u) \geq 0$  whenever  $u > 0$ .
- (B3) For any uniformly bounded subset  $A$  of  $C$ , the set  $\{M(u)(\theta, x) : u \in A, \theta \in [-\tau, 0], x \in \mathbb{H}\}$  is bounded in  $\mathbb{R}^k$ .
- (B4)  $M(\mathcal{R}(u)) = \mathcal{R}(M(u))$ ,  $T_y(M(u)) = M(T_y(u))$ ,  $\forall u \in C, y \in \mathbb{H}$ .
- (B5) For some  $\Delta \in (0, \infty]$ ,  $M$  can be extended to a linear operator on the linear space

$$\begin{aligned} \tilde{C} := \{ & u = u_1(\theta, x)e^{\mu_1 x} + u_2(\theta, x)e^{\mu_2 x} : \\ & u_1, u_2 \in C, \mu_1, \mu_2 \in (-\Delta, \Delta), \theta \in [-\tau, 0], x \in \mathbb{H}\}, \end{aligned}$$

such that if  $u_n, u \in \tilde{C}$  and  $u_n(\theta, x) \rightarrow u(\theta, x)$  uniformly on any bounded set of  $[-\tau, 0] \times \mathbb{H}$ , then  $M(u_n)(\theta, x) \rightarrow M(u)(\theta, x)$  uniformly on any bounded set of  $[-\tau, 0] \times \mathbb{H}$ .

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

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

In particular,  $B_0 = M$  on  $\mathbb{Y}$ . If  $\sigma_n, \sigma \in \mathbb{Y}$  and  $\sigma_n \rightarrow \sigma$  as  $n \rightarrow \infty$ , then  $\sigma_n(\theta)e^{-\mu x} \rightarrow \sigma(\theta)e^{-\mu x}$  uniformly on any bounded subset of  $[-\tau, 0] \times \mathbb{H}$ . Thus,

$$B_\mu(\sigma_n) = M(\sigma_n e^{-\mu x})(\cdot, 0) \rightarrow M(\sigma e^{-\mu x})(\cdot, 0) = B_\mu(\sigma),$$

and hence,  $B_\mu$  is continuous. Moreover,  $B_\mu$  is a positive operator on  $\mathbb{Y}$ . Assume that

- (B6) For any  $\mu \in [0, \Delta)$ ,  $B_\mu$  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  $\mathbb{Y}$ .

- (B7) The principle 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 principle eigenvalue of  $B_\mu$ . The following result is useful for the estimate of the spreading speed.

**Theorem 2.3.2** ([53, Theorem 3.10]) *Let  $Q$  be an operator on  $C_{b^*}$  satisfying (A1)-(A5) and  $c^*$  be the asymptotic speed of spread of  $Q$ . Assume that the linear operator  $M$  satisfies (B1)-(B7), and that either  $M$  has compact support or the infimum of  $\Phi(\mu)$  is attained at some finite value  $\mu^*$  and  $\Phi(\Delta) > \Phi(\mu^*)$ . Then the following statements are valid:*

- (i) *If  $Q(u) \leq M(u)$  for all  $u \in C_{b^*}$ , then  $c^* \leq \inf_{\mu \in (0, \Delta)} \Phi(\mu)$ .*
- (ii) *If there is some  $\eta \in \mathbb{Y}$  with  $\eta \gg 0$  such that  $Q(u) \geq M(u)$  for any  $u \in C_\eta$ , then  $c^* \geq \inf_{\mu \in (0, \Delta)} \Phi(\mu)$ .*

**Definition 2.3.1** *Let  $\omega > 0$ . A family of operators  $\{\Phi_t\}_{t \geq 0}$  is an  $\omega$ -periodic semiflow on a metric space  $(E, \rho)$  with the metric  $\rho$ , provided that  $\{\Phi_t\}$  satisfies*

- (i)  $\Phi_0(v) = v, \forall v \in E$ ;
- (ii)  $\Phi_t(\Phi_\omega(v)) = \Phi_{t+\omega}(v), \forall t \geq 0, v \in E$ ;
- (iii)  $\Phi(t, v) = \Phi_t(v)$  is continuous in  $(t, v)$  on  $[0, +\infty) \times E$ .

**Theorem 2.3.3** ([52, Theorem 2.1]) *Let  $\{Q_t\}_{t \geq 0}$  be an  $\omega$ -periodic semiflow on  $C_{b^*}$  with two  $x$ -independent  $\omega$ -periodic orbits  $0 \ll u^*(t)$ . Suppose that the Poincaré map  $Q = Q_\omega$  satisfies all hypotheses (A1)-(A5) with  $b^* = u^*(0)$ , and  $Q_t$  satisfies (A1) for any  $t > 0$ . Let  $c^*$  be the asymptotic speed of spread of  $Q_\omega$ . Then the following statements are valid:*

- (1) *For any  $c > c^*/\omega$ , if  $v \in C_{b^*}$  with  $0 \leq v \ll b^*$ , and  $v(\cdot, x) = 0$  for  $x$  outside a bounded interval, then  $\lim_{t \rightarrow \infty, |x| \geq ct} Q_t(v)(\theta, x) = 0$  uniformly for  $\theta \in [-\tau, 0]$ .*
- (2) *For any  $c < c^*/\omega$  and  $\sigma \in \mathbb{Y}_{b^*}$  with  $\sigma \gg 0$ , there is a positive number  $r_\sigma$  such that if  $v \in C_{b^*}$  and  $v(\cdot, x) \gg \sigma(\cdot)$  for  $x$  on an interval of length  $2r_\sigma$ , then  $\lim_{t \rightarrow \infty, |x| \leq ct} (Q_t(v)(\theta, x) - u^*(t)(\theta)) = 0$  uniformly for  $\theta \in [-\tau, 0]$ . If, in addition,  $Q_\omega$  is subhomogeneous, then  $r_\sigma$  can be chosen to be independent of  $\sigma \gg 0$ .*

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

$$Q_t(W(\cdot, 0, \cdot))(\theta, x) = W(\theta, t, x - ct),$$

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

**Theorem 2.3.4** ([52, Theorems 2.2 and 2.3]) *Let  $\{Q_t\}_{t \geq 0}$  be an  $\omega$ -periodic semiflow on  $C_b$  with two  $x$ -independent  $\omega$ -periodic orbits  $0 \ll u^*(t)$ . Suppose that  $Q = Q_\omega$  satisfies hypotheses (A1)-(A5) with  $b^* = u^*(0)$  and let  $c^*$  be the asymptotic speed of spread of  $Q_\omega$ . Then the following statements are valid.*

- (1) *For any  $0 < c < c^*/\omega$ ,  $\{Q_t\}_{t \geq 0}$  has no  $\omega$ -periodic traveling wave  $W(\theta, t, x - ct)$  connecting  $u^*(t)$  to 0.*
- (2) *Suppose that  $\mathbb{H} = \mathbb{R}$ , that  $Q_\omega$  further satisfies (A6) with  $b^* = u^*(0)$ , and that  $Q_t$  satisfies (A1) and (A4) for each  $t > 0$ . Then for any  $c \geq c^*/\omega$ ,  $\{Q_t\}_{t \geq 0}$  has an  $\omega$ -periodic traveling wave  $W(\theta, t, x - ct)$  connecting  $u^*(t)$  to 0 such that  $W(\theta, t, s)$  is continuous and nonincreasing in  $s \in \mathbb{R}$ .*

## 2.4 Discrete-time systems in a periodic habitat

Let  $\mathcal{H}$  be an unbounded closed  $d$ -dimensional subset of  $\mathbb{R}^d$  with  $d \geq 1$ . The recursion

$$u_{n+1} = Q(u_n), \quad u_n(x) \in \mathbb{R}^d, \quad \forall x \in \mathcal{H}, \quad n \in \mathbb{N},$$

has two nonnegative fixed points 0 and  $\pi_1(x)$ . Define

$$\mathcal{M} := \{u : u \text{ is continuous on } \mathcal{H}, 0 \leq u(x) \leq \pi_1(x), \forall x \in \mathcal{H}\}.$$

The following assumptions come from [86, Hypotheses 2.1].

- (C1) *The habitat  $\mathcal{H}$  is a closed subset of  $\mathbb{R}^d$ , which is not contained in any lower-dimensional linear subspace of  $\mathbb{R}^d$ .*

- (C2)  $Q$  is order preserving in the sense that if  $u(x) \leq v(x)$  on  $\mathcal{H}$ , then  $Q(u)(x) \leq Q(v)(x)$ . That is, an increase throughout  $\mathcal{H}$  in the population  $u_n$  at time  $n$  increases the population  $u_{n+1} = Q(u_n)$  throughout  $\mathcal{H}$  at the next time step.
- (C3) There is a closed  $d$ -dimensional lattice  $\mathcal{L}$  such that  $\mathcal{H}$  is invariant under translation by any element of  $\mathcal{L}$ , and  $Q$  is periodic with respect to  $\mathcal{L}$  in the sense that  $Q(T_a(u)) = T_a(Q(u))$  holds for all  $u \in \mathcal{M}$  and  $a \in \mathcal{L}$ , where  $T$  is the translation operator defined as  $T_a(u)(x) := u(x - a)$ . Moreover, there is a bounded subset  $\mathcal{P}$  of  $\mathcal{H}$  such that every  $x \in \mathcal{H}$  has a unique representation of the form  $x = z + p$  with  $z$  in  $\mathcal{L}$  and  $p$  in  $\mathcal{P}$ .
- (C4)  $Q(0) = 0$ , and there are  $\mathcal{L}$ -periodic equilibria  $\pi_0(x)$  and  $\pi_1(x)$  such that  $0 \leq \pi_0 < \pi_1$ ,  $Q(\pi_0) = \pi_0$  and  $Q(\pi_1) = \pi_1$ . Moreover, if  $\pi_0 \leq u_0 \leq \pi_1$ ,  $u_0$  is periodic with respect to  $\mathcal{L}$ , and  $u_0 \not\equiv \pi_0$ , then the solution  $u_n$  of the recursion  $u_{n+1} = Q(u_n)$ , which is again periodic with respect to  $\mathcal{L}$ , converges to  $\pi_1$  as  $n \rightarrow \infty$  uniformly on  $\mathcal{H}$ . (That is,  $\pi_0$  is unstable and  $\pi_1$  is stable.) In addition, any  $\mathcal{L}$ -periodic equilibrium  $\pi$  other than  $\pi_1$  which satisfies the inequalities  $0 \leq \pi \leq \pi_1$  also satisfies  $\pi \leq \pi_0$ .
- (C5)  $Q$  is continuous in the sense that if the sequence  $u_m \in \mathcal{M}$  converges to  $u \in \mathcal{M}$ , uniformly on every bounded subset of  $\mathcal{H}$ , then  $Q(u_m)$  converges to  $Q(u)$ , uniformly on every bounded subset of  $\mathcal{H}$ . That is, a change in  $u$  far from the point  $x$  has very little effect on the value of  $Q(u)$  at  $x$ .
- (C6) Every sequence  $\{u_m\}$  of functions in  $\mathcal{M}$  contains a subsequence  $\{u_{m_i}\}$  such that  $\{Q(u_{m_i})\}$  converges to some function, uniformly on every bounded set.

**Theorem 2.4.1** ([86, Theorem 2.1]) *Let (C1)-(C6) hold. For each unit vector  $\vec{\xi}$  there exists a spreading speed  $c^*(\vec{\xi}) \in (-\infty, +\infty]$  such that solutions of the recursion  $u_{n+1} = Q(u_n)$  have the following spreading properties:*

- (1) *If  $u_0(x) \geq 0$ ,  $\inf[\pi_1(x) - u_0(x)] > 0$ , and  $u_0(x) = 0$  in a half-space of the form*

$\vec{\xi} \cdot x \geq L$  and if  $c^*(\vec{\xi}) < \infty$ , then for every  $c > c^*(\vec{\xi})$ ,

$$\limsup_{n \rightarrow \infty} \left[ \sup_{\vec{\xi} \cdot x \geq cn} [u_n(x) - \pi_0(x)] \right] \leq 0;$$

and

(2) If  $0 \leq u_0 \leq \pi_1$  and there is a constant  $K$  such that  $\inf_{\vec{\xi} \cdot x \leq -K} [u_0(x) - \pi_0(x)] > 0$ , then for every  $c < c^*(\vec{\xi})$ ,

$$\lim_{n \rightarrow \infty} \left[ \sup_{\vec{\xi} \cdot x \leq cn} [\pi_1(x) - u_n(x)] \right] = 0.$$

Let  $L$  be a linear operator on nonnegative functions which are continuous on  $\mathcal{H}$ . Suppose that  $L$  is strongly order preserving in the sense that if  $u \geq 0$  and  $u \not\equiv 0$ , then  $L(u) > 0$ . Also suppose that  $L$  is periodic with respect to  $\mathcal{L}$  if  $T_a L = L T_a$  for all  $a \in \mathcal{L}$ , where  $T_a$  is the translation operator. For each  $\mu$ , we say that  $L[e^{\mu|x|}]$  exists if the nondecreasing sequence  $L[\min\{n, e^{\mu|x|}\}](y)$  converges to a function, which we call  $L[e^{\mu|x|}](y)$ . If  $L[e^{\mu|x|}]$  exists, we define

$$L_{\mu\vec{\xi}}[\psi](y) := e^{\mu\vec{\xi} \cdot y} L[e^{-\mu\vec{\xi} \cdot x} \psi(x)](y),$$

for all nonnegative periodic (with respect to  $\mathcal{L}$ ) functions  $\psi : \mathcal{H} \rightarrow \mathbb{R}_+^d$ .

**Theorem 2.4.2** ([86, Theorem 2.4, Theorem 2.5, Corollary 2.1]) *Suppose that the linearization  $M$  of  $Q$  at  $u = 0$  satisfies*

- (1)  $Q(u) \leq M(u)$  for all  $u$  with  $0 \leq u \leq \pi_1$ ;
- (2)  $M$  is  $\mathcal{L}$ -periodic and strongly order-preserving, and  $M[e^{\mu|x|}]$  is defined for all  $\mu$ .
- (3) There is a positive  $\mathcal{L}$ -periodic function  $r$  such that  $M(r) > r$ , and the truncated operator  $Q^{[M,r]}(u) := \min\{M(u), r\}$  satisfies (C1)-(C6).

Moreover, assume that for each small positive  $\delta$ , there is a positive number  $\eta$  such that  $Q(u) \geq (1 - \delta)M(u)$  for every  $u$  with  $0 \leq u \leq \eta$ , and that above assumptions (2) and (9) also hold if  $M$  is replaced with  $(1 - \delta)M$ . Then

$$c^*(\vec{\xi}) = \inf_{\mu > 0} \left[ \frac{\ln \lambda(\mu \vec{\xi})}{\mu} \right],$$

where  $\lambda(\mu \vec{\xi})$  is the principal eigenvalue of  $M_{\mu \vec{\xi}}$ . Thus, the spreading speed is linearly determinate in all directions under these conditions.

**Definition 2.4.1** ([86, Definition 2.1]) A solution  $u_n$  of the recursion  $u_{n+1} = Q(u_n)$  is called a *spatially periodic traveling wave of speed  $c$  in the direction of the unit vector  $\vec{\xi}$*  if it has the form  $u_n(x) = W(\vec{\xi} \cdot x - cn, x)$ , where the function  $W(s, x)$  has the properties:

- (a) For each  $s$  the function  $W(\vec{\xi} \cdot x + s, x)$  is continuous in  $x \in \mathcal{H}$ .
- (b) For each  $s$ ,  $W(s, x)$  is  $\mathcal{L}$ -periodic in  $x$ ;
- (c) For each  $x \in \mathcal{H}$ ,  $W(s, x)$  is nonincreasing in  $s$ ;
- (d)  $W(-\infty, x) = \pi_1(x)$ ;
- (e)  $W(\infty, x) = 0$ .

**Theorem 2.4.3** ([86, Theorem 2.6]) Suppose that  $\pi_0 \equiv 0$ . Then there is a spatially periodic traveling wave of speed  $c$  in the direction  $\vec{\xi}$  if and only if  $c \geq c^*(\vec{\xi})$ .

## 2.5 Functional differential equations

Let  $\tau$  be a positive number,  $Y = C([- \tau, 0], \mathbb{R})$  and  $Y_+ = C([- \tau, 0], \mathbb{R}_+)$ .

**Theorem 2.5.1** ([93, Proposition 2.1]) Assume that  $a(t)$  and  $b(t)$  are  $T$ -periodic and continuous on  $[0, \infty)$  and  $b(t) > 0, \forall t \geq 0$ . Let  $P : Y_+ \rightarrow Y_+$  be the Poincaré map of

$$\dot{u} = a(t)u(t) + b(t)u(t - \tau).$$

Then the spectral radius of  $P$ ,  $r(P)$ , is positive and is an eigenvalue of  $P$  with a positive eigenfunction  $\varphi^*$ . Moreover, if  $\tau = kT$  for some integer  $k \geq 0$ , then  $r(P) - 1$  has the same sign as  $\int_0^T (a(t) + b(t))dt$ .

Consider a nonlinear  $T$ -periodic equation

$$\begin{cases} \dot{u} = f(t, u(t), u(t - \tau)), \\ u(s) = \varphi(s), \quad -\tau \leq s \leq 0, \end{cases} \quad (2.1)$$

where  $\varphi \in Y_+$  is an initial function.

Assume that the continuous function  $f(t, v_1, v_2)$  is  $T$ -periodic in  $t$  and Lipschitzian in  $(v_1, v_2)$  in any bounded subset of  $\mathbb{R}_+^2$ . Moreover,  $f(t, 0, 0) = 0$ ,  $f(t, 0, v_2) \geq 0$ ,  $(\partial/\partial v_2)f(t, v_1, v_2) > 0$ ,  $\forall v_1, v_2 \geq 0$ ;  $f$  is strictly subhomogenous in the sense that for any  $\alpha \in (0, 1)$ ,  $f(t, \alpha v_1, \alpha v_2) > \alpha f(t, v_1, v_2)$ ,  $\forall v_1, v_2 \geq 0$ ; there exists a positive number  $L > 0$  such that  $f(t, L, L) \leq 0$ .

Let  $P_u$  be the Poincaré map of the linearized equation associated with (2.1) at  $u = 0$ , and  $r = r(P_u)$  be the spectral radius of  $P_u$ . Then we have the following results.

**Theorem 2.5.2** ([93, Theorem 2.1]) *Suppose that (2.1) satisfies above assumptions. Then the following statements are valid.*

- (1) *If  $r \leq 1$ , then zero solution is globally asymptotically stable for (2.1) with respect to  $Y_+$ .*
- (2) *If  $r > 1$ , then (2.1) has a unique positive  $T$ -periodic solution  $u(t, \varphi_0)$ , which is globally asymptotically stable with respect to  $Y_+ \setminus \{0\}$ .*

Let  $X$  be a real or complex Banach space with norm denoted by  $|\cdot|$  and  $\tau$  be a positive number. Denote by  $\mathbb{Y} := C([- \tau, 0], X)$  the space of all continuous functions  $\varphi : [- \tau, 0] \rightarrow X$  with  $\|\varphi\| = \max\{|\varphi(\theta)| : -\tau \leq \theta \leq 0\}$ . For any continuous function  $w(\cdot) : [- \tau, b) \rightarrow X$ ,  $b > 0$ , we define  $w_t \in \mathbb{Y}$  by  $w_t(s) = w(t + s)$ ,  $\forall t \in [0, b)$ ,  $s \in [- \tau, 0]$ . It is then easy to see that  $t \rightarrow w_t$  is a continuous function from  $[0, b)$  to  $\mathbb{Y}$ . Let  $a$  be a real number and  $D$  be a closed subset of  $[a - \tau, \infty) \times X$ , and assume

$D(t) := \{x \in X : (t, x) \in D\}$  is nonempty for each  $t \geq a - \tau$ . Let  $\mathcal{D}$  is the closed subset of  $[a, \infty) \times \mathbb{Y}$  defined by  $\mathcal{D} := \{(t, \varphi) : \varphi(\theta) \in D(t+\theta), \forall -\tau \leq \theta \leq 0\}$ . Define  $\mathcal{D}(t) := \{\varphi \in \mathbb{Y} : (t, \varphi) \in \mathcal{D}\}, \forall t \geq a$ , and assume that  $\mathcal{D}(t)$  is nonempty for each set  $t \geq a$ . Let  $E$  be a subset of  $[a - \tau, \infty) \times X$  such that  $E(t) := \{x \in X : (t, x) \in E\}$  is nonempty for all  $t$ .

Let  $B$  be a continuous operator from  $[a, \infty) \times \mathbb{Y}$  into  $X$  satisfying that for each  $R > 0$ , there are an  $L_R > 0$  and a continuous  $v_R : [0, \infty) \rightarrow [0, \infty)$  such that  $v_R(0) = 0$  and

$$|B(t, \varphi) - B(s, \psi)| \leq v_R(|t - s|) + L_R \|\varphi - \psi\|$$

for all  $(t, \varphi), (s, \psi) \in [a, \infty) \times \mathbb{Y}$  with  $\|\varphi\|, \|\psi\| \leq R$  and  $a \leq s, t \leq a + R$ .

Let  $S = \{S(t, s) : t \geq s \geq a\}$  be a family of bounded linear operators from  $X$  into  $X$ . Assume that  $S(t, t)x = x$  and  $S(t, s)S(s, r)x = S(t, r)x$  for all  $t \geq s \geq r \geq a$ , that for each  $x \in X$ , the map  $(t, s) \rightarrow S(t, s)x$  is continuous for  $t \geq s \geq a$ , and that there are numbers  $\hat{M} \geq 1$  and  $\omega \in \mathbb{R}$  such that

$$\|S(t, s)\| := \sup\{|S(t, s)x| : |x| \leq 1\} \leq \hat{M}e^{\omega(t-s)}, \quad \forall t \geq s \geq a.$$

Suppose that  $v^-$  and  $v^+$  are continuous functions from  $[a - \tau, b)$  into  $X$  such that  $v^-(t) \leq v^+(t)$  for  $t \in [a - \tau, b)$ , and that  $[v^-(t), v^+(t)] \subset E(t)$  for all  $a - \tau \leq t \leq b$ . Assume that for each  $a < c < b$ , there exists a continuous and increasing function  $\bar{v}_c : [0, c - a] \rightarrow [0, \infty)$  with  $\bar{v}_c(0) = 0$  such that

$$|v^\pm(t) - v^\pm(s)| \leq \bar{v}_c(|t - s|), \quad \text{for all } a \leq t, s \leq c.$$

Moreover, assume that

$$v^-(t+h) \leq S(t+h, t)v^-(t) + \int_t^{t+h} S(t+h, r)B(r, v_r^-)dr$$

and

$$v^+(t+h) \geq S(t+h, t)v^+(t) + \int_t^{t+h} S(t+h, r)B(r, v_r^+)dr$$

for  $a \leq t \leq t+h < b$ .

**Theorem 2.5.3** ([58, Corollary 5]) *Suppose that  $B$  is quasi-monotone on  $\mathbb{Y}$  in the sense that*

$$\lim_{h \rightarrow 0^+} d(\psi(0) - \phi(0) + h[B(t, \psi) - B(t, \phi)], X_+) = 0, \quad (2.2)$$

*for all  $\phi, \psi \in \mathbb{Y}$  with  $\phi(s) \leq \psi(s), \forall s \in [-\tau, 0]$ . Then for each  $\chi \in \mathbb{Y}$  with  $v_a^- \leq \chi \leq v_a^+$ , the equation*

$$\begin{cases} u(t) = S(t, a)\chi(0) + \int_a^t S(t, r)B(r, u_r)dr, & a \leq t < b, \\ u(a + \theta) = \chi(\theta) \text{ for } -\tau \leq \theta \leq 0, \\ \chi \in \mathcal{D}(a) \end{cases}$$

*has a (unique) solution  $u(\cdot, \chi)$  on  $[a, \bar{b}]$  where  $a < \bar{b} = \bar{b}(\chi)$ . Furthermore, if  $v_a^- \leq \chi \leq \psi \leq v_a^+$ , then*

$$v^-(t) \leq u(t, \chi) \leq u(t, \psi) \leq v^+(t), \quad \forall t \in [a, \hat{b}),$$

*where  $\hat{b} = \min\{\bar{b}(\chi), \bar{b}(\psi)\}$ .*

## Chapter 3

# A Periodic Population Model with Dispersal

### 3.1 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, 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., [10, 15, 84]. These models, however, represent the habitat by discrete 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, e.g., [5, 65, 94]. However, reaction-diffusion models may underestimate speeds of invasion [16, 43]. Further, there are more general dispersal processes than diffusion and advection as well as long-range effects.

Recently, integro-differential models 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, see, e.g., [24, 41, 44, 55, 59, 60, 67, 88]. In particular, Medlock and Kot [59] investigated the effects of population dispersal using the DI epidemic model

$$\frac{\partial I}{\partial t} = \beta I(N - I) - DI + D \int_{\Omega} k(x, y) I(t, y) dy, \quad (3.1)$$

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  $t \geq 0$ ,  $\beta \geq 0$  is the transmission rate,  $D \geq 0$  is the rate at which infective individuals move from one location to another,  $k(x, y)$  is the dispersal kernel (i.e., the density function that prescribes the proportion of infectives leaving  $y$  to  $x$ ). Lutscher, Pachepsky and Lewis [55] presented and analyzed a stream population model

$$\frac{\partial u(t, x)}{\partial t} = f(u(t, x)) - \mu u(t, x) + \mu \int_{\Omega} k(x, y) u(t, y) dy, \quad (3.2)$$

where  $u(t, x)$  is the density of a stream population at the point  $x \in \Omega$  at  $t \geq 0$ ,  $f(u)$  describes the population dynamics such as birth and death,  $\mu \geq 0$  is the jumping rate, and  $k(x, y)$  is the dispersal kernel. Similar models were also studied by Fedotov [24] and Méndez et al. [60]. Medlock and Kot [59] derived the minimal wave speed by the “linear conjecture” approach [63] and gave some approximation of the shape of traveling waves. Lutscher, Pachepsky and Lewis [55] also used the same method as in [59] to obtain the minimal wave speed for (3.2), 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. Actually, in their works,  $c_{\pm}^*$  are called the spreading speeds in the positive and negative directions, if

$$\lim_{t \rightarrow \infty} u(t, x + ct) = \begin{cases} \bar{u}, & c_-^* < c < c_+^*, \\ 0, & c < c_-^* \text{ or } c > c_+^*, \end{cases}$$

for any  $x \in \Omega$ , where  $\bar{u} > 0$  is a positive equilibrium of (3.2), see also (3.13) in [55].

Note that (3.1) and (3.2) are special cases of the following general integro-differential equation

$$\frac{\partial u(t, x)}{\partial t} = F(u(t, x)) + a \int_{\mathbf{R}} k(x, y) u(t, y) dy,$$

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

For simplicity, we assume that the dispersal kernel  $k(x, y)$  depends on the distance between  $x$  and  $y$ , that is, we write  $k(x, y) = k(x - y)$ . Then we obtain the following system:

$$\frac{\partial u(t, x)}{\partial t} = F(u(t, x)) + a \int_{\mathbf{R}} k(x - y) u(t, y) dy, \quad (3.3)$$

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

$$\mu(B) = \int_B \chi_B(0, y) k(y) dy,$$

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

$$\mu * u(t, x) := \int_{s \in \mathbf{R}_+, y \in \mathbf{R}} u(t - s, x - y) \mu(ds, dy) = \int_{\mathbf{R}} u(t, x - y) k(y) dy,$$

and (3.3) can be written as

$$\frac{\partial u(t, x)}{\partial t} = f(u, \mu * g(u)), \quad (3.4)$$

where  $f(u, v) = F(u) + av$ ,  $g(u) = u$ . Schumacher [68] established the spreading speed and the existence and nonexistence of traveling wave solutions for (3.4) under appropriate conditions on  $f$  and  $g$ . We should point out that the spreading speed in [68] was also defined in a weak sense (see, e.g., (3.13) in [55]).

It is observed that time-varying environments (e.g., due to seasonal variation) affect population dynamics very much. This suggests that nonautonomous systems

be more realistic for some populations. Therefore, in this chapter we consider the following periodic evolution equation

$$\frac{\partial u(t, x)}{\partial t} = F(t, u(t, x)) + a(t) \int_{\mathbb{R}} k(x - y) u(t, y) dy, \quad (3.5)$$

where  $u(t, x)$  is the spatial density of a population at the position  $x \in \mathbb{R}$  at time  $t \geq 0$ ,  $F(t, u(t, x))$  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 position  $x \in \mathbb{R}$  at time  $t \geq 0$ ,  $a(t) \geq 0$  is the rate at which an individual leaves its current location at time  $t \geq 0$ ,  $k(x, y)$  is the dispersal kernel that describes the probability that an individual moves from position  $y$  to position  $x$ . Moreover, two continuous functions  $F$  and  $a$  are  $\omega$ -periodic in  $t$  for some  $\omega > 0$ , and  $a(t) \not\equiv 0$ . 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”).

We adopt the definition of spreading speeds in a strong sense (see Theorem 3.3.1) and study the spreading speed and periodic traveling waves for (3.5). It seems to be difficult to apply the approach in [68] to the periodic equation (3.5). However, it is natural to use the theory in [85] for monotone discrete-time systems to study the spreading speed for the time period map associated with (3.5). In order to carry over the results to (3.5), we appeal to the theory recently developed in [52] for monotone periodic semiflows. More precisely, we use this theory to establish the existence of the asymptotic speed of spread  $c^*$  and its explicit formula, and the nonexistence of periodic traveling waves with the wave speed  $c < c^*$ . However, we cannot apply this theory to prove the existence of monotone periodic traveling waves with the wave speed  $c \geq c^*$ . This is because the solution maps associated with (3.5) lack the compactness with respect to the compact open topology (see [50, 53]). In the autonomous case of (3.5), we are able to prove the existence of monotone traveling waves via the method of upper and lower solutions and the limiting argument.

This chapter is organized as follows. In section 3.2, we prove the well-posedness and the comparison principle for (3.5). In section 3.3, we establish the existence of

the spreading speed  $c^*$  for solutions of (3.5) with initial data having compact supports by using the general results in section 2.3 (see also [53, 52]). In section 3.4, we show the nonexistence of periodic traveling waves of (3.5) with the wave speed  $c \in (0, c^*)$  by Theorem 2.3.4, and the existence of monotone traveling waves with the wave speed  $c \geq c^*$  in the autonomous case. A short discussion section completes the chapter.

### 3.2 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 (3.5). Assume that

(H1)  $F(t, u) = ug(t, u)$  with  $g \in C(\mathbb{R}_+^2, \mathbb{R})$  and  $g_u(t, u) < 0$ ,  $\forall (t, u) \in \mathbb{R}_+^2$ ,  $\int_0^\omega (g(t, 0) + a(t))dt > 0$ , and there exist  $\hat{u} > 0$  and  $L > 0$  such that  $g(t, \hat{u}) + a(t) \leq 0$ ,  $\forall t \geq 0$ , and  $|F(t, u_1) - F(t, u_2)| \leq L|u_1 - u_2|$ ,  $\forall t \geq 0, u_1, u_2 \in W := [0, \hat{u}]$ .

(H2)  $k(y) \geq 0$ ,  $k(-y) = k(y)$ ,  $\int_{\mathbb{R}} k(y)dy = 1$ , and the integral  $\int_{\mathbb{R}} k(y)e^{\alpha y}dy$  converges for all  $\alpha \in [0, \Delta)$ , where  $\Delta > 0$  is the abscissa of convergence and it may be infinity.

For convenience, we set

$$m_1 = \max_{t \in [0, \omega]} a(t).$$

Consider the spatially homogeneous system associated with (3.5)

$$\frac{du(t)}{dt} = F(t, u(t)) + a(t)u(t). \quad (3.6)$$

By [97, Theorem 3.1.2], it then follows that (3.6) has a positive  $\omega$ -periodic solution  $u^*(t)$ , which is globally asymptotically stable in  $[0, \hat{u}] \setminus \{0\}$ .

The subsequent result is on the global existence, uniqueness and forward invariance of solutions of (3.5).

**Theorem 3.2.1** For any  $u_0 \in C(\mathbb{R}, W)$ , (3.5) has a unique solution  $u(t, \cdot; u_0)$  satisfying  $u(0, \cdot; u_0) = u_0$  and  $u(\cdot; u_0) \in C(\mathbb{R}_+ \times \mathbb{R}, W)$ .

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

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

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

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

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, (3.5) can be written as

$$\frac{\partial u(t, x)}{\partial t} = -\alpha u(t, x) + Q[u](t, x), \quad \alpha > L. \quad (3.7)$$

Given the initial condition  $u(0, \cdot) = u_0 \in C(\mathbb{R}, W)$ , (3.7) is equivalent to the integral equation

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

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

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

Then

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

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

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

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

where  $\lambda > 0$  is a constant. Then  $S$  is a complete metric space with metric  $d_\lambda$ . For any  $u, \tilde{u} \in S$ , we have

$$\begin{aligned} & |G[u](t, x) - G[\tilde{u}](t, x)|e^{-\lambda t} \\ &= \left| \int_0^t e^{-\alpha(t-s)} (Q[u](s, x) - Q[\tilde{u}](s, x)) ds \right| e^{-\lambda t} \\ &\leq \int_0^t e^{-(\alpha+\lambda)(t-s)} d_\lambda(u, \tilde{u}) (\alpha + L + a(s)) \int_{\mathbf{R}} k(x-y) dy ds \\ &\leq \frac{\alpha + L + m_1}{\alpha + \lambda} d_\lambda(u, \tilde{u}). \end{aligned}$$

This implies that

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

Choose  $\lambda > 0$  large enough such that  $\frac{\alpha+L+m_1}{\alpha+\lambda} < 1$ . Then  $G$  is a contracting mapping on  $(S, d_\lambda)$ . By the contracting mapping theorem,  $G$  has a unique fixed point in  $S$ , which is a solution of (3.5) with  $u(0, \cdot) = u_0$ . ■

In order to establish the comparison principle for upper and lower solutions of (3.5), we first introduce the following concepts.

**Definition 3.2.1** A function  $\bar{u} \in C(\mathbb{R}_+ \times \mathbb{R}, W)$  is called an upper solution of (3.5) if  $\frac{\partial \bar{u}}{\partial t}$  exists and

$$\frac{\partial \bar{u}(t, x)}{\partial t} \geq F(t, \bar{u}(t, x)) + a(t) \int_{\mathbf{R}} k(x-y) \bar{u}(t, y) dy.$$

A function  $\underline{u} \in C(\mathbb{R}_+ \times \mathbb{R}, W)$  is called a lower solution of (3.5) if  $\frac{\partial \underline{u}(t, x)}{\partial t}$  exists and

$$\frac{\partial \underline{u}(t, x)}{\partial t} \leq F(t, \underline{u}(t, x)) + a(t) \int_{\mathbf{R}} k(x-y) \underline{u}(t, y) dy.$$

**Theorem 3.2.2** Let  $\bar{u}(t, x)$  and  $\underline{u}(t, x)$  be upper and lower solutions of (3.5), respectively. If  $\bar{u}(0, \cdot) \geq \underline{u}(0, \cdot)$ , then  $\bar{u}(t, \cdot) \geq \underline{u}(t, \cdot)$  for all  $t \geq 0$ .

**Proof** Define  $v(t, x) = \bar{u}(t, x) - \underline{u}(t, x)$ ,  $\forall (t, x) \in \mathbb{R}_+ \times \mathbb{R}$ , and  $w(t) = \inf_{x \in \mathbf{R}} v(t, x)$ ,  $\forall t \geq 0$ . Obviously,  $w(t)$  is continuous in  $t$  and  $w(0) \geq 0$ . Now we show that  $w(t) \geq 0$ ,

$\forall t \geq 0$ . 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

$$w(t_0)e^{-\delta t_0} = \min_{t \in [0, t_0]} w(t)e^{-\delta t} < w(\tau)e^{-\delta \tau}, \quad \forall \tau \in [0, t_0]. \quad (3.8)$$

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

$$v(t_k, x_k)e^{-\delta t_k} = \min_{t \in [0, t_0]} v(t, x_k)e^{-\delta t}. \quad (3.9)$$

For any  $\varepsilon \in (0, t_0)$ , let  $m_\varepsilon = \min_{t \in [0, t_0 - \varepsilon]} w(t)e^{-\delta t}$ . By (3.8), we have

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

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

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

By (3.9), we obtain

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

and hence,  $t_k \in [t_0 - \varepsilon, t_0], \forall k \geq K_\varepsilon$ . It then follows that,  $\lim_{k \rightarrow \infty} t_k = t_0$ . Since

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

we have

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

Letting  $k \rightarrow \infty$ , we obtain  $\lim_{k \rightarrow \infty} v(t_k, x_k) = w(t_0)$ . Then (3.9) implies that,

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

and hence,  $\frac{\partial v(t_k, x_k)}{\partial t} \leq \delta v(t_k, x_k)$ . Since  $v(t_k, x_k) < 0$ , we have

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

Then

$$\begin{aligned}
0 &\leq \frac{\partial v(t_k, x_k)}{\partial t} - Lv(t_k, x_k) - a(t_k) \int_{\mathbb{R}} k(x_k - y)v(t_k, y)dy \\
&\leq (\delta - L)v(t_k, x_k) - a(t_k) \int_{\mathbb{R}} k(x_k - y)v(t_k, y)dy \\
&\leq (\delta - L)v(t_k, x_k) - a(t_k)w(t_k) \\
&\leq (\delta - L)v(t_k, x_k) - m_1w(t_k).
\end{aligned}$$

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

### 3.3 The asymptotic speed of spread

In this section, we use the theory developed in [85, 53, 52] to prove the existence of the asymptotic speed of spread and obtain its explicit formula.

Let  $C$  be the set of all bounded and continuous functions from  $\mathbb{R}$  to  $\mathbb{R}$  and  $C_r = \{u \in C : 0 \leq u(x) \leq r, \forall x \in \mathbb{R}\}$ , for any  $r > 0$ . Throughout this section, we equip  $C$  with the compact open topology, that is,  $v^n \rightarrow v$  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

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

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

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

$$Q_t(\varphi)(x) := u(t, x; \varphi), \quad \forall x \in \mathbb{R}, t \geq 0,$$

where  $u(t, \cdot; \varphi)$  is the solution of (3.5) satisfying  $u(0, \cdot; \varphi) = \varphi$ .

**Lemma 3.3.1**  $\{Q_t\}_{t \geq 0}$  is a monotone periodic semiflow on  $C(\mathbb{R}, W)$ .

**Proof** We prove that  $Q_t$  is a periodic semiflow on  $C(\mathbb{R}, W)$ .  $Q_t$  satisfies Definition 2.3.1 (i) obviously. It follows from the existence and uniqueness of solutions to (3.5) that  $Q_t$  satisfies Definition 2.3.1 (ii). It remains to prove that  $Q_t$  satisfies Definition 2.3.1 (iii).

Given  $\varphi \in C(\mathbb{R}, W)$ . By the form of (3.5), it is easy to see that  $\frac{\partial u(t, x; \varphi)}{\partial t}$  is bounded for all  $(t, x) \in \mathbb{R}_+ \times \mathbb{R}$  and hence, there exists  $\bar{L} = \bar{L}(\varphi) > 0$  such that  $|\frac{\partial u(t, x; \varphi)}{\partial t}| \leq \bar{L}$ . This implies that

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

Thus,  $Q_t(\varphi) = u(t, \cdot; \varphi)$  is continuous in  $t \in \mathbb{R}_+$  with respect to the compact open topology.

**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  $|\varphi_1(x) - \varphi_2(x)| < \delta, \forall x \in [z - M, z + M]$  for some  $z \in \mathbb{R}$ , then  $|u(t, z; \varphi_1) - u(t, z; \varphi_2)| < \varepsilon, \forall t \in [0, t_0]$ .

By the spatial translation invariance of (3.5), it suffices to prove the claim for  $z = 0$ . Let  $w(t, x) = u(t, x; \varphi_1) - u(t, x; \varphi_2)$ . 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.  $\varphi_1 \geq \varphi_2$ . By Theorem 3.2.2,  $u(\cdot; \varphi_1) \geq u(\cdot; \varphi_2)$ . Then  $w(t, x) \geq 0$  and

$$\frac{\partial w(t, x)}{\partial t} \leq Lw(t, x) + a(t) \int_{\mathbb{R}} k(x - y)w(t, y)dy.$$

We write the linear integro-differential system

$$\frac{\partial v(t, x)}{\partial t} = Lv(t, x) + a(t) \int_{\mathbb{R}} k(x - y)v(t, y)dy \quad (3.10)$$

as a system of integral equations

$$v(t, x) = e^{Lt}\varphi(x) + \int_0^t e^{L(t-s)}a(s) \int_{\mathbb{R}} k(x - y)v(s, y)dyds, \quad (3.11)$$

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

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

$$V_m(t, x) = e^{Lt}\varphi(x) + \int_0^t e^{L(t-s)}a(s) \int_{\mathbb{R}} k(x-y)V_{m-1}(s, y)dyds, \quad \forall t \geq 0, x \in \mathbb{R}, m \geq 1. \quad (3.12)$$

By induction, we have

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

where

$$\begin{aligned} a_0(\varphi)(t, x) &= e^{Lt}\varphi(x), \\ a_k(\varphi)(t, x) &= \int_0^t e^{L(t-s)}a(s) \int_{\mathbb{R}} k(x-y)a_{k-1}(\varphi)(s, y)dyds, \quad \forall k \geq 1. \end{aligned}$$

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

$$P(\varphi)(x) = \int_{\mathbb{R}} k(x-y)\varphi(y)dy, \quad \forall \varphi \in C_{\hat{a}}, x \in \mathbb{R}.$$

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

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

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

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

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

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

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

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

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

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  $m \rightarrow \infty$  in (3.12), we see that  $V(t, x)$  satisfies (3.11) and  $V(0, x) = \varphi(x)$ , and hence  $V(t, x)$  is a solution of (3.10) with  $V(0, \cdot) = \varphi$ .

Suppose that  $\bar{V}(t, x)$  is another solution of (3.10) with  $\bar{V}(0, x) = \varphi(x)$ . It follows that

$$\begin{aligned} |V(t, x) - \bar{V}(t, x)| &= \left| \int_0^t e^{L(t-s)} a(s) \int_{\mathbb{R}} k(x-y)(V(s, y) - \bar{V}(s, y)) dy ds \right| \\ &\leq \int_0^t e^{L(t-s)} a(s) \int_{\mathbb{R}} k(x-y) |V(s, y) - \bar{V}(s, y)| dy ds. \end{aligned}$$

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

$$G(t) \leq \int_0^t e^{L(t-s)} a(s) \int_{\mathbb{R}} k(x-y) G(s) dy ds = \int_0^t e^{L(t-s)} a(s) G(s) ds, \quad \forall t \geq 0,$$

which implies that

$$G(t)e^{-Lt} \leq m_1 \int_0^t e^{-Ls} G(s) ds \leq \varepsilon + m_1 \int_0^t e^{-Ls} G(s) ds, \quad \forall \varepsilon > 0.$$

By the Gronwall inequality, this implies that  $G(t)e^{-Lt} \leq \varepsilon e^{m_1 t}$ ,  $\forall \varepsilon > 0$ , and hence  $G(t) \equiv 0$ . This proves the uniqueness of the solution of (3.10) with  $V(0, \cdot) = \varphi$ .

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

By the continuity of  $P(\varphi)$  at  $\varphi = 0$ , we see that for any  $k \geq 0$ ,  $P^k(\varphi) : C_{\mathfrak{a}} \rightarrow C$  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  $P^k(\varphi)(0) < \varepsilon$ ,  $\forall 0 \leq k \leq N$ , provided that  $\varphi \in C(\mathbb{R}, W)$  with  $\varphi(x) < \delta$ ,  $\forall x \in [-M, M]$ . Thus,

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

It follows that

$$V(t, 0) < \varepsilon + \varepsilon e^{(m_1+L)t_0}, \quad \forall t \in [0, t_0]$$

provided that  $\varphi \in C(\mathbb{R}, W)$  with  $\varphi(x) < \delta$ ,  $\forall x \in [-M, M]$ .

