

Seasonal influences on population spread and persistence in streams: spreading speeds ^{*}

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Abstract: The drift paradox asks how stream-dwelling organisms can persist, without being washed out, when they are continuously subject to the unidirectional stream flow. To date, mathematical analyses of the stream paradox have investigated the interplay of growth, drift and flow needed for species persistence under the assumption that the stream environment is temporally constant. However, in reality, streams are subject to major seasonal variations in environmental factors that govern population growth and dispersal. We consider the influence of such seasonal variations on the drift paradox, using a time-periodic integrodifferential equation model. We establish upstream and downstream spreading speeds under the assumption of periodically fluctuating environments, and also show the existence of periodic traveling waves. The sign of the upstream spreading speed then determines persistence. Fluctuating environments are characterized by seasonal correlations between the flow, transfer rates, diffusion and settling rates, and we investigate the effect of such correlations on the population spread and persistence. We also show how results in this paper can formally connect to those for autonomous integrodifferential equations, through the appropriate weighted averaging methods. Finally, for a specific dispersal function, we show that the upstream spreading speed is nonnegative if and only if the critical domain size exists in this temporally fluctuating environment.

Key words: Seasonal environment, population, stream, spreading speeds, periodic traveling waves

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1 Introduction

Because stream species are subject to unidirectional flows for much of their lives, their growth, movement and persistence in the flow has attracted increasing scientific scrutiny. Indeed, the influences of population dynamics, individual random diffusion and flow velocity on the spread and persistence of a population in a stream have been extensively investigated by mathematicians and ecologists; see, e.g., [11, 12, 18, 20, 22, 23, 25, 26, 28]. However, to date, these investigations have focused on temporally constant stream environments, even though typical temperate stream environments can exhibit strong seasonal fluctuations in both population growth rates and hydrodynamical properties such as flow rates and random dispersal. This seasonality may be a key factor that can affect the population spread or persistence and thus its influence cannot be neglected in long term studies of stream species. One approach to investigate such seasonality is to ask how mathematical predictions for population persistence and invasion in streams change, both quantitatively and qualitatively, when the seasonality is included in models for stream populations.

Traditional mathematical models for populations in streams are partial differential equations, in which population dispersal consists of local random diffusion and movements caused by water advection; see e.g., [18, 25, 26]. In recent years, integrodifference and integrodifferential equations have been used to describe biological invasions and population persistence; see e.g., [9, 11, 12, 20, 28]. Integrodifferential equations provide a flexible modelling framework for population dispersal in streams because both asymmetric dispersal and long-range effects are taken into account [20]. In these models, the long distance dispersal of a population is described by a dispersal kernel, $k(x, y)$, which represents the proportion of individuals moving from location y to location x over a given dispersal event.

For many aquatic organisms it is reasonable to expect that dispersal will operate on a fast fine scale of days or weeks relative to a slower fine scale of months or years for population dynamics. In these cases, a simple form for the dispersal kernels can be derived from a submodel (see Appendix A) operating on the fast fine scale that involves population diffusion (D), water advection (v) and population settling from water to benthos (β) (see also [20] for a derivation of the time-independent version). This gives rise to an asymmetric dispersal kernel

$$k(t, x, y) = \begin{cases} A(t) \exp(b_1(t)(x - y)), & x - y \leq 0 \\ A(t) \exp(b_2(t)(x - y)), & x - y > 0 \end{cases} \quad (1.1)$$

where

$$b_{1,2}(t) = \frac{v(t)}{2D(t)} \pm \sqrt{\frac{v^2(t)}{4D^2(t)} + \frac{\beta(t)}{D(t)}}$$

and

$$A(t) = \frac{b_1(t)b_2(t)}{b_2(t) - b_1(t)},$$

where the asymmetry arises from the advection $v(t)$. Figure 1 (a) and (b) give examples of symmetric and asymmetric versions of this dispersal kernel, respectively. It is clear that in natural streams, the stream factors such as water discharge, temperature, light and etc, and population dynamics usually vary in time, especially in different seasons. Therefore, it is reasonable to introduce a time-dependent dispersal kernel $k(t, x, y)$ into a stream population model. Moreover, note that many previous authors have imposed symmetry condition on the dispersal kernel $k(t, x, y) = k(t, y, x)$, which means that the proportion that the population moving from location x to location y is the same as that from y to x . While this may be true for many population systems, it is unreasonable when we consider a species dispersing in a river or stream where the individuals face a unidirectional flow (see Figure 2). The water advection reduces the probability of upstream movement and increases the probability of downstream movement, and hence provides reasons for assuming an asymmetric dispersal kernel $k(t, x, y)$ for stream species.