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

$$u(t, 0; \varphi_1) - u(t, 0; \varphi_2) = w(t, 0) \leq V(t, 0) < (1 + e^{(m_1+L)t_0})\varepsilon, \quad \forall t \in [0, t_0],$$

provided that  $0 \leq \varphi_1(x) - \varphi_2(x) < \delta$ ,  $\forall x \in [-M, M]$ .

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

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

Then  $\hat{\varphi}_1(x) - \hat{\varphi}_2(x) = |\varphi_1(x) - \varphi_2(x)|$  and

$$u(t, x; \hat{\varphi}_2(x)) \leq u(t, x; \varphi_1), \quad u(t, x; \varphi_2) \leq u(t, x; \hat{\varphi}_1(x)), \quad \forall (t, x) \in \mathbb{R}_+ \times \mathbb{R}.$$

Thus,

$$|u(t, x; \varphi_1) - u(t, x; \varphi_2)| \leq u(t, x; \hat{\varphi}_1(x)) - u(t, x; \hat{\varphi}_2(x)).$$

By case 1, we see that the claim also holds for  $\varphi_1$  and  $\varphi_2$  with  $\varphi_1 \not\leq \varphi_2$ .

By the claim above,  $Q_t(\varphi) = u(t, \cdot; \varphi)$  is continuous in  $\varphi$  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 2.3.1 (iii). Therefore,  $Q_t$  is a continuous  $\omega$ -periodic semiflow on  $C(\mathbb{R}, W)$ . By Theorem 3.2.2, the map  $Q_t$  is monotone on  $C(\mathbb{R}, W)$  for each  $t > 0$ . ■

**Lemma 3.3.2** *Assume that (H1) holds. Then for each  $t > 0$ , the solution map  $Q_t$  of (3.5) satisfies (A1)-(A4) with  $b^* = \hat{u}$  and  $Q_\omega$  satisfies (A5) with  $b^* = u^*(0)$ .*

**Proof** By Lemma 3.3.1, it is easy to see that  $Q_t$  satisfies (A1)-(A4) with  $b^* = \hat{u}$ .

Let  $\hat{Q}_t = Q_t|_{[0, \hat{u}]}$ . Then  $\hat{Q}_t : [0, \hat{u}] \rightarrow [0, \hat{u}]$  is the  $\omega$ -periodic semiflow generated by (3.6). Since (3.6) is a scalar equation, the uniqueness of solutions implies that  $\hat{Q}_t$  is strongly monotone on  $[0, \hat{u}]$ . Note that (3.6) has a positive  $\omega$ -periodic solution  $u^*(t)$  which is globally asymptotically stable in  $[0, \hat{u}] \setminus \{0\}$ . We see that  $\hat{Q}_\omega$  is strongly monotone 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., Theorem 2.2.1), the map  $\hat{Q}_\omega$  admits a strongly monotone full orbit connecting 0 to  $u^*(0)$ . Therefore,  $Q_\omega$  satisfies (A5) with  $b^* = u^*(0)$ . ■

By Lemma 3.3.2 and Theorem 2.3.1, it follows that  $Q_\omega$  has an asymptotic speed of spread  $c_\omega^* > 0$ .

Consider the linearized system of (3.5) at the zero solution

$$\begin{aligned} \frac{\partial u(t, x)}{\partial t} &= g(t, 0)u(t, x) + a(t) \int_{\mathbb{R}} k(x - y)u(t, y)dy \\ &= g(t, 0)u(t, x) + a(t) \int_{\mathbb{R}} k(y)u(t, x - y)dy. \end{aligned} \quad (3.13)$$

For any  $\alpha \in (0, \Delta)$ , let  $u(t, x) = e^{-\alpha x}v(t)$ . Substituting  $u(t, x)$  into (3.13) yields

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

Then

$$v'(t) = A(\alpha, t)v(t), \quad (3.14)$$

where

$$A(\alpha, t) = g(t, 0) + a(t) \int_{\mathbb{R}} k(y)e^{\alpha y}dy. \quad (3.15)$$

Thus, if  $v(t)$  is a solution of (3.14), then  $u(t, x) = e^{-\alpha x}v(t)$  is a solution of (3.13).

Note that the solution of (3.14) can be expressed as  $v(t, v_0) = v_0 e^{\int_0^t A(\alpha, s)ds}$ ,  $\forall v_0 \in \mathbb{R}$ . Define

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

where  $M_t$  is the linear solution map defined by (3.13) and  $v(t, v_0)$  is the solution of (3.14) with  $v(0, v_0) = v_0$ . Therefore,  $B_\alpha^t$  is the solution map associated with (3.14) on  $\mathbb{R}$  and  $B_\alpha^t$  is strongly positive for each  $t > 0$ . Then  $B_\alpha^\omega(v_0) = v_0 e^{\int_0^\omega A(\alpha, s)ds}$ . Let  $\gamma(\alpha) := e^{\int_0^\omega A(\alpha, s)ds}$ , and define a function

$$\Phi(\alpha) := \frac{1}{\alpha} \ln \gamma(\alpha) = \frac{1}{\alpha} \ln e^{\int_0^\omega A(\alpha, s)ds} = \frac{\int_0^\omega A(\alpha, s)ds}{\alpha}. \quad (3.16)$$

By [53, Theorem 3.8], we have the following result.

**Lemma 3.3.3** *The following statements are valid*

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

**Proposition 3.3.1** *Assume that (H1) and (H2) hold. Let  $c_\omega^*$  be the asymptotic speed of spread of  $Q_\omega$ . Then*

$$c_\omega^* = \inf_{0 < \alpha < \Delta} \Phi(\alpha) = \inf_{0 < \alpha < \Delta} \frac{\int_0^\omega A(\alpha, s) ds}{\alpha}.$$

**Proof** By the definitions of  $A(\alpha, t)$  and  $\gamma(\alpha)$  and (H1), 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, the condition (B7) is satisfied.

Now we prove that  $\Phi(\Delta) = \infty$ . First we consider the case  $\Delta = \infty$ . 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

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

and hence,

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

i.e.,  $\Phi(\infty) = \infty$ . In the case where  $\Delta < \infty$ , we have  $\lim_{\alpha \rightarrow \Delta^-} \int_{\mathbb{R}} k(y) e^{\alpha y} dy = \infty$  and hence,  $\lim_{\alpha \rightarrow \Delta^-} \Phi(\alpha) = \infty$ . Therefore, the infimum of  $\Phi(\alpha)$  is attained at some value  $\bar{\alpha} \in (0, \Delta)$ .

Note that  $M_\omega$  and  $B_\alpha^\omega$  satisfy (B1)-(B7) and that (H1) implies  $F(t, u) \leq g(t, 0)u$ ,  $\forall u \geq 0$ . By the comparison theorem, we have  $Q_\omega(\varphi) \leq M_\omega(\varphi)$  for  $\varphi \in C_{u^*}(0)$ . Thus, Theorem 2.3.2 implies that  $c_\omega^* \leq \inf_{0 < \alpha < \Delta} \Phi(\alpha)$ .

By (H1),  $\lim_{u \rightarrow 0^+} \frac{F(t,u)}{u} = g(t,0)$  uniformly for  $t \in [0, \omega]$ . It follows that for any  $\varepsilon \in (0, 1)$ , there exists  $\delta > 0$  such that

$$F(t, u) > (g(t, 0) - \varepsilon)u, \quad \forall 0 < u < \delta, t \in [0, \omega].$$

Moreover, there is  $\eta = \eta(\delta) > 0$  such that for any  $\varphi \in C_\eta$ , we have

$$0 \leq u(t, x; \varphi) \leq u(t, \eta) < \delta, \quad \forall x \in \mathbb{R}, t \in [0, \omega].$$

Thus, for any  $\varphi \in C_\eta$ ,  $u(t, x) := u(t, x; \varphi)$  satisfies

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

Let  $M_t^\varepsilon$ ,  $t \geq 0$ , 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  $M_t^\varepsilon(\varphi) \leq Q_t(\varphi)$ ,  $\forall \varphi \in C_\eta$ ,  $t \in [0, \omega]$ . In particular,  $M_\omega^\varepsilon(\varphi) \leq Q_\omega(\varphi)$ ,  $\forall \varphi \in C_\eta$ . A similar analysis can be made for  $M_t^\varepsilon$  as for  $M_t$ . It follows from Theorem 2.3.2 that  $\inf_{0 < \alpha < \Delta} \Phi_\varepsilon(\alpha) \leq c_\omega^*$ . Thus,

$$\inf_{0 < \alpha < \Delta} \Phi_\varepsilon(\alpha) \leq c_\omega^* \leq \inf_{0 < \alpha < \Delta} \Phi(\alpha), \quad \forall \varepsilon \in (0, 1).$$

Letting  $\varepsilon \rightarrow 0$ , we have  $c_\omega^* = \inf_{0 < \alpha < \Delta} \Phi(\alpha)$ . ■

The following result shows that  $c^* := \frac{c_\omega^*}{\omega} = \frac{1}{\omega} \inf_{0 < \alpha < \Delta} \frac{\int_0^\omega A(\alpha, s)ds}{\alpha}$  is the spreading speed of solutions of (3.5) with initial functions having compact supports.

**Theorem 3.3.1** *Assume that (H1) and (H2) hold and let  $c^* = c_\omega^*/\omega$ . Then the following statements are valid:*

- (1) *For any  $c > c^*$ , if  $\varphi \in C_{u^*(0)}$  with  $\varphi(x) = 0$  for  $x$  outside a bounded interval, then  $\lim_{t \rightarrow \infty, |x| \geq ct} u(t, x; \varphi) = 0$ .*
- (2) *For any  $0 < c < c^*$ , there is a positive number  $r$  such that if  $\varphi \in C_{u^*(0)}$  with  $\varphi(x) > 0$  for  $x$  on an interval of length  $2r$ , then  $\lim_{t \rightarrow \infty, |x| \leq ct} (u(t, x; \varphi) - u^*(t)) = 0$ .*

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

**Proof** The conclusion (1) follows from Theorem 2.3.3.

By (H1), we have  $F(t, u) \leq g(t, 0)u$  for all  $u \in [0, u^*(0)]$ . Then the proof of Proposition 3.3.1 implies that there is a sequence of linear operators  $\{M_n\}_{n=1}^{+\infty}$  with  $\varepsilon_n = \frac{1}{n}, \forall n \in \mathbb{N}$ , such that each  $M_n[\varphi] \leq Q_\omega[\varphi], \forall \varphi \in C_{\sigma_n}$ , for some  $\sigma_n > 0, n \in \mathbb{N}$ . Moreover, each  $M_n$  satisfies (B1)–(B7) and the spreading speed  $c_n^*$  of  $M_n$  converges to  $c_\omega^*$  as  $n \rightarrow \infty$ . Let  $c < c^*$  be given. It then follows from [53, Theorem 3.5] that  $r_\sigma$  can be chosen to be independent of  $\sigma > 0$ . Thus, Theorem 2.3.3 implies the conclusion (2).

In the case where  $a(t) > 0, \forall t \in \mathbb{R}$ , 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 (3.5) through  $\varphi$  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  $\varphi(x) > 0, \forall x \in [-r, r]$  for some  $r > 0$ . Let  $u(t, x) = u(t, x; \varphi)$ . It follows from the continuity of  $u(t, x)$ , there is an  $\varepsilon > 0$  such that  $u(t, x) > 0, \forall (t, x) \in [0, \varepsilon] \times (-r, r)$ .

Let  $\alpha$  be sufficiently large such that  $\alpha u + F(t, u)$  is increasing in  $u \in [0, \hat{u}]$ . Then  $\alpha u + F(t, u) \geq 0, \forall u \in [0, \hat{u}]$  and  $t \geq 0$ . By the proof of Theorem 3.2.1, we have

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

Set  $[a_0, b_0] = [-r, r]$ . Since  $\int_{\mathbb{R}} k(y)dy = 1$ , 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  $\int_0^t \int_{\mathbb{R}} e^{-\alpha(t-s)} k(x-y)u(s, y)dy ds > 0$  for any  $t \in (0, \varepsilon]$  and  $x \in (a_0 + p, b_0 + p + r_0)$ , which implies that  $u(t, x) > 0, \forall t \in (0, \varepsilon], x \in (a_0 + p, b_0 + p + r_0)$ . By induction,  $u(t, x) > 0$  for

all  $(t, x) \in (0, \varepsilon] \times (a_0 + mp, b_0 + mp + mr_0)$ ,  $\forall m \geq 1$ ,  $m \in \mathbb{Z}$ . Let  $a_m = a_0 + mp$ ,  $b_m = b_0 + mp + mr_0$ . Thus,  $b_m - a_m \rightarrow \infty$  as  $m \rightarrow \infty$  and there exists an integer  $m^* > 0$  such that  $a_{m+1} - b_m < 0$ ,  $\forall m \geq m^*$ . Let  $a^* = a_{m^*}$ . It follows that  $u(t, x) > 0$  for all  $x \in \cup_{m \geq m^*} (a_m, b_m) = (a^*, +\infty)$  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,  $u(t, x) > 0$ ,  $\forall (t, x) \in (0, \varepsilon] \times (a^* - mp - mr_0, +\infty)$  for all  $m \geq 0$ , which implies that  $u(t, x) > 0$ ,  $\forall (t, x) \in (0, \varepsilon] \times \mathbb{R}$ .

By (3.5), we have

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

Given  $x \in \mathbb{R}$ . Let  $w(t)$ ,  $t \geq \varepsilon$ , be the unique solution of the ordinary differential system  $\frac{dw}{dt} = F(t, w)$  satisfying  $w(\varepsilon) = u(\varepsilon, x) > 0$ . Then the standard comparison principle implies that  $u(t, x) \geq w(t) > 0$ ,  $\forall t \geq \varepsilon$ . Thus,  $u(t, x) > 0$ ,  $\forall (t, x) \in [\varepsilon, +\infty) \times \mathbb{R}$ . 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  $u(t_0, \cdot; \varphi)$  as a new initial value for  $u(t, \cdot; \varphi)$ . By the claim above, we have  $u(t_0, x; \varphi) > 0$ ,  $\forall x \in \mathbb{R}$ , and hence, the conclusion (3) follows from the conclusion (2). ■

### 3.4 Traveling waves

**Definition 3.4.1**  $u(t, x) = U(t, x + ct)$  is an  $\omega$ -periodic traveling wave of (3.5) connecting 0 to  $u^*(t)$  if it is a solution of (1.5),  $U(t, \xi)$  is  $\omega$ -periodic in  $t$ , and  $U(t, -\infty) = 0$  and  $U(t, \infty) = u^*(t)$  uniformly for  $t \in [0, \omega]$ .

As a straightforward consequence of Theorem 2.3.4, we have the following result on the nonexistence of monotone periodic traveling waves of (3.5).

**Theorem 3.4.1** *Assume that (H1) and (H2) hold. Let  $c_\omega^*$  be the asymptotic speed of spread of  $Q_\omega$  and  $c^* = c_\omega^*/\omega$ . Then for any  $c \in (0, c^*)$ , system (3.5) admits no  $\omega$ -periodic traveling wave solution  $\phi(t, x + ct)$  connecting 0 and  $u^*(t)$ .*

As mentioned in the introduction, the theory in [53, 52] cannot be applied to establish the existence of monotone  $\omega$ -periodic traveling waves for periodic equation (3.5). However, we are able to prove the existence of traveling waves for the autonomous equation (3.3) under the following assumption:

(H1)'  $F(0) = 0$ ,  $F''(0)$  exists,  $F'(0) + a > 0$  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  $F(u) \leq F'(0)u$  for all  $u \in [0, u^*]$ .

Throughout this section, we assume that (H1)' and (H2) hold. Let  $c^*$  be the spreading speed of (3.3), which is defined as in Theorem 3.3.1. Then

$$c^* = \inf_{0 < \alpha < \Delta} \Phi(\alpha), \quad (3.17)$$

where  $\Phi(\alpha) := A(\alpha)/\alpha$  and  $A(\alpha) := F'(0) + a \int_{\mathbb{R}} k(y)e^{\alpha y} dy$ .

A traveling wave solution of (3.3) is a solution with the form

$$u(t, x) = \phi(x + ct) = \phi(s), \quad s = x + ct. \quad (3.18)$$

Thus, the wave profile  $\phi$  satisfies

$$c \frac{d\phi(s)}{ds} = F(\phi(s)) + a \int_{\mathbb{R}} k(y)\phi(s - y)dy. \quad (3.19)$$

**Definition 3.4.2** *A function  $\bar{\rho} \in C(\mathbb{R}, W)$  is called an upper solution of (3.19) if it is differentiable almost everywhere and satisfies the inequality*

$$c \frac{d\bar{\rho}(s)}{ds} \geq F(\bar{\rho}(s)) + a \int_{\mathbb{R}} k(y)\bar{\rho}(s - y)dy;$$

*a lower solution  $\underline{\rho} \in C(\mathbb{R}, W)$  of (3.19) can be defined by reversing the inequality.*

We consider the function  $\Phi(\alpha) = \frac{A(\alpha)}{\alpha} = \frac{F'(0) + a \int_{\mathbf{R}} k(y) e^{\alpha y} dy}{\alpha}$ ,  $0 < \alpha < \Delta$ . As discussed in section 3.3, there is  $\bar{\alpha} \in (0, \Delta)$  such that  $c^* = \Phi(\bar{\alpha}) = \inf_{0 < \alpha < \Delta} \Phi(\alpha)$ . Let  $c = \Phi(\alpha)$ . Given  $c > c^*$ , there exists at least one  $\alpha \in (0, \Delta)$  such that  $\Phi(\alpha) = c$ . If there are more than one values of  $\alpha$  such that  $\phi(\alpha) = c$ , we choose the smallest one, say,  $\alpha_1$ , such that  $\phi(\alpha_1) = c$ .

Note that for any  $\alpha \in (0, \Delta)$ , if  $v(t, v_0)$  is a solution of

$$v'(t) = A(\alpha)v(t), \quad (3.20)$$

then  $u(t, x) = e^{-\alpha x}v(t, v_0)$  and  $u(t, -x) = e^{\alpha x}v(t, v_0)$  are solutions of

$$\begin{aligned} \frac{\partial u(t, x)}{\partial t} &= F'(0)u(t, x) + a \int_{\mathbf{R}} k(x-y)u(t, y)dy \\ &= F'(0)u(t, x) + a \int_{\mathbf{R}} k(y)u(t, x-y)dy. \end{aligned} \quad (3.21)$$

Let  $\alpha = \alpha_1$ ,  $v(0) = v_0 > 0$ ,  $s = x + \frac{A(\alpha_1)}{\alpha_1}t$ . Then

$$u(t, -x) = e^{\alpha_1 x}v(t, v_0) = e^{\alpha_1 x} \cdot e^{A(\alpha_1)t}v_0 = e^{\alpha_1(x + \frac{A(\alpha_1)}{\alpha_1}t)}v_0 = e^{\alpha_1 s}v_0 = \psi(s).$$

Note that  $u(t, -x)$  satisfies the equation

$$\frac{\partial u(t, x)}{\partial t} = F'(0)u(t, x) + a \int_{\mathbf{R}} k(x-y)u(t, y)dy,$$

and that  $\psi(s)$  is the solution of the linearized equations of (3.19) at zero solution

$$c \frac{d\psi(s)}{ds} = F'(0)\psi(s) + a \int_{\mathbf{R}} k(s-y)\psi(y)dy. \quad (3.22)$$

Substituting  $\psi(s) = e^{\alpha_1 s}v_0$  into (3.22) yields

$$c\alpha_1 e^{\alpha_1 s}v_0 = F'(0)e^{\alpha_1 s}v_0 + a \int_{\mathbf{R}} k(s-y)e^{\alpha_1 y}v_0 dy = F'(0)e^{\alpha_1 s}v_0 + a \int_{\mathbf{R}} k(y)e^{\alpha_1(s-y)}v_0 dy,$$

which implies that

$$c\alpha_1 - F'(0) - a \int_{\mathbf{R}} k(y)e^{-\alpha_1 y} dy = 0.$$

Letting  $\varepsilon > 0$  be sufficiently small, we can obtain  $\alpha_\varepsilon = \alpha_1 + \varepsilon \in (0, \Delta)$  and  $c^* < c_\varepsilon < c$ , where  $c_\varepsilon = \Phi(\alpha_\varepsilon) = \frac{A(\alpha_\varepsilon)}{\alpha_\varepsilon}$ . Since

$$u(t, -x) = e^{\alpha_\varepsilon x}e^{A(\alpha_\varepsilon)t}v_0^\varepsilon = e^{\alpha_\varepsilon s}v_0^\varepsilon = \psi_\varepsilon(s)$$

is also a solution of (3.21) with  $v_0^\varepsilon > 0$ , it follows that  $c_\varepsilon$  and  $\alpha_\varepsilon$  satisfy

$$c_\varepsilon \alpha_\varepsilon - F'(0) - a \int_{\mathbb{R}} k(y) e^{-\alpha_\varepsilon y} dy = 0.$$

Let  $\delta_\varepsilon = c - c_\varepsilon > 0$ . We then have

$$c \alpha_\varepsilon - F'(0) - a \int_{\mathbb{R}} k(y) e^{-\alpha_\varepsilon y} dy = \delta_\varepsilon \alpha_\varepsilon > 0.$$

By (H1)', we can choose  $k > 0$  and  $\delta_0 \in (0, u^*)$  such that  $F(u) \geq F'(0)u - ku^2$ ,  $\forall u \in [0, \delta_0]$ .

Motivated by [19] and [78], we define two functions

$$\bar{\rho}(s) := \min\{u^*, u^* e^{\alpha_1 s}\}, \quad \underline{\rho}(s) := \max\{0, \delta_0 e^{\alpha_1 s} - \delta_0 M e^{\alpha_\varepsilon s}\}, \quad \forall s \in \mathbb{R},$$

where  $M$  satisfies  $\delta_\varepsilon \alpha_\varepsilon M - k\delta_0 \geq 0$  and  $M > 1$ . Clearly,  $\underline{\rho}(s) \leq \bar{\rho}(s)$ . Set

$$f(s) = \delta_0 e^{\alpha_1 s} - \delta_0 M e^{\alpha_\varepsilon s} = \delta_0 e^{\alpha_1 s} (1 - M e^{\varepsilon s}), \quad \tau = -\frac{1}{\varepsilon} \ln M < 0.$$

Then  $f(\tau) = 0$ ,  $f(s) > 0$ ,  $\forall s < \tau$ , and  $f(s) < 0$ ,  $\forall s > \tau$ . Let  $0 < \varepsilon < \alpha_1$ . Then we have  $\underline{\rho}^2(s) \leq \delta_0^2 e^{(\alpha_1 + \varepsilon)s} = \delta_0^2 e^{\alpha_\varepsilon s}$ ,  $\forall s \in \mathbb{R}$ .

**Lemma 3.4.1** *For any  $c > c^*$ , the above defined  $\bar{\rho}(s)$  and  $\underline{\rho}(s)$  are upper and lower solutions of (3.19), respectively.*

**Proof** If  $s \geq 0$ ,  $\bar{\rho}(s) = u^*$  and

$$-c \frac{d\bar{\rho}(s)}{ds} + F(\bar{\rho}(s)) + a \int_{\mathbb{R}} k(y) \bar{\rho}(s-y) dy \leq F(u^*) + a \int_{\mathbb{R}} k(y) u^* dy = 0.$$

If  $s < 0$ ,  $\bar{\rho}(s) = u^* e^{\alpha_1 s}$  and

$$-c \frac{d\bar{\rho}(s)}{ds} + F(\bar{\rho}(s)) + a \int_{\mathbb{R}} k(y) \bar{\rho}(s-y) dy \leq (-c\alpha_1 + F'(0) + a \int_{\mathbb{R}} k(y) e^{-\alpha_1 y} dy) e^{\alpha_1 s} u^* = 0.$$

Thus,  $\bar{\rho}(s)$  is an upper solution of (3.19).

Now we consider  $\underline{\rho}(s)$ . If  $s > \tau$ , then  $f(s) < 0$ ,  $\underline{\rho}(s) = 0$  and

$$-c \frac{d\underline{\rho}(s)}{ds} + F(\underline{\rho}(s)) + a \int_{\mathbb{R}} k(y) \underline{\rho}(s-y) dy = a \int_{\mathbb{R}} k(y) \underline{\rho}(s-y) dy \geq 0.$$

If  $s < \tau$ , then  $f(s) > 0$ ,  $\underline{\rho}(s) = \delta_0 e^{\alpha_1 s} - \delta_0 M e^{\alpha_\epsilon s}$  and

$$\begin{aligned}
& -c \frac{d\underline{\rho}(s)}{ds} + F(\underline{\rho}(s)) + a \int_{\mathbb{R}} k(y) \underline{\rho}(s-y) dy \\
&= -c \alpha_1 \delta_0 e^{\alpha_1 s} + c \delta_0 M \alpha_\epsilon e^{\alpha_\epsilon s} + F(\underline{\rho}(s)) + a \int_{-\infty}^{\tau} k(s-y) \underline{\rho}(y) dy \\
&\geq -c \alpha_1 \delta_0 e^{\alpha_1 s} + c \delta_0 M \alpha_\epsilon e^{\alpha_\epsilon s} + F(\underline{\rho}(s)) + a \int_{\mathbb{R}} k(s-y) f(y) dy \\
&= -c \alpha_1 \delta_0 e^{\alpha_1 s} + c \delta_0 M \alpha_\epsilon e^{\alpha_\epsilon s} + F(\underline{\rho}(s)) + a \int_{\mathbb{R}} k(y) f(s-y) dy \\
&\geq \delta_0 e^{\alpha_1 s} (-c \alpha_1 + a \int_{\mathbb{R}} k(y) e^{-\alpha_1 y} dy + F'(0)) \\
&\quad + \delta_0 M e^{\alpha_\epsilon s} (c \alpha_\epsilon - a \int_{\mathbb{R}} k(y) e^{-\alpha_\epsilon y} dy - F'(0)) - k \underline{\rho}^2(s) \\
&\geq \delta_0 e^{\alpha_\epsilon s} (\delta_\epsilon \alpha_\epsilon M - k \delta_0) \\
&\geq 0.
\end{aligned}$$

Thus,  $\underline{\rho}(s)$  is a lower solution of (3.19). ■

Note that the wave profile equation (3.19) is equivalent to

$$\frac{d\phi(s)}{ds} + \delta\phi(s) = \delta\phi(s) + \frac{1}{c} F(\phi(s)) + \frac{a}{c} \int_{\mathbb{R}} k(y) \phi(s-y) dy, \quad \delta \in \mathbb{R}. \quad (3.23)$$

Since we are interested in traveling wave solutions connecting 0 to  $u^*$ , we always suppose  $\phi(-\infty) = 0$ . Then (3.23) is reduced to

$$\phi(s) = e^{-\delta s} \int_{-\infty}^s e^{\delta t} G[\phi](t) dt,$$

where  $G[\phi](s) = \delta\phi(s) + \frac{1}{c} F(\phi(s)) + \frac{a}{c} \int_{\mathbb{R}} k(y) \phi(s-y) dy$ .

Suppose that  $\phi, \psi \in C(\mathbb{R}, W)$  with  $\phi(t) \geq \psi(t)$ ,  $\forall t \in \mathbb{R}$ . Then

$$\begin{aligned}
& G[\phi](t) - G[\psi](t) \\
&= \delta(\phi - \psi)(t) + \frac{1}{c} (F(\phi(t)) - F(\psi(t))) + \frac{a}{c} \int_{\mathbb{R}} k(y) (\phi(t-y) - \psi(t-y)) dy \\
&\geq (\delta - \frac{L}{c})(\phi - \psi)(t) + \frac{a}{c} \int_{\mathbb{R}} k(y) (\phi(t-y) - \psi(t-y)) dy.
\end{aligned}$$

Thus, for sufficiently large  $\delta$  such that  $\delta - \frac{L}{c} \geq 0$ , we have  $G[\phi](t) \geq G[\psi](t)$ ,  $\forall t \in \mathbb{R}$ , provided that  $\phi(t) \geq \psi(t)$ ,  $\forall t \in \mathbb{R}$ . Moreover,  $G(0) = 0$  and  $G(u^*) = \delta u^*$ .

Define an operator  $T$  on  $C(\mathbb{R}, W)$  by

$$T(\phi)(s) := e^{-\delta s} \int_{-\infty}^s e^{\delta t} G[\phi](t) dt, \quad \forall s \in \mathbb{R}.$$

It is easy to obtain the following results.

**Lemma 3.4.2** *The operator  $T$  has the following properties:*

- (1) *If  $\phi \in C(\mathbb{R}, W)$  is nondecreasing, then so is  $T\phi$ ;*
- (2) *If  $\phi \geq \psi$ , then  $T\phi \geq T\psi$ ;*
- (3) *If  $\phi$  is an upper (lower) solution of (3.19), then  $\phi(s) \geq (T\phi)(s)$  ( $\phi(s) \leq (T\phi)(s)$ ),  $\forall s \in \mathbb{R}$ ;*
- (4) *If  $\phi$  is an upper (lower) solution of (3.19), then  $T\phi$  is also an upper (lower) solution of (3.19).*

Now we are in the position to prove the existence of monotone traveling waves.

**Theorem 3.4.2** *Assume that (H1)' and (H2) hold. Let  $c^*$  be defined in (3.17). Then for any  $c \geq c^*$ , system (3.3) has a traveling wave  $\phi(x + ct)$  connecting 0 to  $u^*$  such that  $\phi(s)$  is continuous and nondecreasing in  $s \in \mathbb{R}$ .*

**Proof** Case 1.  $c > c^*$ . By Lemma 3.4.1, there exist an upper solution  $\bar{\rho}(s)$  and a lower solution  $\underline{\rho}(s)$  for (3.19). Let  $\phi_0 = \bar{\rho}$ ,  $\phi_m = T\phi_{m-1}$ ,  $\forall m \geq 1$ . By Lemma 3.4.2, we then have

$$0 \leq \underline{\rho}(s) \leq \dots \leq \phi_m(s) \leq \phi_{m-1}(s) \leq \dots \leq \bar{\rho}(s) \leq u^*, \quad \forall s \in \mathbb{R}.$$

By the monotone convergence theorem, there is a continuous function  $\phi(s)$  such that  $\phi(s) = \lim_{m \rightarrow \infty} \phi_m(s)$ . By the construction of  $\phi_m$ , we see that  $\phi$  is a fixed point of  $T$ ,  $\phi$  is nondecreasing and  $\underline{\rho}(s) \leq \phi(s) \leq \bar{\rho}(s)$ ,  $\forall s \in \mathbb{R}$ .

Since  $\bar{\rho}(-\infty) = 0$ , we have  $\phi(-\infty) = 0$ . Moreover, since  $\underline{\rho}(s) \leq \phi(s) \leq \phi(+\infty) \leq u^*$  and  $\underline{\rho} \not\equiv 0$ , we have  $\phi(+\infty) > 0$ . Since  $\lim_{s \rightarrow +\infty} \frac{d\phi}{ds} = 0$ , it is easy to see that  $\phi(+\infty)$  is an equilibrium of

$$\frac{du(t)}{dt} = F(u(t)) + au(t). \quad (3.24)$$

Thus,  $\phi(+\infty) = u^*$ , and hence,  $\phi(x + ct)$  is a monotone traveling wave solution of (3.3) connecting 0 and  $u^*$ .

Case 2.  $c = c^*$ . Let  $\{c_m\} \subseteq (c^*, c^* + 1)$  with  $\lim_{m \rightarrow \infty} c_m = c^*$ . Since  $c_m > c^*$ , by Case 1, (3.19) admits a nondecreasing solution  $\phi^{(m)}(s)$  for each  $c_m$ , such that  $\phi^{(m)}(-\infty) = 0$  and  $\phi^{(m)}(+\infty) = u^*$ . Without loss of generality, we may assume that  $\phi^{(m)}(0) = \frac{1}{2}u^*$ ,  $\forall m \geq 1$ . Note that  $\phi^{(m)}(s)$  satisfies

$$c_m \frac{d\phi^{(m)}(s)}{ds} = F(\phi^{(m)}(s)) + a \int_{\mathbb{R}} k(y)\phi^{(m)}(s-y)dy$$

and

$$\phi^{(m)}(s) = e^{-\delta s} \int_{-\infty}^s e^{\delta t} [\delta \phi^{(m)}(t) + \frac{1}{c_m} F(\phi^{(m)}(t)) + \frac{a}{c_m} \int_{\mathbb{R}} k(y)\phi^{(m)}(t-y)dy] dt, \quad (3.25)$$

where  $\delta - \frac{L}{c^*} \geq 0$ . Since  $\{\phi^{(m)}(s)\}$  and  $\left\{\frac{d\phi^{(m)}(s)}{ds}\right\}$  are uniformly bounded on  $\mathbb{R}$ ,  $\{\phi^{(m)}(s)\}$  is equi-continuous on  $\mathbb{R}$ . Using the Ascoli theorem and the standard diagonal method, we can obtain a subsequence of functions  $\{\phi_{m_k}\}$ , which converges to  $\phi^*(s)$  as  $k \rightarrow \infty$ , uniformly for  $s$  in any bounded subset of  $\mathbb{R}$ .

Note that  $\phi^*(s)$  is nondecreasing and  $\phi^*(0) = \frac{1}{2}u^*$ . Letting  $m \rightarrow \infty$  in (3.25) and using the Lebesgue dominated convergence theorem, we obtain

$$\phi^*(s) = e^{-\delta s} \int_{-\infty}^s e^{\delta t} [\delta \phi^*(t) + \frac{1}{c^*} F(\phi^*(t)) + \frac{a}{c^*} \int_{\mathbb{R}} k(y)\phi^*(t-y)dy] dt, \quad \forall s \in \mathbb{R},$$

which implies that  $\phi^*$  is also a solution of (3.19). By the L'Hospital rule and  $\phi^*(-\infty) < \phi^*(+\infty)$ , we have  $\phi^*(-\infty) = 0$  and  $\phi^*(+\infty) = u^*$ . Thus,  $\phi^*(x + c^*t)$  is a monotone traveling wave of (3.3) connecting 0 to  $u^*$ . ■

By Theorems 3.4.1 and Theorem 3.4.2, it follows that the asymptotic speed of spread for the autonomous equation (3.3) coincides with the minimal wave speed for monotone traveling waves.

### 3.5 Numerical simulations

In this section, we provide numerical simulations for the DI model presented in [59]

$$\frac{\partial u}{\partial t} = \beta u(N - u) - Du + D \int_{\mathbf{R}} k(x - y)u(t, y)dy, \quad (3.26)$$

which is a special case of (3.3). We choose  $\beta = 1$ ,  $N = 2$ ,  $D = 1$  and the Gaussian kernel  $k(y) = \frac{1}{\theta\sqrt{\pi}}e^{-\frac{y^2}{\theta^2}}$  with  $\theta = \frac{1}{4}\sqrt{\frac{2}{c}}$ . Then  $F(u) = u(1 - u)$ , the integration  $\int_{\mathbf{R}} k(y)e^{\alpha y}dy$  converges for all  $\alpha \in (0, +\infty)$ , and (3.26) satisfies (H1)' and (H2) with  $u^* = 2$ . Moreover,  $F(u) \leq F'(0)u$ ,  $\forall u \in [0, u^*]$ . By (3.15),  $A(\alpha) = 1 + e^{\frac{\alpha^2}{32}}$ . It follows from Theorem 3.3.1 that the asymptotic speed  $c^* = \inf_{\alpha > 0} \frac{A(\alpha)}{\alpha} \approx 8.016706232$ , and that for any continuous initial function  $\varphi$  with compact support, we have  $\lim_{t \rightarrow \infty, |x| \geq tc} u(t, x; \varphi) = 0$ ,  $\forall c > c^*$ , and  $\lim_{t \rightarrow \infty, |x| \leq tc} u(t, x; \varphi) = 2$ ,  $\forall c \in (0, c^*)$ .

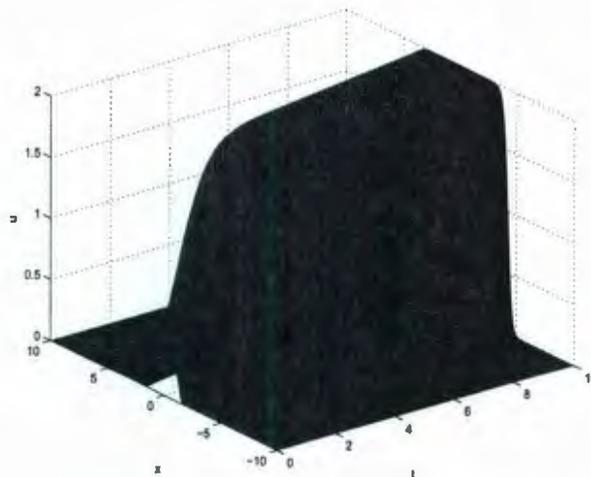


Figure 3.1: The solution of (3.26) with the initial function  $\varphi_1(x)$ .

We discretize (3.26) by the finite difference method coupled with the composite trapezoidal rule for integration on a finite spatial interval, which is sufficiently large in comparison with the domain in which the solutions rapidly change shapes. We

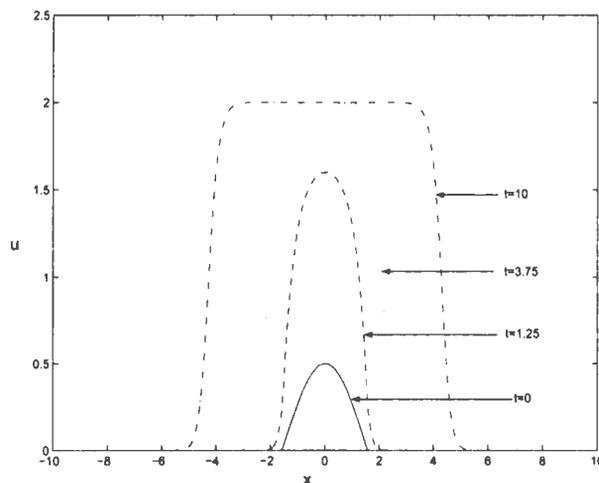


Figure 3.2: The solution of (3.26) with the initial function  $\varphi_1(x)$  for some  $t$ 's.

choose the initial function as

$$\varphi_1(x) = \begin{cases} 0, & \text{if } x \leq -\pi/2, \\ \cos(x)/2, & \text{if } x \in (-\pi/2, \pi/2), \\ 0, & \text{if } x \geq \pi/2, \end{cases}$$

and show the corresponding solution of (3.26) in Figures 3.1 and 3.2.

Furthermore, choosing function

$$\varphi_2(x) = \begin{cases} 0, & \text{if } x \leq -2, \\ (2+x)/2, & \text{if } x \in (-2, 2), \\ 0, & \text{if } x \geq 2, \end{cases}$$

we show that the shape of the solution of (3.26) with initial function  $\varphi_2(x)$  converges to a traveling wave very quickly. The wave moves in the negative  $x$ -direction as time  $t$  increases (see Figures 3.3 and 3.4).

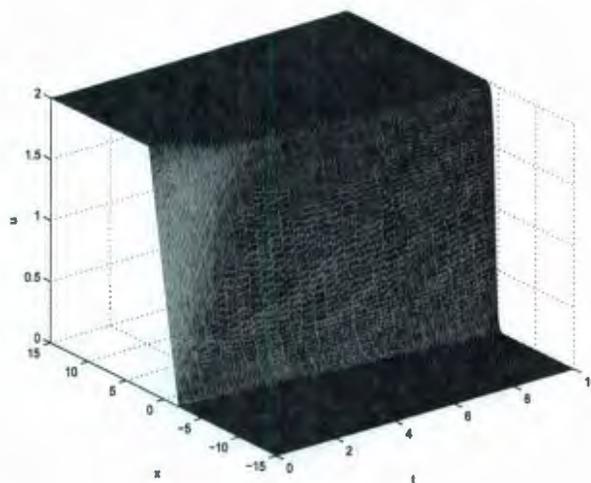


Figure 3.3: The solution of (3.26) with the initial function  $\varphi_2(x)$ .

### 3.6 Discussions

Population dispersal is an important strategy in ecology since it may influence, for example, the distribution of a population or the spread of an disease. In this chapter, we have investigated the spatial dynamics of a class of periodic integro-differential equations which describe population dispersal in a periodic environment. The autonomous version of this model is essentially the same as those in [55, 59]. It is very interesting that the autonomous equation (3.3) can be written as a special case of the general model studied in [68] via a specific probability measure. However, our analysis for periodic equation (3.5) improves and complements the earlier results for (3.3). More precisely, we proved the well-posedness and the comparison principle for the periodic model (3.5), and then established the existence of the spreading speed, its computation formula, the nonexistence of periodic traveling waves, and the existence of traveling waves in the autonomous case. Our work has two advantages over the earlier ones. First, we used the concept of “spreading speeds” in a strong sense for the periodic equation (3.5) (see Theorem 3.3.1) and showed that, in the autonomous case, the asymptotic speed of spread coincides with the minimal wave speed for monotone

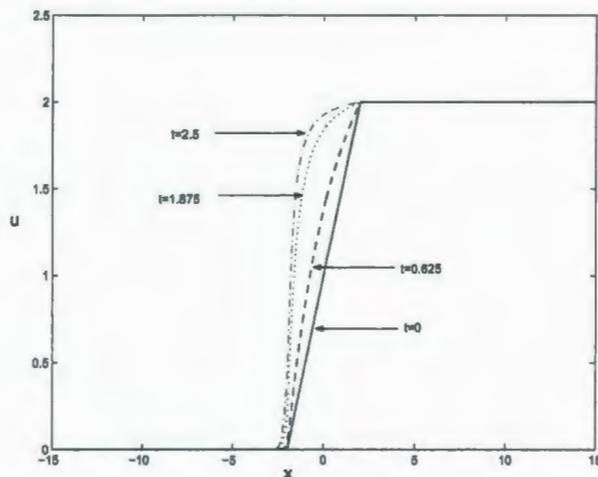


Figure 3.4: The solution of (3.26) with the initial function  $\varphi_2(x)$  for some  $t$ 's.

traveling waves. Secondly, we allowed the convergence abscissa  $\Delta$  of  $\int_{\mathbf{R}} k(y)e^{\alpha y} dy$  to be either finite or infinite.

Since the theory of spreading speeds and traveling waves were developed in [53, 52] for monotone semiflows under a general setting, its application to a specific evolution system with spatial structure is nontrivial technically. For example, we need to prove that the periodic equation (3.5) admits the comparison principle (see Theorem 3.2.2) and generates a periodic semiflow which is continuous with respect to the compact open topology (see Lemma 3.3.1). Further, one should choose appropriate linear equations to obtain an explicit formula for the spreading speed (see Proposition 3.3.1). In the autonomous case, although the method of upper and lower solutions have been applied to prove the existence of monostable traveling waves by numerous researchers (see, e.g., [19, 78, 88, 90] and the references therein), the key point is to construct and verify an ordered pair of upper and lower solutions for the wave profile equation associated with a specific evolution system (see, e.g., Lemma 3.4.1).

With the theory developed in [53, 52], we only obtained the nonexistence of periodic traveling waves with the wave speed  $c < c^*$  for the periodic system (3.5).

Regarding the existence of periodic traveling waves with the wave speed  $c \geq c^*$ , we can not appeal to the same theory since the compactness assumption does not hold for (3.5). As illustrated in [69], we can employ the “vanishing viscosity” approach to obtain monotone periodic traveling wave solutions with  $c \geq c^*$  in the sense of distribution. However, we are not able to prove that this traveling wave is a classic solution of (3.5). Thus, the existence of periodic traveling waves of the periodic equation (3.5) remains open. We leave this problem for future investigation.

## Chapter 4

# A Non-Local Periodic Reaction-Diffusion Model with Stage-Structure

### 4.1 Introduction

Age structure has been an interesting topic in population dynamics (see, e.g., [1, 3, 4, 27, 28, 29, 51, 61, 75, 78, 91]), since we can investigate the separate quantities of immature and mature populations in an age-structured population model. To derive a model for a single species of population with age-structure and diffusion, we usually assume that individuals move around not only after matured, but also while immature. For a standard argument, [61] gives

$$\frac{\partial u}{\partial t} + \frac{\partial u}{\partial a} = D(a) \frac{\partial^2 u}{\partial x^2} - \mu(a)u,$$

where  $u(t, a, x)$  is the density of the population of the species at time  $t \geq 0$ , age  $a \geq 0$  and location  $x$  in a spatial domain  $\Omega$ ;  $D(a) \geq 0$  and  $\mu(a) \geq 0$  are the diffusion rate and the death rate of the population at age  $a$ , respectively.

To study the behaviors of immature individuals and mature individuals, we can also divide the population of a species into two groups: immature population and

mature population. For simplicity, we assume that the maturation time (or the length of the juvenile period) is the same for all juvenile individuals, denoted by  $\tau \geq 0$ . For distributed maturation delay, see [3, 4]. Assume that the diffusion rate and death rate are age-dependent for immature individuals, but age-independent for mature individuals. As a result, we have the following system for a single species of population with age-structure and diffusion (see also [27, 75, 78, 91]):

$$\begin{cases} \partial_t u(t, a, x) + \partial_a u(t, a, x) = d_j(a) \Delta u - \mu_j(a) u(t, a, x), & t > 0, 0 < a < \tau, x \in \Omega, \\ u(t, 0, x) = f(u_m(t, x)), & t \geq -\tau, x \in \Omega, \\ \partial_t u_m(t, x) = d_m \Delta u_m - g(u_m(t, x)) + u(t, \tau, x), & t > 0, x \in \Omega, \end{cases} \quad (4.1)$$

where  $u(t, a, x)$  is the density of the population at time  $t \geq -\tau$ , age  $a \geq 0$  and location  $x \in \Omega$ ,  $u_m(t, x)$  is the density of the mature population,  $f(u_m)$  and  $g(u_m)$  are the birth rate and the mortality rate of mature individuals, respectively,  $d_j(a) \geq 0$  is the diffusion rate of the immature individuals at age  $a \in (0, \tau)$ ,  $d_m \geq 0$  is the diffusion rate of the mature individuals,  $\mu_j(a) > 0$  denotes the per capita mortality rate of juveniles at age  $a$ ,  $u(t, \tau, x)$  is the adults recruitment term, being those of maturation age  $\tau$ ,  $\Delta$  is the Laplacian operator on  $\mathbb{R}$ .

In fact, the dynamics of many populations are influenced greatly by time varying environments (e.g., due to seasonal variation). For example, in a year period, the birth rate may be high in spring and summer and low in winter, while in winter more individuals might be at the risk of death because of low temperature, lack of food or some other reasons. Moreover, populations usually like to move in good weather during the spring and summer time. Therefore, it is more realistic to consider a nonautonomous version of (4.1) for population dynamics. In particular, a periodic model, in which the birth rate, mortality rates and diffusion rates are assumed to be periodic in time, is probably the simplest but an interesting and realistic case. In this

chapter, we consider the following model:

$$\begin{cases} \partial_t u(t, a, x) + \partial_a u(t, a, x) = d_j(t, a)\Delta u - \mu_j(t, a)u(t, a, x), & t > 0, a \in (0, \tau), x \in \Omega, \\ u(t, 0, x) = f(t, u_m(t, x)), & t \geq -\tau, x \in \Omega, \\ \partial_t u_m(t, x) = d_m(t)\Delta u_m - g(t, u_m(t, x)) + u(t, \tau, x), & t > 0, x \in \Omega, \end{cases} \quad (4.2)$$

where  $\Omega \subseteq \mathbb{R}$ ,  $d_j(t, a) \geq 0$  and  $\mu_j(t, a) \geq 0$  denote the diffusion rate and the per capita mortality rate of juveniles at age  $a$  at time  $t$ , respectively;  $d_m(t) \geq 0$  denotes the diffusion rate of mature individuals at time  $t$ ;  $f(t, u_m)$  and  $g(t, u_m)$  are the birth and mortality rates of mature individuals at time  $t$ , respectively.

Similarly as in [78] (see also [73]), we integrate along characteristics to reduce the system (4.2) to one equation with nonlocal term. Let  $v(r, a, x) = u(a+r, a, x)$ , where  $r$  is regarded as a parameter. It follows that

$$\begin{cases} \partial_a v(r, a, x) = [\partial_t u(t, a, x) + \partial_a u(t, a, x)]_{t=r+a} \\ \quad = d_j(a+r, a)\Delta v(r, a, x) - \mu_j(a+r, a)v(r, a, x), \\ v(r, 0, x) = f(r, u_m(r, x)). \end{cases}$$

Integrating the last equation, we obtain

$$v(r, a, x) = \int_{\Omega} \Gamma(\zeta(r, a), x - y) F(r, a) f(r, u_m(r, y)) dy,$$

where  $\Gamma$  is the fundamental solution associated with the partial differential operator  $\partial_t - \Delta$  and

$$\zeta(r, a) = \int_0^a d_j(s+r, s) ds, \quad F(r, a) = \exp\left(-\int_0^a \mu_j(s+r, s) ds\right). \quad (4.3)$$

Since  $u(t, a, x) = v(t-a, a, x)$ , it follows that

$$u(t, a, x) = \int_{\Omega} \Gamma(\zeta(t-a, a), x - y) F(t-a, a) f(t-a, u_m(t-a, y)) dy. \quad (4.4)$$

Set

$$a(t) := \zeta(t - \tau, \tau), \quad b(t) := F(t - \tau, \tau), \quad f_{-\tau}(t, u) := f(t - \tau, u).$$

Substituting (4.4) into the equation for  $u_m$  in (4.2), we finally reduce the age-structured population model (4.2) to the following time-delayed reaction-diffusion equation for mature individuals:

$$\begin{cases} \partial_t u_m(t, x) = d_m(t)\Delta u_m - g(t, u_m(t, x)), \\ \quad + b(t) \int_{\Omega} \Gamma(a(t), x - y) f_{-\tau}(t, u_m(t - \tau, y)) dy, \quad t > 0, x \in \Omega, \\ u_m(s, x) = \phi(s, x), \quad s \in [-\tau, 0], x \in \Omega, \end{cases} \quad (4.5)$$

where  $\phi(t, x)$  is an initial function to be specified later. For simplicity, dropping all  $m$ 's and writing  $u_m(t, x)$  as  $u(t, x)$ , we investigate the following system

$$\begin{cases} \partial_t u(t, x) = d(t)\Delta u - g(t, u(t, x)) \\ \quad + b(t) \int_{\Omega} \Gamma(a(t), x - y) f_{-\tau}(t, u(t - \tau, y)) dy, \quad t > 0, x \in \Omega, \\ u(s, x) = \phi(s, x), \quad s \in [-\tau, 0], x \in \Omega. \end{cases} \quad (4.6)$$

Basically we assume that  $d_j(t, a)$  and  $\mu_j(t, a)$  are periodic in  $t \geq 0$  with the period  $\omega > 0$  for  $a \in (0, \tau)$ , and that  $d(t)$ ,  $g(t, u)$  and  $f(t, u)$  are periodic in  $t$  with the period  $\omega > 0$  for  $u \in \mathbb{R}_+$ . This implies that  $a(t) = a(t + \omega)$ ,  $d(t) = d(t + \omega)$ ,  $b(t) = b(t + \omega)$ ,  $g(t, u) = g(t + \omega, u)$  and  $f(t, u) = f(t + \omega, u)$  for all  $t \geq 0$ ,  $u \in \mathbb{R}_+$ . Moreover, we assume  $d(t) \geq d > 0$ ,  $\forall t \geq 0$ , and

(H3)  $f \in C^1([-\tau, +\infty) \times \mathbb{R}_+, \mathbb{R}_+)$ ,  $g \in C^1(\mathbb{R}_+^2, \mathbb{R}_+)$ ,  $f(t, 0) = 0$  for  $t \geq -\tau$ ,  $f_u(t, u) > 0$  for all  $t \geq -\tau$  and  $u \geq 0$ ;  $g(t, 0) = 0$  for  $t \geq 0$ , and there exists  $l_1 > 0$  such that  $|g(t, u) - g(t, v)| \leq l_1|u - v|$ , for all  $t \geq 0$  and  $u, v \in \mathbb{R}_+$ .

(H4)  $G(t, u, v) := -g(t, u) + b(t)f_{-\tau}(t, v)$  is strictly subhomogeneous in  $(u, v)$  in the sense that for any  $\alpha \in (0, 1)$ ,  $G(t, \alpha u, \alpha v) > \alpha G(t, u, v)$ ,  $\forall u, v \geq 0$ .

(H5) There exists a positive number  $L > 0$  such that  $G(t, \bar{L}, \bar{L}) \leq 0$ ,  $\forall t \geq 0$ ,  $\bar{L} \geq L$ .

The purpose of this chapter is to study the asymptotic speed of spread and periodic traveling waves of (4.6) in the infinite spatial domain, and the global attractivity of zero or a positive periodic solution of (4.6) in a bounded spatial domain. For the autonomous case of (4.6), the dynamics, including the spreading speed and traveling

waves, have been studied extensively. So, Wu and Zou [75] investigated traveling wave fronts in the case where  $\Omega = \mathbb{R}$ ,  $g(u) = \beta u$ . Gourley and Kuang [27] established the linear stabilities of two spatially homogeneous equilibrium solutions, studied traveling wave fronts in the case where  $\Omega = \mathbb{R}$ ,  $f(u) = \alpha u$  and  $g(u) = \beta u^2$ , and obtained a global convergence theorem in the case of bounded intervals. Thieme and Zhao [78] studied the traveling wave solutions, minimal wave speed and asymptotic speed of spread in the case of  $\Omega = \mathbb{R}^n$ . Xu and Zhao [91] established a threshold dynamics and global attractivity of the positive steady state when  $\Omega$  is a bounded domain in  $\mathbb{R}^n$ .

This chapter is organized as follows. In section 4.2, we first establish the well-posedness and the comparison principle for (4.6) with  $\Omega = \mathbb{R}$ , then prove the existence of the spreading speed  $c^*$  for solutions of (4.6) with initial data having compact supports and show that it coincides with the minimal wave speed for monotone periodic traveling waves, by appealing to the theory of the spreading speed and traveling waves for monotone periodic semiflows in section 2.3 (see also [52, 53]). In section 4.3, we use the theory of monotone and subhomogeneous dynamical systems to investigate the global dynamics of (4.6) in a bounded domain  $\Omega \subseteq \mathbb{R}$ , and obtain a threshold result for global attractivity of zero and a positive periodic solution.

## 4.2 Spreading speed and traveling waves

In this section, we consider that the population diffuses in an unbounded spatial domain and study (4.6) with  $\Omega = \mathbb{R}$ :

$$\begin{cases} \partial_t u(t, x) = d(t)\Delta u - g(t, u(t, x)) \\ \quad + b(t) \int_{\mathbb{R}} \Gamma(a(t), x - y) f_{-\tau}(t, u(t - \tau, y)) dy, & t > 0, x \in \mathbb{R}, \\ u(t, x) = \phi(t, x), & t \in [-\tau, 0], x \in \mathbb{R}. \end{cases} \quad (4.7)$$

In the following, we first apply the threshold dynamics in a scalar periodic and time-delayed equation, Theorems 2.5.1 and 2.5.2, to the spatially homogeneous system associated with (4.7), to find a periodic solution of (4.7). Then we use the theory of

abstract functional differential equations and reaction-diffusion systems to establish the existence of solutions to (4.7) and comparison principle. Finally, we prove that the solution periodic semiflow of (4.7) satisfies all the assumptions on monotone periodic semiflows in section 2.3, and hence, we obtain the existence of the spreading speed and periodic traveling wave solutions for (4.7).

Let  $\mathbb{Y}$  be the space of all continuous functions from  $[-\tau, 0]$  to  $\mathbb{R}$  with the usual supreme norm  $\|\cdot\|_{\mathbb{Y}}$  (i.e.,  $\mathbb{Y} = C([-\tau, 0], \mathbb{R})$ ), and  $\mathbb{Y}_+ = C([-\tau, 0], \mathbb{R}_+)$ . Then  $(\mathbb{Y}, \mathbb{Y}_+)$  is an ordered Banach space. For  $\varphi, \psi \in \mathbb{Y}$ , we write  $\varphi \leq \psi$  if  $\psi - \varphi \in \mathbb{Y}_+$ ,  $\varphi < \psi$  if  $\psi - \varphi \in \mathbb{Y}_+ \setminus \{0\}$ ,  $\varphi \ll \psi$  if  $\psi - \varphi \in \text{int}(\mathbb{Y}_+)$ . Moreover, we define  $\mathbb{Y}_r = \{\varphi \in \mathbb{Y} : 0 \leq \varphi \leq r\}$  for any  $r \in \mathbb{Y}$  with  $r \gg 0$ .

Let  $\mathbb{X}$  be the set of all bounded and continuous functions from  $\mathbb{R}$  into  $\mathbb{R}$  and  $\mathbb{X}_+ = \{\varphi \in \mathbb{X} ; \varphi(x) \geq 0, \forall x \in \mathbb{R}\}$ . For  $\varphi, \psi \in \mathbb{X}$ , we write  $\varphi \leq \psi$  ( $\varphi \ll \psi$ ) if  $\varphi(x) \leq \psi(x)$  ( $\varphi(x) < \psi(x)$ ),  $\forall x \in \mathbb{R}$ ,  $\varphi < \psi$  if  $\varphi \leq \psi$  but  $\varphi \neq \psi$ . It is easy to see that  $\mathbb{X}_+$  is a positive cone of  $\mathbb{X}$ . Define  $\mathbb{X}_r = \{\varphi \in \mathbb{X} : 0 \leq \varphi \leq r\}$  for any  $r \in \mathbb{X}$  with  $r \gg 0$ . We equip  $\mathbb{X}$  with the compact open topology, i.e.,  $u^m \rightarrow u$  in  $\mathbb{X}$  means that the sequence of  $u^m(x)$  converges to  $u(x)$  as  $m \rightarrow \infty$  uniformly for  $x$  in any compact set on  $\mathbb{R}$ . Define

$$\|u\|_{\mathbb{X}} = \sum_{k=1}^{\infty} \frac{\max_{|x| \leq k} |u(x)|}{2^k}, \quad \forall u \in \mathbb{X},$$

where  $|\cdot|$  denotes the usual norm in  $\mathbb{R}$ . Then  $(\mathbb{X}, \|\cdot\|_{\mathbb{X}})$  is a normed space. Let  $d_{\mathbb{X}}(\cdot, \cdot)$  be the distance induced by the norm  $\|\cdot\|_{\mathbb{X}}$ . It follows that the topology in the metric space  $(\mathbb{X}, d_{\mathbb{X}})$  is the same as the compact open topology in  $\mathbb{X}$ . Moreover,  $(\mathbb{X}_r, d_{\mathbb{X}})$  is a complete metric space.

Let  $C$  be the set of continuous functions from  $[-\tau, 0]$  into  $\mathbb{X}$ ,  $C_+ = \{\varphi \in C, \varphi(s) \in \mathbb{X}_+, s \in [-\tau, 0]\}$  and  $C_r = \{\varphi \in C : 0 \leq \varphi \leq r\}$  for any  $r \in \mathbb{Y}$  with  $r \gg 0$ . Then  $C_+$  is a positive cone of  $C$ . For convenience, we also identify an element  $\varphi \in C$  as a function from  $[-\tau, 0] \times \mathbb{R}$  into  $\mathbb{R}$  defined by  $\varphi(s, x) = \varphi(s)(x)$ , for any  $s \in [-\tau, 0]$  and  $x \in \mathbb{R}$ . For  $\varphi, \psi \in C$ , we write  $\varphi \leq \psi$  ( $\varphi \ll \psi$ ) if  $\varphi(s, x) \leq \psi(s, x)$  ( $\varphi(s, x) < \psi(s, x)$ ),  $\forall s \in [-\tau, 0], x \in \mathbb{R}$ ,  $\varphi < \psi$  if  $\varphi \leq \psi$  but  $\varphi \neq \psi$ . For any continuous function  $w(\cdot) : [-\tau, b) \rightarrow \mathbb{X}$ ,  $b > 0$ , we define  $w_t \in C$  by  $w_t(s) = w(t + s)$ ,  $\forall t \in [0, b)$ ,

$s \in [-\tau, 0]$ . It is then easy to see that  $t \rightarrow w_t$  is a continuous function from  $[0, b)$  to  $C$ . Moreover, we also equip  $C$  with the compact open topology and define the norm on  $C$ :

$$\|u\|_C = \sum_{k=1}^{\infty} \frac{\max_{|x| \leq k, s \in [-\tau, 0]} |u(s, x)|}{2^k}, \quad \forall u \in C,$$

where  $|\cdot|$  denotes the usual norm in  $\mathbb{R}$ .

For any constant  $N > 0$ ,  $\widehat{N}$  denotes the constant function with value  $N$  in  $\mathbb{Y}$ ,  $\mathbb{X}$  or  $C$ .

Now we consider the spatially homogeneous system associated with (4.7). Letting  $u(t, x) = w(t)$ , we have

$$\begin{cases} \frac{dw(t)}{dt} = -g(t, w(t)) + b(t)f_{-\tau}(t, w(t-\tau)), & t > 0, \\ w(t) = \varphi(t), & t \in [-\tau, 0], \quad \varphi \in \mathbb{Y}_+. \end{cases} \quad (4.8)$$

The linearized equation associated with (4.8) at  $w = 0$  is

$$\begin{cases} \frac{dw(t)}{dt} = -g_u(t, 0)w(t) + b(t)\partial_u f_{-\tau}(t, 0)w(t-\tau), & t > 0, \\ w(t) = \varphi(t), & t \in [-\tau, 0], \quad \varphi \in \mathbb{Y}_+. \end{cases} \quad (4.9)$$

Since  $g$ ,  $b$  and  $f_{-\tau}$  are periodic functions in  $t \geq 0$ , we can easily see that for any  $\varphi \in \mathbb{Y}_+$ , (4.9) admits a unique solution  $w(t, \varphi)$  existing for all  $t \geq -\tau$  with  $w(s, \varphi) = \varphi(s)$  for  $s \in [-\tau, 0]$ , and  $w_t(\varphi) \in \mathbb{Y}_+$ ,  $\forall t \geq 0$ , where  $\{w_t\}_{t \geq 0}$  is the solution semiflow for (4.9) defined by  $w_t(\varphi)(s) = w(t+s, \varphi)$ ,  $\forall s \in [-\tau, 0]$ ,  $t > 0$ .

Define the Poincaré map of (4.9)  $P : \mathbb{Y}_+ \rightarrow \mathbb{Y}_+$  by  $P(\varphi) = w_\omega(\varphi)$ ,  $\forall \varphi \in \mathbb{Y}_+$ , and let  $r = r(P)$  be the spectral radius of  $P$ . The following two results follow from Theorems 2.5.1 and 2.5.2.

**Proposition 4.2.1**  $r = r(P)$  is positive and is an eigenvalue of  $P$  with a positive eigenfunction  $\varphi^*$ . Moreover, if  $\tau = k\omega$  for some integer  $k \geq 0$ , then  $r - 1$  has the same sign as  $\int_0^\omega [-g_u(t, 0) + b(t)\partial_u f_{-\tau}(t, 0)] dt$ .

**Theorem 4.2.1** Let (H3)-(H5) hold. The following statements are valid.

(i) If  $r \leq 1$ , then zero solution is globally asymptotically stable for (4.8) with respect to  $\mathbb{Y}_+$ .

(ii) If  $r > 1$ , then (4.8) has a unique positive  $\omega$ -periodic solution  $\beta^*(t)$ , and  $\beta^*(t)$  is globally asymptotically stable with respect to  $\mathbb{Y}_+ \setminus \{0\}$ .

In the remainder of this section, we further assume that

(H6)  $r = r(P) > 1$ .

By (H5) and the proof of Theorem 2.5.2 in [93], it is easy to see that  $\beta^*(t) \in [0, L]$  for all  $t \geq -\tau$  and  $[\hat{0}, \hat{L}]$  is positively invariant for (4.7). Define  $\beta_0^* \in \mathbb{Y}_{\hat{L}}$  as

$$\beta_0^*(s) = \beta^*(s), \quad \forall s \in [-\tau, 0].$$

Consider

$$\begin{cases} \partial_t u(t, x) = d(t)\Delta u, & t > 0, \\ u(0, x) = \phi(x), & x \in \mathbb{R}, \phi \in \mathbb{X}. \end{cases} \quad (4.10)$$

The solution of (4.10) can be expressed as

$$u(t, x, \phi) = \int_{\mathbb{R}} \Gamma(\eta(t), x - y)\phi(y)dy, \quad t \geq 0, \quad (4.11)$$

where  $\eta(t) = \int_0^t d(s)ds$ . According to [35, Chapter II], (4.10) admits an evolution operator  $U(t, s) : \mathbb{X} \rightarrow \mathbb{X}$ ,  $0 \leq s \leq t$ , which satisfies  $U(t, t) = I$ ,  $U(t, s)U(s, \rho) = U(t, \rho)$ ,  $\forall 0 \leq \rho \leq s \leq t$ , and  $U(t, 0)(\phi)(x) = u(t, x, \phi)$ , for  $t \geq 0$ ,  $x \in \mathbb{R}$  and  $\phi \in \mathbb{X}$ , where  $u(t, x, \phi)$  is the solution of (4.10). Moreover, for any  $0 \leq s < t$ ,  $U(t, s)$  is a compact and positive operator on  $\mathbb{X}$ ; and  $U(t, s)(\phi)(x) > 0$  for all  $0 \leq s < t$ ,  $x \in \mathbb{R}$  and  $\phi \in \mathbb{X}$  provided that  $\phi(x) \geq 0$  and  $\phi \neq 0$ .

Define  $B : [0, \infty) \times C \rightarrow \mathbb{X}$  by

$$B(t, \phi) := -g(t, \phi(0, \cdot)) + b(t) \int_{\mathbb{R}} \Gamma(a(t), \cdot - y)f_{-\tau}(t, \phi(-\tau, y))dy,$$

for any  $t \in [0, \infty)$ ,  $\phi \in C$ . Then (4.7) becomes

$$\begin{cases} \partial_t u(t, x) = d(t)\Delta u + B(t, u_t), & t > 0, \\ u(t, x) = \phi(t, x), & t \in [-\tau, 0], x \in \mathbb{R}, \end{cases} \quad (4.12)$$

which can be written as an integral equation

$$u(t, \cdot, \phi) = U(t, 0)\phi(0, \cdot) + \int_0^t U(t, s)B(s, u_s)ds, \quad t \geq 0, \quad \phi \in C, \quad (4.13)$$

whose solutions are called mild solutions to (4.12).

**Theorem 4.2.2** *Let (H3)-(H6) hold. For any  $\phi \in C_{\bar{L}}$ , system (4.7) has a unique mild solution  $u(t, x, \phi)$  with  $u_0(\cdot, \cdot, \phi) = \phi$  and  $u_t(\cdot, \cdot, \phi) \in C_{\bar{L}}, \forall t \geq 0$ , and  $u(t, x, \phi)$  is a classic solution when  $t > \tau$ . Moreover, if  $\hat{u}(t, x)$  and  $\bar{u}(t, x)$  are a pair of lower and upper solutions of (4.7), respectively, with  $\hat{u}_0(\cdot, \cdot) \leq \bar{u}_0(\cdot, \cdot)$ , then  $\hat{u}_t(\cdot, \cdot) \leq \bar{u}_t(\cdot, \cdot), \forall t \geq 0$ .*

**Proof** We first show that  $B$  is quasi-monotone on  $[0, \infty) \times C_{\bar{L}}$  in the sense that

$$\lim_{h \rightarrow 0^+} d(\psi(0, \cdot) - \phi(0, \cdot) + h[B(t, \psi) - B(t, \phi)], \mathbf{X}_+) = 0, \quad (4.14)$$

for all  $\phi, \psi \in C_{\bar{L}}$  with  $\phi(s, x) \leq \psi(s, x), \forall s \in [-\tau, 0], x \in \mathbb{R}$ . In fact, for any  $\phi, \psi \in C_{\bar{L}}$  with  $\phi(s, x) \leq \psi(s, x), \forall (s, x) \in [-\tau, 0] \times \mathbb{R}$ , we have

$$\begin{aligned} & \psi(0, \cdot) - \phi(0, \cdot) + h[B(t, \psi) - B(t, \phi)] \\ &= \psi(0, \cdot) - \phi(0, \cdot) + h[-(g(t, \psi(0, \cdot)) - g(t, \phi(0, \cdot)))] \\ & \quad + h \int_{\mathbb{R}} \Gamma(a(t), \cdot - y)b(t)(f_{-\tau}(t, \psi(-\tau, y)) - f_{-\tau}(t, \phi(-\tau, y)))dy \\ & \geq \psi(0, \cdot) - \phi(0, \cdot) - h(g(t, \psi(0, \cdot)) - g(t, \phi(0, \cdot))) \\ & \geq (1 - hl_1)(\psi(0, \cdot) - \phi(0, \cdot)). \end{aligned}$$

Thus, for  $1 - hl_1 > 0$ ,  $\psi(0, \cdot) - \phi(0, \cdot) + h[B(t, \psi) - B(t, \phi)] \in \mathbf{X}_+$ , and hence, (4.14) holds. Then by Theorem 2.5.3 (for  $v^- = \hat{0}$ ,  $v^+ = \hat{L}$ ,  $S \equiv U$ ), (4.7) admits a unique mild solution  $u(t, \cdot, \phi)$  on  $[-\tau, \infty)$  for any  $\phi \in C_{\bar{L}}$  and  $u_t(\cdot, \cdot, \phi) \in C_{\bar{L}}, \forall t \geq 0$ . Moreover, the comparison principle holds for lower and upper solutions. ■

In the following, we study the spreading speed and periodic traveling waves for (4.7).

Define a family of operators  $\{Q_t\}_{t \geq 0}$  on  $C_{\tilde{L}}$  by

$$Q_t(\phi)(s, x) = u(t + s, x, \phi), \quad \forall t \geq 0, \quad s \in [-\tau, 0], \quad x \in \mathbb{R}, \quad \phi \in C_{\tilde{L}},$$

where  $u(t, x, \phi)$  is the mild solution of (4.7) with  $u(s, x) = \phi(s, x)$  for  $s \in [-\tau, 0]$ ,  $x \in \mathbb{R}$ . Note that for any  $(t_0, \phi_0) \in \mathbb{R}_+ \times C_{\tilde{L}}$ , we have

$$\|Q_t(\phi) - Q_{t_0}(\phi_0)\|_C \leq \|Q_t(\phi) - Q_t(\phi_0)\|_C + \|Q_t(\phi_0) - Q_{t_0}(\phi_0)\|_C$$

and that  $U(t, 0)\varphi$  is continuous in  $(t, \varphi) \in [0, \infty) \times \mathbb{X}$  with respect to the compact open topology. By a similar argument as in [57, Theorem 8.5.2], it follows that  $Q_t(\phi)$  is continuous at  $(t_0, \phi_0)$  with respect to the compact open topology. Thus,  $\{Q_t\}_{t \geq 0}$  is an  $\omega$ -periodic semiflow on  $C_{\tilde{L}}$ .

**Lemma 4.2.1** *For each  $t > 0$ ,  $Q_t$  is strictly subhomogeneous.*

**Proof** For any  $\phi \in C_{\tilde{L}}$  with  $\phi \not\equiv 0$ , let  $u(t, x, \phi)$  be the solution of (4.7) with  $u(s, x) = \phi(s, x)$  for  $s \in [-\tau, 0]$ ,  $x \in \mathbb{R}$ . Fix  $k \in (0, 1)$ . Since  $G(t, u, v)$  is strictly subhomogeneous in  $(u, v)$ , we have

$$\begin{aligned} & \partial_t(ku(t, x)) \\ &= d(t)\Delta(ku) - kg(t, u(t, x)) + kb(t) \int_{\mathbb{R}} \Gamma(a(t), x - y) f_{-\tau}(t, u(t - \tau, y)) dy \\ &\leq d(t)\Delta(ku) - g(t, ku(t, x)) + b(t) \int_{\mathbb{R}} \Gamma(a(t), x - y) f_{-\tau}(t, ku(t - \tau, y)) dy. \end{aligned}$$

Thus,  $ku(t, x, \phi)$  is a lower solution of (4.7) with  $ku(s, x, \phi) = k\phi(s, x)$  for  $s \in [-\tau, 0]$ ,  $x \in \mathbb{R}$ . Then,  $ku(t, x, \phi) \leq u(t, x, k\phi)$  for  $t \geq 0$ , where  $u(t, x, k\phi)$  is the solution of (4.7) with  $u(s, x, k\phi) = k\phi(s, x)$  for  $(s, x) \in [-\tau, 0] \times \mathbb{R}$ .

Let  $w(t, x) = u(t, x, k\phi) - ku(t, x, \phi)$ . Then  $w(s, x) = 0$  for  $(s, x) \in [-\tau, 0] \times \mathbb{R}$  and  $w(s, x) \geq 0$ , for  $(s, x) \in [-\tau, \infty) \times \mathbb{R}$ . We further show that  $w(t, x) > 0$  for all  $t > 0, x \in \mathbb{R}$ . For simplicity, we write

$$\tilde{F}(t, u(t, x), v(t, x)) = -g(t, u(t, x)) + b(t) \int_{\mathbb{R}} \Gamma(a(t), x - y) f_{-\tau}(t, v(t, y)) dy.$$

It follows that

$$\begin{aligned}
& \frac{\partial w(t, x)}{\partial t} \\
&= \frac{\partial u(t, x, k\phi)}{\partial t} - k \frac{\partial u(t, x, \phi)}{\partial t} \\
&= d(t)\Delta u(t, x, k\phi) + \tilde{F}(t, u(t, x, k\phi), u(t - \tau, x, k\phi)) \\
&\quad - k[d(t)\Delta u(t, x, \phi) + \tilde{F}(t, u(t, x, \phi), u(t - \tau, x, \phi))] \\
&= d(t)\Delta w(t, x) + [\tilde{F}(t, u(t, x, k\phi), u(t - \tau, x, k\phi)) - \tilde{F}(t, ku(t, x, \phi), ku(t - \tau, x, \phi))] \\
&\quad + [\tilde{F}(t, ku(t, x, \phi), ku(t - \tau, x, \phi)) - k\tilde{F}(t, u(t, x, \phi), u(t - \tau, x, \phi))] \\
&= d(t)\Delta w(t, x) - g(t, u(t, x, k\phi)) + g(t, ku(t, x, \phi)) \\
&\quad + b(t) \int_{\mathbb{R}} \Gamma(a(t), x - y) [f_{-\tau}(t, u(t - \tau, y, k\phi)) - f_{-\tau}(t, ku(t - \tau, y, \phi))] dy + h(t, x) \\
&\geq d(t)\Delta w(t, x) - g(t, u(t, x, k\phi)) + g(t, ku(t, x, \phi)) + h(t, x) \\
&\geq d(t)\Delta w(t, x) - l_1 w(t, x) + h(t, x),
\end{aligned} \tag{4.15}$$

where

$$h(t, x) = \tilde{F}(t, ku(t, x, \phi), ku(t - \tau, x, \phi)) - k\tilde{F}(t, u(t, x, \phi), u(t - \tau, x, \phi)).$$

Let  $\tilde{U}(t, s) : \mathbb{X} \rightarrow \mathbb{X}$ ,  $0 \leq s \leq t$ , be the evolution operator of

$$\begin{cases} \partial_t u(t, x) = d(t)\Delta u - l_1 u(t, x), & t > 0, \\ u(0, x) = \psi(x), & x \in \mathbb{R}, \psi \in \mathbb{X}. \end{cases}$$

Then

$$\tilde{U}(t, s)(\psi)(x) = e^{-l_1(t-s)} U(t, s)(\psi)(x), \quad \forall t \geq s \geq 0, x \in \Omega, \psi \in C,$$

where  $U(t, s)$  is the evolution operator of (4.10). Thus, the equation

$$\begin{cases} \partial_t u(t, x) = d(t)\Delta u - l_1 u(t, x) + h(t, x) \\ u(0, x) = \psi(x), \quad x \in \mathbb{R}, \psi \in \mathbb{X} \end{cases} \tag{4.16}$$

can be written as

$$u(t, x, \psi) = \tilde{U}(t, 0)(\psi)(x) + \int_0^t \tilde{U}(t, s)h(s, x)ds, \quad t \geq 0, x \in \mathbb{R}, \psi \in C. \tag{4.17}$$

By (H4), we have  $h(t, x) > 0$  for all  $t > 0, x \in \mathbb{R}$ . It then follows from (4.17) and the property of  $\tilde{U}(t, s)$  that for any  $\psi \geq 0$  with  $\psi \not\equiv 0$ , the solution of (4.16) satisfies  $u(t, x, \psi) > 0, \forall t > 0, x \in \mathbb{R}$ . Then by (4.15) and the comparison principle, we have  $w(t, x) > 0, \forall t > 0, x \in \mathbb{R}$ . Therefore,  $u(t, x, k\phi) > ku(t, x, \phi), \forall t > 0, x \in \mathbb{R}$ , and hence,  $Q_t(k\phi) > kQ_t(\phi)$  for all  $t > 0$ , which indicates that for each  $t > 0, Q_t$  is strictly subhomogeneous. ■

**Lemma 4.2.2** For any  $\varphi \in C_{\tilde{L}}$  with  $\varphi \not\equiv 0, u(t, x, \varphi) > 0$ , for all  $t \geq \tau, x \in \mathbb{R}$ .

**Proof** Let  $\varphi \in C_{\tilde{L}}$  with  $\varphi \not\equiv 0$ . By Theorem 4.2.2,  $u(t, x, \varphi) \geq 0$  for all  $t \geq 0$  and  $x \in \mathbb{R}$ . It follows from (H3) that for any  $t > 0, u(t, x, \varphi)$  satisfies

$$\begin{aligned} \partial_t u(t, x) &= d(t)\Delta u - g(t, u(t, x, \varphi)) + b(t) \int_{\mathbb{R}} \Gamma(a(t), x - y) f_{-\tau}(t, u(t - \tau, y, \varphi)) dy \\ &\geq d(t)\Delta u - g(t, u(t, x, \varphi)) \\ &\geq d(t)\Delta u - l_1 u(t, x, \varphi). \end{aligned}$$

By [82, Theorem 5.5.4],  $u(t, x, \varphi) > 0, \forall t > 0, x \in \mathbb{R}$ , provided that  $\varphi(0, \cdot) > 0$ .

Now we show that for any  $\varphi \in C_{\tilde{L}}$  with  $\varphi \not\equiv 0$  and  $\varphi(0, \cdot) = 0$ , there exists  $t_0 = t_0(\varphi) \in [0, \tau]$  such that  $u(t_0, \cdot, \varphi) > 0$ . Assume, by contradiction, that for some  $\varphi \in C_{\tilde{L}}$  with  $\varphi \not\equiv 0$  and  $\varphi(0, \cdot) = 0$ , we have  $u(t, \cdot, \varphi) \equiv 0$  for all  $t \in [0, \tau]$ . It follows from (4.13) that

$$0 = \int_0^t U(t, s) b(s) \int_{\mathbb{R}} \Gamma(a(s), x - y) f_{-\tau}(s, u_s(-\tau, y)) dy ds, \quad t \in [0, \tau],$$

which implies that  $\int_{\mathbb{R}} \Gamma(a(s), x - y) f_{-\tau}(s, u_s(-\tau, y)) dy = 0$  for any  $s \in [0, \tau]$ , and hence,  $f_{-\tau}(s, u_s(-\tau, y)) = 0$  for any  $s \in [0, \tau], y \in \mathbb{R}$ . Then by (H3),  $u_s(-\tau, y) = 0$  for any  $s \in [0, \tau], y \in \mathbb{R}$ . That is,  $\varphi \equiv 0$ . A contradiction. Thus, we have  $u(t_0, \cdot, \varphi) > 0$  for some  $t_0 = t_0(\varphi) \in [0, \tau]$ . Then for any  $t > t_0$ ,

$$\tilde{U}(t, t_0)[u(t_0, \cdot, \varphi)](x) = e^{-l_1(t-t_0)} U(t, t_0)[u(t_0, \cdot, \varphi)](x) > 0,$$

and hence, by the comparison principle, we have  $u(t, x, \varphi) > 0$  for all  $t > t_0, x \in \mathbb{R}$ .

Therefore, for any  $\varphi \in C_{\tilde{L}}$  with  $\varphi \not\equiv 0, u(t, x, \varphi) > 0$  for all  $t > \tau, x \in \mathbb{R}$ . ■

**Lemma 4.2.3** For any  $t > 0$ ,  $Q_t$  satisfies (A1), (A2), (A4) and (A6) with  $b^* = \widehat{L}$ , and  $Q_\omega$  satisfies (A5) with  $b^* = \beta_0^*$ , where  $\beta_0^* \in Y_{\widehat{L}}$  with  $\beta_0^*(s) = \beta^*(s)$ ,  $\forall s \in [-\tau, 0]$ .

**Proof** It is easy to see that  $Q_t$  satisfies (A1), (A2) and (A4) with  $b^* = \widehat{L}$  for any  $t > 0$ .

Let  $\widehat{Q}_t = Q_t|_{Y_{\widehat{L}}}$ . Then  $\widehat{Q}_t : Y_{\widehat{L}} \rightarrow Y_{\widehat{L}}$  is the  $\omega$ -periodic semiflow generated by (4.8). Moreover, it is not difficult to see that  $\widehat{Q}_t$  is strictly monotone for any  $t \geq \tau$  and strongly monotone for any  $t \geq 2\tau$  on  $Y_{\widehat{L}}$ . Note that (4.8) has a positive  $\omega$ -periodic solution  $\beta^*(t)$  which is globally asymptotically stable in  $Y_{\widehat{L}} \setminus \{0\}$ . We see that  $\widehat{Q}_\omega$  has only two fixed points 0 and  $\beta_0^*$  in  $Y_{\widehat{L}}$ , where  $\beta_0^*(s) = \beta^*(s)$ ,  $\forall s \in [-\tau, 0]$ . Thus, by the Dancer-Hess connecting orbit lemma (see Theorem 2.2.1), the map  $\widehat{Q}_\omega$  admits a strictly monotone full orbit  $\{\varphi_n\}_{-\infty}^{\infty} \subseteq Y_{\beta_0^*}$  connecting 0 to  $\beta_0^*$  and  $\varphi_n < \varphi_{n+1}$  for any  $n = 0, \pm 1, \pm 2, \dots$ . For any  $\bar{n} \in \mathbb{N}$  such that  $\bar{n}\omega \geq 2\tau$ , since  $\widehat{Q}_{\bar{n}\omega}$  is strongly monotone, we have  $\widehat{Q}_{\bar{n}\omega}(\varphi_n) = \widehat{Q}_\omega^{\bar{n}}(\varphi_n) \ll \widehat{Q}_\omega^{\bar{n}}(\varphi_{n+1}) = \widehat{Q}_{\bar{n}\omega}(\varphi_{n+1})$ , for any  $n = 0, \pm 1, \pm 2, \dots$ . That is,  $\varphi_{n+\bar{n}\omega} \ll \varphi_{n+1+\bar{n}\omega}$ , for any  $n = 0, \pm 1, \pm 2, \dots$ . Therefore,  $\varphi_n \ll \varphi_{n+1}$  for any  $n = 0, \pm 1, \pm 2, \dots$ , and hence,  $Q_\omega$  satisfies (A5) with  $b^* = \beta_0^*$ .

Now we show that  $Q_t$  satisfies (A6)(a) with  $b^* = \widehat{L}$  for  $t > \tau$ . Fix  $t_0 > \tau$  and set  $a = t_0 - \tau$ ,  $b = t_0$ . Let  $u(t, \varphi)$  be the solution of (4.7) with  $u_0(\varphi) = \varphi \in C_{\widehat{L}}$  and define the Kuratowski measure of noncompactness of a subset  $A$  of  $\mathbf{X}$  as

$$\alpha(A) = \inf\{r > 0 : A \text{ has a finite cover of diameter } \leq r\}.$$

First we prove that  $\overline{\{u(t, \varphi) : a \leq t \leq b, \varphi \in C_{\widehat{L}}\}}$  is compact in  $\mathbf{X}$ . By (4.13), for any  $\epsilon \in (0, a)$ ,  $t \in [a, b]$  and  $\varphi \in C_{\widehat{L}}$ , we have

$$\begin{aligned} & u(t, \varphi) \\ &= U(t, 0)\varphi(0, \cdot) + \int_0^{t-\epsilon} U(t, s)B(s, u_s)ds + \int_{t-\epsilon}^t U(t, s)B(s, u_s)ds \\ &= U(t, t-\epsilon)[U(t-\epsilon, 0)\varphi(0, \cdot) + \int_0^{t-\epsilon} U(t-\epsilon, s)B(s, u_s)ds] + \int_{t-\epsilon}^t U(t, s)B(s, u_s)ds \\ &= U(t, t-\epsilon)u(t-\epsilon, \varphi) + \int_{t-\epsilon}^t U(t, s)B(s, u_s)ds. \end{aligned}$$

Since  $\{u(t - \epsilon, \varphi), t \in [a, b], \varphi \in C_{\bar{L}}\}$  is bounded in  $\mathbf{X}_+$  and  $U(t, t - \epsilon)$  is compact, we have

$$\alpha(\{U(t, t - \epsilon)u(t - \epsilon, \varphi), t \in [a, b], \varphi \in C_{\bar{L}}\}) = 0.$$

It is easy to see  $\{U(t, s)B(s, u_s) : t \in [a, b], s \in [0, t], \varphi \in C_{\bar{L}}\}$  is bounded in  $\mathbf{X}_+$ . Let  $N > 0$  such that  $\|U(t, s)B(s, u_s)\|_{\mathbf{X}} \leq N$  for all  $t \in [a, b], s \in [0, t], \varphi \in C_{\bar{L}}$ . By the fact of  $\alpha(A) \leq \delta(A)$ , where  $\delta(A)$  is the diameter of  $A \subseteq \mathbf{X}$ , we have

$$\alpha\left(\left\{\int_{t-\epsilon}^t U(t, s)B(s, u_s)ds : t \in [a, b], s \in [t - \epsilon, t], \varphi \in C_{\bar{L}}\right\}\right) \leq 2\epsilon N.$$

Thus,

$$\begin{aligned} & \alpha(\{u(t, \varphi) : t \in [a, b], \varphi \in C_{\bar{L}}\}) \\ & \leq \alpha(\{U(t, t - \epsilon)u(t - \epsilon, \varphi), t \in [a, b], \varphi \in C_{\bar{L}}\}) \\ & \quad + \alpha\left(\left\{\int_{t-\epsilon}^t U(t, s)B(s, u_s)ds : t \in [a, b], s \in [t - \epsilon, t], \varphi \in C_{\bar{L}}\right\}\right) \\ & \leq 2\epsilon N. \end{aligned}$$

Letting  $\epsilon \rightarrow 0$ , we have  $\alpha(\{u(t, \varphi) : t \in [a, b], \varphi \in C_{\bar{L}}\}) = 0$ , and hence,  $\{u(t, \varphi) : t \in [a, b], \varphi \in C_{\bar{L}}\}$  is precompact in  $\mathbf{X}$ .

Given a compact interval  $I \subseteq \mathbb{R}$ . Let  $K = \min\{K_1 > 0 : I \subseteq [-K_1, K_1]\}$ . Since  $\{u(t, \varphi) : t \in [a, b], \varphi \in C_{\bar{L}}\}$  is precompact in  $\mathbf{X}$ ,  $\{u(t, \varphi)|_I : t \in [a, b], \varphi \in C_{\bar{L}}\}$  is equicontinuous in  $\mathbf{X}$ , that is, for any  $\epsilon > 0$ , there exists  $\delta > 0$ , such that

$$|u(t, x_1, \varphi) - u(t, x_2, \varphi)| < \epsilon, \quad (4.18)$$

for all  $t \in [a, b]$  and  $\varphi \in C_{\bar{L}}$ , provided that  $x_1, x_2 \in I$  and  $|x_1 - x_2| < \delta$ .