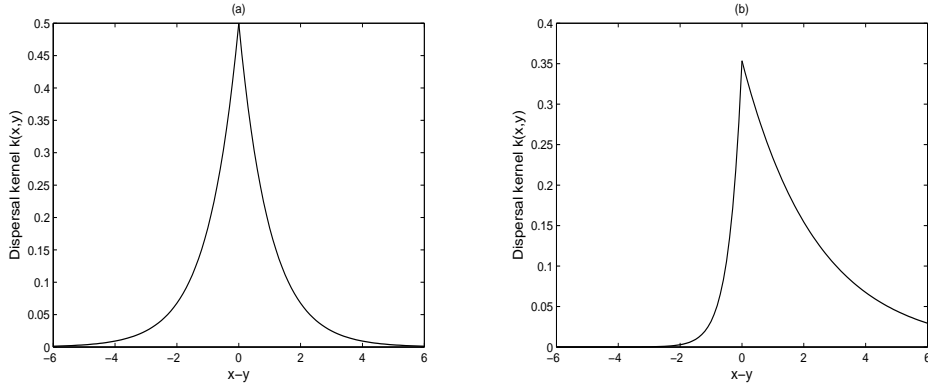


Figure 1: Time-independent dispersal kernels $k(t, x, y)$ defined in (1.1), where the diffusion rate $D(t) \equiv 1$, the settling rate $\beta(t) \equiv 1$. In (a), the flow velocity $v(t) \equiv 0$; in (b), the flow velocity $v(t) \equiv 2$.

In this work, based on an extension of the autonomous integro-differential equation in [20], we will investigate the influences of the seasonal variations of population dynamics and dispersal on the population spread and persistence in streams. We consider the following periodic model for stream species

$$\frac{\partial u(t, x)}{\partial t} = \underbrace{u(t, x)g(t, u(t, x))}_{\text{growth}} - \underbrace{a(t)u(t, x)}_{\text{emigration}} + a(t) \underbrace{\int_{\Omega} k(t, x, y)u(t, y)dy}_{\text{immigration}}, \quad t \geq 0, x \in \Omega, \quad (1.2)$$

where $\Omega = \mathbb{R}$ represents a stream in one dimensional space, $u(t, x)$ is the spatial density of a population at the point $x \in \Omega$ at time $t \geq 0$, $g(t, u)$ is the per capita growth rate at the density u at time $t \geq 0$, $a(t)$ is the rate at which an individual leaves its current location at time $t \geq 0$, or the transfer rate of the population from stationary state to the mobile state at time $t \geq 0$, and $k(t, x, y)$ is the dispersal kernel that describes the proportion of individuals that moves from point y to point x at time $t \geq 0$ and is not symmetric in x and y . Moreover, we assume that g , a and k are ω -periodic in t for some $\omega > 0$. In the sense of seasonality variation, ω can be considered as the length of one year. This model can be derived from a two-stage (mobile and stationary) population model; see Appendix A.

As first introduced by Aronson and Weinberger [3] for reaction-diffusion equations, the asymptotic speed of spread (in short, spreading speed) is an important ecological metric in a wide range of ecological applications. It describes the asymptotic tendency of the spread or invasion phenomenon of species in spatial habitats and predicts the long term invasion of a population (see Figure 2 for population spreading in a stream environment). It has been extensively investigated for many ecological models; see, e.g., [14, 15, 30, 31]. Traveling wave solutions have also been studied for a variety of evolution equations (see, e.g., [14, 15, 20, 30, 31, 33]), as they represent a kind of special evolution dynamics.