Let  $[a_1, b_1]$  be any bounded interval on  $\mathbb{R}$  with  $a_1 > 0$  and  $U_0(t)$  be the semigroup generated by  $u_t = \Delta u$ . Then

$$U_0(t)\varphi(x) = \int_{-\infty}^{+\infty} \Gamma(t, x - y)\varphi(y)dy, \quad \forall t > 0, x \in \mathbb{R}, \varphi \in \mathbf{X}.$$

By the properties of  $\Gamma$ , we can find an  $N_0 > 0$  such that  $\int_{|y| \geq N_0} \Gamma(b_1, y)dy \leq \epsilon$ . Since  $\frac{\partial \Gamma(t, y)}{\partial t} > 0$  for all  $t > 0$  and  $y^2 > 2t$ , we have  $\int_{|y| \geq N_1} \Gamma(t, y)dy \leq \epsilon$ , for all

$t \in [a_1, b_1]$ , where  $N_1 = \max\{N_0, \sqrt{2b_1}\}$ . Moreover, since  $\int_{-N_1}^{N_1} \Gamma(t, y) dy$  is continuous in  $t \in [a_1, b_1]$ , there is a  $\delta_1 > 0$ , such that  $|\int_{-N_1}^{N_1} (\Gamma(t_1, y) - \Gamma(t_2, y)) dy| < \epsilon$  provided that  $t_1, t_2 \in [a_1, b_1]$  and  $|t_1 - t_2| < \delta_1$ . Therefore, for any  $t_1, t_2 \in [a_1, b_1]$  and  $|t_1 - t_2| < \delta_1$ ,  $\psi \in \mathbb{X}_{\bar{L}}, x \in I$ , we have

$$\begin{aligned} & |(U_0(t_1)\psi)(x) - (U_0(t_2)\psi)(x)| \\ &= \left| \int_{\mathbb{R}} \Gamma(t_1, x-y)\psi(y) dy - \int_{\mathbb{R}} \Gamma(t_2, x-y)\psi(y) dy \right| \\ &= \left| \int_{\mathbb{R}} (\Gamma(t_1, y) - \Gamma(t_2, y))\psi(x-y) dy \right| \\ &\leq \left| \int_{|y| \leq N_1} (\Gamma(t_1, y) - \Gamma(t_2, y))\psi(x-y) dy \right| + \left| \int_{|y| \geq N_1} (\Gamma(t_1, y) - \Gamma(t_2, y))\psi(x-y) dy \right| \\ &< 2\epsilon L. \end{aligned}$$

It follows from the continuity of  $\eta(t)$  in  $t \in \mathbb{R}_+$  and definitions of  $U_0(t)$  and  $U(t, s)$  that there exists  $\delta_2 > 0$ , such that

$$|(U(t_1, 0)\varphi(0, \cdot))(x) - (U(t_2, 0)\varphi(0, \cdot))(x)| < 2\epsilon L,$$

for all  $x \in I$ ,  $\varphi \in C_{\bar{L}}$ , provided that  $t_1, t_2 \in [a, b]$  and  $|t_1 - t_2| < \delta_2$ . Let  $\bar{\delta} \in (0, \min\{\epsilon, \delta_2\})$ . Then for  $x \in I$ ,  $\varphi \in C_{\bar{L}}$ ,  $t_1, t_2 \in [a, b]$  and  $|t_1 - t_2| < \bar{\delta}$ , we have

$$\begin{aligned} & |u(t_1, x, \varphi) - u(t_2, x, \varphi)| \\ &\leq |(U(t_1, 0)\varphi(0, \cdot))(x) - (U(t_2, 0)\varphi(0, \cdot))(x)| \\ &\quad + \left| \int_0^{t_1} (U(t_1, s)B(s, u_s))(x) ds - \int_0^{t_2} (U(t_2, s)B(s, u_s))(x) ds \right| \quad (4.19) \\ &\leq 2L\epsilon + 2N \cdot 2^K \bar{\delta} \\ &\leq 2(L + 2^K N)\epsilon, \end{aligned}$$

where  $N$  was defined in the former paragraph of this proof. This implies that  $u(t, x, \varphi)$  is equicontinuous in  $t \in [a, b]$  for  $x \in I$  and  $\varphi \in C_{\bar{L}}$ .

Consequently, by (4.18) and (4.19), for any  $\varphi \in C_{\bar{L}}$ ,  $\theta_1, \theta_2 \in [-\tau, 0]$ ,  $x_1, x_2 \in I$

with  $|\theta_1 - \theta_2| < \bar{\delta}$  and  $|x_1 - x_2| < \delta$ , we have

$$\begin{aligned}
& |u_{t_0}(\varphi)(\theta_1, x_1) - u_{t_0}(\varphi)(\theta_2, x_2)| \\
&= |u(t_0 + \theta_1, x_1, \varphi) - u(t_0 + \theta_2, x_2, \varphi)| \\
&\leq |u(t_0 + \theta_1, x_1, \varphi) - u(t_0 + \theta_1, x_2, \varphi)| + |u(t_0 + \theta_1, x_2, \varphi) - u(t_0 + \theta_2, x_2, \varphi)| \\
&\leq (2L + 2^{K+1}N + 1)\epsilon,
\end{aligned}$$

which indicates that  $\{u_{t_0}(\varphi) : \varphi \in C_{\bar{L}}\}$  is equicontinuous for  $(\theta, x) \in [-\tau, 0] \times I$ . Therefore,  $\{u_{t_0}(\varphi) : \varphi \in C_{\bar{L}}\}$  is precompact in  $C_{\bar{L}}$  and (A6)(a) follows from  $Q_{t_0}(C_{\bar{L}}) = \{u_{t_0}(\varphi) : \varphi \in C_{\bar{L}}\}$  for  $t_0 > \tau$ .

Finally, we show that  $Q_t$  satisfies (A6)(b) with  $b^* = \hat{L}$  for  $0 < t \leq \tau$ . Fix  $t_1 \in (0, \tau]$  and define

$$S[\varphi](\theta, x) := \begin{cases} \varphi(0, x), & -\tau \leq \theta < -t_1, \\ Q_{t_1}(\varphi)(\theta, x), & -t_1 \leq \theta \leq 0, \end{cases}$$

for any  $\varphi \in C_{\bar{L}}$ . By the above analysis, we know that  $\{u(t, \varphi) : a \leq t \leq b, \varphi \in C_{\bar{L}}\}$  is precompact in  $\mathbf{X}$ , for any  $0 < a \leq b$ . In particular, fixing  $a = b = t_1$ , we can easily see that  $\{u_{t_1}(\varphi)(0, \cdot), \varphi \in C_{\bar{L}}\} = \{u(t_1, \cdot, \varphi), \varphi \in C_{\bar{L}}\}$  is precompact in  $\mathbf{X}$ , that is,  $Q_{t_1}[C_{\bar{L}}](0, \cdot)$  is precompact in  $\mathbf{X}$ .

Since  $Q_t$  is an  $\omega$ -periodic semiflow, it is easy to see that  $S[\varphi]$  is continuous on  $C_{\bar{L}}$ . Let  $D$  be a  $T$ -invariant subset of  $C_{\bar{L}}$  (i.e.,  $T_y D = D, \forall y \in \mathbb{R}$ ) with  $D(0, \cdot)$  being precompact in  $\mathbf{X}$ . Now we show that for any given compact interval  $I \subseteq \mathbb{R}$ ,  $S[D]$  is equicontinuous on  $[-\tau, 0] \times I$ , that is, for any  $\epsilon > 0$ , there exist  $\delta_1, \delta_2 > 0$ , such that  $|S[\varphi](\theta_1, x_1) - S[\varphi](\theta_2, x_2)| < \epsilon$  for any  $\varphi \in D$ , if  $\theta_1, \theta_2 \in [-\tau, 0], x_1, x_2 \in I$  and  $|\theta_1 - \theta_2| < \delta_1, |x_1 - x_2| < \delta_2$ .

Since  $S[\varphi](\theta, x) = \varphi(0, x), \forall \varphi \in D, \theta \in [-\tau, -t_1], x \in I$ , and  $D(0, \cdot)$  is precompact in  $\mathbf{X}$ , it is obvious that  $S[D]$  is equicontinuous on  $[-\tau, -t_1] \times I$ .

Note that there exists  $N > 0$ , such that  $\|U(t, s)B(s, u_s)\|_{\mathbf{X}} \leq N$  for all  $t \in [0, t_1], s \in [0, t], \varphi \in C_{\bar{L}}$ . Let  $\delta_0 = \min\{\epsilon/(2^K N), t_1\}$ . Then for any  $t < \delta_0, x \in I$  and  $\varphi \in D$ , we have

$$\left| \int_0^t U(t, s)B(s, u_s)(x) ds \right| < 2^K N \delta_0 = \epsilon. \quad (4.20)$$

Let  $\mathcal{F}(t, \psi) := U(t, 0)\psi$ , for  $(t, \psi) \in [0, \delta_0] \times D(0, \cdot)$ . Then  $\mathcal{F}$  is continuous on  $[0, \delta_0] \times D(0, \cdot)$  and  $\mathcal{F}([0, \delta_0] \times D(0, \cdot))$  is precompact in  $\mathbb{X}$ . Thus, for above  $I$ , there exists  $\delta_2 > 0$ , such that for  $x_1, x_2 \in I$  and  $|x_1 - x_2| < \delta_2$ , we have

$$|U(t, 0)\psi(x_1) - U(t, 0)\psi(x_2)| < \epsilon, \quad \forall t \in [0, \delta_0], \psi \in D(0, \cdot). \quad (4.21)$$

Moreover, since  $\mathcal{F}$  is uniformly continuous on  $[0, \delta_0] \times D(0, \cdot)$ , there exists  $\delta_1 > 0$ ,  $\delta_3 > 0$ , such that  $\|\mathcal{F}(\bar{t}_1, \psi_1) - \mathcal{F}(\bar{t}_2, \psi_2)\|_{\mathbb{X}} < \epsilon/2^K$ , if  $\bar{t}_1, \bar{t}_2 \in [0, \delta_0]$ ,  $\psi_1, \psi_2 \in D(0, \cdot)$  and  $|\bar{t}_1 - \bar{t}_2| < \delta_1$ ,  $\|\psi_1 - \psi_2\|_{\mathbb{X}} < \delta_3$ . In particular, we have  $\|U(\bar{t}_1, 0)\psi - U(\bar{t}_2, 0)\psi\|_{\mathbb{X}} < \epsilon/2^K$ , if  $\bar{t}_1, \bar{t}_2 \in [0, \delta_0]$ ,  $\psi \in D(0, \cdot)$  and  $|\bar{t}_1 - \bar{t}_2| < \delta_1$ . Then

$$|U(\bar{t}_1, 0)\psi(x) - U(\bar{t}_2, 0)\psi(x)| < \epsilon, \quad (4.22)$$

for any  $\psi \in D(0, \cdot)$ ,  $x \in I$ , and  $\bar{t}_1, \bar{t}_2 \in [0, \delta_0]$  with  $|\bar{t}_1 - \bar{t}_2| < \delta_1$ . By (4.20)-(4.22), we can easily obtain that if  $\theta_1, \theta_2 \in [-t_1, \delta_0 - t_1]$ ,  $x_1, x_2 \in I$  and  $|\theta_1 - \theta_2| < \delta_1$ ,  $|x_1 - x_2| < \delta_2$ , then for any  $\varphi \in D$ ,

$$\begin{aligned} & |S[\varphi](\theta_1, x_1) - S[\varphi](\theta_2, x_2)| \\ &= |Q_{t_1}[\varphi](\theta_1, x_1) - Q_{t_1}[\varphi](\theta_2, x_2)| \\ &= |u(t_1 + \theta_1, x_1, \varphi) - u(t_1 + \theta_2, x_2, \varphi)| \\ &\leq |(U(t_1 + \theta_1, 0)\varphi(0, \cdot))(x_1) - (U(t_1 + \theta_2, 0)\varphi(0, \cdot))(x_2)| \\ &\quad + \left| \int_0^{t_1 + \theta_1} U(t_1 + \theta_1, s)B(s, u_s)(x_1)ds - \int_0^{t_1 + \theta_2} U(t_1 + \theta_2, s)B(s, u_s)(x_2)ds \right| \\ &\leq |(U(t_1 + \theta_1, 0)\varphi(0, \cdot))(x_1) - (U(t_1 + \theta_1, 0)\varphi(0, \cdot))(x_2)| + \\ &\quad |(U(t_1 + \theta_1, 0)\varphi(0, \cdot))(x_2) - (U(t_1 + \theta_2, 0)\varphi(0, \cdot))(x_2)| + 2\epsilon \\ &< 4\epsilon, \end{aligned}$$

which implies that  $S[D]$  is equicontinuous on  $[-t_1, \delta_0 - t_1] \times I$ .

By a similar argument as for (A6)(a), it is easy to see that  $S[D]$  is equicontinuous on  $[\delta_0 - t_1, 0] \times I$ .

Therefore,  $S[D]$  is equicontinuous on  $[-\tau, 0] \times I$ , and hence,  $S[D]$  is precompact in  $C_{\bar{t}}$ . Thus, (A6)(b) is valid for  $Q_t$ ,  $t \in (0, \tau]$ . ■

It then follows from Lemma 4.2.3 and Theorems 2.3.1 that  $Q_\omega$  has an asymptotic speed of spread  $c_\omega^* > 0$ .

Consider the linearized system of (4.7) at the zero solution:

$$\begin{cases} \partial_t u(t, x) = d(t)\Delta u - g_u(t, 0)u(t, x) \\ \quad + b(t)\partial_u f_{-\tau}(t, 0) \int_{\mathbb{R}} \Gamma(a(t), x-y)u(t-\tau, y)dy, \quad t > 0, x \in \mathbb{R}, \\ u(t, x) = \phi(t, x), \quad t \in [-\tau, 0], x \in \mathbb{R}. \end{cases} \quad (4.23)$$

For  $\alpha > 0$ , let  $u(t, x) = e^{-\alpha x}v(t)$ . Substituting  $u(t, x)$  into (4.23) yields

$$\begin{aligned} e^{-\alpha x}v'(t) &= d(t)\alpha^2 e^{-\alpha x}v(t) - g_u(t, 0)v(t)e^{-\alpha x} \\ &\quad + b(t)\partial_u f_{-\tau}(t, 0)v(t-\tau) \int_{\mathbb{R}} \Gamma(a(t), y)e^{-\alpha(x-y)}dy. \end{aligned}$$

Since  $\Gamma(t, x)$  is even in  $x$  and by [78, Proposition 4.2], we obtain

$$\begin{aligned} v'(t) &= d(t)\alpha^2 v(t) - g_u(t, 0)v(t) + b(t)\partial_u f_{-\tau}(t, 0)v(t-\tau) \int_{\mathbb{R}} \Gamma(a(t), y)e^{\alpha y}dy, \\ &= d(t)\alpha^2 v(t) - g_u(t, 0)v(t) + b(t)\partial_u f_{-\tau}(t, 0)v(t-\tau) \int_{\mathbb{R}} \Gamma(a(t), y)e^{-\alpha y}dy, \\ &= d(t)\alpha^2 v(t) - g_u(t, 0)v(t) + b(t)\partial_u f_{-\tau}(t, 0)v(t-\tau)e^{\alpha^2 a(t)}. \end{aligned} \quad (4.24)$$

Then  $u(t, x) = e^{-\alpha x}v(t)$  satisfies (4.23) with  $\phi(s, x) = e^{-\alpha x}v(s)$  for  $s \in [-\tau, 0]$  and  $x \in \mathbb{R}$ , if  $v(t)$  satisfies (4.24) for  $t \geq 0$ .

Let  $M_t$  be the linear solution map defined by (4.23) and  $v(t, v_0)$  be the solution of (4.24) with  $v(s, v_0) = v_0(s)$  for  $s \in [-\tau, 0]$ ,  $v_0 \in \mathbb{Y}$ . Define

$$B_\alpha^t(v_0) := M_t(v_0 e^{-\alpha x})(0), \quad v_0 \in \mathbb{Y}.$$

It is not difficult to see  $B_\alpha^t(v_0) = v(t, v_0)$ , and hence,  $B_\alpha^t$  is the solution map associated with (4.24) on  $\mathbb{Y}$ .

Let  $\gamma(\alpha)$  be the spectral radius of the Poincaré map associated with (4.24). Then Theorem 2.5.1 implies that  $\gamma(\alpha) > 0$ . Moreover, it follows from the proof of Theorem 2.5.1 in [93] that there exists a positive  $\omega$ -periodic function  $w(t)$  such that  $v(t) = e^{\lambda(\alpha)t}w(t)$  is a solution of (4.24), where  $\lambda(\alpha) = \frac{\ln \gamma(\alpha)}{\omega}$ . Define  $\psi \in \mathbb{Y}$  by  $\psi(\theta) = e^{\lambda(\alpha)\theta}w(\theta)$ ,  $\forall \theta \in [-\tau, 0]$ . Clearly,  $v(t, \psi) = e^{\lambda(\alpha)t}w(t)$ ,  $\forall t \geq 0$ . Then we have

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

By the  $\omega$ -periodicity of  $w(t)$ , it follows that

$$B_\alpha^\omega(\psi)(\theta) = e^{\lambda(\alpha)\omega} e^{\lambda(\alpha)\theta} w(\theta) = e^{\lambda(\alpha)\omega} \psi(\theta), \quad \forall \theta \in [-\tau, 0],$$

that is,  $B_\alpha^\omega(\psi) = e^{\lambda(\alpha)\omega} \psi$ . This implies that  $e^{\lambda(\alpha)\omega}$  is the principle eigenvalue of  $B_\alpha^\omega$  with positive eigenfunction  $\psi$ .

Let

$$\Phi(\alpha) := \frac{1}{\alpha} \ln e^{\lambda(\alpha)\omega} = \frac{\lambda(\alpha)\omega}{\alpha} = \frac{\ln \gamma(\alpha)}{\alpha}.$$

Then we have the following result.

**Proposition 4.2.2** *Assume that (H3)-(H6) hold. Let  $c_\omega^*$  be the asymptotic speed of spread of  $Q_\omega$ . Then  $c_\omega^* = \inf_{\alpha > 0} \Phi(\alpha) = \inf_{\alpha > 0} \frac{\ln \gamma(\alpha)}{\alpha}$ .*

**Proof** When  $\alpha = 0$ , (4.24) becomes (4.9). It follows from (H6) that  $\gamma(0) > 1$ , and hence (B7) in section 2.3 is satisfied. Now we prove that  $\Phi(\infty) = \infty$ . By (4.24), we have

$$v'(t) \geq [\alpha^2 d(t) - g_u(t, 0)]v(t), \quad \forall t \geq 0,$$

and hence,

$$\frac{w'(t)}{w(t)} \geq \alpha^2 d(t) - g_u(t, 0) - \lambda(\alpha).$$

Then

$$0 = \int_0^\omega \frac{w'(t)}{w(t)} dt \geq \int_0^\omega (\alpha^2 d(t) - g_u(t, 0)) dt - \lambda(\alpha)\omega,$$

which implies that

$$\lambda(\alpha)\omega \geq \alpha^2 \int_0^\omega d(t) dt - \int_0^\omega g_u(t, 0) dt.$$

Therefore,

$$\Phi(\alpha) = \frac{\lambda(\alpha)\omega}{\alpha} \geq \alpha \int_0^\omega d(t) dt - \frac{\int_0^\omega g_u(t, 0) dt}{\alpha}.$$

Letting  $\alpha \rightarrow \infty$ , we can easily obtain  $\Phi(\infty) = \infty$ .

Since  $G(t, \cdot, \cdot)$  is subhomogeneous in  $(u, v)$ , it follows from Theorem 2.2.6 that  $G(t, u, v) \leq G_u(t, 0, 0)u + G_v(t, 0, 0)v$ , that is,

$$-g(t, u) + b(t)f_{-\tau}(t, v) \leq -g_u(t, 0)u + b(t)\partial_u f_{-\tau}(t, 0)v,$$

and hence, we have

$$\begin{aligned} & -g(t, u(t, x)) + b(t) \int_{\mathbb{R}} \Gamma(a(t), x - y) f_{-\tau}(t, u(t - \tau, y)) dy \\ & \leq -g_u(t, 0)u(t, x) + b(t) \partial_u f_{-\tau}(t, 0) \int_{\mathbb{R}} \Gamma(a(t), x - y) u(t - \tau, y) dy. \end{aligned}$$

By the comparison principle, we have  $Q_\omega(\varphi) \leq M_\omega(\varphi)$  for any  $\varphi \in C_{\beta_0^*}$ . Thus, Theorem 2.3.2 implies that  $c_\omega^* \leq \inf_{\alpha > 0} \Phi(\alpha)$ .

Let  $K > 0$  such that  $K - g_u(t, 0) > 0, \forall t \in [0, \omega]$ . Set  $\bar{G}(t, u, v) = Ku + G(t, u, v)$ . Then  $\bar{G}_u(t, 0, 0) > 0, \bar{G}_v(t, 0, 0) > 0, \forall t \in [0, \omega]$ . It is easy to see that for any  $\epsilon \in (0, 1)$ , there exists  $\delta = \delta(\epsilon) \in (0, L)$ , s.t.,

$$\bar{G}(t, u, v) \geq (1 - \epsilon)\bar{G}_u(t, 0, 0)u + (1 - \epsilon)\bar{G}_v(t, 0, 0)v, \quad \forall (u, v) \in [0, \delta]^2,$$

and hence, for any  $(u, v) \in [0, \delta]^2$ ,

$$G(t, u, v) = -Ku + \bar{G}(t, u, v) \geq [(1 - \epsilon)G_u(t, 0, 0) - \epsilon K]u + (1 - \epsilon)G_v(t, 0, 0)v.$$

Moreover, there exists  $\xi = \xi(\delta) > 0$  such that for any  $\varphi \in C_{\hat{\xi}}$ , we have

$$0 \leq u(t, x, \varphi) \leq u(t, x, \hat{\xi}) < \delta, \quad \forall x \in \mathbb{R}, t \in [0, \omega].$$

Thus, for any  $\varphi \in C_{\hat{\xi}}$ ,  $u(t, x, \varphi)$  satisfies

$$\begin{aligned} \partial_t u(t, x) & \geq d(t)\Delta u(t, x) + [(1 - \epsilon)g_u(t, 0) - \epsilon K]u(t, x) \\ & \quad + (1 - \epsilon)b(t)\partial_u f_{-\tau}(t, 0) \int_{\mathbb{R}} \Gamma(a(t), x - y) u(t - \tau, y) dy, \quad \forall t \in [0, \omega]. \end{aligned}$$

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

$$\begin{aligned} \partial_t u(t, x) & = d(t)\Delta u(t, x) + [(1 - \epsilon)g_u(t, 0) - \epsilon K]u(t, x) \\ & \quad + (1 - \epsilon)b(t)\partial_u f_{-\tau}(t, 0) \int_{\mathbb{R}} \Gamma(a(t), x - y) u(t - \tau, y) dy, \quad \forall t \in [0, \omega]. \end{aligned}$$

The comparison principle implies that  $M_t^\epsilon(\varphi) \leq Q_t(\varphi), \forall \varphi \in C_{\hat{\xi}}, t \in [0, \omega]$ . In particular,  $M_\omega^\epsilon(\varphi) \leq Q_\omega(\varphi), \forall \varphi \in C_{\hat{\xi}}$ . By a similar analysis for  $M_t^\epsilon$  as for  $M_t$ , it follows from Theorem 2.3.2 that  $\inf_{\alpha > 0} \Phi_\epsilon(\alpha) \leq c_\omega^*$ .

Therefore,  $\inf_{\alpha > 0} \Phi_\epsilon(\alpha) \leq c_\omega^* \leq \inf_{\alpha > 0} \Phi(\alpha), \forall \epsilon \in (0, 1)$ . Letting  $\epsilon \rightarrow 0$ , we have  $c_\omega^* = \inf_{\alpha > 0} \Phi(\alpha)$ . ■

Let

$$c^* = \frac{C_\omega^*}{\omega} = \frac{1}{\omega} \inf_{\alpha > 0} \Phi(\alpha) = \frac{1}{\omega} \inf_{\alpha > 0} \frac{\ln \gamma(\alpha)}{\alpha}. \quad (4.25)$$

The following result shows that  $c^*$  is the spreading speed of solutions of (4.7) with initial functions having compact support.

**Theorem 4.2.3** *Assume that (H3)-(H6) hold. Then the following statements are valid.*

- (1) *For any  $c > c^*$ , if  $\varphi \in C_{\beta_0^*}$  with  $0 \leq \varphi \ll \beta_0^*$  and  $\varphi(\cdot, x) = 0$  for  $x$  outside a bounded interval, then*

$$\lim_{t \rightarrow \infty, |x| \geq ct} u(t, x, \varphi) = 0.$$

- (2) *For any  $c < c^*$ , if  $\varphi \in C_{\beta_0^*}$  with  $\varphi \not\equiv 0$ , then*

$$\lim_{t \rightarrow \infty, |x| \leq ct} (u(t, x, \varphi) - \beta^*(t)) = 0.$$

**Proof** Conclusion (1) follows from Theorem 2.3.3. By Lemma 4.2.1 and Theorem 2.3.3, for any  $c < c^*$ , there is a positive number  $\sigma$  s.t., if  $\varphi \in C_{\beta_0^*}$  with  $\varphi(\cdot, x) > 0$  for  $x$  on an interval of length  $2\sigma$ , then  $\lim_{t \rightarrow \infty, |x| \leq ct} (u(t, x, \varphi) - \beta^*(t)) = 0$ . It follows from Lemma 4.2.2 that for any  $\varphi \in C_{\beta_0^*}$  with  $\varphi \not\equiv 0$ ,  $Q_t(\varphi) \gg 0$  for all  $t > 2\tau$ . We can fix  $t_0 > 2\tau$  and take  $Q_{t_0}(\varphi)$  as a new initial value for  $u(t, x, \varphi)$ . Then by above analysis, conclusion (2) is valid. ■

We say  $u(t, x) = \mathcal{U}(t, x - ct)$  is an  $\omega$ -periodic traveling wave of (4.7) connecting  $\beta^*(t)$  to 0 if it is a solution of (4.7),  $\mathcal{U}(t, \xi)$  is  $\omega$ -periodic in  $t$ , and  $\mathcal{U}(t, -\infty) = \beta^*(t)$  and  $\mathcal{U}(t, \infty) = 0$  uniformly for  $t \in [0, \omega]$ . By Theorem 2.3.4, we have the following result about traveling waves of (4.7).

**Theorem 4.2.4** *Assume that (H3)-(H6) hold. Let  $c^*$  be defined in (4.25). Then for any  $c \geq c^*$ , (4.7) has an  $\omega$ -periodic traveling wave solution  $\mathcal{U}(t, x - ct)$  connecting  $\beta^*(t)$  to 0 such that  $\mathcal{U}(t, s)$  is continuous and nonincreasing in  $s$ . Moreover, for any  $c < c^*$ , (4.7) has no  $\omega$ -periodic traveling wave  $\mathcal{U}(t, x - ct)$  connecting  $\beta^*(t)$  to 0.*

### 4.3 Dynamics in a bounded domain

In this section, we consider (4.6) in a bounded spatial domain

$$\left\{ \begin{array}{l} \partial_t u(t, x) = d(t)\Delta u - g(t, u) + b(t) \int_{\Omega} \Gamma(a(t), x - y) f_{-\tau}(t, u(t - \tau, y)) dy, \\ \quad (t, x) \in (0, \infty) \times \Omega, \\ Bu(t, x) = 0 \text{ on } (0, \infty) \times \partial\Omega, \\ u(t, x) = \phi(t, x), \quad t \in [-\tau, 0], x \in \Omega, \end{array} \right. \quad (4.26)$$

where  $\Omega \subseteq \mathbb{R}^n$  is a bounded domain with boundary  $\partial\Omega$  of class  $C^{1+\theta}$  ( $0 < \theta \leq 1$ ), the boundary condition is either  $Bu = u$  (Dirichlet boundary condition) or  $Bu = (\partial u / \partial \nu) + \alpha(x)u$  (Robin type boundary condition) for some nonnegative function  $\alpha \in C^{1+\theta}(\partial\Omega, \mathbb{R}^n)$ ,  $\partial u / \partial \nu$  denotes the differentiation in the direction of outward normal  $\nu$  to  $\partial\Omega$ .

Let  $p \in (1, \infty)$  be fixed. For each  $\beta \in (\frac{1}{2} + \frac{1}{2p}, 1)$ , let  $\mathbb{X}_\beta$  be the fractional power space of  $L^p(\Omega)$  with respect to  $-\Delta$  and the boundary condition  $Bu = 0$  (see, e.g., [35]). Then  $\mathbb{X}_\beta$  is an ordered Banach space with the positive cone  $\mathbb{X}_\beta^+$  consisting of all nonnegative functions in  $\mathbb{X}_\beta$ , and  $\mathbb{X}_\beta^+$  has non-empty interior  $\text{int}(\mathbb{X}_\beta^+)$ . Moreover,  $\mathbb{X}_\beta \subseteq C^{1+\nu}(\bar{\Omega})$  with continuous inclusion for  $\nu \in [0, 2\beta - 1 - \frac{1}{p}]$ . Denote the norm on  $\mathbb{X}_\beta$  by  $\|\cdot\|_\beta$ . Then there exists a constant  $k_\beta > 0$  such that  $\|\phi\|_\infty := \max_{x \in \bar{\Omega}} |\phi(x)| \leq k_\beta \|\phi\|_\beta, \forall \phi \in \mathbb{X}_\beta$ .

Let  $\bar{C} = C([-\tau, 0], \mathbb{X}_\beta)$  and  $\bar{C}^+ = C([-\tau, 0], \mathbb{X}_\beta^+)$ . For convenience, we identify an element  $\phi \in \bar{C}$  as a function from  $[-\tau, 0] \times \bar{\Omega}$  to  $\mathbb{R}^n$  defined by  $\phi(s, x) = \phi(s)(x)$ . For any  $N \geq L$ , let  $\bar{C}_N^+ = \{\phi \in \bar{C} : 0 \leq \phi(s, x) \leq N, (s, x) \in [-\tau, 0] \times \bar{\Omega}\}$ . For any function  $y(\cdot) : [-\tau, b] \rightarrow \mathbb{X}_\beta$ , where  $b > 0$ , define  $y_t \in \bar{C}$ , by  $y_t(s) = y(t + s), \forall s \in [-\tau, 0], t \in [0, b]$ .

Note that the differential operator  $\Delta$  generates an analytic semigroup  $\bar{U}_0(t)$  on  $L^p(\Omega)$  and that the standard parabolic maximum principle (see, e.g., [72, Corollary 7.2.3]) implies that the semigroup  $\bar{U}_0(t) : \mathbb{X}_\beta \rightarrow \mathbb{X}_\beta$  is strongly positive in the sense that  $\bar{U}_0(t)(\mathbb{X}_\beta^+ \setminus \{0\}) \subseteq \text{int}(\mathbb{X}_\beta^+), \forall t > 0$ . By the similar analysis as in section 2, we

can write equation (4.26) as an integral equation (4.13) with  $u_0 = \phi \in \bar{C}^+$ . It then follows from Theorem 2.5.3 that, for any  $\phi \in \bar{C}_L^+$ , (4.26) has a unique mild solution  $u(t, x, \phi)$  with  $u_0(\cdot, \cdot, \phi) = \phi$  and  $u_t(\cdot, \cdot, \phi) \in \bar{C}_L^+$ ,  $\forall t \geq 0$ . Moreover,  $u(t, x, \phi)$  is a classic solution when  $t > \tau$  and the comparison theorem holds for (4.26).

Define a family of operators  $\{Q_t\}_{t \geq 0}$  on  $\bar{C}^+$  by

$$Q_t(\phi)(s, x) = u(t + s, x, \phi), \quad \forall \phi \in \bar{C}^+, x \in \bar{\Omega}, t \geq 0, s \in [-\tau, 0].$$

Similarly as in section 2, we can show that  $\{Q_t\}_{t \geq 0}$  is a monotone  $\omega$ -periodic semiflow on  $\bar{C}^+$ ;  $u(t, x, \phi) > 0$  for  $t > \tau$ ,  $x \in \bar{\Omega}$ ,  $\phi \in \bar{C}^+$  with  $\phi \not\equiv 0$ , and hence,  $Q_t$  is strongly positive for  $t > 2\tau$ ; moreover,  $Q_t$  is compact on  $\bar{C}^+$  for all  $t > \tau$ . Let  $n_1 = \min\{n \in \mathbb{N}, n\omega > 2\tau\}$ . Then  $Q_{n_1\omega}$  is compact and strongly positive on  $\bar{C}^+$ . We can further show that the periodic semiflow  $\{Q_t\}_{t \geq 0}$  is point dissipative on  $\bar{C}^+$ .

**Theorem 4.3.1** *Let (H3)-(H5) hold. Then  $Q_{n_1\omega}$  admits a global attractor on  $\bar{C}^+$ .*

**Proof** We show that  $Q_t$  is point dissipative for any  $t \geq 0$ . In the case where (H6) holds, Theorem 4.2.1 implies that for any  $\phi \in \mathbb{Y}_+$  with  $\phi \not\equiv 0$ , the unique solution  $w(t, \phi)$  of (4.8) with  $w(s, \phi) = \phi(s)$ ,  $\forall s \in [-\tau, 0]$ , satisfies  $\lim_{t \rightarrow \infty} \|w(t, \phi) - \beta^*(t)\|_\infty = 0$ . Let  $\bar{\beta}^* = \max_{t \in [0, \omega]} \beta^*(t)$ . It follows that  $\limsup_{t \rightarrow \infty} w(t, \phi) < 2\bar{\beta}^*$ ,  $\forall \phi \in \mathbb{Y}_+$ . In the case where (H6) doesn't hold, also by Theorem 4.2.1, this limit inequality is valid for any  $\bar{\beta}^* > 0$ .

For any given  $\phi \in \bar{C}^+$ , let  $\tilde{\phi}(s) = \max\{\phi(\theta, x) : \theta \in [-\tau, 0], x \in \bar{\Omega}\}$ ,  $\forall s \in [-\tau, 0]$ . Then  $\limsup_{t \rightarrow \infty} w(t, \tilde{\phi}) \leq 2\bar{\beta}^*$ . Note that for any given  $t \geq 0$  and  $\varsigma \in \bar{C}^+$  with  $\varsigma(s, \cdot) \leq w(t + s, \tilde{\phi})$ ,  $\forall s \in [-\tau, 0]$ , we have

$$\begin{aligned} & w(t, \tilde{\phi}) - \varsigma(0, x) + h(-g(t, w(t, \tilde{\phi})) + b(t)f_{-\tau}(t, w(t - \tau, \tilde{\phi}))) \\ & \quad - h(-g(t, \varsigma(0, x)) + b(t)f_{-\tau}(t, \varsigma(-\tau, x))) \\ & \geq w(t, \tilde{\phi}) - \varsigma(0, x) - hg(t, w(t, \tilde{\phi})) + hg(t, \varsigma(0, x)) \\ & \geq 0, \end{aligned}$$

for  $0 < h \ll 1$ ,  $x \in \bar{\Omega}$ . By [58, Proposition 3],  $u(t, x, \phi) \leq w(t, \tilde{\phi})$ ,  $\forall x \in \bar{\Omega}, t \geq -\tau$ . Then  $\limsup_{t \rightarrow \infty} u(t, x, \phi) \leq 2\bar{\beta}^*$ ,  $\forall x \in \bar{\Omega}$ , and hence,  $\limsup_{t \rightarrow \infty} \|u(t, \cdot, \phi)\|_\infty \leq 2\bar{\beta}^*$ . Thus,

there exists  $t_0 > 0$  such that  $\|u(t, \cdot, \phi)\|_\infty \leq 2\bar{\beta}^*$ ,  $\forall t \geq t_0$ . By the definition of  $\|\cdot\|_0$  on  $\mathbf{X}_0 = \mathbf{X}$ , we have

$$\|u(t, \cdot, \phi)\|_0 \leq k_0 \|u(t, \cdot, \phi)\|_\infty \leq 2k_0\bar{\beta}^*$$

for some positive number  $k_0$ ,  $\forall t \geq t_0$ . For any  $t \geq t_0 + 2\omega$ , let  $\tilde{n} = [\frac{t}{\omega}] - 1$ . Then  $\tilde{n}\omega > t_0$  and  $(\tilde{n} + 1)\omega \leq t \leq (\tilde{n} + 2)\omega$ . Moreover, similarly as (4.13), (4.26) can be written as

$$u(t, \cdot, \phi) = U(t, \tilde{n}\omega)u(\tilde{n}\omega, \cdot, \phi) + \int_{\tilde{n}\omega}^t U(t, s)B(s, u_s)ds, \quad t \geq \tilde{n}\omega,$$

where  $U(t, s)$  is the evolution operator of

$$\begin{cases} \partial_t u(t, x) = d(t)\Delta u, & t > 0, \quad x \in \Omega, \\ u(0, x) = \varphi(x), & x \in \Omega, \quad \varphi \in \mathbf{X}_\beta. \end{cases} \quad (4.27)$$

Since (4.27) is an  $\omega$ -periodic system, we have  $U(t + \omega, s + \omega)\varphi = U(t, s)\varphi$  for all  $0 \leq s \leq t$  and  $\varphi \in \mathbf{X}_\beta$ . By (11.9) in [35], there exists  $c_1 \equiv c_1(0, \beta, \gamma_1) > 0$  such that  $\|U(t, s)\|_{0, \beta} \leq c_1(t - s)^{-\gamma_1}$  for  $0 \leq s \leq t \leq 2\omega$ ,  $\beta < \gamma_1 < 1$ . Moreover, there exists  $c_3 > 0$  such that  $\|\varphi\|_0 \leq c_3 \|\varphi\|_\beta$  for all  $\varphi \in \mathbf{X}_\beta$  since  $\mathbf{X}_\beta \hookrightarrow \mathbf{X}_0$  is a continuous injection. Then for any  $t \geq t_0 + 2\omega$ ,

$$\begin{aligned} & \|u(t, \cdot, \phi)\|_\beta \\ & \leq \|U(t, \tilde{n}\omega)u(\tilde{n}\omega, \cdot, \phi)\|_\beta + \left\| \int_{\tilde{n}\omega}^t U(t, s)B(s, u_s)ds \right\|_\beta \\ & = \|U(t - \tilde{n}\omega, 0)u(\tilde{n}\omega, \cdot, \phi)\|_\beta + \left\| \int_{\tilde{n}\omega}^t U(t - \tilde{n}\omega, s - \tilde{n}\omega)B(s, u_s)ds \right\|_\beta \\ & \leq \|U(t - \tilde{n}\omega, 0)\|_{0, \beta} \cdot \|u(\tilde{n}\omega, \cdot, \phi)\|_0 \\ & \quad + \int_{\tilde{n}\omega}^t \|U(t - \tilde{n}\omega, s - \tilde{n}\omega)\|_{0, \beta} \cdot \|B(s, u_s)\|_0 ds \\ & \leq c_1(t - \tilde{n}\omega)^{-\gamma_1} \|u(\tilde{n}\omega, \cdot, \phi)\|_0 + \int_{\tilde{n}\omega}^t c_1(t - s)^{-\gamma_1} c_2 \|u(s, \cdot, \phi)\|_0 ds \\ & \leq c_1(t - \tilde{n}\omega)^{-\gamma_1} \|u(\tilde{n}\omega, \cdot, \phi)\|_0 + \int_{\tilde{n}\omega}^t c_1(t - s)^{-\gamma_1} c_2 c_3 \|u(s, \cdot, \phi)\|_\beta ds, \end{aligned}$$

where  $c_2 > 0$  depends on  $2k_0\bar{\beta}^*$  by (H3). A general Gronwall inequality implies that

$$\begin{aligned} \|u(t, \cdot, \phi)\|_{\beta} &\leq c_1(t - \tilde{n}\omega)^{-\gamma_1} \|u(\tilde{n}\omega, \cdot, \phi)\|_0 \cdot e^{\int_{\tilde{n}\omega}^t c_1 c_2 c_3 (t-s)^{-\gamma_1} ds} \\ &\leq c_1(t - \tilde{n}\omega)^{-\gamma_1} \|u(\tilde{n}\omega, \cdot, \phi)\|_0 \cdot e^{c_1 c_2 c_3 \cdot \frac{(2\omega)^{1-\gamma_1}}{1-\gamma_1}} \\ &\leq c_1 \cdot \omega^{-\gamma_1} \cdot 2k_0\bar{\beta}^* \cdot e^{c_1 c_2 c_3 \cdot \frac{(2\omega)^{1-\gamma_1}}{1-\gamma_1}}, \quad \forall t \geq t_0 + 2\omega, \end{aligned}$$

where we have applied the inequality  $\int_{\tilde{n}\omega}^t (t-s)^{-\gamma_1} ds \leq \frac{(2\omega)^{1-\gamma_1}}{1-\gamma_1}$ , for  $\tilde{n}\omega \leq s < t \leq (\tilde{n}+2)\omega$ . Therefore,

$$\limsup_{t \rightarrow \infty} \|u(t, \cdot, \phi)\|_{\beta} \leq c_1 \cdot \omega^{-\gamma_1} \cdot 2k_0\bar{\beta}^* \cdot e^{c_1 c_2 c_3 \cdot \frac{(2\omega)^{1-\gamma_1}}{1-\gamma_1}}.$$

It follows that  $Q_t : \bar{C}^+ \rightarrow \bar{C}^+$  is point dissipative. In particular,  $Q_{n_1\omega}$  is point dissipative.

Note that  $Q_{n_1\omega}$  is compact on  $\bar{C}^+$ . By Theorem 2.1.1,  $Q_{n_1\omega}$  admits a global attractor on  $\bar{C}^+$ , which attracts any bounded set in  $\bar{C}^+$ . ■

Consider the linearized system of (4.26) at the zero solution

$$\begin{cases} \partial_t \tilde{u}(t, x) = d(t)\Delta \tilde{u} - g_u(t, 0)\tilde{u}(t, x) \\ \quad + b(t)\partial_u f_{-\tau}(t, 0) \int_{\Omega} \Gamma(a(t), x-y)\tilde{u}(t-\tau, y)dy, \quad t > 0, x \in \Omega, \\ B\tilde{u}(t, x) = 0, \quad t > 0, x \in \partial\Omega, \\ \tilde{u}(s, x) = \phi(s, x), \quad s \in [-\tau, 0], x \in \Omega, \phi \in \bar{C}. \end{cases} \quad (4.28)$$

Similarly as in Theorem 4.2.2, we can show that the comparison principle holds for (4.28), and hence, the solution map  $\tilde{u}_t$  of (4.28) is monotone increasing for all  $t \geq 0$ .

Now we consider (4.26) and (4.28) as  $n_1\omega$ -periodic systems. Define the Poincaré map of (4.28)  $P_1 : \bar{C} \rightarrow \bar{C}$  by

$$P_1(\phi) = \tilde{u}_{n_1\omega}(\phi), \quad \forall \phi \in \bar{C},$$

where  $\tilde{u}_{n_1\omega}(\phi)(s, x) = \tilde{u}(n_1\omega + s, x, \phi)$ ,  $\forall (s, x) \in [-\tau, 0] \times \bar{\Omega}$ , and  $\tilde{u}(t, x, \phi)$  is the solution of (4.28) with  $\tilde{u}(s, x) = \phi(s, x)$ ,  $\forall (s, x) \in [-\tau, 0] \times \bar{\Omega}$ . Similarly as in section 2, we can obtain that  $P_1$  is also compact and strongly positive. Let  $r_1 = r(P_1)$  be the spectral radius of  $P_1$ . By the Krein-Rutman Theorem (see, e.g., [35, Theorem 7.2]),  $r_1 > 0$  and  $P_1$  has a positive eigenfunction  $\bar{\phi} \in \text{int}(\bar{C}^+)$  corresponding to  $r_1$ .

**Lemma 4.3.1** *Let  $\mu = -\frac{1}{n_1\omega} \ln r_1$ . Then there exists a positive  $n_1\omega$ -periodic function  $v(t, x)$  such that  $e^{-\mu t}v(t, x)$  is a solution of (4.28).*

**Proof** By the definitions of  $r_1$  and  $\bar{\phi}$ , we have  $P_1\bar{\phi} = r_1\bar{\phi}$ . Let  $\tilde{u}(t, x, \bar{\phi})$  be the solution of (4.28) with  $\tilde{u}(s, x) = \bar{\phi}(s, x)$ ,  $\forall s \in [-\tau, 0], x \in \Omega$ . Since  $\bar{\phi} \gg 0$ , it is not difficult to see that  $\tilde{u}(\cdot, \cdot, \bar{\phi}) \gg 0$ . Let  $\mu = -\frac{1}{n_1\omega} \ln r_1$  and  $v(t, x) = e^{\mu t}\tilde{u}(t, x, \bar{\phi})$ ,  $\forall t \geq -\tau, x \in \Omega$ . Then  $r_1 = e^{-n_1\omega\mu}$  and  $v(t, x) > 0$ ,  $\forall t \in [-\tau, \infty), x \in \Omega$ . Moreover,

$$\begin{aligned} v_t(t, x) &= e^{\mu t}\tilde{u}_t(t, x, \bar{\phi}) + \mu e^{\mu t}\tilde{u}(t, x, \bar{\phi}) \\ &= e^{\mu t}[d(t)\Delta\tilde{u} - g_u(t, 0)\tilde{u}(t, x, \bar{\phi})] + \\ &\quad e^{\mu t}b(t)\partial_u f_{-\tau}(t, 0) \int_{\Omega} \Gamma(a(t), x - y)\tilde{u}(t - \tau, y, \bar{\phi})dy + \mu v \quad (4.29) \\ &= d(t)\Delta v - g_u(t, 0)v(t, x) \\ &\quad + e^{\mu\tau}b(t)\partial_u f_{-\tau}(t, 0) \int_{\Omega} \Gamma(a(t), x - y)v(t - \tau, y)dy + \mu v, \end{aligned}$$

for all  $(t, x) \in (0, \infty) \times \Omega$ . Thus,  $v(t, x)$  is a solution of  $n_1\omega$ -periodic equation (4.29) with  $Bv = 0$  on  $(0, \infty) \times \partial\Omega$  and  $v(s, x) = e^{\mu s}\bar{\phi}(s, x)$ ,  $\forall s \in [-\tau, 0], x \in \Omega$ .

For any  $\theta \in [-\tau, 0], x \in \Omega$ , we have

$$v(n_1\omega + \theta, x) = e^{\mu(n_1\omega + \theta)} \cdot P_1(\bar{\phi})(\theta, x) = e^{\mu(n_1\omega + \theta)} \cdot r_1\bar{\phi}(\theta, x) = e^{\mu\theta} \cdot \tilde{u}(\theta, x, \bar{\phi}) = v(\theta, x).$$

Therefore,  $v_0(\theta, \cdot) = v_{n_1\omega}(\theta, \cdot)$ ,  $\forall \theta \in [-\tau, 0]$ , and hence, the existence and uniqueness of solutions of (4.29) implies that

$$v(t, x) = v(t + n_1\omega, x), \quad \forall t \geq -\tau, x \in \Omega,$$

that is,  $v(t, x)$  is an  $n_1\omega$ -periodic solution of (4.29). Clearly,  $e^{-\mu t}v(t, x)$  is a solution of (4.28). ■

Define  $P_0 : \bar{C} \rightarrow \bar{C}$  by

$$P_0(\phi) = \tilde{u}_\omega(\phi), \quad \forall \phi \in \bar{C},$$

where  $\tilde{u}(t, x, \phi)$  is the solution of (4.28) with  $\tilde{u}(s, x) = \phi(s, x)$ ,  $\forall s \in [-\tau, 0], x \in \Omega$ . Let  $r_0 = r(P_0)$  be the spectral radius of  $P_0$ .

**Theorem 4.3.2** *Let (H3)-(H5) hold. For any  $\phi \in \bar{C}^+$ , denote by  $u(t, x, \phi)$  the solution of (4.26) with  $u(s, x) = \phi(s, x)$  for all  $(t, x) \in [-\tau, 0] \times \Omega$ . Then the following two statements are valid.*

(i) *If  $r_0 < 1$ ,  $\lim_{t \rightarrow \infty} \|u(t, \cdot, \phi)\|_\beta = 0$  for every  $\phi \in \bar{C}^+$ .*

(ii) *If  $r_0 > 1$ , then (4.26) admits a unique positive  $\omega$ -periodic solution  $u^*(t, x)$  and  $\lim_{t \rightarrow \infty} \|u(t, \cdot, \phi) - u^*(t, \cdot)\|_\beta = 0$  for all  $\phi \in \bar{C}^+ \setminus \{0\}$ .*

**Proof** Since  $P_1 = \tilde{u}_{n_1\omega}$ ,  $P_0 = \tilde{u}_\omega$  and  $\tilde{u}_{n_1\omega} = \tilde{u}_\omega^{n_1}$ , where  $\tilde{u}_t$  is the solution map of (4.28), by the properties of spectral radius of linear operators, we know that  $r(P_1) = (r(P_0))^{n_1}$ , i.e.,  $r_1 = (r_0)^{n_1}$ . Note that the qualitatives of solutions of (4.26) and (4.28) do not change whether we consider them as  $n_1\omega$ -periodic systems or  $\omega$ -periodic systems. The conditions in Theorem 4.3.2 can be replaced by  $r_1 < 1$  and  $r_1 > 1$ , respectively. In the following, we will consider (4.26) and (4.28) as  $n_1\omega$ -periodic systems and prove the theorem under the conditions of  $r_1 < 1$  and  $r_1 > 1$ .

In the case where  $r_1 < 1$ , we have  $\mu = -\frac{1}{n_1\omega} \ln r_1 > 0$ . By Lemma 4.3.1, (4.28) has a solution  $\tilde{u}(t, x) := \tilde{u}(t, x, \bar{\phi}) = e^{-\mu t} v(t, x)$  with  $\tilde{u}(s, x) = \bar{\phi}(s, x)$ ,  $\forall (s, x) \in [-\tau, 0] \times \Omega$ , where  $\bar{\phi} \in \text{int}(\bar{C}^+)$  is the positive eigenfunction of  $P_1$  corresponding to  $r_1$  and  $v(t, x)$  is  $n_1\omega$ -periodic in  $t \geq -\tau$ . Then  $v$  is bounded on  $[-\tau, \infty) \times \bar{\Omega}$ , and hence, there exists  $\rho > 0$  such that  $\|v(t, \cdot)\|_\infty \leq \rho$ ,  $\forall t \geq -\tau$ . Thus,  $\lim_{t \rightarrow \infty} \|\tilde{u}(t, \cdot)\|_\infty = 0$ . By a similar argument as in Theorem 4.3.1, it follows that  $\lim_{t \rightarrow \infty} \|\tilde{u}(t, \cdot)\|_\beta = 0$ .

Given  $\phi \in \bar{C}^+$ . Since  $\lim_{\delta \rightarrow 0^+} (\bar{\phi} - \delta\phi) = \bar{\phi} \in \text{int}(\bar{C}^+)$ , for any  $\epsilon > 0$ , there exists  $\delta_\phi > 0$ , such that,  $\bar{\phi} - \delta\phi \in B_\epsilon(\bar{\phi}) \subseteq \bar{C}^+$ , for  $0 < \delta \leq \delta_\phi$ , where  $B_\epsilon(\bar{\phi})$  is an open ball in  $\bar{C}^+$  centered at  $\bar{\phi}$  with radius  $\epsilon$ . Therefore,  $\bar{\phi} \geq \delta_\phi\phi$  in  $\bar{C}^+$ . It then follows from the comparison principle that  $\tilde{u}(t, x) \geq \delta_\phi\tilde{u}(t, x, \phi)$ ,  $\forall t \geq -\tau, x \in \bar{\Omega}$ , where  $\tilde{u}(t, \cdot, \phi)$  is the solution of (4.28) with  $\tilde{u}(s, x) = \phi(s, x)$ ,  $\forall (s, x) \in [-\tau, 0] \times \Omega$ . Thus,  $\lim_{t \rightarrow \infty} \|\tilde{u}(t, \cdot, \phi)\|_\infty = 0$ , and hence,  $\lim_{t \rightarrow \infty} \|\tilde{u}(t, \cdot, \phi)\|_\beta = 0$  for any  $\phi \in \bar{C}^+$ .

Note that every solution of (4.26) satisfies

$$\partial_t u(t, x) \leq d(t)\Delta u - g_u(t, 0)u(t, x) + b(t)\partial_u f_{-\tau}(t, 0) \int_{\Omega} \Gamma(a(t), x - y)u(t - \tau, y)dy,$$

for  $t > 0$ ,  $x \in \Omega$ . Similarly as in the proof of Theorem 4.2.2, we can show that the comparison theorem for abstract functional differential equations [58, Proposition 3] can be applied to (4.26) and (4.28). Therefore, for any  $\phi \in \bar{C}^+$ ,  $u(t, \cdot, \phi) \leq \tilde{u}(t, \cdot, \phi)$ ,  $\forall t \geq -\tau$ , where  $u(t, \cdot, \phi)$  and  $\tilde{u}(t, \cdot, \phi)$  are solutions of (4.26) and (4.28), respectively. It then follows that solutions of (4.26) satisfy  $\lim_{t \rightarrow \infty} \|u(t, \cdot, \phi)\|_{\beta} = 0$ ,  $\forall \phi \in \bar{C}^+$ .

In the case where  $r_1 > 1$ , we have  $\mu < 0$ . Let  $\bar{C}_0 = \{\phi \in \bar{C}^+ : \phi \not\equiv 0\}$ ,  $\partial\bar{C}_0 = \bar{C}^+ \setminus \bar{C}_0 = \{0\}$ . Similarly as in the proof of Lemma 4.2.2, we can show that for any  $\phi \in \bar{C}_0$ , the solution  $u(t, x, \phi)$  of (4.26) satisfies  $u(t, x, \phi) > 0$ , for all  $t > \tau$ ,  $x \in \Omega$ . It follows that  $Q_t(\bar{C}_0) \subseteq \text{int}(\bar{C}^+)$ ,  $\forall t > 2\tau$ . Clearly,  $Q_t(0) = 0$ ,  $\forall t \geq 0$ . We future claim that

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

Indeed, we consider the following system

$$\begin{cases} \partial_t u^\varepsilon(t, x) = d(t)\Delta u^\varepsilon - (g_u(t, 0) + \varepsilon)u^\varepsilon(t, x) \\ \quad + b(t)(\partial_u f_{-\tau}(t, 0) - \varepsilon) \int_{\Omega} \Gamma(a(t), x - y)u^\varepsilon(t - \tau, y)dy, & t > 0, x \in \Omega, \\ Bu^\varepsilon(t, x) = 0, & t > 0, x \in \partial\Omega, \\ u^\varepsilon(s, x) = \phi(s, x), & s \in [-\tau, 0], x \in \Omega, \phi \in \bar{C}. \end{cases} \quad (4.30)$$

Define the Poincaré map of (4.30)  $P_\varepsilon : \bar{C} \rightarrow \bar{C}$  by

$$P_\varepsilon(\phi) = u_{n_1\omega}^\varepsilon(\phi), \quad \forall \phi \in \bar{C},$$

where

$$u_{n_1\omega}^\varepsilon(\phi)(s, x) = u^\varepsilon(n_1\omega + s, x, \phi), \quad \forall (s, x) \in [-\tau, 0] \times \bar{\Omega}$$

and  $u^\varepsilon(t, x, \phi)$  is the solution of (4.30) with  $u^\varepsilon(s, x) = \phi(s, x)$ ,  $\forall s \in [-\tau, 0]$ ,  $x \in \Omega$ . Let  $r_\varepsilon = r(P_\varepsilon)$  be the spectral radius of  $P_\varepsilon$ . Since  $r_1 = r(P_1) > 1$ , there exists a sufficiently small positive number  $\varepsilon_1$  such that  $r_\varepsilon > 1$  for all  $\varepsilon \in [0, \varepsilon_1)$ . We fix an  $\varepsilon \in (0, \varepsilon_1)$ . Since  $\lim_{u \rightarrow 0^+} \frac{g(t, u)}{u} = g_u(t, 0)$  and  $\lim_{u \rightarrow 0^+} \frac{f_{-\tau}(t, u)}{u} = \partial_u f_{-\tau}(t, 0)$  uniformly for  $t \in [0, n_1\omega]$ , there exists  $\delta_\varepsilon > 0$ , such that  $g(t, u) < (g_u(t, 0) + \varepsilon)u$  and  $f_{-\tau}(t, u) > (\partial_u f_{-\tau}(t, 0) - \varepsilon)u$  for  $u \in (0, \delta_\varepsilon)$ ,  $t \in [0, n_1\omega]$ . Let  $\delta_0 = \delta_\varepsilon/k_\beta$ . Suppose, by contradiction, that there

exists  $\phi_0 \in \bar{C}_0$  such that  $\limsup_{t \rightarrow \infty} \|Q_t(\phi)\|_\beta < \delta_0$ . Then there exists  $t_0 > \tau$  such that  $\|u(t, \cdot, \phi_0)\|_\infty \leq k_\beta \|u(t, \cdot, \phi_0)\|_\beta < \delta_\varepsilon$  for all  $t \geq t_0$ . Therefore,  $u(t, x, \phi_0)$  satisfies

$$\begin{aligned} \partial_t u(t, x) &> d(t)\Delta u - (g_u(t, 0) + \varepsilon)u(t, x) \\ &\quad + b(t)(\partial_u f_{-\tau}(t, 0) - \varepsilon) \int_\Omega \Gamma(a(t), x - y)u(t - \tau, y)dy, \end{aligned} \quad (4.31)$$

for  $t \geq t_0, x \in \Omega$ . Let  $\bar{\phi}_\varepsilon$  be the positive eigenfunction of  $P_\varepsilon$  associated with  $r_\varepsilon$  and  $\mu_\varepsilon = -\frac{1}{n_1\omega} \ln r_\varepsilon$ . Then by Lemma 4.3.1, the solution  $u^\varepsilon(t, x, \bar{\phi}_\varepsilon)$  of (4.30) with  $u^\varepsilon(s, x) = \bar{\phi}_\varepsilon(s, x), \forall s \in [-\tau, 0], x \in \Omega$ , satisfies  $u^\varepsilon(t, x, \bar{\phi}_\varepsilon) = e^{-\mu_\varepsilon t} v_\varepsilon(t, x)$ , where  $v_\varepsilon(t, x)$  is a positive  $n_1\omega$ -periodic function in  $t \geq -\tau$ . Since  $u(t, x, \phi_0) > 0, \forall t \geq \tau, x \in \Omega$ , there exists  $\zeta > 0$  such that

$$u(t_0 + s, x, \phi_0) \geq \zeta u^\varepsilon(s, x, \bar{\phi}_\varepsilon) = \zeta \bar{\phi}_\varepsilon(s, x), \quad \forall s \in [-\tau, 0], x \in \bar{\Omega}.$$

By (4.31) and the comparison theorem, we have

$$u(t, x, \phi_0) \geq \zeta u^\varepsilon(t - t_0, x, \bar{\phi}_\varepsilon) = \zeta e^{-\mu_\varepsilon(t-t_0)} v_\varepsilon(t, x), \quad \forall t \geq t_0, x \in \bar{\Omega}.$$

Since  $\mu_\varepsilon < 0$ , it follows that  $u(t, x, \phi_0)$  is unbounded, a contradiction. Thus, the claim is true.

By the claim above,  $Q_{n_1\omega}$  is weakly uniformly persistent with respect to  $(\bar{C}_0, \partial\bar{C}_0)$ . Since  $Q_{n_1\omega}$  admits a global attractor on  $\bar{C}^+$ , it follows from Theorem 2.1.2 that  $Q_{n_1\omega}$  is uniformly persistent with respect to  $(\bar{C}_0, \partial\bar{C}_0)$  in the sense that there exists  $\delta_1 > 0$  such that  $\liminf_{n \rightarrow \infty} \|Q_{n_1\omega}^n(\phi)\|_\beta \geq \delta_1, \forall \phi \in \bar{C}_0$ .

Note that  $Q_{n_1\omega}$  is compact, point dissipative and uniformly persistent. It follows from Theorem 2.1.3 that  $Q_{n_1\omega} : \bar{C}_0 \rightarrow \bar{C}_0$  admits a global attractor  $A_0$  and has a fixed point  $\hat{\phi}$  in  $A_0$ . Similarly as in the proof of Lemma 4.2.1, we can show that  $Q_{n_1\omega}$  is strictly subhomogeneous. Then Theorem 2.2.4 implies that  $Q_{n_1\omega}$  has at most one fixed point. Thus,  $Q_{n_1\omega}$  has a unique equilibrium  $\hat{\phi}$  in  $\bar{C}_0$ . Clearly, by the strong monotonicity of  $Q_{n_1\omega}$ , we have  $\hat{\phi} \in \text{int}(\bar{C}^+)$ . Moreover, it follows from Theorem 2.2.5 that  $A_0 = \{\hat{\phi}\}$  since  $Q_{n_1\omega}$  is strongly monotone and strictly subhomogeneous. Thus,  $\hat{\phi}$  is globally attractive in  $\bar{C}_0$  for  $Q_{n_1\omega}$ .

Let  $u(t, x, \hat{\phi})$  be the solution of (4.26) with  $u(s, x) = \hat{\phi}(s, x)$ ,  $\forall (s, x) \in [-\tau, 0] \times \Omega$ . Since  $\hat{\phi}$  is a fixed point of  $Q_{n_1\omega}$  and is globally attractive in  $\bar{C}_0$ ,  $u(t, x, \hat{\phi})$  is an  $n_1\omega$ -periodic solution of (4.26) which attracts all solutions of (4.26) in  $\bar{C}^+ \setminus \{0\}$ . That is,

$$\lim_{t \rightarrow \infty} \|u(t, \cdot, \phi) - u(t, \cdot, \hat{\phi})\|_{\beta} = 0 \text{ for all } \phi \in \bar{C}_0.$$

Now we show that  $u(t, x, \hat{\phi})$  is also  $\omega$ -periodic. Since  $Q_{n_1\omega}(\hat{\phi}) = \hat{\phi}$ , we have

$$Q_{\omega}(\hat{\phi}) = Q_{\omega}(Q_{n_1\omega}(\hat{\phi})) = Q_{n_1\omega}(Q_{\omega}(\hat{\phi})),$$

which implies that  $Q_{\omega}(\hat{\phi})$  is also a fixed point of  $Q_{n_1\omega}$ . By the facts that  $\hat{\phi} \gg 0$  and  $Q_{\omega}$  is monotone, it follows that  $Q_{\omega}(\hat{\phi}) \gg 0$ . Note that  $Q_{n_1\omega}$  has a unique fixed point in  $\text{int}(\bar{C}^+)$ . Then  $Q_{\omega}(\hat{\phi}) = \hat{\phi}$ , that is,  $\hat{\phi}$  is a fixed point of  $Q_{\omega}$ , and hence,  $u(t, x, \hat{\phi})$  is an  $\omega$ -periodic solution of (4.26). Thus,  $u^*(t, x) := u(t, x, \hat{\phi})$ ,  $\forall (t, x) \in [-\tau, \infty) \times \bar{\Omega}$ , is the desired  $\omega$ -periodic solution. ■

## Chapter 5

# A Discrete-Time Population Model in A Periodic Lattice Habitat

### 5.1 Introduction

Integrodifference models have been attracting more and more attention since they consider the importance of nonoverlapping generations and various types of dispersal kernels, see [38, 40, 49, 81, 87]. A simple case among them is the following discrete-time model in a homogeneous habitat:

$$u_{n+1}(x) = \int_{\mathbb{R}} k(x, y) f(u_n(y)) dy, \quad x \in \mathbb{R}, \quad n \in \mathbb{N}, \quad (5.1)$$

where  $u_n(x)$  is the density of the  $n$ -th generation of the population at location  $x \in \mathbb{R}$ ,  $k(x, y)$  is the dispersal kernel,  $f$  is the recruitment function of the population.

Although most of earlier studies assumed that the environment is spatially homogeneous, the real environment is generally heterogeneous, due to natural phenomena or exposure to artificial disturbances. The investigation of aliens in Chile ([64]) states that roads and city streets constitute less competitive habitats than do agricultural fields, allowing apparently for colonization by a greater diversity of alien species, and hence, roads, city streets and vacant lots constitute more stable habitats than agricultural fields. More examples can be found in [7, 8, 11, 25, 26, 30, 40, 70, 71, 81, 86, 87].

This indicates that in the study of biological invasion it is important to understand how spatial heterogeneities influence the characteristics of front propagation such as front speeds, front profiles and front location. As a generalization of (5.1), one may consider the following discrete-time model in a heterogeneous habitat:

$$u_{n+1}(x) = \int_{\mathbf{R}} k(x, y) f(y, u_n(y)) dy, \quad x \in \mathbf{R}, n \in \mathbf{N}, \quad (5.2)$$

where  $k(x, y)$  is still the dispersal kernel, which may not be symmetric,  $f(x, u)$  is the recruitment function of the population with density  $u$  at location  $x \in \mathbf{R}$ .

The simplest case of the spatial heterogeneity is a periodic habitat, by which we mean that the recruitment function (or the growth function) and dispersal properties vary periodically in the habitat. Freidin and Gärtner [25, 26] used probabilistic methods to study the spreading speed for an equation of Fisher's type in which the mobility and the growth function vary periodically in space. In the ecological context, Shigesada et al [71] first introduced a reaction-diffusion model for the spread of a single species in a patchy environment with periodic variations in diffusivity and growth rate. Weinberger [86] presented a general model in periodically varying environments and investigated the spreading speed and spatially periodic traveling waves in the case where the recursion operator is monotone. Guo and Hamel [30] studied the front propagation of a monotone lattice model in a periodic habitat. More recently, Kawasaki and Shigesada [40] considered propagating waves in a periodic environment in the framework of integrodifference equations (an example of (5.2)), by the linearization method and numerical simulations. Weinberger et al. [87] established the spreading speed for (5.2) in a periodic habitat in the case where the recruitment function is not necessarily monotone in the density of the species. However, the proof of the existence of periodic traveling waves for (5.2) in this case is still an open problem.

It is impractical to measure the population densities at all points at all times and computations for continuous models are often obtained as the approximation of the related discrete models ([11, 85, 98]). It is then reasonable to consider the following lattice version of (5.2) in a periodic habitat in the case where the recruitment function

is not necessarily monotone:

$$u_{n+1}^i = \sum_{j=-\infty}^{+\infty} P_{ij} f_j(u_n^j), \quad i \in \mathbb{Z}, \quad n \in \mathbb{N}, \quad (5.3)$$

where  $u_n^i$  is the density of the  $n$ -th generation of the population at the  $i$ -th location,  $P_{ij}$  is the dispersal kernel, which is the fraction of those individuals who successfully migrate from the  $j$ -th location to the  $i$ -th location,  $f_j(u) := f(j, u)$  is the recruitment function of the population with density  $u$  at location  $j \in \mathbb{Z}$ . The purpose of the current chapter is to study the spreading speeds and spatially periodic traveling waves for (5.3) in both monotone and non-monotone cases of  $f_j(u)$ .

Throughout this chapter, we always assume that (5.3) satisfies the following conditions:

(H7)  $P_{ij}$  is nonnegative;  $P_{ij} = P_{i+L, j+L}$ ,  $\forall i, j \in \mathbb{Z}$ , for some  $L > 0$ ;  $\sum_{j=-\infty}^{+\infty} P_{ij} = 1$ ,  $\forall i \in \mathbb{Z}$ ; and  $\sum_{j=-\infty}^{+\infty} P_{ij} e^{-\mu(i-j)}$  is uniformly bounded for  $\mu \in (-\Delta^+, \Delta^-)$ ,  $i \in \mathbb{Z}$ , where  $\Delta^+$  and  $\Delta^-$  are positive and can be infinity.

(H8) For any  $i \in \mathbb{Z}$ ,  $f_i \in C^1(\mathbb{R}_+, \mathbb{R})$ ;  $f_i(0) = 0$ ,  $f_i'(0) > 1$ ;  $f_i([0, b]) \subseteq [0, b]$  for some  $b > 0$ ;  $f_i(u) = f_{i+L}(u)$ ,  $\forall u \in [0, b]$ ;  $\frac{f_i(u)}{u}$  is strictly decreasing in  $u \in [0, b]$ . There exists  $\hat{L} > 0$  such that  $|f_i(u_1) - f_i(u_2)| \leq \hat{L}|u_1 - u_2|$ ,  $\forall u_1, u_2 \in [0, b]$ ,  $\forall i \in \mathbb{Z}$ .

We also use the following notations:

$$\begin{aligned} X &= \{ \{ \varphi^i \}_{i \in \mathbb{Z}} : \varphi^i \in \mathbb{R}_+, \forall i \in \mathbb{Z} \}, \\ X^L &= \{ \{ \varphi^i \}_{i \in \mathbb{Z}} \in X : \varphi^i = \varphi^{i+L}, \forall i \in \mathbb{Z} \}, \\ X_b^L &= \{ \{ \varphi^i \}_{i \in \mathbb{Z}} \in X^L : \varphi^i \in [0, b], \forall i \in \mathbb{Z} \}. \end{aligned}$$

For  $u \in X$ ,  $v \in X$ ,  $u \leq v$  means  $u^i \leq v^i, \forall i \in \mathbb{Z}$ ;  $u < v$  means  $u^i \leq v^i, \forall i \in \mathbb{Z}$  but  $u \neq v$ ; and  $u \ll v$  means  $u^i < v^i, \forall i \in \mathbb{Z}$ .

The rest of this chapter is organized as follows. In section 5.2, we consider the case where the recruitment function  $f_i(u)$  is monotone in  $u$  for all  $i \in \mathbb{Z}$  and establish the existence and computation formula of spreading speeds and their coincidence with the

minimal wave speeds for spatially periodic traveling waves in both positive and negative directions. In section 5.3, we extend these results to the case of non-monotone recruitment functions by using the comparison method (for spreading speeds) and the Schauder fixed point theorem (for spatially periodic traveling waves). An example is also given in section 5.4 to illustrate the obtained analytic results.

## 5.2 Monotone case

In this section, we consider model (5.3) with a monotone recruitment function. In addition to (H7) and (H8), we further assume that

(H9)  $f_i(u)$  is nondecreasing in  $u \in [0, b]$  for any  $i \in \mathbb{Z}$ .

Define an operator  $Q$  on  $X$  by

$$(Q(\varphi))^i = \sum_{j=-\infty}^{+\infty} P_{ij} f_j(\varphi^j), \quad i \in \mathbb{Z}, \quad \varphi \in X. \quad (5.4)$$

Then for  $u_n = \{u_n^i\}_{i \in \mathbb{Z}} \in X$ , (5.3) can be written as

$$u_{n+1} = Q(u_n).$$

To find a fixed point of  $Q$  in  $X^L$ , we restrict  $Q$  on  $X^L$  as  $\bar{Q}$ :

$$(\bar{Q}(\varphi))^i = \sum_{j=-\infty}^{+\infty} P_{ij} f_j(\varphi^j), \quad i \in \mathbb{Z}, \quad \varphi \in X^L.$$

By using the periodicity properties of  $f$  and  $\varphi$ , we can write  $\bar{Q}$  as

$$\begin{aligned} (\bar{Q}(\varphi))^i &= \sum_{j=-\infty}^{+\infty} P_{ij} f_j(\varphi^j) \\ &= \sum_{k=-\infty}^{+\infty} \sum_{m=1}^L P_{i, kL+m} f_{kL+m}(\varphi^{kL+m}) \\ &= \sum_{k=-\infty}^{+\infty} \sum_{m=1}^L P_{i, kL+m} f_m(\varphi^m) \\ &= \sum_{m=1}^L \left( \sum_{k=-\infty}^{+\infty} P_{i, kL+m} \right) f_m(\varphi^m), \end{aligned}$$

for any  $i \in \mathbb{Z}$ ,  $\varphi \in X^L$ . Since  $P_{ij} = P_{i+Lj+L}$  for any  $i \in \mathbb{Z}, j \in \mathbb{Z}$ , we have  $(\bar{Q}(\varphi))^i = (\bar{Q}(\varphi))^{i+L}$ ,  $\forall i \in \mathbb{Z}$ , and hence,  $\bar{Q} : X^L \rightarrow X^L$ . By the periodicity of elements in  $X^L$ , it is easy to see that  $X^L$  is actually equivalent to  $\mathbb{R}_+^L$ . Thus,  $\bar{Q}$  can be considered as an operator from  $\mathbb{R}_+^L$  to  $\mathbb{R}_+^L$ :

$$(\bar{Q}(\varphi))^i = \sum_{m=1}^L \bar{a}_{im} f_m(\varphi^m), \quad \forall i \in \{1, 2, \dots, L\}, \quad \varphi \in \mathbb{R}_+^L,$$

where  $\bar{a}_{im} = \sum_{k=-\infty}^{+\infty} P_{i, kL+m}$ , for  $i, m \in \{1, 2, \dots, L\}$ .

Let  $\bar{L}_0 = D\bar{Q}(0)$  be the derivative of  $\bar{Q}$  at 0. It then follows that

$$(\bar{L}_0(\varphi))^i = \sum_{j=-\infty}^{+\infty} P_{ij} f'_j(0) \varphi^j, \quad \forall i \in \mathbb{Z}, \quad \varphi \in X^L.$$

Similarly as we do for  $\bar{Q}$ , we can also show that  $\bar{L}_0 : X^L \rightarrow X^L$  and then consider  $\bar{L}_0$  as a linear operator from  $\mathbb{R}^L$  to  $\mathbb{R}^L$ . Moreover,

$$\bar{L}_0(\varphi) = A\varphi, \quad \forall \varphi \in \mathbb{R}^L, \quad (5.5)$$

where  $A = (a_{im})_{L \times L}$ ,  $a_{im} = \sum_{k=-\infty}^{+\infty} P_{i, kL+m} f'_m(0)$ , for  $i, m \in \{1, 2, \dots, L\}$ .

We further assume that

(H10)  $A$  is irreducible, and for any  $u_0 \in \mathbb{R}_+^L$ , there exists  $k = k(u_0) \in \mathbb{N}$ , such that  $\bar{Q}^k(u_0) \gg 0$ .

Let

$$r(\bar{L}_0) = \max\{|\lambda|, \lambda \text{ is an eigenvalue of } A\}.$$

Then by [74, Theorem A.4], it follows that  $r(\bar{L}_0)$  is a positive eigenvalue of  $A$  and that there is a strongly positive eigenvector of  $A$  associated with  $r(\bar{L}_0)$ .

**Lemma 5.2.1** *Let (H7)-(H10) hold. If  $r(\bar{L}_0) > 1$ , then there exists a unique fixed point  $\beta^* \gg 0$  in  $X_b^L$  such that every forward orbit of  $\bar{Q}$  in  $X_b^L \setminus \{0\}$  converges to  $\beta^*$ .*

**Proof** Let  $\hat{b} := (b, b, \dots, b) \in \mathbb{R}^L$  and  $\mathbb{R}_b^L := \{\varphi \in \mathbb{R}^L : 0 \leq \varphi \leq \hat{b}\}$ . Consider  $\bar{Q}$  and  $\bar{L}_0$  as operators on  $\mathbb{R}_+^L$  and  $\mathbb{R}^L$ , respectively. Obviously,  $\bar{Q}(0) = 0$ . For any  $\varphi \in \mathbb{R}_b^L$ , it follows from  $f_i([0, b]) \subseteq [0, b]$  that  $0 \leq (\bar{Q}(\varphi))^i \leq b, \forall i \in \mathbb{Z}$ . This implies that  $\bar{Q} : \mathbb{R}_b^L \rightarrow \mathbb{R}_b^L$ .

For  $\varphi, \psi \in \mathbb{R}_b^L$  with  $\varphi < \psi$ , i.e.,  $0 \leq \varphi^i \leq \psi^i \leq b, \forall 1 \leq i \leq L$ , and  $\varphi \neq \psi$ , we have

$$(\bar{Q}(\varphi))^i = \sum_{m=1}^L \bar{a}_{im} f_m(\varphi^m) \leq \sum_{m=1}^L \bar{a}_{im} f_m(\psi^m) = (\bar{Q}(\psi))^i, \quad \forall 1 \leq i \leq L.$$

Thus,  $\bar{Q}(\varphi) \leq \bar{Q}(\psi)$  and  $\bar{Q}$  is monotone on  $\mathbb{R}_b^L$ .

Let  $\alpha \in (0, 1)$  and  $\varphi \in \mathbb{R}_b^L$  with  $\varphi \gg 0$ . Since  $\frac{f_i(u)}{u}$  is strictly decreasing in  $u \in [0, b]$ , it follows that for any  $i \in \mathbb{Z}$ ,  $f_i$  is strictly subhomogeneous on  $[0, b]$  in the sense that

$$f_i(\alpha u) > \alpha f_i(u), \quad \forall u \in [0, b], \quad \alpha \in (0, 1),$$

and hence,

$$(\bar{Q}(\alpha\varphi))^i = \sum_{m=1}^L \bar{a}_{im} f_m(\alpha\varphi^m) > \sum_{m=1}^L \bar{a}_{im} \cdot \alpha \cdot f_m(\varphi^m) = \alpha \sum_{m=1}^L \bar{a}_{im} f_m(\varphi^m) = \alpha (\bar{Q}(\varphi))^i,$$

for all  $1 \leq i \leq L$ . Then  $\bar{Q}(\alpha\varphi) \gg \alpha\bar{Q}(\varphi)$  in  $\mathbb{R}^L$ , which indicates that  $\bar{Q}$  is strongly subhomogeneous on  $\mathbb{R}_b^L$ .

Note that  $r(\bar{L}_0)$  is a positive eigenvalue of  $\bar{L}_0$  with a strongly positive eigenvector  $e \in \mathbb{R}_b^L$ . Since  $r(\bar{L}_0) > 1$ , as argued in the proof of Theorem 2.2.2 in [99], we see that there exists  $\varepsilon_0 > 0$  such that  $\bar{Q}(\varepsilon e) \gg \varepsilon e, \forall \varepsilon \in (0, \varepsilon_0]$ . For any given  $u \in \mathbb{R}_b^L$  with  $u \gg 0$ , there exists sufficiently small  $\varepsilon > 0$  such that  $u \geq \varepsilon e$ . Then we have

$$\bar{Q}(u) \geq \bar{Q}(\varepsilon e) \gg \varepsilon e,$$

and hence,

$$\bar{Q}^n(u) \geq \varepsilon e, \quad \forall n \geq 1.$$

Therefore, the  $\omega$ -limit set of  $u, \omega(u)$ , is a nonempty compact invariant set in  $Int(\mathbb{R}_+^L)$ . By Theorem 2.2.5,  $\bar{Q} : \mathbb{R}_b^L \rightarrow \mathbb{R}_b^L$  has a fixed point  $\beta^* \in Int(\mathbb{R}_+^L)$  such that every

nonempty compact invariant set of  $\bar{Q}$  in  $Int(\mathbb{R}_+^L)$  consists of  $\beta^*$ . Thus, for any  $u \in Int(\mathbb{R}_+^L) \cap \mathbb{R}_b^L$ ,  $\beta^*$  attracts the forward orbit of  $u$ . Moreover, (H10) implies that  $\beta^*$  is globally attractive in  $\mathbb{R}_b^L \setminus \{0\}$ . ■

To study the dynamics of invasion for (5.3), in the rest of this section we always assume that

$$(H11) \quad r(\bar{L}_0) > 1.$$

Thus,  $Q$  admits a globally attractive fixed point  $\beta^* \gg 0$  in  $X_b^L \setminus \{0\}$ .

In the following we study the spreading speeds and spatially periodic traveling waves by the theories in section 2.4.

**Lemma 5.2.2** *The operator  $Q$  in (5.4) satisfies (C1)-(C6) with  $\mathcal{H} = \mathbb{Z}$ ,  $\mathcal{L} = \{nL : n \in \mathbb{Z}\}$ ,  $\mathcal{P} = \{1, 2, \dots, L\}$ ,  $\pi_0 = 0$ ,  $\pi_1 = \beta^*$ , and  $\mathcal{M} := \{\varphi \in X : 0 \leq \varphi^i \leq \beta^{*i}, \forall i \in \mathbb{Z}\}$ .*

**Proof** (C1) and (C2) are obvious. It remains to verify (C3)-(C6). We define the translation operator

$$(T_a(u))^i = u^{i-a}, \quad \forall i \in \mathbb{Z}, \quad a \in \mathcal{H}, \quad u \in X.$$

Clearly,  $\mathcal{H}$  is invariant under translation by any element of  $\mathcal{L}$  and every  $x \in \mathcal{H}$  has a unique representation of the form  $x = z + p$  with  $z \in \mathcal{L}$  and  $p \in \mathcal{P}$ . For any  $a \in \mathcal{L}$ ,  $u \in \mathcal{M}$ , we have

$$(T_a(Q(u)))^i = (Q(u))^{i-a} = \sum_{j=-\infty}^{+\infty} P_{i-a,j} f_j(u^j),$$

$$(Q(T_a(u)))^i = \sum_{j=-\infty}^{+\infty} P_{ij} f_j(u^{j-a}) \underset{z=j-a}{=} \sum_{z=-\infty}^{+\infty} P_{i,z+a} f_{z+a}(u^z) = \sum_{z=-\infty}^{+\infty} P_{i-a,z} f_z(u^z).$$

Therefore,

$$(T_a(Q(u)))^i = (Q(T_a(u)))^i, \quad \forall a \in \mathcal{L}, \quad u \in \mathcal{M}, \quad i \in \mathbb{Z},$$

which indicates that  $Q$  is periodic with respect to  $\mathcal{L}$ . This verifies (C3).

By Lemma 5.2.1, it follows that if  $0 \leq u_0 \leq \beta^*$ ,  $u_0$  is periodic with respect to  $\mathcal{L}$  and  $u_0 \neq 0$ , then the solution  $u_n$  of  $u_{n+1} = Q(u_n)$  through  $u_0$ , which is again periodic with respect to  $\mathcal{L}$ , converges to  $\beta^*$  as  $n \rightarrow \infty$  uniformly on  $\mathcal{H}$ . Then (C4) is valid.

To verify (C5), let  $\{u_m\}_{m \in \mathbb{N}} \subseteq \mathcal{M}$  with  $u_m = \{u_m^i\}_{i \in \mathbb{Z}} \in X$  be a sequence such that  $u_m \rightarrow u \in \mathcal{M}$  uniformly on every bounded subset of  $\mathcal{H}$ , as  $m \rightarrow \infty$ . Given a bounded subset  $B$  of  $\mathcal{H}$ , for any  $\varepsilon > 0$ ,  $i \in B$ , we have

$$\begin{aligned} |(Q(u_m))^i - (Q(u))^i| &= \left| \sum_{j=-\infty}^{+\infty} P_{ij} f_j(u_m^j) - \sum_{j=-\infty}^{+\infty} P_{ij} f_j(u^j) \right| \\ &= \left| \sum_{j=-\infty}^{+\infty} P_{ij} (f_j(u_m^j) - f_j(u^j)) \right| \\ &\leq \hat{L} \sum_{j=-\infty}^{+\infty} P_{ij} |u_m^j - u^j|. \end{aligned}$$

Since  $\sum_{j=-\infty}^{+\infty} P_{ij} = 1$  for any  $i \in \mathbb{Z}$ , there exists  $M > 0$ , such that  $\sum_{|j| \geq M} P_{ij} < \varepsilon$  for  $i \in B$ .

Thus, there exists  $N_1 \in \mathbb{Z}$ ,  $N_1 > 0$ , such that  $|(Q(u_m))^i - (Q(u))^i| \leq \hat{L}(\varepsilon \cdot 2\beta_0 + \varepsilon)$  for any  $i \in B$ , where  $\beta_0 = \max_{i \in \{1, 2, \dots, L\}} |\beta^{*i}|$  and  $N_1$  satisfies that for  $m \geq N_1$ ,  $|u_m^j - u^j| < \varepsilon$ , for all  $j \in \{-M, \dots, M\}$ . This implies that  $Q(u_m)$  converges to  $Q(u)$  uniformly on every bounded subset of  $\mathcal{H}$ .

Any sequence  $\{u_m\}_{m \in \mathbb{N}}$  in  $\mathcal{M}$  is uniformly bounded. Moreover, since  $\mathcal{H}$  is countable, it is easy to see that  $\{Q(u_m)\}_{m \in \mathbb{N}}$  is equicontinuous on  $\mathcal{H}$ . Therefore, there exists a subsequence  $\{u_{m_k}\}_{k \in \mathbb{N}}$  of  $\{u_m\}_{m \in \mathbb{N}}$  such that  $\{Q(u_{m_k})\}_{k \in \mathbb{N}}$  converges to some function uniformly on every bounded subset of  $\mathcal{H}$ . Thus, (C6) is valid. ■

Let  $L_0 = DQ(0)$  be the derivative of  $Q$  at 0. Consider the negative direction  $\vec{\xi} = -1$ . Following section 2.4 (see also [86, Section 2]), we define  $L_{-\mu} : X^L \rightarrow X^L$  by

$$(L_{-\mu}(u))^i = e^{-\mu i} (L_0(v))^i, \quad \forall i \in \mathbb{Z}, \quad (5.6)$$

for  $\mu \in (0, \Delta^-)$ ,  $u \in X^L$ , where  $v = \{e^{\mu i} u^i\}_{i \in \mathbb{Z}}$ . It is easy to see that

$$(L_{-\mu}(u))^i = (L_{-\mu}(u))^{i+L}, \quad \forall i \in \mathbb{Z}, u \in X^L.$$

Moreover,

$$\begin{aligned}
(L_{-\mu}(u))^i &= e^{-\mu \cdot i} \sum_{j=-\infty}^{+\infty} P_{ij} f'_j(0) e^{\mu j} u^j \\
&= \sum_{j=-\infty}^{+\infty} P_{ij} f'_j(0) e^{-\mu(i-j)} u^j \\
&= \sum_{k=-\infty}^{+\infty} \sum_{m=1}^L P_{i,kL+m} f'_{kL+m}(0) e^{-\mu(i-kL-m)} u^{kL+m} \\
&= \sum_{m=1}^L \left( \sum_{k=-\infty}^{+\infty} (P_{i,kL+m} e^{\mu kL}) \cdot e^{\mu m} f'_m(0) e^{-\mu i} \right) u^m,
\end{aligned}$$

for any  $i \in \mathbb{Z}$ ,  $u \in X^L$ . Thus,  $L_{-\mu}$  can be considered as a linear operator from  $\mathbb{R}^L$  to  $\mathbb{R}^L$ :

$$L_{-\mu}(u) = A_{-\mu} u, \quad \forall u \in \mathbb{R}^L,$$

where  $A_{-\mu} = (a_{im}^{-\mu})_{L \times L}$  with

$$a_{im}^{-\mu} = \sum_{k=-\infty}^{+\infty} (P_{i,kL+m} e^{\mu kL}) e^{\mu m} f'_m(0) e^{-\mu i},$$

for all  $i, m \in \{1, 2, \dots, L\}$ .

For the positive direction  $\vec{\xi} = 1$ , we can define  $L_{\mu} : X^L \rightarrow X^L$  by

$$(L_{\mu}(u))^i = e^{\mu i} (L_0(v))^i, \quad \forall i \in \mathbb{Z}, \quad (5.7)$$

for  $\mu \in (0, \Delta^+)$ ,  $u \in X^L$ , where  $v = \{e^{-\mu i} u^i\}_{i \in \mathbb{Z}}$ . Furthermore,  $L_{\mu}$  can also be considered as a linear operator from  $\mathbb{R}^L$  to  $\mathbb{R}^L$ :

$$L_{\mu}(u) = A_{\mu} u, \quad \forall u \in \mathbb{R}^L,$$

where  $A_{\mu} = (a_{im}^{\mu})_{L \times L}$  with

$$a_{im}^{\mu} = \sum_{k=-\infty}^{+\infty} (P_{i,kL+m} e^{-\mu kL}) e^{-\mu m} f'_m(0) e^{\mu i},$$

for all  $i, m \in \{1, 2, \dots, L\}$ .