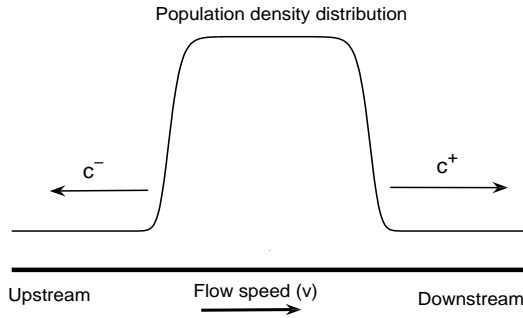


Figure 2: The flow speed v , upstream spreading speed c^- and downstream spreading speed c^+ of a population in a stream. The directions of the arrows indicate the positive direction of the corresponding variables. That is, $v > 0$ corresponds to the flow to the downstream and $v < 0$ to the flow to the upstream; $c^+ > 0$ corresponds to population spreading to the downstream and $c^+ < 0$ to population spreading to the upstream; $c^- > 0$ corresponds to population spreading to the upstream and $c^- < 0$ to population spreading to the downstream. Due to the definition of c^- , the relation between the sign of c^- and population's spreading direction in this paper is different from that in some previous works (e.g., [20]), where $c^- > 0$ corresponds to population spreading to the downstream and $c^- < 0$ to population spreading to the upstream.

The *drift paradox* problem (see, e.g., [22, 23]) asks how aquatic species can avoid washout when living in environments with unidirectional flow. Since the problem was proposed by Müller in 1954 [22], one line of research has shown that the drift paradox relates to the upstream spreading speed for the population and its dependence on the flow speed. The population will be washed downstream if the water flow speed is too high, but will persist, i.e., spread to both upstream and downstream, if the water velocity is relatively low and the reproduction is sufficiently large [16, 20, 22, 23, 25, 26]. In this work, we attempt to provide some solutions to the drift paradox problem via the study of spreading speeds, especially, the upstream spreading speed.

This paper is the sequel to [8], where the seasonal influences on population invasions have been investigated mathematically from the perspective of the critical domain size, which is the minimal size of the habitat needed for a species to persist. The analysis in [8] showed that seasonal variations of population birth, death, transfer from stationary to mobile states, diffusion, settling, and the flow velocity greatly influence the critical domain size and hence the possibility of population persistence in a bounded stream.

In this paper, we assume spatially uniform time-dependent asymmetric dispersal so, at any point in time, dispersal between two locations depends on the signed distance between them. Thus k is rewritten as $k(t, x - y)$ and equation (1.2) becomes

$$\frac{\partial u(t, x)}{\partial t} = u(t, x)g(t, u(t, x)) - a(t)u(t, x) + a(t) \int_{\mathbb{R}} k(t, x - y)u(t, y)dy. \quad (1.3)$$

For the case where k is independent of time t and symmetric (i.e., $k(x) = k(-x)$ for any $x \in \mathbb{R}$), spreading speeds and periodic traveling waves for (1.3) have been studied [9]. As these assumptions violate a real stream situations, results are not suitable for a stream species. We start in Section 2 by considering upstream and downstream spreading speeds for our more realistic model. Although spread can vary on the short times scales between seasons, we consider the year-to-year spread on longer times scales via a Poincaré map, and determine a formula for calculating the speed of this spread. We show that, when the dispersal kernel has a moment generating function, this spread has finite speeds in both upstream and downstream directions and they coincide with the minimal wave speeds for periodic traveling waves, in both directions, respectively. We interpret a positive upstream spreading speed as persistence of the population in the time-periodic river environment. When the moment generating function does not exist, the population spreads at accelerating speeds and has infinite spreading speeds. This translates into unconditional persistence in the time-periodic river environment. Section 3 analyses the spreading speeds in a two-season environment and obtains the approximate effects of the normalized covariances between the flow velocity and the transfer rate, the diffusion rate and the settling rate, on the spreading speeds. By

this approximation, we see very interesting results about the co-effects, in the sense of normalized covariances, of the flow velocity and the transfer rate, the diffusion rate and the settling rate, on the spreading speeds and population persistence. In Section 4, as we analyze the expressions of spreading speeds for the periodic model (1.3) and its autonomous case, we find that the spreading speeds are equal to those of an associated autonomous model which is obtained by averaging the functions $g(t, u)$ and $a(t)k(t, x - y)$ with respect to t . Moreover, for (1.3) with the dispersal kernel in (1.1) but constant β , v and D , by comparing the conditions for the critical domain size to exist in [8] and those for the upstream spreading speed to be positive in this paper, we see that the conditions for the upstream spreading speed to be nonnegative in an infinitely long stream are exactly those for the population to persist in a bounded stream.

2 Spreading speeds and periodic traveling waves

In this section, we will study the upstream and downstream spreading speeds and the existence of periodic traveling waves for the system (1.3). Firstly, we make some biologically reasonable assumptions for the model that facilitate the mathematical analysis of the model:

- (H1) (i) $g \in C(\mathbb{R}_+^2, \mathbb{R})$ and $g_u(t, u) < 0$ for all $(t, u) \in \mathbb{R}_+^2$, i.e., the per capita growth rate $g(t, u)$ decreases with respect to the population density; $\int_0^\omega g(t, 0)dt > 0$, which leads to the instability of the zero solution, and hence, population with a low density does not become extinct; there exists $\hat{u} > 0$ such that $g(t, \hat{u}) \leq 0$ for all $t \geq 0$, i.e., the growth rate is negative if the population density is over \hat{u} , and hence, the population will not explode;
- (ii) the transfer rate $a(t) > 0$ and continuous, that is, transfer occurs continuously during the cycle;
- (iii) there exists $\bar{L} > 0$ such that $|[u_1g(t, u_1) - a(t)u_1] - [u_2g(t, u_2) - a(t)u_2]| \leq \bar{L}|u_1 - u_2|$ for all $t \geq 0, u_1, u_2 \in W$ with

$$W := [0, \hat{u}],$$

which implies $ug(t, u) - a(t)u$ is uniformly Lipschitz continuous in u on W ;

- (H2) (i) $k(t, x) \geq 0$ for all $t \geq 0, x \in \mathbb{R}$, and $\int_{\mathbb{R}} k(t, y)dy = 1$ for all $t \geq 0$, which mean that the proportion of individuals that moves from one point to another point is nonnegative and that the total proportion of individuals that moves from one point to all possible points on the real line should be 1;
- (ii) $k(t, x)$ is continuous in $t \in \mathbb{R}$ uniformly for x in any bounded interval on \mathbb{R} , i.e., the dispersal of the population continuously varies in any bounded part of the stream;

(iii) the moment generating function

$$M(t, \alpha) = \int_{\mathbb{R}} k(t, y) e^{\alpha y} dy$$

exists for all $\alpha \in (-\Delta_-, \Delta_+)$ and $t \geq 0$ with $M(t_0, -\Delta_-) = \infty$ and $M(t_1, \Delta_+) = \infty$ for some $t_0, t_1 \geq 0$, where $\Delta_{\pm} > 0$, and $-\Delta_-$ and Δ_+ are the abscissae of convergence and may be infinity, which implies that at any time $t \geq 0$, the dispersal kernel $k(t, x)$ has exponentially bounded tails and the tails are uniformly bounded for all $t \geq 0$; this assumption is later relaxed in Section 2.2 where we consider the possibility of accelerating spread.

Remark The dispersal kernel k defined in (1.1) satisfies (H2) with $\Delta_- = \min_{t \geq 0} \{b_1(t)\}$ and $\Delta_+ = -\max_{t \geq 0} \{b_2(t)\}$, for positive, periodic and continuous functions $v(t)$, $D(t)$ and $\beta(t)$, if $x - y$ is considered as one argument in (1.1).

2.1 Finite spreading speeds and periodic traveling waves

Let C be the set of all bounded and continuous functions from \mathbb{R} to \mathbb{R} . For any $r > 0$, we define $C_r := \{u \in C : 0 \leq u(x) \leq r \text{ for all } x \in \mathbb{R}\}$. For $u, v \in C$, we write $u \geq v$ ($u \gg v$) provided that $u(x) \geq v(x)$ ($u(x) > v(x)$) for all $x \in \mathbb{R}$, and $u > v$ provided $u \geq v$ but $u \neq v$. 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.