Let

$$c^*(1) = \inf_{0 < \mu < \Delta^+} \frac{1}{\mu} \ln \lambda_{\mu} \quad (5.8)$$

and

$$c^*(-1) = \inf_{0 < \mu < \Delta^-} \frac{1}{\mu} \ln \lambda_{-\mu}, \quad (5.9)$$

where  $\lambda_\mu$  and  $\lambda_{-\mu}$  are the principle eigenvalues of  $A_\mu$  and  $A_{-\mu}$ , respectively.

**Lemma 5.2.3** *Let (H7), (H8) and (H10) hold. If  $\Delta^+ = \Delta^-$  and  $P_{ij} = P_{ji}$ ,  $\forall i, j \in \mathbb{Z}$ , then  $c^*(1) = c^*(-1)$ .*

**Proof** Let  $C = \text{diag}(f'_1(0) \cdots f'_L(0))$  and  $B = (B_{im})_{L \times L}$  with

$$B_{im} = \sum_{k=-\infty}^{+\infty} (P_{i, kL+m} e^{\mu k L}) e^{\mu m} e^{-\mu i}, \quad \forall i, m \in \{1, 2, \dots, L\}.$$

It is easy to see that  $A_{-\mu} = BC$ . Moreover, we have

$$\begin{aligned} a_{mi}^\mu &= \sum_{k=-\infty}^{+\infty} (P_{m, kL+i} e^{-\mu k L}) e^{-\mu i} f'_i(0) e^{\mu m} \\ &= \sum_{k=-\infty}^{+\infty} (P_{m, -kL+i} e^{\mu k L}) e^{-\mu i} f'_i(0) e^{\mu m} \\ &= \sum_{k=-\infty}^{+\infty} (P_{m+kL, i} e^{\mu k L}) e^{-\mu i} f'_i(0) e^{\mu m} \\ &= \sum_{k=-\infty}^{+\infty} (P_{i, m+kL} e^{\mu k L}) e^{-\mu i} f'_i(0) e^{\mu m}, \end{aligned}$$

for all  $i, m \in \{1, 2, \dots, L\}$ . Then  $A_\mu = B^T C$ , where  $B^T$  is the transpose of  $B$ , and hence,  $A_\mu^T = CB$ . Since  $C$  is invertible, we obtain  $C \cdot BC \cdot C^{-1} = CB$ , which indicates that  $BC$  and  $CB$  are similar, and hence,  $\sigma(A_{-\mu}) = \sigma(A_\mu^T) = \sigma(A_\mu)$ , where  $\sigma(M)$  denotes the set of all eigenvalues of matrix  $M$ . By the definition of  $c^*(\vec{\xi})$ , it then follows that  $c^*(1) = c^*(-1)$  provided that  $\Delta^+ = \Delta^-$ . ■

The following result shows that  $c^*(\vec{\xi})$  is the spreading speed in the directions  $\vec{\xi} = \pm 1$ .

**Theorem 5.2.1** *Let (H7)-(H11) hold. Then the following statements are valid:*

- (i) *For any  $u_0 \in \mathcal{M} := \{\varphi \in X : 0 \leq \varphi^i \leq \beta^{*i}, \forall i \in \mathbb{Z}\}$  with  $u_0^i = 0$  for  $i \in \mathbb{Z}$  and  $i \geq K$  for some  $K \in \mathbb{Z}$ , the solution of (5.3) satisfies*

$$\lim_{n \rightarrow \infty, i \geq cn} u_n^i = 0, \quad \forall c > c^*(1).$$

For any  $u_0 \in \mathcal{M} \setminus \{0\}$ , the solution of (5.3) satisfies

$$\lim_{n \rightarrow \infty, i \leq cn} (u_n^i - \beta^{*i}) = 0, \quad \forall c < c^*(1).$$

(ii) For any  $u_0 \in \mathcal{M}$  with  $u_0^i = 0$  for  $i \in \mathbb{Z}$  and  $i \leq K$  for some  $K \in \mathbb{Z}$ , the solution of (5.3) satisfies

$$\lim_{n \rightarrow \infty, i \leq -cn} u_n^i = 0, \quad \forall c > c^*(-1).$$

For any  $u_0 \in \mathcal{M} \setminus \{0\}$ , the solution of (5.3) satisfies

$$\lim_{n \rightarrow \infty, i \geq -cn} (u_n^i - \beta^{*i}) = 0, \quad \forall c < c^*(-1).$$

(iii) For any  $u_0 \in \mathcal{M}$  with  $u_0^i = 0$  for  $i$  outside a bounded subset of  $\mathbb{Z}$ , the solution of (5.3) satisfies

$$\lim_{n \rightarrow \infty, i \leq -c_1 n \text{ or } i \geq c_2 n} u_n^i = 0, \quad \forall c_1 > c^*(-1), \quad \forall c_2 > c^*(1).$$

(iv) For any  $u_0 \in \mathcal{M} \setminus \{0\}$ , the solution of (5.3) satisfies

$$\lim_{n \rightarrow \infty, -c_1 n \leq i \leq c_2 n} (u_n^i - \beta^{*i}) = 0, \quad \forall c_1 < c^*(-1), \quad \forall c_2 < c^*(1).$$

**Proof** In view of Lemma 5.2.2, it suffices to verify conditions in Theorem 2.4.2.

Since  $f_i(u)/u$  is strictly decreasing for  $i \in \mathbb{Z}$ ,  $u \in [0, b]$ , we see that  $f_i$  is strictly subhomogeneous in  $u \in [0, b]$  for any  $i \in \mathbb{Z}$ . This implies that

$$f_i(u) \leq f_i'(0)u, \quad \forall i \in \mathbb{Z}, u \in [0, b],$$

and hence, for any  $u \in \mathcal{M}$ ,

$$(Q(u))^i = \sum_{j=-\infty}^{+\infty} P_{ij} f_j(u^j) \leq \sum_{j=-\infty}^{+\infty} P_{ij} f_j'(0)u^j = (L_0(u))^i, \quad \forall i \in \mathbb{Z}.$$

Thus,  $Q(u) \leq L_0(u)$  for all  $0 \leq u \leq \beta^*$ .

Clearly  $L_0$  is  $\mathcal{L}$ -periodic and strongly order-preserving. For any  $n \in \mathbb{Z}$ , let  $\varphi_n = \{\varphi_n^i\}_{i \in \mathbb{Z}} \in X$  with  $\varphi_n^i = \min\{n, e^{\mu|i}|\}$ ,  $\forall i \in \mathbb{Z}$ . Then

$$(L_0(\varphi_n))^i = \sum_{j=-\infty}^{+\infty} P_{ij} f_j'(0) \varphi_n^j = \sum_{|j| > \lfloor \frac{\ln n}{\mu} \rfloor} P_{ij} f_j'(0) n + \sum_{|j| \leq \lfloor \frac{\ln n}{\mu} \rfloor} P_{ij} f_j'(0) e^{\mu|j|}, \quad \forall i \in \mathbb{Z}, n \in \mathbb{N}.$$

Given a bounded subset  $B$  of  $\mathbb{Z}$ . Since  $\sum_{j=-\infty}^{+\infty} P_{ij}e^{\mu j}$  is uniformly bounded for  $\mu \in [0, \Delta^-)$ ,  $i \in \mathbb{Z}$ , and

$$\sum_{|j| \leq \lfloor \frac{\ln n}{\mu} \rfloor} P_{ij} f'_j(0) e^{\mu |j|} \leq \max_{j \in \{1, 2, \dots, L\}} \{f'_j(0)\} \sum_{|j| \leq \lfloor \frac{\ln n}{\mu} \rfloor} P_{ij} e^{\mu |j|},$$

we can obtain that  $\sum_{|j| \leq \lfloor \frac{\ln n}{\mu} \rfloor} P_{ij} f'_j(0) e^{\mu |j|}$  is uniformly bounded for all  $i \in B$  and  $n > 0$ .

Fix  $\alpha \in (0, \Delta^-)$  such that  $0 < \mu < \alpha < \Delta^-$ . Since  $\sum_{j=-\infty}^{+\infty} P_{ij} e^{\alpha j} < \infty$ , we have  $P_{ij} e^{\alpha j} \rightarrow 0$  as  $j \rightarrow \infty$  uniformly for  $i \in B$ . Then there exists  $M > 0$  such that  $P_{ij} e^{\alpha j} < 1$  for  $i \in B$ ,  $j > M$ , and hence,  $P_{ij} < e^{-\alpha j}$  for  $i \in B$ ,  $j > M$ . Therefore, when  $\lfloor \frac{\ln n}{\mu} \rfloor > M$ , for any  $i \in B$ , we have

$$\begin{aligned} \sum_{j > \lfloor \frac{\ln n}{\mu} \rfloor} P_{ij} f'_j(0) n &\leq \max_{j \in \{1, 2, \dots, L\}} \{f'_j(0)\} \sum_{j > \lfloor \frac{\ln n}{\mu} \rfloor} P_{ij} n \\ &\leq \max_{j \in \{1, 2, \dots, L\}} \{f'_j(0)\} \sum_{j > \lfloor \frac{\ln n}{\mu} \rfloor} e^{-\alpha j} n \\ &\leq \max_{j \in \{1, 2, \dots, L\}} \{f'_j(0)\} \frac{n e^{\alpha(1 - \frac{\ln n}{\mu})}}{e^\alpha - 1}, \end{aligned}$$

which indicates that  $\sum_{j > \lfloor \frac{\ln n}{\mu} \rfloor} P_{ij} f'_j(0) n$  tends to 0 as  $n \rightarrow \infty$  uniformly for  $i \in B$ .

Similarly, we can prove that  $\sum_{j < -\lfloor \frac{\ln n}{\mu} \rfloor} P_{ij} f'_j(0) n$  tends to 0 as  $n \rightarrow \infty$  uniformly for

$i \in B$ . Thus,  $\sum_{|j| > \lfloor \frac{\ln n}{\mu} \rfloor} P_{ij} f'_j(0) n$  is uniformly bounded for all  $i \in B$  and  $n > 0$ , and

hence,  $(L_0(\varphi_n))^i$  is uniformly bounded for all  $i \in B$  and  $n > 0$ . The equicontinuity of  $\{L_0(\varphi_n)\}_{n \in \mathbb{N}}$  in  $i \in B$  is obvious since  $B \subseteq \mathbb{Z}$ . Then by the Arzelà-Ascoli theorem,  $\{L_0(\varphi_n)\}_{n \in \mathbb{N}}$  has a subsequence  $\{L_0(\varphi_{n_k})\}_{k \in \mathbb{N}}$ , which converges to some function  $\tilde{f}$  on every bounded set of  $\mathbb{Z}$ . By the definitions of  $L_0$  and  $\varphi_n$ , it is easy to see that  $\{L_0(\varphi_n)\}_{n \in \mathbb{N}}$  is increasing in  $n$ . Thus,  $\{L_0(\varphi_n)\}_{n \in \mathbb{N}}$  itself converges to  $\tilde{f}$  on every bounded set of  $\mathbb{Z}$ . By the theory developed in [86], we can define  $L_0(e^{\mu \cdot}) = \tilde{f}$ .

Since  $f_i(u) < f'_i(0)u$ ,  $\forall i \in \mathbb{Z}$ ,  $u \in [0, b]$ , we have

$$(L_0(\beta^*))^i = \sum_{j=-\infty}^{+\infty} P_{ij} f'_j(0) \beta^{*j} > \sum_{j=-\infty}^{+\infty} P_{ij} f_j(\beta^{*j}) = (Q(\beta^*))^i = \beta^{*i}, \forall i \in \mathbb{Z},$$

that is,  $L_0(\beta^*) > \beta^*$ . Define a translated operator  $Q^{[L_0, \beta^*]}$  by

$$Q^{[L_0, \beta^*]}(u) = \min\{L_0(u), \beta^*\}, \quad \forall u \in X \text{ with } 0 \leq u^i \leq \beta^{*i}, \forall i \in \mathbb{Z}.$$

Then we have the following observation.

*Claim.*  $Q^{[L_0, \beta^*]}(u)$  satisfies (C1)-(C6) with  $\mathcal{H} = \mathbb{Z}$ ,  $\mathcal{P} = \{1, 2, \dots, L\}$ ,  $\mathcal{L} = \{nL : n \in \mathbb{Z}\}$ , and  $\mathcal{M} = \{\{\varphi^i\}_{i \in \mathbb{Z}} \in X : 0 \leq \varphi^i \leq \beta^{*i}, \forall i \in \mathbb{Z}\}$ .

Indeed, (C1) is obvious. By the monotonicity of  $L_0$ , for  $u \in \mathcal{M}$ ,  $v \in \mathcal{M}$ , we have

$$(Q^{[L_0, \beta^*]}(u))^i = \min\{(L_0(u))^i, \beta^{*i}\} \leq \min\{(L_0(v))^i, \beta^{*i}\} = (Q^{[L_0, \beta^*]}(v))^i, \quad \forall i \in \mathbb{Z}.$$

Thus,  $Q^{[L_0, \beta^*]}$  is monotone.  $L_0$  is periodic with respect to  $\mathcal{L}$ , so is  $Q^{[L_0, \beta^*]}(u)$ .  $Q^{[L_0, \beta^*]}(0) = 0$ ,  $Q^{[L_0, \beta^*]}(\beta^*) = \min\{L_0(\beta^*), \beta^*\} = \beta^*$ . By the properties of  $L_0$ , if  $0 \leq u_0 \leq \beta^*$  with  $u_0$  periodic with respect to  $\mathcal{L}$  and  $u_0 \not\equiv 0$ , then the the solution  $u_n$  of  $u_{n+1} = Q^{[L_0, \beta^*]}(u_n)$  is again periodic with respect to  $\mathcal{L}$ . Since  $\bar{Q}(u_0) \leq L_0(u_0)$  and  $\bar{Q}(u_0) \leq \bar{Q}(\beta^*) = \beta^*$ , we have  $\bar{Q}(u_0) \leq Q^{[L_0, \beta^*]}(u_0) \leq Q^{[L_0, \beta^*]}(\beta^*) = \beta^*$ . Then it follows from  $\bar{Q}(u_n) \rightarrow \beta^*$  as  $n \rightarrow \infty$  that  $u_{n+1} = Q^{[L_0, \beta^*]}(u_n) \rightarrow \beta^*$  as  $n \rightarrow \infty$ . Let  $\{u_m\}_{m \in \mathbb{N}} \subseteq \mathcal{M}$  be a sequence such that  $u_m \rightarrow u \in \mathcal{M}$  as  $m \rightarrow \infty$  uniformly on every bounded subset of  $\mathbb{Z}$ . Given a bounded subset  $B$  of  $\mathbb{Z}$ . For any  $\varepsilon > 0$  and  $i \in B$ , by the continuity of  $L_0$  and uniform convergence of  $u_m$  on  $B$ , we can obtain

$$\begin{aligned} & |(Q^{[L_0, \beta^*]}(u_m))^i - (Q^{[L_0, \beta^*]}(u))^i| \\ &= |\min\{(L_0(u_m))^i, \beta^{*i}\} - \min\{(L_0(u))^i, \beta^{*i}\}| \\ &= \begin{cases} |(L_0(u_m))^i - (L_0(u))^i|, & \text{if } \beta^{*i} \geq \max\{(L_0(u_m))^i, (L_0(u))^i\} \\ |\beta^{*i} - \beta^{*i}|, & \text{if } \beta^{*i} \leq \min\{(L_0(u_m))^i, (L_0(u))^i\} \\ |(L_0(u_m))^i - \beta^{*i}|, & \text{if } (L_0(u_m))^i \leq \beta^{*i} \leq (L_0(u))^i \\ |\beta^{*i} - (L_0(u))^i|, & \text{if } (L_0(u))^i \leq \beta^{*i} \leq (L_0(u_m))^i \end{cases} \\ &\leq |(L_0(u_m))^i - (L_0(u))^i| \\ &< \varepsilon, \end{aligned}$$

for  $m > N_i$  for some  $N_i > 0$ . Note that  $B$  is a finite subset of  $\mathbb{Z}$ . We can further find an  $N > 0$ , such that

$$|(Q^{[L_0, \beta^*]}(u_m))^i - (Q^{[L_0, \beta^*]}(u))^i| < \varepsilon, \quad \forall i \in B, \quad m > N.$$

For any sequence  $\{u_m\}_{m \in \mathbb{N}}$  in  $\mathcal{M}$ ,  $\{Q^{[L_0, \beta^*]}(u_m)\}_{m \in \mathbb{N}}$  is clearly uniformly bounded by  $\beta^*$ . For any bounded subset  $B$  of  $\mathbb{Z}$ , the equicontinuity of  $\{Q^{[L_0, \beta^*]}(u_m)\}_{m \in \mathbb{N}}$  on  $B$  follows from the fact that  $N$  contains only countable elements. Therefore,  $\{u_m\}_{m \in \mathbb{N}}$  contains a subsequence  $\{u_{m_k}\}_{k \in \mathbb{N}}$  such that  $\{Q(u_{m_k})\}_{k \in \mathbb{N}}$  converges to some function on every bounded subset of  $\mathbb{Z}$ . Therefore,  $Q^{[L_0, \beta^*]}$  satisfies (C1)-(C6). This proves our claim above.

Since  $r(\bar{L}_0) > 1$ , there exists  $\delta_0 > 0$  such that  $r((1 - \delta)\bar{L}_0) > 1, \forall \delta \in [0, \delta_0)$ . Since  $f_i$  is increasing in  $u \in [0, b]$  and  $f_i = f_{i+L}, i \in \mathbb{Z}$ , we can find  $a_1, a_2 > 0$  such that  $0 < a_1 \leq f'_i(0) \leq a_2$ , for all  $i \in \{1, 2, \dots, L\}$ . For any  $\delta$  in  $(0, \delta_0)$ , there exists  $\varsigma > 0$  such that

$$f_i(u) > (f'_i(0) - a_1\delta)u, \text{ for all } 0 \leq u \leq \varsigma, i \in \{1, 2, \dots, L\},$$

and hence,

$$f_i(u) > (f'_i(0) - a_1\delta)u \geq f'_i(0) \cdot u - \delta f'_i(0) \cdot u = (1 - \delta)f'_i(0) \cdot u,$$

for  $0 \leq u \leq \varsigma, i \in \{1, 2, \dots, L\}$ . Thus, for any  $u \in [0, \varsigma]$ ,

$$(Q(u))^i = \sum_{j=-\infty}^{+\infty} P_{ij} f_j(u^j) \geq \sum_{j=-\infty}^{+\infty} P_{ij} (1 - \delta) f'_j(0) u^j = (1 - \delta) (L_0(u))^i, \quad \forall i \in \mathbb{Z},$$

i.e.,  $Q(u) \geq (1 - \delta)L_0(u), \forall 0 \leq u \leq \varsigma$ .

Clearly,  $(1 - \delta)L_0$  is  $\mathcal{L}$ -periodic and strongly order preserving. Similarly as we did for  $L_0$ , we can define  $(1 - \delta)L_0(e^{|\mu|})$  for all  $\mu \in (0, \Delta^-)$ .

For simplicity, we let  $M := (1 - \delta)L_0$ . Then  $r((1 - \delta)\bar{L}_0) > 1$  and there exists  $\varphi \in X_b^L$  such that  $\varphi$  is an eigenvector of  $(1 - \delta)\bar{L}_0$ , corresponding to  $r((1 - \delta)\bar{L}_0)$ . Noting that  $(1 - \delta)\bar{L}_0$  is the restriction of  $M$  on  $X_b^L$ , we have  $M(\varphi) = r((1 - \delta)\bar{L}_0)\varphi > \varphi$ . Moreover, we can choose  $\varphi \leq \varsigma$  (i.e.,  $\varphi^i \leq \varsigma^i, \forall i \in \mathbb{Z}$ ). Define

$$(Q^{[M, \varphi]}(u))^i = \min\{(M(u))^i, \varphi^i\}, \quad \forall u \in X \text{ with } 0 \leq u^i \leq \varsigma^i, \forall i \in \mathbb{Z}.$$

Then  $Q^{[M, \varphi]}(0) = 0$  and  $Q^{[M, \varphi]}(\varphi) = \varphi$ . By similar arguments as in [53, Lemma 3.3], we can prove that  $Q^{[M, \varphi]}$  admits exactly two fixed points 0 and  $\varphi$  in  $[0, \varphi] \subseteq X_b^L$ .

Note that  $Q^{[M,\varphi]}$  is strongly positive and monotone increasing in  $u \in [0, \varsigma]$ . Similarly as we did for  $Q^{[L_0,\beta^*]}$ , we can verify that  $Q^{[M,\varphi]}$  satisfies (C1)-(C6).

By Theorem 2.4.2, it then follows that the statements (i) and (ii) are valid. Statements (iii) and (iv) are straightforward consequences of (i) and (ii) (see also [87, Remarks 2]). ■

Motivated by Definition 2.4.1, below we introduce the concept of spatially periodic traveling waves for system (5.3).

**Definition 5.2.1** *A solution  $\{u_n^i\}_{i \in \mathbb{Z}}$  of the recursion (5.3) is called a spatially periodic traveling wave with speed  $c$  in the direction of the unit vector  $\vec{\xi} = -1$  if it has the form  $u_n^i = W(i, i + cn)$ , for some function  $W : \mathbb{Z} \times \{i + cn : i \in \mathbb{Z}, n \in \mathbb{N}\} \rightarrow \mathbb{R}_+$ , with  $W(i, s)$  being  $L$ -periodic in  $i$  for each  $s$ ; Such a wave is said to be nondecreasing if  $W(i, s)$  is nondecreasing in  $s$ , and to connect 0 to  $\{\beta^{*i}\}_{i \in \mathbb{Z}}$  if  $\lim_{s \rightarrow -\infty} W(i, s) = 0$  and  $\lim_{s \rightarrow +\infty} W(i, s) = \beta^{*i}$  uniformly for  $i \in \mathbb{Z}$ . Similarly, a solution  $\{u_n^i\}_{i \in \mathbb{Z}}$  of the recursion (5.3) is called a spatially periodic traveling wave with speed  $c$  in the direction of the unit vector  $\vec{\xi} = 1$  if it has the form  $u_n^i = W(i, i - cn)$ , for some function  $W : \mathbb{Z} \times \{i - cn : i \in \mathbb{Z}, n \in \mathbb{N}\} \rightarrow \mathbb{R}_+$ , with  $W(i, s)$  being  $L$ -periodic in  $i$  for each  $s$ ; Such a wave is said to be nonincreasing if  $W(i, s)$  is nonincreasing in  $s$ , and to connect  $\{\beta^{*i}\}_{i \in \mathbb{Z}}$  to 0 if  $\lim_{s \rightarrow -\infty} W(i, s) = \beta^{*i}$  and  $\lim_{s \rightarrow +\infty} W(i, s) = 0$  uniformly for  $i \in \mathbb{Z}$ .*

The subsequent result is a consequence of Lemma 5.2.2, Theorem 5.2.1 and Theorem 2.4.3, which shows that  $c^*(\vec{\xi})$  is the minimal wave speed for spatially periodic traveling waves in the direction  $\vec{\xi}$ .

**Theorem 5.2.2** *Let (H7)-(H11) hold. Then the following statements are valid.*

- (i) *For any  $c \geq c^*(1)$ , (5.3) admits a nonincreasing spatially periodic traveling wave  $W(i, i - cn)$  connecting  $\{\beta^{*i}\}_{i \in \mathbb{Z}}$  to 0; and for any  $c < c^*(1)$ , (5.3) has no spatially periodic traveling wave  $W(i, i - cn)$  connecting  $\{\beta^{*i}\}_{i \in \mathbb{Z}}$  to 0.*
- (ii) *For any  $c \geq c^*(-1)$ , (5.3) admits a nondecreasing spatially periodic traveling wave  $W(i, i + cn)$  connecting 0 to  $\{\beta^{*i}\}_{i \in \mathbb{Z}}$ ; and for any  $c < c^*(-1)$ , (5.3) has no spatially periodic traveling wave  $W(i, i + cn)$  connecting 0 to  $\{\beta^{*i}\}_{i \in \mathbb{Z}}$ .*

### 5.3 Non-monotone case

In this section, we study spatial dynamics of system (5.3) with a non-monotone recruitment function. Motivated by the recent works in [38, 87], we employ the comparison method and Schauder fixed point theorem to establish spreading speeds and spatially periodic traveling waves for (5.3).

Firstly, we define a nondecreasing function

$$f_i^+(u) := \max_{v \in [0, u]} \{f_i(v)\}, \quad \forall i \in \mathbb{Z}, u \in [0, b].$$

It follows that that  $f_i^+$  is Lipschitz continuous in  $u$  with the same Lipschitz constant  $\hat{L}$  as  $f_i$  has, that is,

$$|f_i^+(u_1) - f_i^+(u_2)| \leq \hat{L}|u_1 - u_2|, \quad \forall i \in \mathbb{Z}, u_1, u_2 \in [0, b].$$

Then for the monotone system

$$u_{n+1}^i = \sum_{j=-\infty}^{+\infty} P_{ij} f_j^+(u_n^j), \quad i \in \mathbb{Z}, n \in \mathbb{N}, \quad (5.10)$$

by Lemma 5.2.1, there exists  $u_{+*} = \{u_{+*}^i\}_{i \in \mathbb{Z}} \in X_b^L$  with  $u_{+*}^i = u_{+*}^{i+L}$ ,  $\forall i \in \mathbb{Z}$ , such that  $u_{+*}$  is a fixed point of (5.10).

We define another function

$$f_i^-(u) = \min_{v \in [u, u_{+*}^i]} \{f_i(v)\}, \quad \forall u \in [0, u_{+*}^i], i \in \mathbb{Z}.$$

It then follows that  $f_i^-$  is nondecreasing in  $u \in [0, u_{+*}^i]$  for all  $i \in \mathbb{Z}$ , and that  $f_i^-$  is Lipschitz continuous in  $u \in [0, u_{+*}^i]$  with the Lipschitz constant  $\hat{L}$ , that is,

$$|f_i^-(u_1) - f_i^-(u_2)| \leq \hat{L}|u_1 - u_2|, \quad \forall u_1, u_2 \in [0, u_{+*}^i], i \in \mathbb{Z}.$$

Similarly, by Lemma 5.2.1, the monotone system

$$u_{n+1}^i = \sum_{j=-\infty}^{+\infty} P_{ij} f_j^-(u_n^j), \quad i \in \mathbb{Z}, n \in \mathbb{N} \quad (5.11)$$

admits a fixed point  $u_{-*} = \{u_{-i}^i\}_{i \in \mathbb{Z}} \in X_{u_{+*}}^L$  with  $u_{-i}^i = u_{+*}^{i+L}$ ,  $\forall i \in \mathbb{Z}$ .

By the definitions of  $f^\pm$ , it is easy to see that the recruitment function  $f$  is bounded above and below by  $f^\pm$ , that is,

$$f_i^-(u) \leq f_i(u) \leq f_i^+(u), \quad \forall i \in \mathbb{Z}, \quad u \in [0, u_{+*}^i],$$

and  $0 < u_{-i}^i \leq u_{+*}^i \leq b$ . Moreover, it follows from Theorem 5.2.1, (5.10) and (5.11) admit spreading speeds  $c_+^*(\pm 1)$  and  $c_-^*(\pm 1)$  (in the directions of  $\vec{\xi} = \pm 1$ ), respectively. By  $f_i'(0) > 1$ ,  $\forall i \in \mathbb{Z}$  and the periodicity of  $f_i$ , there exists  $\delta_0 \in (0, \min_{j \in \{1, 2, \dots, L\}} u_{-i}^j]$ , such that  $f_i^\pm(u) = f_i(u)$ ,  $\forall i \in \mathbb{Z}$ ,  $u \in [0, \delta_0]$ , and hence,  $f_i^{+'}(0) = f_i^{-'}(0) = f_i'(0)$ . Since  $c_+^*(\pm 1)$  and  $c_-^*(\pm 1)$  are determined by the linearization systems of (5.10) and (5.11) at  $u = 0$ , respectively, we then obtain  $c_+^*(1) = c_-^*(1)$  and  $c_+^*(-1) = c_-^*(-1)$ . Let  $c^*(1) := c_+^*(1) = c_-^*(1)$  and  $c^*(-1) := c_+^*(-1) = c_-^*(-1)$ . By Theorem 5.2.1,  $c^*(1)$  and  $c^*(-1)$  are actually defined in (5.8) and (5.9), respectively.

We restrict  $Q$  on  $X^L$  as  $\bar{Q}$  as we did in section 2 and consider that  $\bar{Q}$  is an operator from  $\mathbb{R}_+^L$  to  $\mathbb{R}_+^L$ . It then follows that

$$u_{-*} = Q^-(u_{-*}) \leq Q^-(u) \leq \bar{Q}(u) \leq Q^+(u) \leq Q^+(u_{+*}) = u_{+*}, \quad \forall u \in [u_{-*}, u_{+*}] \subseteq \mathbb{R}_+^L,$$

and hence,  $\bar{Q} : [u_{-*}, u_{+*}] \rightarrow [u_{-*}, u_{+*}]$ . By the Brower fixed point theorem,  $\bar{Q}$  admits a fixed point  $\beta^*$  in  $[u_{-*}, u_{+*}] \subseteq \mathbb{R}^L$ , and hence,  $Q$  admits a fixed point  $\beta^*$  in  $X_b^L$  with  $u_{-i}^i \leq \beta^{*i} \leq u_{+*}^i$ ,  $\forall i \in \mathbb{Z}$ .

Instead of hypothesis (H9), we assume that

(H9)' There exists  $\sigma > 1$ ,  $\delta^* > 0$ ,  $\alpha > 0$  such that  $f_i(u) \geq f_i'(0)u - \alpha u^\sigma$ ,  $\forall i \in \mathbb{Z}$ ,

$$u \in [0, \delta^*] \subseteq [0, \min_{j \in \{1, 2, \dots, L\}} u_{+*}^j].$$

We then have the following result on spreading speeds for (5.3).

**Theorem 5.3.1** *Let (H7), (H8), (H9)', (H10) and (H11) hold. Then the following statements are valid:*

- (i) *For any  $u_0 = \{u_0^i\}_{i \in \mathbb{Z}} \in [0, u_{+*}]$  with  $u_0^i = 0$  for  $i \in \mathbb{Z}$  and  $i \geq K$  for some  $K \in \mathbb{Z}$ , the solution of (5.9) satisfies*

$$\lim_{n \rightarrow \infty, i \geq cn} u_n^i = 0, \quad \forall c > c^*(1),$$

and for any  $u_0 = \{u_0^i\}_{i \in \mathbb{Z}} \in [0, u_{+*}] \setminus \{0\}$ , the solution of (5.3) satisfies

$$\limsup_{n \rightarrow \infty, i \leq cn} (u_n^i - u_{+*}^i) \leq 0 \leq \liminf_{n \rightarrow \infty, i \leq cn} (u_n^i - u_{-}^i), \quad \forall c < c^*(1).$$

(ii) For any  $u_0 = \{u_0^i\}_{i \in \mathbb{Z}} \in [0, u_{+*}]$  with  $u_0^i = 0$  for  $i \in \mathbb{Z}$  and  $i \leq K$  for some  $K \in \mathbb{Z}$ , the solution of (5.3) satisfies

$$\lim_{n \rightarrow \infty, i \leq -cn} u_n^i = 0, \quad \forall c > c^*(-1),$$

and for any  $u_0 = \{u_0^i\}_{i \in \mathbb{Z}} \in [0, u_{+*}] \setminus \{0\}$ , the solution of (5.3) satisfies

$$\limsup_{n \rightarrow \infty, i \geq -cn} (u_n^i - u_{+*}^i) \leq 0 \leq \liminf_{n \rightarrow \infty, i \geq -cn} (u_n^i - u_{-}^i), \quad \forall c < c^*(-1).$$

**Proof** For convenience, we define

$$(Q^+(\varphi))^i = \sum_{j=-\infty}^{+\infty} P_{ij} f_j^+(\varphi^j), \quad (Q^-(\varphi))^i = \sum_{j=-\infty}^{+\infty} P_{ij} f_j^-(\varphi^j), \quad i \in \mathbb{Z},$$

for any  $\varphi \in X$  with  $\varphi^i \in [0, u_{+*}^i], \forall i \in \mathbb{Z}$ . Then  $Q^+$  and  $Q^-$  are monotone on  $X$  and  $Q^-(\varphi) \leq Q(\varphi) \leq Q^+(\varphi)$ , for any  $\varphi \in X$  with  $\varphi^i \in [0, u_{+*}^i]$ . Moreover,  $c^*(\pm 1)$  are spreading speeds for  $u_{n+1} = Q^+(u_n)$  and  $u_{n+1} = Q^-(u_n)$  (i.e., (5.10) and (5.11)), in the directions of  $\vec{\xi} = 1$  and  $\vec{\xi} = -1$ , respectively.

We only show that statement (i) is valid since the proof of statement (ii) is similar. For any  $u_0 = \{u_0^i\}_{i \in \mathbb{Z}} \in [0, u_{+*}]$  with  $u_0^i = 0$  for  $i \in \mathbb{Z}$  and  $i \geq K$  for some  $K \in \mathbb{Z}$ , let

$$u_n = Q^n(u_0), \quad u_n^+ = (Q^+)^n(u_0), \quad \forall n \geq 0.$$

By the comparison principle, we have

$$0 \leq u_n^i \leq u_n^{+i}, \quad \forall i \in \mathbb{Z}, \quad n \geq 0.$$

For any  $c > c^*(1)$ , Theorem 5.2.1 implies that  $\lim_{n \rightarrow \infty, i \geq cn} u_n^{+i} = 0$ , and hence,  $\lim_{n \rightarrow \infty, i \geq cn} u_n^i = 0$ .

For any  $u_0 = \{u_0^i\}_{i \in \mathbb{Z}} \in [0, u_{+*}] \setminus \{0\}$ , define  $v_0 = \{v_0^i\}_{i \in \mathbb{Z}}$  with  $v_0^i = \min\{u_0^i, u_{-}^i\}$ ,  $\forall i \in \mathbb{Z}$ . Then  $v_0 \in [0, u_{-*}] \setminus \{0\}$ . Let

$$u_n^- = (Q^-)^n(v_0), \quad u_n = Q^n(u_0), \quad u_n^+ = (Q^+)^n(u_0), \quad \forall n \geq 0.$$

Since  $v_0 \leq u_0$ , it follows from the comparison principle that

$$0 \leq u_n^{-i} \leq u_n^i \leq u_n^{+i}, \quad \forall i \in \mathbb{Z}, \quad n \geq 0.$$

For any  $c < c^*(1)$ , Theorem 5.2.1 implies that

$$\lim_{n \rightarrow \infty, i \leq cn} (u_n^{-i} - u_{-*}^i) = 0, \quad \lim_{n \rightarrow \infty, i \leq cn} (u_n^{+i} - u_{+*}^i) = 0.$$

Thus, for any  $c < c^*(1)$ , we have

$$\begin{aligned} \liminf_{n \rightarrow \infty, i \leq cn} (u_n^i - u_{-*}^i) &\geq \liminf_{n \rightarrow \infty, i \leq cn} (u_n^{-i} - u_{-*}^i) = 0, \\ \limsup_{n \rightarrow \infty, i \leq cn} (u_n^i - u_{+*}^i) &\leq \limsup_{n \rightarrow \infty, i \leq cn} (u_n^{+i} - u_{+*}^i) = 0. \end{aligned}$$

This completes the proof of statement (i). ■

Now we consider spatially periodic traveling waves in the direction  $\tilde{\xi} = -1$ . Let  $c \in \mathbb{R}$  and  $a > 0$  be given, and define

$$X_c = \{i + cn : i \in \mathbb{Z}, n \in \mathbb{N}\}$$

and  $\mathcal{F}_{c,a}$  as the set of all functions from  $\mathbb{Z} \times X_c$  to  $[0, a]$ . Let  $U \in \mathcal{F}_{c,b}$ . By Definition 5.2.1, we say that  $U(i, i + cn)$  is a spatially periodic traveling wave solution of (5.3) with wave speed  $c$  if  $\{u_n^i\}_{i \in \mathbb{Z}} = \{U(i, i + cn)\}_{i \in \mathbb{Z}}, \forall n \in \mathbb{N}$ , satisfies (5.3) and  $U(i, s) = U(i + L, s), \forall i \in \mathbb{Z}, s \in X_c$ .

Note that one should take  $X_c = \{i - cn : i \in \mathbb{Z}, n \in \mathbb{N}\}$  and replace  $U(i, i + cn)$  with  $U(i, i - cn)$  in order to obtain spatially periodic traveling waves in the direction  $\tilde{\xi} = 1$ .

**Theorem 5.3.2** *Let (H7), (H8), (H9)', (H10) and (H11) hold. Then the following statements are valid:*

- (i) *For any  $c < c^*(-1)$ , (5.3) has no spatially periodic traveling wave  $U(i, i + cn)$  with  $U \in \mathcal{F}_{c,u_{+*}} \setminus \{0\}$ ,  $U(i, -\infty) = 0, \forall i \in \mathbb{Z}$ , and  $U(i, i + cn) \not\equiv 0$  for  $(i, n) \in \mathbb{Z} \times \mathbb{N}$ .*

(ii) For any  $c > c^*(-1)$ , (5.9) has a spatially periodic traveling wave  $U(i, i + cn)$  such that  $U \in \mathcal{F}_{c, u_{+,*}} \setminus \{0\}$ ,  $U(i, -\infty) = 0$ , and for any  $i \in \mathbb{Z}$ ,

$$\min_{1 \leq j \leq L} \{u_{-,*}^j\} \leq \liminf_{n \rightarrow \infty} U(i, i + cn) \leq \limsup_{n \rightarrow \infty} U(i, i + cn) \leq \max_{1 \leq j \leq L} \{u_{+,*}^j\}.$$

(iii) For  $\tilde{\xi} = 1$ , similar results hold for spatially periodic traveling waves  $U(i, i - cn)$  with  $U(i, \infty) = 0$ .

**Proof** For any  $c \in \mathbb{R}$ , let  $u_n^i = U(i, i + cn)$ ,  $\forall i \in \mathbb{Z}$ ,  $n \in \mathbb{N}$ . Then (5.3) becomes

$$U(i, i + c + cn) = \sum_{j=-\infty}^{+\infty} P_{ij} f_j(U(j, j + cn)).$$

Let  $s = i + c + cn$ . This equation is written as

$$\begin{aligned} U(i, s) &= \sum_{j=-\infty}^{+\infty} P_{ij} f_j(U(j, j + s - i - c)) \\ &\quad \underline{k = i - j} \sum_{k=-\infty}^{-\infty} P_{i, i-k} f_{i-k}(U(i - k, s - k - c)) \\ &\quad \underline{j = k} \sum_{j=-\infty}^{+\infty} P_{i, i-j} f_{i-j}(U(i - j, s - j - c)). \end{aligned}$$

Thus, we only need to consider the following wave profile equation

$$U(i, s) = \sum_{j=-\infty}^{\infty} P_{i, i-j} f_{i-j}(U(i - j, s - j - c)). \quad (5.12)$$

For any  $U \in C(\mathbb{Z} \times X_c, [0, b])$ , define

$$T(U)(i, s) = \sum_{j=-\infty}^{\infty} P_{i, i-j} f_{i-j}(U(i - j, s - j - c)), \quad \forall i \in \mathbb{Z}, \quad s \in X_c. \quad (5.13)$$

Similarly, we define  $T^+$  and  $T^-$  as in (5.13) with  $f$  replaced by  $f^+$  and  $f^-$ , respectively.

It then follows that  $T^\pm$  are nondecreasing and that

$$T^-(U)(i, s) \leq T(U)(i, s) \leq T^+(U)(i, s), \quad \forall U \in C(\mathbb{Z} \times X_c, [0, b]), \quad i \in \mathbb{Z}, \quad s \in X_c.$$

In the following, we only prove (i) and (ii) (i.e., in the case where  $\tilde{\xi} = -1$ ). The proof for  $\tilde{\xi} = 1$  is similar.

Assume, by contradiction, that for some  $c_0 < c^*(-1)$ , (5.3) has a spatially periodic traveling wave  $U(i, i + c_0 n)$  with  $U \in C(\mathbb{Z} \times X_{c_0}, [0, u_{+*}) \setminus \{0\})$ ,  $U(i, -\infty) = 0$ ,  $\forall i \in \mathbb{Z}$ , and  $U(i, i + c_0 n) \not\equiv 0$  for  $(i, n) \in \mathbb{Z} \times \mathbb{N}$ . Let  $u_n^i = U(i, i + c_0 n)$ . Fix two real numbers  $c_1$  and  $c_2$  such that  $c_0 < c_1 < c_2 < c^*(-1)$ . Since  $U(i, i + c_0 n) \not\equiv 0$ , there exist  $n_0$  and  $i_0$ , such that  $U(i_0, i_0 + c_0 n_0) \neq 0$ , i.e.,  $u_{n_0}^{i_0} \neq 0$ . Regarding  $u_{n_0}$  as a new initial value, we then see from Theorem 5.3.1 (ii) that  $\liminf_{n \rightarrow \infty, i \geq -c_2 n} (u_n^i - u_{-}^i) \geq 0$ , and hence,  $\liminf_{n \rightarrow \infty, i \geq -c_2 n} u_n^i > 0$ . By letting  $i = \lfloor -c_1 n \rfloor$ , it follows that

$$\liminf_{n \rightarrow \infty} u_n^{\lfloor -c_1 n \rfloor} = \liminf_{n \rightarrow \infty} U(\lfloor -c_1 n \rfloor, c_0 n + \lfloor -c_1 n \rfloor) > 0.$$

Since  $\lim_{s \rightarrow -\infty} U(i, s) = 0$  uniformly for  $i \in \mathbb{Z}$ , we have

$$\liminf_{n \rightarrow \infty} U(\lfloor -c_1 n \rfloor, c_0 n + \lfloor -c_1 n \rfloor) = 0.$$

A contradiction.