It is not hard to see that the arguments for the well-posedness, monotonicity and continuity of solutions for the model (1.3) with k being independent of time (i.e., $k(t, x) = k(x)$ for all $t \geq 0$ and $x \in \mathbb{R}$) in [9] are also true for (1.3) with slight modifications. It then follows from the results in Section 2 and Lemma 3.1 in [9] that (1.3) admits a positive ω -periodic solution $u^*(t)$, which is globally asymptotically stable for all initial values in $(0, \hat{u}]$ for the spatially homogeneous system associated with (1.3), and that (1.3) generates a monotone periodic semiflow $\{Q_t\}_{t \geq 0}$ on $C(\mathbb{R}, W)$, where Q_t is defined by

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

where $u(t, x; \varphi)$ is the solution of (1.3) satisfying $u(0, x; \varphi) = \varphi(x)$ for all $x \in \mathbb{R}$. $\{Q_t\}_{t \geq 0}$ is a periodic semiflow in the sense that $Q_0[\varphi] = \varphi$ for all $\varphi \in C(\mathbb{R}, W)$, that $Q_t[Q_\omega[\varphi]] = Q_{t+\omega}[\varphi]$ for

all $t \geq 0$ and $\varphi \in C(\mathbb{R}, W)$, and that $Q[t, \varphi] := Q_t[\varphi]$ is continuous in (t, φ) on $[0, +\infty) \times C(\mathbb{R}, W)$. The continuity of $u(t, x; \varphi)$ in (t, φ) is with respect to the compact open topology. Moreover, $Q_t[\varphi_1] \geq Q_t[\varphi_2]$ for all $t \geq 0$ and $\varphi_1, \varphi_2 \in C(\mathbb{R}, W)$ with $\varphi_1 \geq \varphi_2$. In this section, we use both $u(t, x)$ and $u(t, x; \varphi)$ to represent a solution to (1.3), where the latter notation specifies the initial function φ .

Let Q_ω be the Poincaré map of (1.3). We can then apply the theories in [14, 15, 30] and follow a similar derivation as in [9] to obtain the spreading speeds of Q_ω and hence the spreading speeds of the periodic semiflow $\{Q_t\}_{t \geq 0}$. In the case of $\Delta_\pm = \infty$, we apply the theory of spreading speeds for monotone scalar maps in [15, 30] to (1.3) to show the existence of the spreading speeds of Q_ω in the upstream and downstream directions. In the cases of $\Delta_- < \infty$ or $\Delta_+ < \infty$, the existence of the spreading speed in the associated direction follows from a similar limiting argument as in the proof of Proposition 3.4 in [9]. The result is given in the following proposition and the proof is in Appendix B. We can also follow a similar process as for the theories in [15, 30] to obtain the same result.

Proposition 2.1 *Assume that (H1) and (H2) hold. Let Q_ω be the Poincaré map of (1.3). The spreading speeds of Q_ω in the downstream (c_ω^+) and upstream (c_ω^-) directions are, respectively,*

$$c_\omega^+ = \inf_{0 < \alpha < \Delta_+} \frac{\int_0^\omega (g(s, 0) - a(s)) ds + \int_0^\omega a(s) \int_{\mathbb{R}} k(s, y) e^{\alpha y} dy ds}{\alpha} \quad (2.1)$$

and

$$c_\omega^- = \inf_{0 < \alpha < \Delta_-} \frac{\int_0^\omega (g(s, 0) - a(s)) ds + \int_0^\omega a(s) \int_{\mathbb{R}} k(s, y) e^{-\alpha y} dy ds}{\alpha}. \quad (2.2)$$

Let

$$c^+ = \frac{c_\omega^+}{\omega} \quad \text{and} \quad c^- = \frac{c_\omega^-}{\omega}. \quad (2.3)$$

By similar arguments to those in [17, Lemma 2.10], we obtain

$$c^+ + c^- > 0.$$

Then by the proof of [14, Theorem 2.1] with $\tau = 0$, we can obtain the following theorem.