Let  $c > c^*(-1)$  be given. It follows that there exists  $\mu_1 \in (0, \Delta^-)$  such that  $\frac{\ln \lambda_{-\mu_1}}{\mu_1} = c$ . Without loss of generality, suppose that  $\mu_1$  is the smallest  $\mu$  such that  $\frac{\ln \lambda_{-\mu}}{\mu} = c$ . Thus,  $\lambda_{-\mu_1} = e^{c\mu_1}$ . Let  $\{\psi_*^i\}_{i \in \mathbb{Z}}$  be the nonnegative eigenvector of  $L_{-\mu_1}$  corresponding to  $\lambda_{-\mu_1}$  with  $\psi_*^i = \psi_*^{i+L}$ ,  $\forall i \in \mathbb{Z}$ . Then

$$(L_{-\mu_1}(\psi_*))^i = \sum_{j=-\infty}^{\infty} P_{ij} f_j'(0) \psi_*^j e^{-\mu_1(i-j)} = e^{c\mu_1} \psi_*^i, \quad \forall i \in \mathbb{Z}.$$

Define  $\phi^+$  on  $\mathbb{Z} \times X_c$  as

$$\phi^+(i, s) = \min\{\psi_*^i e^{\mu_1 s}, u_{+*}^i\}, \quad \forall i \in \mathbb{Z}, \quad s \in X_c.$$

Then for any  $i \in \mathbb{Z}$ ,  $s \in X_c$ ,

$$\begin{aligned} T^+(\phi^+)(i, s) &= \sum_{j=-\infty}^{\infty} P_{i, i-j} f_{i-j}^+(\phi^+(i-j, s-j-c)) \\ &\leq \sum_{j=-\infty}^{\infty} P_{i, i-j} f_{i-j}^+(u_{+*}^{i-j}) \\ &= \sum_{j=-\infty}^{\infty} P_{ij} f_j^+(u_{+*}^j) \\ &= u_{+*}^i. \end{aligned}$$

Since  $f_i(u) \leq f'_i(0)u$ ,  $\forall u \in [0, b]$ ,  $i \in \mathbb{Z}$ , we have

$$f_i^+(u) = \max_{v \in [0, u]} f_i(v) \leq \max_{v \in [0, u]} f'_i(0)v = f'_i(0)u, \quad \forall u \in [0, b], \quad i \in \mathbb{Z},$$

and hence,

$$\begin{aligned} T^+(\phi^+)(i, s) &= \sum_{j=-\infty}^{\infty} P_{i, i-j} f_{i-j}^+(\phi^+(i-j, s-j-c)) \\ &\leq \sum_{j=-\infty}^{\infty} P_{i, i-j} f'_{i-j}(0) (\phi^+(i-j, s-j-c)) \\ &\leq \sum_{j=-\infty}^{\infty} P_{i, i-j} f'_{i-j}(0) \psi_*^{i-j} e^{\mu_1(s-j-c)} \\ &= e^{\mu_1(s-c)} e^{c\mu_1} \psi_*^i \\ &= \psi_*^i e^{\mu_1 s}, \end{aligned}$$

for any  $i \in \mathbb{Z}$ ,  $s \in X_c$ . Thus,

$$T^+(\phi^+)(i, s) \leq \min\{u_{+*}^i, \psi_*^i e^{\mu_1 s}\} = \phi^+(i, s), \quad \forall i \in \mathbb{Z}, s \in X_c.$$

Let  $\varepsilon > 0$  be sufficiently small such that  $0 < \varepsilon \leq \mu_1(\sigma - 1)$ ,  $\mu_\varepsilon := \mu_1 + \varepsilon \in (0, \Delta^-)$ , and  $c_\varepsilon := \frac{\ln \lambda - \mu_\varepsilon}{\mu_\varepsilon} \in (c^*(-1), c)$ . Then  $\lambda_{-\mu_\varepsilon} = e^{c_\varepsilon \mu_\varepsilon}$  is the principle eigenvalue of  $L_{-\mu_\varepsilon}$  with a nonnegative eigenvector  $\{\psi_{*\varepsilon}^i\}_{i \in \mathbb{Z}}$  with  $\psi_{*\varepsilon}^i = \psi_{*\varepsilon}^{i+L}$ ,  $\forall i \in \mathbb{Z}$ , that is,

$$(L_{-\mu_\varepsilon}(\psi_{*\varepsilon}))^i = \sum_{j=-\infty}^{\infty} P_{ij} f'_j(0) \cdot \psi_{*\varepsilon}^j \cdot e^{-\mu_\varepsilon(i-j)} = e^{c_\varepsilon \mu_\varepsilon} (\psi_{*\varepsilon}^i), \quad \forall i \in \mathbb{Z}.$$

Define  $\phi^-$  on  $\mathbb{Z} \times X_c$  as

$$\phi^-(i, s) = \max\{0, \psi_*^i e^{\mu_1 s} - \psi_{*\varepsilon}^i e^{\mu_\varepsilon s}\}, \quad \forall i \in \mathbb{Z}, s \in X_c.$$

We choose suitable  $\{\psi_*^i\}_{i \in \mathbb{Z}}$  and  $\{\psi_{*\varepsilon}^i\}_{i \in \mathbb{Z}}$  such that

$$\psi_*^i \leq \min\{\delta^*, u_{+*}^i, \psi_{*\varepsilon}^i\}, \quad \forall i \in \mathbb{Z},$$

and

$$\psi_{*\varepsilon}^i \cdot f'_i(0) + \alpha(\psi_*^i)^\sigma \leq e^{(c-c_\varepsilon)\mu_\varepsilon} \psi_{*\varepsilon}^i \cdot f'_i(0), \quad \forall i \in \mathbb{Z}.$$

Then  $\phi^-(i, s) \in [0, \delta^*]$  and  $\phi^-(i, s) \leq \phi^+(i, s)$ ,  $\forall i \in \mathbb{Z}$ ,  $s \in X_c$ . We claim that

$$(\phi^-(i, s))^\sigma \leq [\psi_*^i]^\sigma e^{\mu_\varepsilon s}, \quad \forall i \in \mathbb{Z}, s \in X_c.$$

If  $\phi^-(i, s) = 0$ , it is obvious. If  $\phi^-(i, s) > 0$ , then  $s < 0$ . Since  $0 < \varepsilon \leq \mu_1(\sigma - 1)$ , we have  $\varepsilon s + \mu_1 s \geq \mu_1 \sigma s$ . Thus,

$$(\phi^-(i, s))^\sigma \leq e^{\mu_1 \sigma s} (\psi_*^i)^\sigma \leq e^{\mu_1 s + \varepsilon s} (\psi_*^i)^\sigma = e^{\mu_\varepsilon s} (\psi_*^i)^\sigma,$$

and hence,  $(\phi^-(i, s))^\sigma \leq (\psi_*^i)^\sigma e^{\mu_\varepsilon s}$ ,  $\forall i \in \mathbb{Z}$ ,  $s \in X_c$ .

Clearly,  $T^-(\phi^-)(i, s) \geq 0$ ,  $\forall i \in \mathbb{Z}$ ,  $s \in X_c$ . Moreover,

$$\begin{aligned} & T^-(\phi^-)(i, s) \\ &= \sum_{j=-\infty}^{\infty} P_{i, i-j} f_{i-j}^-(\phi^-(i-j, s-j-c)) \\ &\geq \sum_{j=-\infty}^{\infty} P_{i, i-j} (f_{i-j}'(0) \phi^-(i-j, s-j-c) - \alpha (\phi^-(i-j, s-j-c))^\sigma) \\ &\geq \sum_{j=-\infty}^{\infty} P_{i, i-j} f_{i-j}'(0) (\psi_*^{i-j} e^{\mu_1(s-j-c)} - \psi_{*\varepsilon}^{i-j} e^{\mu_\varepsilon(s-j-c)}) - \sum_{j=-\infty}^{\infty} P_{i, i-j} \alpha (\psi_*^{i-j})^\sigma e^{\mu_\varepsilon(s-j-c)} \\ &= e^{\mu_1(s-c)} \sum_{j=-\infty}^{\infty} P_{i, i-j} f_{i-j}'(0) \psi_*^{i-j} e^{-\mu_1 j} \\ &\quad - e^{\mu_\varepsilon(s-c)} \sum_{j=-\infty}^{\infty} P_{i, i-j} (f_{i-j}'(0) \psi_{*\varepsilon}^{i-j} e^{-\mu_\varepsilon j} + \alpha (\psi_*^{i-j})^\sigma e^{-\mu_\varepsilon j}) \\ &\geq e^{\mu_1(s-c)} \sum_{j=-\infty}^{\infty} P_{i, j} f_j'(0) \psi_*^j e^{-\mu_1(i-j)} - e^{\mu_\varepsilon(s-c)} \sum_{j=-\infty}^{\infty} P_{i, i-j} f_{i-j}'(0) \psi_{*\varepsilon}^{i-j} e^{-\mu_\varepsilon j} \cdot e^{(c-c_\varepsilon)\mu_\varepsilon} \\ &= e^{\mu_1(s-c)} \cdot e^{c\mu_1} \cdot \psi_*^i - e^{\mu_\varepsilon(s-c)} \cdot e^{(c-c_\varepsilon)\mu_\varepsilon} \sum_{j=-\infty}^{\infty} P_{ij} f_j'(0) \psi_{*\varepsilon}^j \cdot e^{-\mu_\varepsilon(i-j)} \\ &= e^{\mu_1 s} \psi_*^i - e^{\mu_\varepsilon(s-c_\varepsilon)} e^{c_\varepsilon \mu_\varepsilon} \psi_{*\varepsilon}^i \\ &= e^{\mu_1 s} \psi_*^i - e^{\mu_\varepsilon s} \psi_{*\varepsilon}^i, \end{aligned}$$

for any  $i \in \mathbb{Z}$ ,  $s \in X_c$ . Thus,  $T^-(\phi^-)(i, s) \geq \phi^-(i, s)$ ,  $\forall i \in \mathbb{Z}$ ,  $s \in X_c$ .

Fix some  $\mu \in (0, \mu_1)$  and define

$$\begin{aligned} X_\mu &:= \{ \phi | \phi : \mathbb{Z} \times X_c \rightarrow \mathbb{R}, \sup_{s \in X_c} \max_{1 \leq i \leq L} |\phi(i, s)| e^{-\mu s} < \infty, \\ &\quad \phi(i, s) = \phi(i+L, s), \quad \forall (i, s) \in \mathbb{Z} \times X_c \} \end{aligned}$$

and

$$\|\phi\|_\mu = \sup_{s \in X_c} \max_{1 \leq i \leq L} |\phi(i, s)| e^{-\mu s}, \quad \forall \phi \in X_\mu.$$

It follows that  $(X_\mu, \|\cdot\|_\mu)$  is a Banach space. Then  $\phi^+, \phi^- \in X_\mu$ . Let

$$Y := \{ \phi \in X_\mu : \phi^-(i, s) \leq \phi(i, s) \leq \phi^+(i, s), \quad \forall i \in \mathbb{Z}, s \in X_c \}.$$

It is easy to see that  $Y$  is nonempty, closed, convex in  $X_\mu$ . For any  $\phi \in Y$ ,

$$\phi^- \leq T^-(\phi^-) \leq T^-(\phi) \leq T(\phi) \leq T^+(\phi) \leq T^+(\phi^+) \leq \phi^+.$$

Moreover, we have

$$\begin{aligned} T(\phi)(i+L, s) &= \sum_{j=-\infty}^{\infty} P_{i+L, i+L-j} f_{i+L-j}(\phi(i+L-j, s-j-c)) \\ &= \sum_{j=-\infty}^{\infty} P_{i, i-j} f_{i-j}(\phi(i-j, s-j-c)) \\ &= T(\phi)(i, s) \end{aligned}$$

for any  $i \in \mathbb{Z}$  and  $s \in X_c$ , and

$$\begin{aligned} 0 &\leq \sup_{s \in X_c} \max_{1 \leq i \leq L} |T(\phi)(i, s)| e^{-\mu s} \\ &= \sup_{s \in X_c} \max_{1 \leq i \leq L} \sum_{j=-\infty}^{\infty} P_{i, i-j} f_{i-j}(\phi(i-j, s-j-c)) e^{-\mu s} \\ &\leq \sup_{s \in X_c} \max_{1 \leq i \leq L} \sum_{j=-\infty}^{\infty} P_{i, i-j} f_{i-j}^+(\phi^+(i-j, s-j-c)) e^{-\mu s} \\ &= \sup_{s \in X_c} \max_{1 \leq i \leq L} T^+(\phi^+)(i, s) e^{-\mu s} \\ &\leq \sup_{s \in X_c} \max_{1 \leq i \leq L} \phi^+(i, s) e^{-\mu s} \\ &= \|\phi^+\|_\mu. \end{aligned} \tag{5.14}$$

Therefore, for any  $\phi \in Y$ ,  $T(\phi) \in Y$ , and hence,  $T(Y) \subseteq Y$ .

For any  $\varphi, \psi \in Y$ , we have

$$\begin{aligned} &\|T(\varphi) - T(\psi)\|_\mu \\ &= \sup_{s \in X_c} \max_{1 \leq i \leq L} |T(\varphi)(i, s) - T(\psi)(i, s)| e^{-\mu s} \\ &= \sup_{s \in X_c} \max_{1 \leq i \leq L} \left| \sum_{j=-\infty}^{\infty} P_{i, i-j} [f_{i-j}(\varphi(i-j, s-j-c)) - f_{i-j}(\psi(i-j, s-j-c))] \right| e^{-\mu s} \\ &\leq \hat{L} \sup_{s \in X_c} \max_{1 \leq i \leq L} \sum_{j=-\infty}^{\infty} P_{i, i-j} |\varphi(i-j, s-j-c) - \psi(i-j, s-j-c)| e^{-\mu s} \\ &\leq \hat{L} \sum_{j=-\infty}^{\infty} P_{i, i-j} \sup_{s \in X_c} \max_{1 \leq i \leq L} |\varphi(i-j, s-j-c) - \psi(i-j, s-j-c)| e^{-\mu(s-j-c)} e^{-\mu(j+c)} \\ &= \hat{L} \sum_{j=-\infty}^{\infty} P_{i, i-j} \|\varphi - \psi\|_\mu e^{-\mu(j+c)} \\ &\leq \tilde{L} \|\varphi - \psi\|_\mu \end{aligned}$$

for some  $\tilde{L} > 0$  since  $\sum_{j=-\infty}^{\infty} P_{i,i-j} e^{-\mu j} < \infty$ . Thus,  $T : Y \rightarrow Y$  is continuous.

By (5.14), it follows that  $\{T(\phi) : \phi \in Y\}$  is uniformly bounded by 0 and  $\|\phi^+\|_{\mu}$ . Since both  $\mathbb{Z}$  and  $X_c$  consist of countable elements, it is obvious that  $\{T(\phi) : \phi \in Y\}$  is equicontinuous on any bounded subset of  $\mathbb{Z} \times X_c$ . It follows from the Arzela-Ascoli theorem that for any given sequence  $\{\psi_n\}_{n \geq 1}$  in  $T(Y)$ , there exist  $n_k \rightarrow \infty$  and  $\psi : \mathbb{Z} \times X_c \rightarrow \mathbb{R}$  such that

$$\lim_{k \rightarrow \infty} \psi_{n_k}(i, s) = \psi(i, s)$$

uniformly for  $(i, s)$  in any bounded subset of  $\mathbb{Z} \times X_c$ . Since

$$\phi^-(i, s) \leq \psi_{n_k}(i, s) \leq \phi^+(i, s), \quad \forall i \in \mathbb{Z}, s \in X_c,$$

we have

$$\phi^-(i, s) \leq \psi(i, s) \leq \phi^+(i, s), \quad \forall i \in \mathbb{Z}, s \in X_c.$$

Moreover, by the periodicity of  $\psi_{n_k}$  with respect to  $L$ , we also have  $\psi(i, s) = \psi(i+L, s)$ ,  $\forall i \in \mathbb{Z}, s \in X_c$ . The boundedness of  $\sup_{s \in X_c} \max_{1 \leq i \leq L} |\psi(i, s)| e^{-\mu s}$  is obvious. Therefore,  $\psi \in Y$ . Note that

$$\begin{aligned} \lim_{s \rightarrow +\infty} (\phi^+(i, s) - \phi^-(i, s)) e^{-\mu s} &= 0, \\ \lim_{s \rightarrow -\infty} (\phi^+(i, s) - \phi^-(i, s)) e^{-\mu s} &= 0, \end{aligned}$$

uniformly for  $i \in \{1, 2, \dots, L\}$ . Therefore, for any  $\varepsilon > 0$ , there exists  $M > 0$  such that

$$0 \leq (\phi^+(i, s) - \phi^-(i, s)) e^{-\mu s} < \varepsilon, \quad \forall s \in X_c, |s| \geq M, 1 \leq i \leq L,$$

and hence,

$$|\psi_{n_k}(i, s) - \psi(i, s)| e^{-\mu s} \leq |\phi^+(i, s) - \phi^-(i, s)| e^{-\mu s} < \varepsilon, \quad \forall s \in X_c, |s| \geq M, 1 \leq i \leq L.$$

Since  $\lim_{k \rightarrow \infty} |\psi_{n_k}(i, s) - \psi(i, s)| e^{-\mu s} = 0$  uniformly for  $1 \leq i \leq L$  and  $s \in X_c$  with  $|s| \leq M$ , there exists an integer  $N > 0$  such that

$$|\psi_{n_k}(i, s) - \psi(i, s)| e^{-\mu s} < \varepsilon, \quad \forall 1 \leq i \leq L, s \in X_c, |s| \leq M, k \geq N.$$

It then follows that

$$\|\psi_{n_k} - \psi\|_\mu = \sup_{s \in X_c} \max_{1 \leq i \leq L} |\psi_{n_k}(i, s) - \psi(i, s)| e^{-\mu s} < \varepsilon, \quad \forall k \geq N,$$

and hence,  $\lim_{k \rightarrow \infty} \psi_{n_k} = \psi$  in  $X_\mu$ . Thus,  $T(Y)$  is precompact in  $X_\mu$ .

Thus, by the Schauder fixed point theorem, there exists  $U \in Y$  such that  $U = T(U)$ , and hence,  $U(i, s)$  is a traveling wave of (5.3). Since

$$\phi^-(i, s) \leq U(i, s) \leq \phi^+(i, s), \quad \forall i \in \mathbb{Z}, s \in X_c,$$

we have  $U(i, -\infty) = 0$  and  $U \in C(\mathbb{Z} \times X_c, [0, u_{+*}]) \setminus \{0\}$ .

Let  $u_n^i = U(i, i + cn)$ ,  $\forall i \in \mathbb{Z}, n \in \mathbb{N}$ . Fix  $\bar{c} < c^*(-1)$ . By Theorem 5.3.1, we have

$$\liminf_{n \rightarrow \infty, i \geq -\bar{c}n} (u_n^i - u_{-*}^i) \geq 0 \quad \text{and} \quad \limsup_{n \rightarrow \infty, i \geq -\bar{c}n} (u_n^i - u_{+*}^i) \leq 0.$$

Then for sufficiently small  $\varepsilon > 0$ , we have

$$\liminf_{n \rightarrow \infty, i \geq -\bar{c}n} u_n^i \geq \min_{1 \leq j \leq L} \{u_{-*}^j\} - \varepsilon > 0 \quad \text{and} \quad \limsup_{n \rightarrow \infty, i \geq -\bar{c}n} u_n^i \leq \max_{1 \leq j \leq L} \{u_{+*}^j\} + \varepsilon,$$

that is,

$$\liminf_{n \rightarrow \infty, i \geq -\bar{c}n} U(i, i + cn) \geq \min_{1 \leq j \leq L} \{u_{-*}^j\} - \varepsilon \quad \text{and} \quad \limsup_{n \rightarrow \infty, i \geq -\bar{c}n} U(i, i + cn) \leq \max_{1 \leq j \leq L} \{u_{+*}^j\} + \varepsilon.$$

Note that for any given  $i \in \mathbb{Z}$ , when  $n$  is sufficiently large,  $i \geq -\bar{c}n$ . Thus,

$$\liminf_{n \rightarrow \infty} U(i, i + cn) \geq \min_{1 \leq j \leq L} \{u_{-*}^j\} - \varepsilon \quad \text{and} \quad \limsup_{n \rightarrow \infty} U(i, i + cn) \leq \max_{1 \leq j \leq L} \{u_{+*}^j\} + \varepsilon.$$

Letting  $\varepsilon \rightarrow 0$ , we obtain

$$\min_{1 \leq j \leq L} \{u_{-*}^j\} \leq \liminf_{n \rightarrow \infty} U(i, i + cn) \leq \limsup_{n \rightarrow \infty} U(i, i + cn) \leq \max_{1 \leq j \leq L} \{u_{+*}^j\}.$$

This completes the proof. ■

As a remark of this section, we point out that the domains for all spatially periodic traveling wave profiles with speed  $c > c^*(\bar{\xi})$  are not the same, and hence, it is not easy to use these wave profiles to approximate the possible spatially periodic traveling wave profile with  $c = c^*(\bar{\xi})$ . Thus, we are not able to prove the existence of the spatially periodic traveling wave with speed  $c = c^*(\bar{\xi})$  at this moment.

## 5.4 An example

In this section, we present an example of (5.3) with a specific recruitment function and dispersal kernel to illustrate our main analytic results.

Consider the Ricker type recruitment function

$$f_i(u) = au e^{r(i)-qu}, \quad \forall i \in \mathbb{Z}, \quad u \in \mathbb{R},$$

where  $q > 0$ ,  $r$  is an  $L$ -periodic function defined on  $\mathbb{Z}$  for some  $L \in \mathbb{N}$ , and  $ae^{r(i)} > 1$ ,  $\forall i \in \mathbb{Z}$ . Inspired by the exponentially damping kernel function for a continuous habitat (see [40]), we choose  $P_{ij} = \frac{e^{\frac{1}{d}} - 1}{e^{\frac{1}{d}} + 1} e^{-\frac{|i-j|}{d}}$  with  $d > 0$ , for any  $i, j \in \mathbb{Z}$ . Then (5.3) becomes

$$u_{n+1}^i = \sum_{j=-\infty}^{+\infty} \frac{e^{\frac{1}{d}} - 1}{e^{\frac{1}{d}} + 1} e^{-\frac{|i-j|}{d}} au_n^j e^{r(j)-qu_n^i}, \quad i \in \mathbb{Z}, \quad n \in \mathbb{Z}. \quad (5.15)$$

Clearly, for any  $i \in \mathbb{Z}$ ,  $f_i \in C^1(\mathbb{R}, \mathbb{R})$ ,  $f_i(0) = 0$ ,  $f_i'(0) = ae^{r(i)} > 1$ ,

$$f_i(u) = au e^{r(i)-qu} = au e^{r(i+L)-qu} = f_{i+L}(u), \quad \forall u \in \mathbb{R},$$

and  $f_i(u)/u = ae^{r(i)-qu}$  is strictly decreasing in  $u \in \mathbb{R}$ . Moreover, for any  $i \in \mathbb{Z}$ ,

$$\max_{u \in [0, +\infty)} f_i(u) = f_i\left(\frac{1}{q}\right) = \frac{a}{q} e^{r(i)-1}. \quad \text{Let}$$

$$\hat{b} = \{b\}_{i \in \mathbb{Z}} \in X \text{ with } b = \max_{i \in \mathbb{Z}} f_i\left(\frac{1}{q}\right),$$

and

$$\hat{L} = \max_{1 \leq i \leq L, u \in [0, b]} |f_i'(u)| = \max_{1 \leq i \leq L, u \in [0, b]} ae^{r(i)-qu} |1 - qu|.$$

Then  $\hat{b} \in X^L$ ,  $f_i([0, b]) \subseteq [0, b]$ ,  $\forall i \in \mathbb{Z}$  and

$$|f_i(u_1) - f_i(u_2)| \leq \hat{L} |u_1 - u_2|, \quad \forall i \in \mathbb{Z}, u_1, u_2 \in [0, b].$$

It is easy to see that  $P_{ij} = P_{i+L, j+L}$ ,  $\forall i, j \in \mathbb{Z}$  and  $\sum_{j=-\infty}^{\infty} P_{ij} = 1$ . Moreover, for  $\mu \in [0, \frac{1}{d})$ ,  $i \in \mathbb{Z}$ ,

$$\begin{aligned} \sum_{j=-\infty}^{\infty} P_{ij} e^{-\mu(i-j)} &= \frac{e^{\frac{1}{d}} - 1}{e^{\frac{1}{d}} + 1} \sum_{j=-\infty}^{\infty} e^{-\frac{|i-j|}{d}} e^{-\mu(i-j)} \\ &= \frac{(e^{\frac{1}{d}} - 1) e^{\mu} (e^{\frac{1}{d}} - 1)}{(e^{\frac{1}{d}} + 1) (e^{\mu + \frac{1}{d}} - 1) (e^{\frac{1}{d}} - e^{\mu})}. \end{aligned}$$

Thus,  $\sum_{j=-\infty}^{\infty} P_{ij} e^{-\mu(i-j)}$  is uniformly bounded for  $\mu \in [0, \frac{1}{d}]$ ,  $i \in \mathbb{Z}$ .

For  $\sigma = 2$  and  $\alpha$  satisfies  $0 < \frac{ae^{r(i)}}{\alpha} \leq \frac{1}{q}$ ,  $\forall i \in \mathbb{Z}$ , we have

$$f_i(u) \geq f'_i(0)u - \alpha u^\sigma, \quad \forall i \in \mathbb{Z}, \quad u \in [0, b].$$

Define  $\bar{L}_0 : \mathbb{R}^L \rightarrow \mathbb{R}^L$  as

$$\bar{L}_0(\varphi) = A\varphi, \quad \forall \varphi \in \mathbb{R}^L,$$

where  $A = (a_{im})_{L \times L}$  with  $a_{im} = \sum_{k=-\infty}^{+\infty} P_{i, kL+m} f'_m(0)$ , for  $i, m \in \{1, 2, \dots, L\}$ , and

$$r(\bar{L}_0) = \max\{|\lambda|, \lambda \text{ is an eigenvalue of } A\}.$$

In this case, we have

$$\begin{aligned} a_{im} &= ae^{r(m)} \frac{e^{\frac{1}{d}} - 1}{e^{\frac{1}{d}} + 1} \sum_{k=-\infty}^{\infty} e^{-\frac{|i-(kL+m)|}{d}} \\ &= \begin{cases} ae^{r(m)} \frac{e^{\frac{1}{d}} - 1}{(e^{\frac{1}{d}} + 1)(1 - e^{-\frac{1}{d}})} \left( e^{-\frac{i+m}{d}} + e^{\frac{i-m-L}{d}} \right), & \text{if } i \geq m, \\ ae^{r(m)} \frac{e^{\frac{1}{d}} - 1}{(e^{\frac{1}{d}} + 1)(1 - e^{-\frac{1}{d}})} \left( e^{-\frac{i+m-L}{d}} + e^{\frac{i-m}{d}} \right), & \text{if } i < m, \end{cases} \end{aligned}$$

for  $i, m \in \{1, 2, \dots, L\}$ .

As long as  $r(\bar{L}_0) > 1$ , the assumptions (H7), (H8), (H9)', (H10) and (H11) hold, and hence, Theorems 5.3.1 and 5.3.2 hold for system (5.15). The spreading speed in the direction of  $\vec{\xi} = -1$  is

$$c^*(-1) = \inf_{\mu \in (0, \frac{1}{d})} \frac{\ln \lambda_{-\mu}}{\mu},$$

where  $\lambda_{-\mu}$  is the principle eigenvalue of  $L_{-\mu} : \mathbb{R}^L \rightarrow \mathbb{R}^L$ :

$$L_{-\mu}(u) = A_{-\mu}u, \quad \forall u \in \mathbb{R}^L,$$

where  $A_{-\mu} = (a_{im}^{-\mu})_{L \times L}$  with

$$\begin{aligned} a_{im}^{-\mu} &= \sum_{k=-\infty}^{+\infty} a \frac{e^{\frac{1}{d}} - 1}{e^{\frac{1}{d}} + 1} e^{-\frac{|i-(kL+m)|}{d}} e^{r(m)} e^{-\mu(i-(kL+m))} \\ &= \begin{cases} a \frac{e^{\frac{1}{d}} - 1}{e^{\frac{1}{d}} + 1} e^{r(m) - \mu(i-m)} \left( \frac{e^{\frac{m-i}{d}}}{1 - e^{-(\mu L + \frac{1}{d})}} + \frac{e^{\frac{i-m-L}{d} + \mu L}}{1 - e^{-(\mu L - \frac{1}{d})}} \right), & \text{if } i \geq m, \\ a \frac{e^{\frac{1}{d}} - 1}{e^{\frac{1}{d}} + 1} e^{r(m) - \mu(i-m)} \left( \frac{e^{\frac{m-i-L}{d} - \mu L}}{1 - e^{-(\mu L + \frac{1}{d})}} + \frac{e^{\frac{i-m}{d}}}{1 - e^{-(\mu L - \frac{1}{d})}} \right), & \text{if } i < m, \end{cases} \end{aligned}$$

for  $i, m \in \{1, 2, \dots, L\}$ .

The spreading speed in the direction of  $\vec{\xi} = 1$  can be similarly defined as

$$c^*(1) = \inf_{\mu \in (0, \frac{1}{d})} \frac{\ln \lambda_\mu}{\mu},$$

where  $\lambda_\mu$  is the principle eigenvalue of  $L_\mu : \mathbb{R}^L \rightarrow \mathbb{R}^L$ :

$$L_\mu(u) = A_\mu u, \quad \forall u \in \mathbb{R}^L,$$

where  $A_\mu = (a_{im}^\mu)_{L \times L}$  with

$$a_{im}^\mu = \begin{cases} a \frac{e^{\frac{1}{d}} - 1}{e^{\frac{1}{d}} + 1} e^{r(m) + \mu(i-m)} \left( \frac{e^{\frac{m-i}{d}}}{1 - e^{(\mu L - \frac{1}{d})}} + \frac{e^{\frac{i-m-L-\mu L}{d}}}{1 - e^{(-\mu L - \frac{1}{d})}} \right), & \text{if } i \geq m, \\ a \frac{e^{\frac{1}{d}} - 1}{e^{\frac{1}{d}} + 1} e^{r(m) + \mu(i-m)} \left( \frac{e^{\frac{m-i-L+\mu L}{d}}}{1 - e^{(\mu L - \frac{1}{d})}} + \frac{e^{\frac{i-m}{d}}}{1 - e^{(-\mu L - \frac{1}{d})}} \right), & \text{if } i < m, \end{cases}$$

for  $i, m \in \{1, 2, \dots, L\}$ .

Since  $P_{ij} = P_{ji}$ ,  $\forall i, j \in \mathbb{Z}$ , it follows from Lemma 5.2.3 that the spreading speeds in the directions of  $\vec{\xi} = 1$  and  $\vec{\xi} = -1$  are the same, i.e.,  $c^*(1) = c^*(-1)$ . Indeed, it is easy to see that  $A_{-\mu} = BC$  and  $A_\mu = B^T C$ , where

$$B_{im} = \begin{cases} a \frac{e^{\frac{1}{d}} - 1}{e^{\frac{1}{d}} + 1} e^{-\mu(i-m)} \left( \frac{e^{\frac{m-i}{d}}}{1 - e^{-(\mu L + \frac{1}{d})}} + \frac{e^{\frac{i-m-L+\mu L}{d}}}{1 - e^{(\mu L - \frac{1}{d})}} \right), & \text{if } i \geq m, \\ a \frac{e^{\frac{1}{d}} - 1}{e^{\frac{1}{d}} + 1} e^{-\mu(i-m)} \left( \frac{e^{\frac{m-i-L-\mu L}{d}}}{1 - e^{-(\mu L + \frac{1}{d})}} + \frac{e^{\frac{i-m}{d}}}{1 - e^{(\mu L - \frac{1}{d})}} \right), & \text{if } i < m, \end{cases}$$

for  $i, m \in \{1, 2, \dots, L\}$ , and  $C = \text{diag}\{e^{r(1)}, e^{r(2)}, \dots, e^{r(L)}\}$ .

In particular, we choose

$$r(i) = \begin{cases} r_1, & nL - L_1 \leq i < nL, \\ r_2, & nL \leq i < nL + L_2, \end{cases}$$

for any  $i \in \mathbb{Z}$ , where  $n \in \mathbb{N}$ ,  $L_1, L_2 \in \mathbb{N}$  and  $L_1 + L_2 = L$ . This indicates that each period part of the whole periodic habitat is composed of a favorable habitat (corresponding to  $\max\{r_1, r_2\}$ ) and an unfavorable habitat (corresponding to  $\min\{r_1, r_2\}$ ).

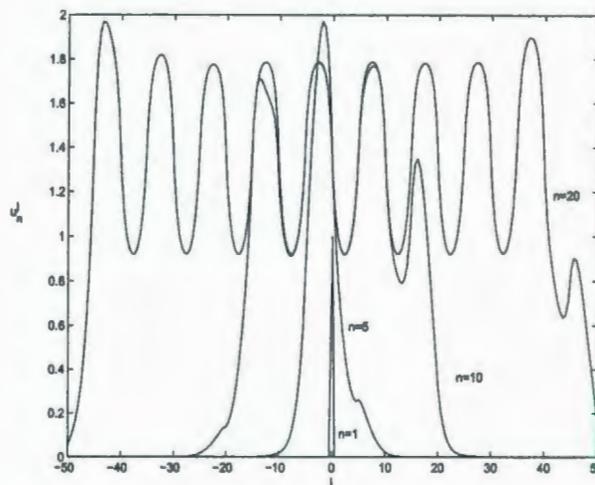


Figure 5.1: A solution  $\{u_n^i\}_{i \in \mathbb{Z}}$  of (5.15) when  $n = 1, 5, 10, 20$ .

Let  $a = 1.2$ ,  $q = 1$ ,  $d = 1$ ,  $L = 2$ ,  $L_1 = L_2 = 1$ ,  $r_1 = 0$ ,  $r_2 = 1$ . Then we have

$$A = \begin{bmatrix} 1.979266244 & 0.4718686397 \\ 1.282671949 & 0.7281313600 \end{bmatrix}$$

and  $r(\bar{L}_0) = 2.351990990 > 1$ . Moreover,

$$A_{-\mu} = \begin{bmatrix} \frac{1.2e(e-1)\left(\frac{1}{1-e^{-2\mu-2}} + \frac{e^{-2+2\mu}}{1-e^{-2+2\mu}}\right)}{(e+1)} & \frac{1.2e^\mu(e-1)\left(\frac{e^{-1-2\mu}}{1-e^{-2\mu-2}} + \frac{e^{-1}}{1-e^{-2+2\mu}}\right)}{(e+1)} \\ \frac{1.2e^{1-\mu}(e-1)\left(\frac{e^{-1}}{1-e^{-2\mu-2}} + \frac{e^{-1+2\mu}}{1-e^{-2+2\mu}}\right)}{(e+1)} & \frac{1.2(e-1)\left(\frac{1}{1-e^{-2\mu-2}} + \frac{e^{-2+2\mu}}{1-e^{-2+2\mu}}\right)}{(e+1)} \end{bmatrix}$$

and

$$c^*(1) = c^*(-1) \approx 2.069595656.$$

Choosing the initial function  $u_1$  as

$$u_1^i = \begin{cases} 1, & i = 0, \\ 0, & \forall i \neq 0, \end{cases}$$

we can draw the graph for the solution  $\{u_n^i\}_{i \in \mathbb{Z}}$  of (5.15) when  $n = 1, 5, 10, 20$ , which is shown in Figure 5.1.

## Chapter 6

# Bistable Waves for A Class of Reaction-Diffusion Systems

### 6.1 Introduction

Classic reaction-diffusion models usually take the form

$$\begin{cases} \frac{\partial u}{\partial t} = D_1 \frac{\partial^2 u}{\partial x^2} + F(u, v), \\ \frac{\partial v}{\partial t} = D_2 \frac{\partial^2 v}{\partial x^2} + G(u, v), \end{cases} \quad (6.1)$$

where  $u$  and  $v$  are densities of two populations (or subpopulations of a population, or two particles) at location  $x$  and time  $t$ ,  $D_1$  and  $D_2$  are positive diffusion constants,  $F(u, v)$  and  $G(u, v)$  are reaction functions. This model has been generally applied to describe the dispersal dynamics of populations, disease transmission dynamics, chemical reactions, and so on ([12, 46, 62, 66]), and it seems to work well in most cases.

However, it has been recently noticed that in some situations during the dispersal process, one of the reacting populations diffuses so slowly in the habitat, compared with the other, that its diffusion can be almost neglected. This phenomenon is very interesting in the study of population dispersal and it naturally suggests that only one of the diffusion constants be positive while the other be zero, when we describe

the dispersal dynamics in reaction-diffusion models. To model fecally-orally transmitted diseases such as cholera, typhoid fever, infections hepatitis, polyometitis etc, Capasso and Maddalena [12] assumed that the bacteria diffuse randomly in the habitat, while the diffusion of the human population can be neglected with respect to that of bacteria. As a result, they studied the following model

$$\begin{cases} \frac{\partial u_1(x, t)}{\partial t} = d \frac{\partial^2 u_1(x, t)}{\partial x^2} - a_{11}u_1(x, t) + a_{12}u_2(x, t), \\ \frac{\partial u_2(x, t)}{\partial t} = -a_{22}u_2(x, t) + g(u_1(x, t)), \end{cases} \quad (6.2)$$

where  $u_1$  and  $u_2$  denote the spatial densities of the infectious agent and infective human population, respectively;  $d > 0$  is the diffusion constant of bacteria;  $1/a_{11}$  is the mean lifetime of the agent in the environment;  $1/a_{22}$  is the mean infectious period of the human infectives;  $a_{12}$  is the multiplicative factor of the infectious agent due to the human population;  $g(u_1)$  is the infection rate of the human population under the assumption that the total susceptible human population is constant during the evolution of the epidemic.

Other examples come from reaction-diffusion models for single species. Recently, some authors assumed that only part of the population is migrating and the other part is sedentary. Cook [65] studied a Verhulst type population model with a sedentary and a migrating subpopulation, assuming that there is a joint carrying capacity for both subpopulations and that the offspring of both groups forms one pool which is then distributed to both subpopulations at constant proportions:

$$\begin{cases} v_t = r_v(u + v)(1 - (u + v)/K) + Dv_{xx}, \\ w_t = r_w(u + v)(1 - (u + v)/K). \end{cases} \quad (6.3)$$

Lewis and Schmitz [48] studied another Verhulst type model in which it was assumed that individuals switch between mobile and stationary states during their lifetime and that the migrants have a positive mortality while the sedentary subpopulation reproduces and is subject to a finite carrying capacity:

$$\begin{cases} v_t = D\Delta v - \mu v - \gamma_2 v + \gamma_1 w, \\ w_t = f(w) - \gamma_1 w + \gamma_2 v, \end{cases} \quad (6.4)$$

where  $f(w) = rw(1 - w/K)$ . Haderer and Lewis [32] proposed a Fisher type equation with a quiescent state:

$$\begin{cases} v_t = D\Delta v + f(v) - \gamma_2 v + \gamma_1 w, \\ w_t = \gamma_2 v - \gamma_1 w, \end{cases} \quad (6.5)$$

where individuals in state  $v$  move and interact as in the standard Fisher's equation while those in state  $w$  are quiescent. Such behavior is typical for invertebrates living in small ponds in arid climates which dry up and reappear subject to rainfall [32].

Motivated by (6.2)-(6.5) and other recent works (see, e.g., [14, 31, 79, 92, 94]), we consider the following general reaction-diffusion system

$$\begin{cases} \frac{\partial u}{\partial t} = D \frac{\partial^2 u}{\partial x^2} + F(u, v), \\ \frac{\partial v}{\partial t} = G(u, v), \end{cases} \quad (6.6)$$

where  $u(t, x)$  and  $v(t, x)$  are densities of the migrating population and sedentary population at the location  $x$  and time  $t$ , respectively;  $D > 0$  is the diffusion constant of the migrating population,  $F(u, v)$  and  $G(u, v)$  are reaction functions.

Systems (6.2)-(6.5) have been investigated extensively and many results have been established in the monostable case, where the corresponding reaction system admits zero equilibrium and a stable nontrivial equilibrium. The stability of the trivial and nontrivial equilibria for (6.2) was studied in [12]; the existence of monotone traveling waves and the minimal wave speed for (6.2) were established in [100], and it was shown in [78] that this minimal wave speed is also the spreading speed for solutions with initial functions having compact supports. The minimal speed for monotone traveling waves for (6.4) was determined in [48] from the linearization at the zero equilibrium, under the assumption that the emigration rate is less than the intrinsic growth rate for the sedentary class; the authors of [32] studied the spreading speed, minimal wave speed, and the persistence of the population in different domains for (6.4); the spreading speed and traveling waves of (6.4) were also established in [83]. System (6.5) was briefly discussed in [32] and it was shown in [94] that the spreading speed coincides with the minimal wave speed for monotone traveling waves.

In epidemiology, large outbreaks usually tend to a nontrivial endemic state, while small outbreaks tend to extinction. This may explain why, even though we are exposed to many infections, only some diseases have evolved into an endemic state [14]. Mathematically, this leads to the study of epidemic models with bistable nonlinearities. There are some results for (6.2) in the bistable case: a saddle point structure was obtained under Neumann boundary conditions in [13] and under Dirichlet boundary conditions in [39]; a complete analysis of the steady states was obtained under Dirichlet boundary conditions in [14]; the existence, uniqueness and global exponential stability with phase shift of bistable traveling waves were established in [92].

In this chapter, we are interested in the existence, uniqueness and global attractivity of traveling waves of the general system (6.6) with bistable nonlinearity. The organization of this chapter is as follows. In section 6.2, we establish the existence of bistable traveling waves for (6.6) by the shooting method (see, e.g., [79]). In section 6.3, we obtain the global attractivity with phase shift and uniqueness (up to translation) of traveling waves via the dynamical system approach (see [92, 97]). In section 6.4, we present some specific examples of (6.6) to illustrate applicability of our main results.

## 6.2 Existence of bistable waves

Throughout this chapter, we make the following assumptions to obtain the cooperative and bistable nonlinearity for system (6.6).

(H12) There exist three points  $E_- = (0, 0)$ ,  $E_0 = (a_1, b_1)$  and  $E_+ = (a_2, b_2)$  with  $0 < a_1 < a_2$  and  $0 < b_1 < b_2$  such that

(i)  $F, G \in C^1(\mathbb{R}_+^2, \mathbb{R})$ ,  $F_v(u, v) \geq 0$ ,  $G_u(u, v) \geq 0$  and  $G_v(u, v) < 0$  on  $\mathbb{R}_+^2$ , and  $G_u(0, 0) > 0$ .

(ii)  $E_-$ ,  $E_0$  and  $E_+$  are only zeros of  $f(u, v) := (F(u, v), G(u, v))$  in the order interval  $[E_-, E_+]$ .

(iii) All eigenvalues of the Jacobian matrices  $Df(E_-)$  and  $Df(E_+)$  have negative real parts; and  $Df(E_0)$  has an eigenvalue with positive real part and another with negative real part.

(iv)  $F_v(u, v) > 0$  for  $(u, v) \in [0, a_2] \times [0, b_2]$ .

Consider the spatially homogeneous system associated with (6.6)

$$\begin{cases} u'(t) = F(u, v), \\ v'(t) = G(u, v). \end{cases} \quad (6.7)$$

By the assumption (H12), (6.7) has only three equilibria  $E_-$ ,  $E_0$  and  $E_+$  in  $[E_-, E_+]$ ,  $E_-$  and  $E_+$  are stable,  $E_0$  is a saddle. In this paper, we will study the existence of bistable waves of (6.6), i.e., traveling wave solutions connecting  $E_-$  and  $E_+$ .

Let  $\tau = x + ct$  and  $(u(t, x), v(t, x)) = (U(x + ct), V(x + ct))$  be a traveling wave solution of (6.6). Then the wave front profile  $(U(\tau), V(\tau))$  satisfies

$$\begin{cases} cU' = DU'' + F(U, V), \\ cV' = G(U, V), \end{cases} \quad (6.8)$$

where  $'$  denotes  $\frac{d}{d\tau}$ . Since we are interested in traveling waves connecting  $E_-$  and  $E_+$ , we impose the following asymptotic boundary conditions on (6.8)

$$\begin{cases} U(-\infty) = 0, V(-\infty) = 0, U'(-\infty) = 0, \\ U(+\infty) = a_2, V(+\infty) = b_2, U'(+\infty) = 0. \end{cases} \quad (6.9)$$

In the case where  $c = 0$ , (6.8) becomes

$$\begin{cases} DU'' + F(U, V) = 0, \\ G(U, V) = 0, \end{cases} \quad (6.10)$$

which is equivalent to

$$\begin{cases} U' = W, \\ W' = -\frac{F(U, V^*(U))}{D}, \end{cases} \quad (6.11)$$

where  $V^*(U)$  satisfies  $G(U, V^*(U)) = 0$ . By (H12) and the implicit function theorem, it is not difficult to see that  $V^*(U)$  is continuously differentiable on  $[0, \infty)$ . Since

$E_-$  and  $E_+$  are stable for (6.7), we can easily see that  $(0, 0)$  and  $(a_2, 0)$  are saddles of (6.11). Then a traveling wave of (6.6) connecting  $E_-$  and  $E_+$  with wave speed  $c = 0$  corresponds to a heteroclinic orbit of (6.11) connecting  $(0, 0)$  and  $(a_2, 0)$ . The solutions of (6.11) through  $(0, 0)$  can be expressed as

$$\frac{W^2}{2} = -\frac{1}{D} \int_0^U F(t, V^*(t)) dt.$$

Thus, (6.11) admits a heteroclinic orbit connecting  $(0, 0)$  and  $(a_2, 0)$  if and only if  $\int_0^{a_2} F(U, V^*(U)) dU = 0$ .

In what follows, we mainly consider the case where  $c > 0$ . It is easy to see that (6.8)-(6.9) is equivalent to

$$\begin{cases} U' = W, \\ V' = \frac{G(U, V)}{c}, \\ W' = \frac{cW^2 - F(U, V)}{D}, \end{cases} \quad (6.12)$$

with boundary conditions

$$U(-\infty) = 0, V(-\infty) = 0, W(-\infty) = 0, \quad (6.13)$$

$$U(+\infty) = a_2, V(+\infty) = b_2, W(+\infty) = 0. \quad (6.14)$$

Clearly, (6.12) has three equilibria  $(E_-, 0)$ ,  $(E_0, 0)$  and  $(E_+, 0)$ . Thus, a traveling wave solution of (6.6) connecting  $E_-$  and  $E_+$  with positive wave speed corresponds to a solution of (6.12) connecting  $(E_-, 0)$  and  $(E_+, 0)$ , i.e., a solution of (6.12)-(6.14).

**Lemma 6.2.1** *For any  $c > 0$ , the Jacobian matrix of (6.12) at  $(E_-, 0)$  has one positive eigenvalue  $\lambda(c)$  and two eigenvalues with negative real parts.*

**Proof** The Jacobian matrix of (6.12) at  $(E_-, 0)$  is

$$J_0 = \begin{bmatrix} 0 & 0 & 1 \\ \frac{G_u(0,0)}{c} & \frac{G_v(0,0)}{c} & 0 \\ -\frac{F_u(0,0)}{D} & -\frac{F_v(0,0)}{D} & \frac{c}{D} \end{bmatrix}.$$

The characteristic equation of  $J_0$  is

$$\left(\lambda - \frac{G_v(0,0)}{c}\right) \left(\lambda^2 - \frac{c\lambda}{D} + \frac{F_u(0,0)}{D}\right) + \frac{G_u(0,0)F_v(0,0)}{Dc} = 0.$$

Consider  $f(\lambda, m) = \left(\lambda - \frac{G_v(0,0)}{c}\right) \left(\lambda^2 - \frac{c\lambda}{D} + \frac{F_u(0,0)}{D}\right) + m$ . Then we have

$$f\left(\lambda, \frac{F_u(0,0)G_v(0,0)}{Dc}\right) = \lambda \left[\lambda^2 - \left(\frac{c}{D} + \frac{G_v(0,0)}{c}\right)\lambda + \frac{F_u(0,0) + G_v(0,0)}{D}\right].$$

Since  $Df(E_-)$  is stable, it follows that

$$F_u(0,0) + G_v(0,0) < 0 \text{ and } F_u(0,0)G_v(0,0) - F_v(0,0)G_u(0,0) > 0.$$

Then it is easy to see that  $f\left(\lambda, \frac{F_u(0,0)G_v(0,0)}{Dc}\right)$  has three solutions  $0$ ,  $\lambda_1$  and  $\lambda_2$  with  $\lambda_1 < 0 < \lambda_2$ , and hence,  $f\left(\lambda, \frac{G_u(0,0)F_v(0,0)}{Dc}\right)$  has one positive solution and two solutions with negative real parts. Thus,  $J_0$  has one positive eigenvalue  $\lambda(c)$  and two eigenvalues with negative real parts. ■

By Lemma 6.2.1, (6.12) has a one-dimensional unstable manifold corresponding to  $\lambda(c)$  at  $(E_-, 0)$ . Let  $\bar{X} = (X_1, X_2, X_3)$  be an eigenvector of  $J_0$  corresponding to  $\lambda(c)$ . Then there is a nonconstant solution of (6.12)-(6.13), which tends to  $(E_-, 0)$  as  $\tau \rightarrow -\infty$  and whose tangent vector at  $\tau = -\infty$  is the eigenvector  $\bar{X}$  or  $-\bar{X}$ . It follows from the equation  $J_0\bar{X} = \lambda(c)\bar{X}$  that

$$\begin{cases} X_3 = \lambda(c)X_1, \\ \frac{G_u(0,0)X_1}{D} + \frac{G_v(0,0)X_2}{D} = \lambda(c)X_2, \\ -\frac{F_u(0,0)X_1}{D} - \frac{F_v(0,0)X_2}{D} + \frac{cX_3}{D} = \lambda(c)X_3. \end{cases}$$

Without loss of generality, we can assume that  $\bar{X} = \left(1, \frac{G_u(0,0)}{c\lambda(c) - G_v(0,0)}, \lambda(c)\right)$ . Since  $G_u(0,0) > 0$ ,  $G_v(0,0) < 0$ ,  $\lambda(c) > 0$ ,  $c > 0$ , we have  $X_i > 0$ ,  $i = 1, 2, 3$ .

In the rest of this section, we assume that  $(U, V, W)$  is a solution of (6.12)-(6.13) with the tangent vector  $\bar{X}$  at  $\tau = -\infty$ . By the above analysis, we can easily obtain the following result.

**Lemma 6.2.2** *Let  $(U, V, W)$  be a solution of (6.12)-(6.13). Then near  $\tau = -\infty$ ,  $(U, V, W)$  satisfies  $U > 0$ ,  $V > 0$ ,  $W = U' > 0$ , and  $V' > 0$ .*

**Definition 6.2.1** *Let  $(U, V, W)$  be a solution of (6.12)-(6.13). Let  $\tau_0 = \tau_0(c)$  be the first zero of  $U'$  if it exists and  $\bar{u} = U(\tau_0)$  ( $\bar{u}$  may be  $+\infty$ ).*

Since  $U > 0$  and  $U' > 0$  on  $(-\infty, \tau_0)$ , we can express  $V$  and  $W$  as functions of  $U$  for  $U \in (0, \bar{u})$ . Let  $\mathcal{V}(U) = V(\tau(U))$  and  $\mathcal{W}(U) = W(\tau(U))$  for  $U \in (0, \bar{u})$ . Then  $\mathcal{V}$  and  $\mathcal{W}$  satisfy the following equations

$$\mathcal{V}' = \frac{d\mathcal{V}}{dU} = \frac{G(U, \mathcal{V})}{c\mathcal{W}}, \quad (6.15)$$

$$\mathcal{W}' = \frac{d\mathcal{W}}{dU} = \frac{c\mathcal{W} - F(U, \mathcal{V})}{D\mathcal{W}}, \quad (6.16)$$

for  $U \in (0, \bar{u})$  with the initial conditions

$$\mathcal{V}(0) = 0, \mathcal{W}(0) = 0. \quad (6.17)$$

**Lemma 6.2.3** *Let  $(U, V, W)$  be a solution of (6.12)-(6.13). Then  $V'(\tau) > 0$  for all  $\tau \in (-\infty, \tau_0)$ .*

**Proof** Since  $V'(\tau) > 0$  near  $\tau = -\infty$  and  $U'(\tau) > 0$  for  $\tau \in (-\infty, \tau_0)$ , we have  $\mathcal{V}'(U) > 0$ , and hence,  $G(U, \mathcal{V}(U)) > 0$  for all  $U \in (0, u_0)$  for some  $u_0 \in (0, \bar{u}]$ . If  $u_0 < \bar{u}$  and  $G(u_0, \mathcal{V}(u_0)) = 0$ , then  $\mathcal{V}'(u_0) = 0$ . However,  $\frac{dG}{dU}|_{U=u_0} < 0$ , that is,  $[\frac{\partial G}{\partial U} + \frac{\partial G}{\partial \mathcal{V}} \cdot \frac{\partial \mathcal{V}}{\partial U}]_{U=u_0} < 0$ , which implies that  $\mathcal{V}'(u_0) > 0$ , a contradiction. Therefore,  $\mathcal{V}'(U) > 0$  for all  $U \in (0, \bar{u})$ , and hence,  $V'(\tau) > 0$  for all  $\tau \in (-\infty, \tau_0)$ . ■

**Lemma 6.2.4** *Let  $(U, V, W)$  be a solution of (6.12)-(6.13). If  $U(\tau) \in (0, a_2)$  for some  $\tau \in (-\infty, \tau_0)$ , then  $V(\tau) \in (0, b_2)$ .*

**Proof** Clearly, we have  $U(\tau) \in (0, a_2)$  and  $V(\tau) \in (0, b_2)$  when  $\tau$  is near  $-\infty$ . Suppose that there exists  $\tilde{\tau} \in (-\infty, \tau_0)$  such that  $U(\tilde{\tau}) \in (0, a_2)$ ,  $V(\tilde{\tau}) = b_2$ . Then  $G(U(\tilde{\tau}), V(\tilde{\tau})) = G(U(\tilde{\tau}), b_2) \leq G(a_2, b_2) = 0$  since  $G_u \geq 0$ . Thus, we have  $V'(\tilde{\tau}) \leq 0$ , a contradiction to  $V'(\tau) > 0$  on  $(-\infty, \tau_0)$ . ■

**Lemma 6.2.5** *There exists no nontrivial solution  $(U, V, W)$  of (6.12)-(6.13) satisfying  $U(\tau_0) = a_2$ ,  $U'(\tau_0) = 0$  and  $U''(\tau_0) \leq 0$  for some finite  $\tau_0$ .*

**Proof** Suppose that there is such a solution. Then either  $U''(\tau_0) < 0$  or  $U''(\tau_0) = 0$ . If  $U''(\tau_0) = 0$ , then by (6.8) we have  $F(U(\tau_0), V(\tau_0)) = 0$ . Since  $U(\tau_0) = a_2$ , we have  $V(\tau_0) = b_2$ , which contradicts the uniqueness of solutions. If  $U''(\tau_0) < 0$ , then  $F(U(\tau_0), V(\tau_0)) > 0$ , i.e.,  $F(a_2, V(\tau_0)) > 0 = F(a_2, b_2)$ . Since  $F_v \geq 0$ , we have  $V(\tau_0) > b_2$ . By  $G_v < 0$ , we have  $G(U(\tau_0), V(\tau_0)) = G(a_2, V(\tau_0)) < G(a_2, b_2) = 0$ . Thus, we have  $V'(\tau_0) < 0$ , which contradicts  $V'(\tau_0) \geq 0$ . ■

**Theorem 6.2.1** *System (6.6) has a monotone increasing traveling wave solution  $(U(x + ct), V(x + ct))$  connecting  $E_-$  to  $E_+$  for some real number  $c$  such that the wave speed  $c$  has the same sign as the integral  $\int_0^{a_2} F(U, V^*(U))dU$ , where  $V^*(U)$  satisfies  $G(U, V^*(U)) = 0$ .*

**Proof** Since  $V^*(U)$  is continuously differentiable on  $[0, a_2]$ ,  $\int_0^{a_2} F(U, V^*(U))dU$  is well defined.

In the case where  $\int_0^{a_2} F(U, V^*(U))dU = 0$ , we have shown that (6.11) has a heteroclinic orbit connecting  $(0, 0)$  and  $(a_2, 0)$ , and hence (6.6) has a monotone traveling wave solution with  $c = 0$ .

Next we consider the case where  $\int_0^{a_2} F(U, V^*(U))dU > 0$ . We proceed with the following four steps.

**Step 1.** We claim that  $\bar{u} > a_1$ . Indeed, it follows from Lemma 6.2.3 that  $\mathcal{V}(U) > 0$ , that is,  $G(U, \mathcal{V}(U)) > 0$  for all  $U \in (0, \bar{u})$ . Since  $G_v < 0$  and  $G(U, V^*(U)) = 0$ , we have  $\mathcal{V}(U) < V^*(U)$  for all  $U \in (0, \bar{u})$ . By (H12) and the implicit function theorem, we can also find a continuously differentiable function  $V_F^*(U)$  on  $[0, a_2]$  such that  $F(U, V_F^*(U)) = 0$  for all  $U \in [0, a_2]$ . Again by (H12) and the qualitative analysis of (6.7), it is not difficult to obtain  $V^*(U) < V_F^*(U)$  for all  $U \in (0, a_1)$ . Assume, by contradiction, that  $\bar{u} \leq a_1$ . Then  $F(U, \mathcal{V}(U)) < F(U, V^*(U)) < F(U, V_F^*(U)) = 0$  on  $(0, \bar{u})$ , and hence by (6.16),  $\mathcal{W}'(U) > \frac{c}{D} > 0$  on  $(0, \bar{u})$ , which implies that  $\mathcal{W}(\bar{u}) > 0$ . This contradicts  $\mathcal{W}(\bar{u}) = 0$ .

**Step 2.** We claim that if  $c$  is sufficiently large, then there exists a finite  $\hat{\tau}$  such that  $U'(\tau) > 0$  on  $(-\infty, \hat{\tau}]$  and  $U(\hat{\tau}) = a_2$ .

Choose  $c_0 > \sqrt{\frac{2|m_1|D}{a_1}}$ , where  $m_1 = \max_{(u,v) \in [0,a_2] \times [0,b_2]} F(u,v)$ . We claim that  $\bar{u} > a_2$  for  $c > c_0$ . Suppose that this is not true. Then there is some  $\bar{c} > c_0$  such that  $\bar{u} \leq a_2$  and  $\bar{W}(\bar{u}) = 0$ , where  $(\bar{V}, \bar{W})$  is the solution of (6.15)-(6.16) corresponding to  $\bar{c}$ . By analysis in step 1,  $\bar{W}' \geq \frac{\bar{c}}{D}$  for  $U \in (0, a_1]$ . Then  $\bar{W}(a_1) \geq \frac{\bar{c}}{D}a_1$ . Since  $\bar{W}(\bar{u}) = 0$  and  $\bar{u} \leq a_2$ , we have  $\bar{W}(U) \geq \frac{\bar{c}}{2D}a_1$  for all  $U \in [a_1, \hat{u}]$  for some  $\hat{u} \in (a_1, a_2)$  and  $\bar{W}(\hat{u}) = \frac{\bar{c}}{2D}a_1 < \bar{W}(a_1)$ . On the other hand, for all  $U \in [a_1, \hat{u}]$ ,  $\bar{W}'(U) = \frac{\bar{c}}{D} - \frac{F(U, \bar{V})}{D\bar{W}} \geq \frac{\bar{c}}{D} - \frac{m_1}{D\bar{W}} \geq \frac{\bar{c}}{D} - \frac{m_1}{D\frac{\bar{c}}{2D}a_1} = \frac{\bar{c}}{D} - \frac{2m_1}{\bar{c}a_1} = \frac{\bar{c}^2 - 2m_1D/a_1}{D\bar{c}} > 0$ . Thus,  $\bar{W}$  increases in  $U \in [a_1, \hat{u})$ , and hence  $\bar{W}(\hat{u}) > \bar{W}(a_1)$ , a contradiction. Thus, if  $c > c_0$ , we have  $\bar{u} > a_2$ , which indicates that there exists some finite  $\hat{\tau}$  such that  $U'(\tau) > 0$  on  $(-\infty, \hat{\tau}]$  and  $U(\hat{\tau}) = a_2$ .

Let  $(U(\tau), V(\tau), W(\tau))$  be a solution of (6.12)-(6.13). Set

$$P_1 = \{c > 0 : U'(\tau) > 0 \text{ on } (-\infty, \hat{\tau}] \text{ and } U(\hat{\tau}) = a_2 \text{ for some finite } \hat{\tau}\}.$$

Then  $P_1$  is not empty and  $P_1$  is open by continuous dependence on  $c$ . Moreover,  $P_1 \supseteq (c_0, +\infty)$ .

**Step 3.** We claim that for sufficiently small  $c > 0$ , there is a finite  $\bar{\tau}$  with  $U'(\bar{\tau}) = 0$  and  $U(\bar{\tau}) \in (a_1, a_2)$ .

Suppose that this is not true. Then there exists a sequence  $\{c_i\}_{i \in \mathbb{N}} \subseteq \mathbb{R}^+$  with  $\lim_{i \rightarrow +\infty} c_i = 0$  such that the corresponding solutions  $(U_i, V_i, W_i)$  of (6.12)-(6.13) satisfy  $(U_i)' > 0$  on  $(-\infty, \bar{\tau}_i)$  and  $U_i(\bar{\tau}_i) = a_2$  for some  $\bar{\tau}_i$  ( $\bar{\tau}_i$  may be infinity). By (6.16), we have

$$\frac{W_i^2(U)}{2} = \int_0^U \left[ \frac{c_i}{D} W_i(s) - \frac{F(s, V_i(s))}{D} \right] ds, \quad \forall U \in [0, a_2]. \quad (6.18)$$

Let

$$A_i = \sup_{U \in [0, a_2]} W_i(U) \text{ and } m_2 = \min_{(u,v) \in [0, a_2] \times [0, b_2]} F(u, v).$$

Then  $A_i > 0$ ,  $m_2 < 0$ , and  $\frac{A_i^2}{2} \leq \frac{c_i A_i a_2}{D} - \frac{m_2 a_2}{D}$ . Thus,  $\frac{A_i}{2} + \frac{m_2 a_2}{DA_i} \leq \frac{c_i a_2}{D}$ . Since  $\frac{x}{2} + \frac{m_2 a_2}{Dx}$  increases in  $x \in (0, +\infty)$  and  $c_i \rightarrow 0$  as  $i \rightarrow +\infty$ , we obtain that for large  $i$ ,  $A_i$  is

uniformly bounded. This implies that  $\mathcal{W}_i(U)$  is uniformly bounded on  $[0, a_2]$  for large  $i \in \mathbb{N}$ .

Let  $M_i(U) = G(U, \mathcal{V}_i(U))$ , for  $U \in [0, a_2]$ . Then

$$M_i'(U) = G_u + G_v \cdot \mathcal{V}_i'(U) = G_u + G_v \cdot \frac{M_i(U)}{c\mathcal{W}_i}$$

and

$$\begin{aligned} M_i(U) &= M_i(0)e^{\int_0^U \frac{G_v(s, \mathcal{V}_i(s))}{c_i \mathcal{W}_i(s)} ds} + \int_0^U G_u(s, \mathcal{V}_i(s))e^{\int_s^U \frac{G_v(t, \mathcal{V}_i(t))}{c_i \mathcal{W}_i(t)} dt} ds \\ &= \int_0^U G_u(s, \mathcal{V}_i(s))e^{\int_s^U \frac{G_v(t, \mathcal{V}_i(t))}{c_i \mathcal{W}_i(t)} dt} ds. \end{aligned} \quad (6.19)$$

Since  $\mathcal{W}_i(U)$  is uniformly bounded on  $[0, a_2]$  for large  $i \in \mathbb{N}$ ,  $c_i \mathcal{W}_i(U) \rightarrow 0$  as  $i \rightarrow \infty$  uniformly for  $U \in [0, a_2]$ .  $G_u(U, \mathcal{V}_i(U))$  is bounded for  $U \in [0, a_2]$  since  $G(u, v) \in C^1(\mathbb{R} \times \mathbb{R})$ . Moreover, there exists  $\delta > 0$  such that  $G_v \leq -\delta$  for  $(U, V) \in [0, a_2] \times [0, b_2]$ . Then we finally obtain  $M_i(U) \rightarrow 0$  as  $i \rightarrow \infty$  uniformly for  $U \in [0, a_2]$ . This, by the definitions of  $M_i(U)$  and  $V^*(U)$ , implies that  $G(U, \mathcal{V}_i(U)) \rightarrow G(U, V^*(U))$  as  $i \rightarrow \infty$ , uniformly for  $U \in [0, a_2]$ , that is,

$$\lim_{i \rightarrow \infty} |G(U, \mathcal{V}_i(U)) - G(U, V^*(U))| = 0, \text{ uniformly for } U \in [0, a_2]. \quad (6.20)$$

For any  $U \in [0, a_2]$  and  $i \in \mathbb{N}$ , we have

$$\begin{aligned} \delta_1 \cdot |\mathcal{V}_i(U) - V^*(U)| &\leq \left| \int_0^1 G_v(U, \mathcal{V}_i(U) + s(V^*(U) - \mathcal{V}_i(U))) ds (V^*(U) - \mathcal{V}_i(U)) \right| \\ &= |G(U, \mathcal{V}_i(U)) - G(U, V^*(U))|, \end{aligned}$$

where  $\delta_1 > 0$  is such that  $G_v \leq -\delta_1$  on  $[0, a_2] \times [0, b_2]$ . Then by (6.20), we have  $\mathcal{V}_i(U) \rightarrow V^*(U)$  as  $i \rightarrow \infty$  uniformly for  $U \in [0, a_2]$ , and hence,  $F(U, \mathcal{V}_i(U)) \rightarrow F(U, V^*(U))$  as  $i \rightarrow \infty$ , uniformly for  $U \in [0, a_2]$ . Then, letting  $U = a_2$  and  $i \rightarrow \infty$  in (6.18), we obtain

$$\lim_{i \rightarrow \infty} -\frac{DW_i^2(a_2)}{2} = \lim_{i \rightarrow \infty} \int_0^{a_2} F(s, \mathcal{V}_i(s)) ds = \int_0^{a_2} F(s, V^*(s)) ds. \quad (6.21)$$

Thus,  $\int_0^{a_2} F(s, V^*(s)) ds \leq 0$ , which contradicts our assumption that  $\int_0^{a_2} F(s, V^*(s)) ds > 0$ .

Let  $(U(\tau), V(\tau), W(\tau))$  be a solution of (6.12)-(6.13). Set

$$P_2 = \{c > 0 : U'(\bar{\tau}) = 0 \text{ for some finite } \bar{\tau} \in \mathbb{R} \text{ and } U(\bar{\tau}) \in (0, a_2)\}.$$

Then  $P_2$  is nonempty and contains  $(0, \bar{c})$  for some finite  $\bar{c} \in \mathbb{R}$ .

Moreover, for each  $c \in P_2$ , since  $\tau_0 = \tau_0(c)$  is the first zero of  $U'$ , we have  $U''(\tau_0) \leq 0$ . Then by Lemma 6.2.5,  $U(\tau_0) \in (a_1, a_2)$ . Suppose that  $U''(\tau_0) = 0$ . By (6.12), we have  $F(U(\tau_0), V(\tau_0)) = 0$  and  $G(U(\tau_0), V(\tau_0)) \geq 0$ . However, by (H12)(ii), we have  $G(U(\tau_0), V(\tau_0)) > 0$ , that is,  $V'(\tau_0) > 0$ . It then follows that

$$\begin{aligned} U'''(\tau_0) &= W'''(\tau_0) = \frac{c}{D}W''(\tau_0) - \frac{1}{D}F_u \cdot U'(\tau_0) - \frac{1}{D}F_v \cdot V'(\tau_0) \\ &= -\frac{1}{D}F_v(U(\tau_0), V(\tau_0))V'(\tau_0) \\ &< 0. \end{aligned}$$

This contradicts the definition of  $\tau_0$ . Thus, we have  $U''(\tau_0) < 0$ , and hence,  $P_2$  is open.

**Step 4.** Let  $c^* = \sup P_2$ . By above two steps,  $c^*$  exists and  $c^* \in \mathbb{R}^+ \setminus (P_1 \cup P_2)$ . Let  $(U^*(\tau), V^*(\tau), W^*(\tau))$  be a solution of (6.12)-(6.13) corresponding to  $c^*$ . Then  $U^{*'} > 0$  and  $V^{*'} > 0$  on  $\mathbb{R}$ . Moreover,  $U^*(\tau) \in (0, a_2)$  and  $V^*(\tau) \in (0, b_2)$  for all  $\tau \in \mathbb{R}$ . Then as  $\tau$  tends to  $+\infty$ ,  $U^*(\tau)$  and  $V^*(\tau)$  have limits. Since  $\bar{u} > a_1$ , we have  $\lim_{\tau \rightarrow +\infty} U^*(\tau) = a_2$  and  $\lim_{\tau \rightarrow +\infty} V^*(\tau) = b_2$ . Thus,  $(U^*(\tau), V^*(\tau))$  is the bistable traveling waves of (6.6) connecting  $E_-$  to  $E_+$  with positive speeds  $c^*$  when  $\int_0^{a_2} F(U, V^*(U))dU > 0$ .

Finally, we consider the case where  $\int_0^{a_2} F(U, V^*(U))dU < 0$ . By a change of variables  $\bar{u} = a_2 - u$ ,  $\bar{v} = b_2 - v$ , (6.6) reduces to

$$\begin{cases} \frac{\partial \bar{u}}{\partial t} = D \frac{\partial^2 \bar{u}}{\partial x^2} + \bar{F}(\bar{u}, \bar{v}), \\ \frac{\partial \bar{v}}{\partial t} = \bar{G}(\bar{u}, \bar{v}), \end{cases} \quad (6.22)$$

where  $\bar{F}(\bar{u}, \bar{v}) = -F(a_2 - \bar{u}, b_2 - \bar{v})$ ,  $\bar{G}(\bar{u}, \bar{v}) = -G(a_2 - \bar{u}, b_2 - \bar{v})$ . Letting  $\bar{G}(\bar{u}, \bar{v}) = 0$ , we have  $\bar{v} = \bar{v}^*(\bar{u}) := b_2 - V^*(a_2 - \bar{u})$ . Then  $\bar{f}(\bar{u}, \bar{v}) := (\bar{F}(\bar{u}, \bar{v}), \bar{G}(\bar{u}, \bar{v}))$  has only three zeros  $E_- = (0, 0)$ ,  $E_+ = (a_2, b_2)$  and  $\bar{E}_0 = (a_2 - a_1, b_2 - b_1)$  on  $[E_-, E_+]$ . Moreover, it

is easy to see that (6.22) satisfies (H12) and

$$\int_0^{a_2} \bar{F}(\bar{u}, \bar{v}^*(\bar{u})) d\bar{u} = - \int_0^{a_2} F(U, V^*(U)) dU > 0.$$

It follows from what we have proved that (6.22) has a monotone increasing traveling wave solution  $(\bar{U}(x+ct), \bar{V}(x+ct))$  connecting  $E_-$  and  $E_+$  for some  $c > 0$ . Define  $U(\xi) = a_2 - \bar{U}(-\xi)$ ,  $V(\xi) = b_2 - \bar{V}(-\xi)$ ,  $\forall \xi \in \mathbb{R}$ . Clearly,  $(U(-\infty), V(-\infty)) = (0, 0)$  and  $(U(\infty), V(\infty)) = (a_2, b_2)$ . It then follows that  $(U(x-ct), V(x-ct))$  is a monotone increasing traveling wave solution of (6.6) connecting  $E_-$  and  $E_+$ . ■

### 6.3 Attractivity and uniqueness of bistable waves

In this section, we discuss the global attractivity with phase shift and uniqueness (up to translation) of the bistable traveling wave of (6.6). In addition to (H12), we further impose the following conditions on  $F$  and  $G$ .

(H13)  $F$  and  $G$  can be extended to the domain  $(-l, \infty)^2$  for some  $l > 0$  such that

(i)  $F, G \in C^2((l, \infty)^2, \mathbb{R})$ ,  $F_u(u, v) < 0$ ,  $F_v(u, v) > 0$ ,  $G_u(u, v) \geq 0$  and  $G_v(u, v) < 0$  for  $(u, v) \in (-l, \infty)^2$ .

(ii) There exists  $L > 0$  such that for any  $l_2 > L$ , there exists  $l_1 > 0$  such that  $F(l_1, l_2) < 0$ .

Let  $\mathbb{X} = BUC(\mathbb{R}, \mathbb{R}^2)$  be the Banach space of all bounded and uniformly continuous functions from  $\mathbb{R}$  to  $\mathbb{R}^2$  with the usual supreme norm. Let  $\mathbb{X}_+ = \{(\psi_1, \psi_2) \in \mathbb{X} : \psi_i(x) \geq 0, \forall x \in \mathbb{R}, i = 1, 2\}$ . Then  $\mathbb{X}_+$  is a closed cone of  $\mathbb{X}$  and its induced partial ordering makes  $\mathbb{X}$  into a Banach lattice. For any  $\psi^1 = (\psi_1^1, \psi_2^1), \psi^2 = (\psi_1^2, \psi_2^2) \in \mathbb{X}$ , we write  $\psi^1 \leq_{\mathbb{X}} \psi^2$  if  $\psi^2 - \psi^1 \in \mathbb{X}_+$ ,  $\psi^1 <_{\mathbb{X}} \psi^2$  if  $\psi^2 - \psi^1 \in \mathbb{X}_+ \setminus \{0\}$ ,  $\psi^1 \ll_{\mathbb{X}} \psi^2$  if  $\psi^2 - \psi^1 \in \text{Int}(\mathbb{X}_+)$ .

By the arguments similar to those in [92, Lemma 3.1], we can prove the following result for (6.6).

**Lemma 6.3.1** For any  $\psi \in \mathbb{X}_+$ , (6.6) has a unique bounded and nonnegative solution  $(\Psi(t)\psi)(x) := (u(t, x, \psi), v(t, x, \psi))$  with  $\Psi(0)\psi = \psi$ , and the solution semiflow  $\Psi(t)$  of (6.6) is monotone on  $\mathbb{X}_+$ . Moreover,  $(\Psi(t)\psi^1)(x) \ll (\Psi(t)\psi^2)(x)$  for all  $t > 0$  and  $x \in \mathbb{R}$  whenever  $\psi^1, \psi^2 \in \mathbb{X}_+$  with  $\psi^1 <_{\mathbb{X}} \psi^2$ .

In view of section 2, we assume that  $\phi(x - ct) = (\phi_1(x - ct), \phi_2(x - ct))$  is a strictly increasing traveling wave solution of (6.6) connecting  $E_-$  and  $E_+$ . Letting  $z = x - ct$ , we transform (6.6) into the following system:

$$\begin{cases} u_t(t, z) = cu_z(t, z) + Du_{zz}(t, z) + F(u(t, z), v(t, z)), \\ v_t(t, z) = cv_z(t, z) + G(u(t, z), v(t, z)). \end{cases} \quad (6.23)$$

It is easy to see that  $\phi(z)$  is an equilibrium of system (6.23). Denote  $(\Phi(t)\psi)(z) := (u(t, z, \psi), v(t, z, \psi))$  as the solution of (6.23) with  $\Phi(0)\psi = \psi \in \mathbb{X}_+$ . Then the solution  $(\Psi(t)\psi)(x)$  of (6.6) with initial value  $\psi$  is given by  $(\Psi(t)\psi)(x) = (\Phi(t)\psi)(x - ct)$ . Moreover, the comparison principle holds for (6.6) and hence for (6.23). By constructing upper and lower solutions for (6.23) in the same way as in [92], we can obtain the following result.

**Lemma 6.3.2** The wave profile  $\phi(z)$  is a Liapunov stable equilibrium of (6.23).

Since  $\Phi(t) : \mathbb{X}_+ \rightarrow \mathbb{X}_+$  is the solution semiflow of (6.23), it follows that  $\Phi(t) : [E_-, E_+] \rightarrow [E_-, E_+]$  is monotone and for any  $s \in \mathbb{R}$ ,  $\phi(\cdot + s)$  is a stable equilibrium of  $\Phi(t)$ . Consequently, by using the convergence theorem Theorem 2.2.3 and the similar arguments as in the proof of [92, Theorem 3.1], we can establish the following result on the global attractivity with phase shift and uniqueness (up to translation) of the bistable wave of (6.6).

**Theorem 6.3.1** Let  $\phi(x - ct)$  be a monotone traveling wave solution of system (6.6) and  $\Psi(t, x, \psi) := (u(t, x, \psi), v(t, x, \psi))$  be the solution of (6.6) with  $\Psi(0, \cdot, \psi) = \psi \in \mathbb{X}_+$ . Then for any  $\psi \in \mathbb{X}_+$  with

$$\limsup_{\xi \rightarrow -\infty} \psi(\xi) \ll E_0 \ll \liminf_{\xi \rightarrow -\infty} \psi(\xi), \quad (6.24)$$

there exists  $s_\psi \in \mathbb{R}$  such that  $\lim_{t \rightarrow +\infty} \|\Psi(t, x, \psi) - \phi(x - ct + s_\psi)\| = 0$  uniformly for  $x \in \mathbb{R}$ . Moreover, any traveling wave solution of system (6.6) connection  $E_-$  and  $E_+$  is a translate of  $\phi$ .

**Remark 6.3.1** By the spectrum analysis of the linearization operator of (6.23) at the equilibrium solution  $\phi(z)$ , as in [92, Section 4], we can obtain the local exponential stability with phase shift of the bistable wave  $\phi(x - ct)$  with  $c \neq 0$ . This, together with Theorem 6.3.1, implies the global exponential stability with phase shift of the bistable wave  $\phi(x - ct)$  with  $c \neq 0$  of (6.6).

**Remark 6.3.2** Recently, Tsai [80] studied the global exponential stability of traveling waves in monotone bistable systems:

$$\begin{cases} \frac{\partial \mathbf{u}}{\partial t} = \mathbf{D} \frac{\partial^2 \mathbf{u}}{\partial x^2} + F(\mathbf{u}), & (t, x) \in (0, \infty) \times \mathbb{R}, \quad \mathbf{u}(t, x) \in \mathbb{R}^n, \\ \mathbf{u}(0, x) = \mathbf{u}_0(x), & x \in \mathbb{R}, \end{cases}$$

where  $\mathbf{D}$  is a diagonal matrix of order  $n$  with elements of the vector  $(D_1, \dots, D_n)$  on the diagonal, with  $D_i > 0$  for  $i = 1, \dots, n_1$ , and  $D_i = 0$  for  $i = n_1 + 1, \dots, n$ . In this work, he used some basic tools of comparison principle, super-sub solutions construction, and squeezing methods, instead of spectrum analysis. However, it was required that  $\partial F^1 / \partial u_i > 0$  and  $\partial F^j / \partial u_1 > 0$ , for all  $i, j \in \{2, \dots, n\}$ , on the interval between two positive equilibria, which is stronger than our conditions in (H12) and (H13).

## 6.4 Examples

In this section, we apply the results in sections 2 and 3 to some reaction-diffusion population models and show the existence and global exponential stability of bistable waves.

**Example 1.** Consider a reaction-diffusion epidemic model (see, e.g., [12] and [92])

$$\begin{cases} \frac{\partial U_1(x, t)}{\partial t} = d \frac{\partial^2 U_1(x, t)}{\partial x^2} - U_1(x, t) + \alpha U_2(x, t), \\ \frac{\partial U_2(x, t)}{\partial t} = -\beta U_2(x, t) + g(U_1(x, t)), \end{cases} \quad (6.25)$$

where  $d$ ,  $\alpha$  and  $\beta$  are positive constants,  $U_1$  and  $U_2$  denote the spatial densities of infectious agent and the infective human population,  $F(U_1, U_2) = -U_1(x, t) + \alpha U_2(x, t)$ ,  $G(U_1, U_2) = -\beta U_2(x, t) + g(U_1(x, t))$ . The existence, uniqueness (up to translation) and global exponential stability with phase shift of the bistable traveling wave with nonzero wave speed were established for (6.25) in [92]. However, it seems that the claim in step 2 of the proof of Theorem 2.1 (for the existence) in [92] needs to be readdressed since the inequality

$$\dot{V}_c(\eta) = \frac{c}{d} - \frac{\eta - \alpha u_2}{md(\eta - b)} \leq \frac{c}{d} + \frac{b - \eta}{md(\eta - b)} = \frac{1}{d} \left( c - \frac{1}{m} \right)$$

cannot be obtained as the authors stated there. By Theorem 6.2.1, we can establish the existence of the bistable wave under the assumptions (A1), (A2) and (A3) in [92].

**Example 2.** Consider a reaction-diffusion model with quiescent phases (see, e.g., [31, 48, 83])

$$\begin{cases} v_t = D\Delta v - \mu v - \gamma_2 v + \gamma_1 w, \\ w_t = g(w) - \gamma_1 w + \gamma_2 v, \end{cases} \quad (6.26)$$

where  $v$  and  $w$  are densities of two particles,  $g$  is smooth,  $D, \mu, \gamma_1, \gamma_2 > 0$ . For system (6.26),  $F(v, w) = -\mu v - \gamma_2 v + \gamma_1 w$ ,  $G(v, w) = g(w) - \gamma_1 w + \gamma_2 v$ . Then  $F_v = -\mu - \gamma_2 < 0$ ,  $F_w = \gamma_1 > 0$ ,  $G_v = \gamma_2 > 0$ . Assume that  $g \in C^2(-l, \infty)$  for some  $l > 0$  such that  $g(0) = 0$ ,  $g'(w) > 0$ ,  $\forall w > 0$ , and  $g'(w) < \gamma_1$  on  $(-l, +\infty)$ , that  $g(w) = \frac{\mu w}{\mu + \gamma_2}$  has only three zeros  $0, b_1, b_2$  on  $[0, b_2]$ , and that  $g''(w) > 0$  for  $w \in (0, b_1)$ ,  $g''(w) < 0$  for  $w > b_1$ . It is easy to check that system (6.26) satisfies (H12)-(H13). By Theorems 6.2.1 and 6.3.1, it then follows that system (6.26) admits a bistable traveling wave, which is globally attractive with phase shift (or even globally exponentially stable with phase shift when the wave speed  $c \neq 0$ ) and unique (up to translation).

**Example 3.** Consider a reaction-diffusion model with a quiescent stage (see, e.g., [32, 94])

$$\begin{cases} \frac{\partial u_1(t, x)}{\partial t} = D\Delta u_1(t, x) + f(u_1(t, x)) - \gamma_2 u_1(t, x) + \gamma_1 u_2(t, x), \\ \frac{\partial u_2(t, x)}{\partial t} = \gamma_2 u_1(t, x) - \gamma_1 u_2(t, x), \end{cases} \quad (6.27)$$

where  $u_1, u_2$  are densities of the dispersal and nondispersal subpopulations,  $D > 0$ ,  $f(u)$  is a nonlinear continuous function,  $\gamma_1$  and  $\gamma_2$  are the emigration and immigration rates, respectively. For system (6.27),  $F(u_1, u_2) = f(u_1) - \gamma_2 u_1 + \gamma_1 u_2$ ,  $G(u_1, u_2) = \gamma_2 u_1 - \gamma_1 u_2$ . Then  $F_{u_2} = \gamma_1 > 0$ ,  $G_{u_1} = \gamma_2 > 0$ ,  $G_{u_2} = -\gamma_1 < 0$ . If we further assume that  $f \in C^2(-l, \infty)$  for some  $l > 0$  such that  $f'(u_1) - \gamma_2 < 0$  for  $u_1 \in (-l, \infty)$ , that  $f(u_1)$  has only three zeros  $0, a_1, a_2$  on  $[0, a_2]$ , and that  $f'(0) < 0$ ,  $f'(a_1) > 0$  and  $f'(a_2) < 0$ , then (6.27) satisfies (H12) and (H13). Thus, Theorems 6.2.1 and 6.3.1 imply that system (6.27) admits a bistable traveling wave, which is globally attractive with phase shift (or even globally exponentially stable with phase shift when the wave speed  $c \neq 0$ ) and unique (up to translation). As a particular example,  $f$  can be chosen as  $f(u_1) = u_1(u_1 - a)(1 - u_1)$  for some  $0 < a < 1$ .

# Chapter 7

## Summary and Future Work

In this chapter, we briefly summarize the results in this thesis and present some possible problems as future work.

In this thesis, we studied the evolution dynamics of four population models with spatial and temporal heterogeneities. The main topics of all these projects are about traveling waves and spreading speeds, which are very important characteristics in biological invasions.

In Chapter 3, motivated by the autonomous integro-differential models in [55, 59, 68], we considered that population dynamics depends on the time-varying environment and proposed a periodic model (3.5). We generalized the results about the spreading speed and traveling waves for the autonomous models in [55, 59, 68] to our periodic model and obtained the existence and formula of the spreading speed  $c^*$ , the nonexistence of periodic traveling waves connecting 0 and a positive periodic solution when  $c < c^*$ , and the existence of traveling waves when  $c \geq c^*$  for the associated autonomous system. Note that in the above three mentioned references, the spreading speed was studied in a weak sense (see Chapter 3) and mainly by the “linear conjecture”, while we studied the spreading speed in a strong sense (see Chapter 3) with rigorous mathematical analysis. One thing that has to be pointed out is that, the existence of periodic traveling waves when  $c \geq c^*$  remains an open problem.

In Chapter 4, motivated by the study of some reaction-diffusion models with stage-structure in [27, 75, 78, 91]), we investigate a non-local periodic reaction-diffusion population model with stage-structure (4.2). We successfully generalized the results of the spreading speed and traveling waves in unbounded domains and the threshold result in a bounded domain for the autonomous models in [27, 75, 78, 91]) to the general periodic system (4.2). More precisely, in the case of unbounded spatial domain, we established the existence of the asymptotic speed of spread and showed that it coincides with the minimal wave speed for monotone periodic traveling waves connecting 0 and a positive periodic solution; in the case of bounded spatial domain, we obtained a threshold result on the global attractivity of either zero or a positive periodic solution.

In Chapter 5, we considered a class of discrete-time population models (5.3), which was proposed in [85], in a periodic lattice habitat. The spreading speeds and traveling waves for the continuous version of this model in homogeneous habitats when the recruitment function is not necessarily monotone have been studied in [38, 49]. The continuous version in periodic habitats when the recruitment function is not necessarily monotone has also been studied numerically in [40] and the spreading speeds have been obtained in [87]. There is no result about the existence of the spatially periodic traveling waves in this case. We studied the lattice model (5.3) in two cases. When the recruitment function is monotone in the population density, we obtained the formula of the spreading speeds and showed that the spreading speeds coincide with the minimal wave speeds for spatially periodic traveling waves in the positive and negative directions. When the recruitment function is not monotone in the population density, we constructed two monotone systems to control the nonmonotone system and used the spreading speeds for the monotone systems to estimate the spreading speeds for the nonmonotone system. In this case, we also showed that for any wave speed greater than the spreading speed, there exists a spatially periodic traveling wave, while for any wave speed less than the spreading speed, there is no spatially periodic traveling wave. However, we did not obtain any result about the existence

of a spatially periodic traveling wave with wave speed equal to the spreading speed.

In Chapter 6, motivated by some specific population models in [12, 32, 48, 65, 92], we proposed a general model of a class of cooperative reaction-diffusion systems (6.6), in which one population (or subpopulation) diffuses while the other is sedentary. The monostable case has been well studied for specific examples of (6.6) in [12, 32, 48, 65], while it seems that the bistable case has only been studied in [92] for a specific example. The existence, uniqueness and global stability of the bistable traveling waves have been obtained there. In our work, for the most general model (6.6), we established the existence of the bistable traveling wave by the shooting method, and then obtained its global attractivity with phase shift and uniqueness (up to translation) via the dynamical system approach. The results can be well applied to the examples in [12, 32, 48, 65, 92] and all other examples which satisfy the basic assumptions for (6.6).

Besides the unsolved problems arising from the finished projects in this thesis, which are mentioned above, there are quite a few related problems which may be my future work. In the first two projects, I considered the time periodic systems which are obvious more realistic than autonomous systems for many species. However, the time periodic systems are still simple cases of most general situations. As future work, I would like to study the almost periodic case of the models or simply assume that the parameters generally depend on the time  $t$ . Moreover, in Chapter 4, I assumed that the maturation time for all individuals are the same, which implies that the maturation recruitment at any time  $t$  simply depends on the population at time  $t - \tau$ . However, in real situations, for some populations, the maturation time is not always the same for all individuals. This results in the possibility of distributed delay or time delay depending on time  $t$ . Therefore, I would also like to study the model (4.2) in the almost periodic case or under the assumption of  $\tau = \tau(t)$ . In the first three projects, I only considered the monostable case, another interesting problem would be to investigate these models in the bistable case. To include the water flow in the stream population models, we may add an advection term in a reaction-diffusion

model and then study the spreading speeds and (periodic) traveling waves. Noting that the dispersal of immature population and mature population may not be the same, we can also incorporate age-structure into a model with long-term dispersal, for instance, (3.5). Finally, it is very important to consider the long time dispersal in a stochastic model. This may also be a part of my future work.

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