Theorem 2.1 *Assume that (H1) and (H2) hold. Let $u(t, x; \varphi)$ be the solution of (1.3) with $u(0, x; \varphi) = \varphi(x)$ for all $x \in \mathbb{R}$. The following results are valid.*

- (i) *For any $c > c^+$ and $c' > c^-$, if $\varphi \in C_{u^*(0)}$ with $\varphi(x) = 0$ for x outside a bounded interval, then*

$$\lim_{t \rightarrow \infty, x \geq ct} u(t, x; \varphi) = 0, \quad \lim_{t \rightarrow \infty, x \leq -c't} u(t, x; \varphi) = 0.$$

(ii) For any $c < c^+$ and $c' < c^-$, there is a positive number $r \in \mathbb{R}$, such that if $\varphi \in C_{u^*(0)}$ and $\varphi(x) > 0$ for x on an interval of length r , then

$$\lim_{t \rightarrow \infty, -c't \leq x \leq ct} (u(t, x; \varphi) - u^*(t)) = 0.$$

Remark Theorem 2.1 (i) and (ii) state that c^+ and c^- are the spreading speeds of solutions to (1.3) in the downstream and upstream directions, respectively.

According to the analysis in [9], we know that the downstream spreading speed c^+ is always positive. To solve the “drift paradox” problem such that the population can spread to the upstream, the upstream spreading speed c^- has to be positive (see Figure 2 for the signs of spreading speeds). By (2.2) and (2.3),

$$c^- > 0 \Leftrightarrow \inf_{0 < \alpha < \Delta_-} \frac{\int_0^\omega (g(s, 0) - a(s)) ds + \int_{\mathbb{R}} \int_0^\omega a(s) k(s, y) ds e^{-\alpha y} dy}{\alpha} > 0,$$

which requires $\int_0^\omega (g(s, 0) - a(s)) ds$ and $\int_0^\omega a(s) k(s, y) ds$ being sufficiently large. Then to ensure that the population can spread to the upstream, it is necessary to assume sufficiently large total population growth in a period $\int_0^\omega g(s, 0) ds$ (or average growth rate $\int_0^\omega g(s, 0) ds / \omega$) when the population density is low, and sufficiently small population transfer over a period $\int_0^\omega a(s) ds$. If the sums of growth and transfer over a period (i.e., $\int_0^\omega (g(s, 0) - a(s)) ds$ and $\int_0^\omega a(s) k(s, y) ds$) are kept constant, then changing the period ω does not change the fact that the population will persist or be washed out, but will change the values of speeds at which the population spreads to the upstream or downstream.

Recall that $u(t, x) = U(t, x + ct)$ is called an ω -periodic traveling wave of (1.3) connecting 0 to $u^*(t)$ provided that it is a solution of (1.3), $U(t, \xi)$ is ω -periodic in t , and $U(t, -\infty) = 0$ and $U(t, \infty) = u^*(t)$ uniformly for $t \in [0, \omega]$. In the following, we further show that the spreading speeds for (1.3) coincide with the minimal wave speeds of periodic traveling waves for (1.3), in the upstream and downstream directions respectively. The following theorem gives the nonexistence of periodic traveling waves for $c < c^\pm$. We omit the proof here as it is very similar to the proofs of [14, Theorem 2.2] and [15, Theorem 4.1].

Theorem 2.2 *Assume that (H1) and (H2) hold. Let c^\pm be the spreading speeds of (1.3) in the downstream and upstream directions, respectively. Then the following two statements are true.*

(i) *For any $c \in (0, c^-)$, system (1.3) admits no continuous ω -periodic traveling wave solution $U(t, x + ct)$ connecting 0 and $u^*(t)$.*

(ii) For any $c \in (0, c^+)$, system (1.3) admits no continuous ω -periodic traveling wave solution $U(t, x - ct)$ connecting $u^*(t)$ and 0.

When $c \geq c^-$ or $c \geq c^+$, since the solution map Q_t does not have compactness, we refer to the theory in [33]. After a similar process as in [9, Section 4] we obtain the existence of left-continuous nondecreasing periodic traveling waves connecting 0 and $u^*(t)$ when $c \geq c^-$. For $c \geq c^+$, introducing $x = -z$ to (1.3) and taking z as the new spatial variable to the new equation, we then obtain left-continuous nondecreasing periodic traveling waves connecting 0 to $u^*(t)$ for the new equation, which correspond to right-continuous nonincreasing periodic traveling waves connecting $u^*(t)$ to 0 for (1.3). The results are stated as follows.

Theorem 2.3 *Assume that (H1) and (H2) hold. Let c^\pm be the spreading speeds of (1.3) in the downstream and upstream directions, respectively. The following results hold true.*

- (i) *For any $c \geq c^-$, there exists a function $U(t, \xi)$ defined on $\mathbb{R}^+ \times \mathbb{R}$ such that $U(t, \xi)$ is differentiable with respect to t , that $U(t, \xi)$ is monotone nondecreasing and left-continuous in ξ , and that $U(t, x + ct)$ is a periodic traveling wave solution of (1.3) connecting 0 and $u^*(t)$.*
- (ii) *For any $c \geq c^+$, there exists a function $U(t, \xi)$ defined on $\mathbb{R}^+ \times \mathbb{R}$ such that $U(t, \xi)$ is differentiable with respect to t , that $U(t, \xi)$ is monotone nonincreasing and right-continuous in ξ , and that $U(t, x - ct)$ is a periodic traveling wave solution of (1.3) connecting $u^*(t)$ and 0.*

2.2 Infinite spreading speeds

In the case that the dispersal kernel does not have a moment generating function, that is, for any $t \geq 0$, $\int_{\mathbb{R}} k(t, y)e^{\alpha y} dy$ does not converge for any positive or negative α , we can obtain that the Poincaré map of (1.3) attains infinite spreading speeds c_ω^+ or c_ω^- , by studying a limiting process of spreading speeds for (1.3) with kernels k_m 's defined as truncations of $k(t, x)$ for $m > 0$ (see (5.5) for k_m when $\int_{\mathbb{R}} k(t, y)e^{\alpha y} dy$ does not converge for $\alpha < 0$). Since $c^+ = c_\omega^+/\omega$ and $c^- = c_\omega^-/\omega$, we then obtain the existence of infinite spreading speeds for the system (1.3). The result is stated as follows.

Theorem 2.4 *The spreading speed c^+ (c^-) of (1.3) in the downstream (upstream) direction is infinity if and only if $\int_{\mathbb{R}} k(t, y)e^{\alpha y} dy = \infty$ for all positive (negative) α and $t \geq 0$.*

As we know, when the downstream spreading speed is positive, the population spreads to the downstream, and when the upstream spreading speed is positive, the population spreads to the

upstream. As the condition $\int_{\mathbb{R}} k(t, y)e^{\alpha y} dy = \infty$ for all negative α guarantees infinite upstream spreading speed, it actually guarantees the persistence of the population in an infinitely long river.

In the following, we approximate the accelerating spread for (1.3) with dispersal kernel k independent of time t :

$$\frac{\partial u(t, x)}{\partial t} = ug(t, u(t, x)) - a(t)u(t, x) + a(t) \int_{\mathbb{R}} k(x - y)u(t, y)dy, \quad (2.4)$$

where k does not have a moment generating function, that is, $\int_{\mathbb{R}} k(y)e^{\alpha y} dy = \infty$ for all positive and negative α . It follows from Theorem 2.4 that $c^+ = \infty$ and $c^- = \infty$.

The linearized equation of (2.4) at $u = 0$ is

$$\frac{\partial u(t, x)}{\partial t} = (g(t, 0) - a(t))u(t, x) + a(t) \int_{\mathbb{R}} k(x - y)u(t, y)dy, \quad \forall t \geq 0, x \in \mathbb{R}. \quad (2.5)$$

Assume that $u(0, x) = u_0\delta(x)$, where $u_0 > 0$ and $\delta(x)$ is the Dirac delta function. Further suppose that the dispersal kernel $k(x)$ has finite moments

$$\zeta_n = \int_{\mathbb{R}} x^n k(x)dx$$

for all orders $n = 0, 1, 2, \dots$. By virtue of the Fourier transform, we can establish an approximation of the solutions to (2.5) with an initial point source.

Theorem 2.5 *The solution to (2.5) with an initial point source of strength u_0 satisfies*

$$u(t, x) \sim u_0 k(x) e^{\int_0^t g(s, 0) ds} \quad (2.6)$$

for $|x| \gg 1$, $t > 0$, provided that

$$\lim_{|x| \rightarrow \infty} \left[\frac{1}{k(x)} \frac{d^n k(x)}{dx^n} \right] = 0 \quad (2.7)$$

uniformly for all $n \geq 0$.

Based on [11, Appendix A], the proof of Theorem 2.5 is given in Appendix C. Then we can estimate the speeds of spread for the linearized equation (2.5) in both upstream and downstream directions, by the approximation (2.6). If we consider that the spreading speeds for (2.4) can be linearly determined, this estimation can also be taken as the approximation to the speeds of spread for (2.4). This is shown in the following example.

Example Consider $g(t, u) = (2 - u)(1 + \sin(t))$ and $a(t) = 1 + \sin(t)$. Then g and a are periodic functions in t with a period 2π . Define

$$k(x) = \begin{cases} A_1 e^{-B_1 \sqrt{-x}}, & x \leq 0, \\ A_2 e^{-B_2 \sqrt{x}}, & x > 0, \end{cases} \quad (2.8)$$

with $A_1/B_1^2 + A_2/B_2^2 = 1/2$. Then $\int_{\mathbb{R}} k(x)dx = 1$; k does not have the moment generating function, but has finite moments $\zeta_n = \int_{\mathbb{R}} x^n k(x)dx$ for all orders $n = 0, 1, 2, \dots$. Moreover, k satisfies (2.7). Let the initial function be

$$u(0, x) = u_0\delta(x)$$

with $u_0 > 0$. Define the extent x_t of a population as the distance from the source where the population first falls below a given sufficiently small threshold, \bar{u} (see, e.g., [11]). By (2.6), the extents for a solution to (2.5) are approximately

$$x_t^- = -\frac{(\ln(\frac{\bar{u}}{u_0 A_1}) - 2t + 2\cos(t) - 2)^2}{B_1^2}, \quad x_t^+ = \frac{(\ln(\frac{\bar{u}}{u_0 A_2}) - 2t + 2\cos(t) - 2)^2}{B_2^2},$$

in the upstream and downstream directions, respectively. Consider x_t^\pm/t as the speeds that the population spreads to downstream and upstream. The extents x_t^\pm and speeds of spread x_t^\pm/t are shown as functions of t in Figure 3. We see that both the extents and the speeds of spread increase in time.

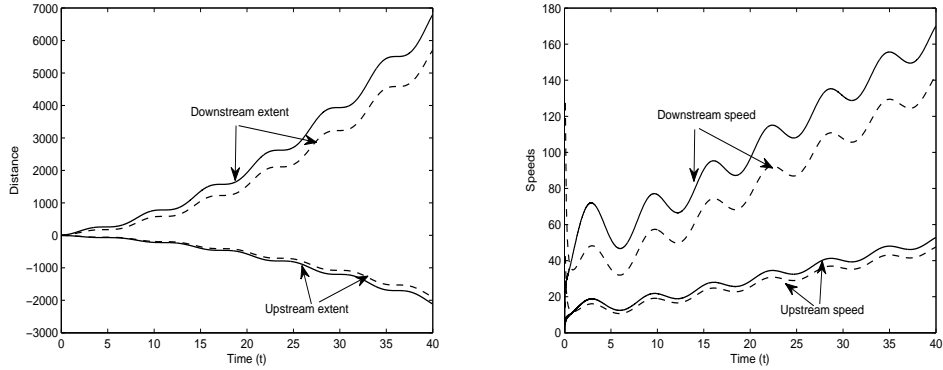


Figure 3: The extents x_t^\pm and speeds of spread x_t^\pm/t for (2.5), based on the exact solution to (2.5) and the approximation (2.6). Here $g(t, u) = (2-u)(1+\sin(t))$ and $a(t) = 1+\sin(t)$, and $k(x)$ is defined in (2.8) with $A_1 = A_2 = 1/2$, $B_1 = 2$, $B_2 = 2/\sqrt{3}$. The initial function for the exact solution to (2.5) is defined in (2.9) with space step $\Delta x = 0.5$ and $u_0 = 1$; the initial function for the approximation (2.6) is $u(0, x) = u_0\delta(x)$ with $u_0 = 1$. The extent threshold \bar{u} is 0.01. The solid curves represents extents or speeds obtained from the exact solution to (2.5); the dash curves represents extents or speeds obtained from the approximation (2.6).

On the other hand, we also obtain the exact solution to (2.5) with above settings except the initial value. Note that $\delta_n(x) := \mathcal{N}(0, 1/n)$, which is the normal distribution with mean 0 and variance $1/n$, satisfies $\lim_{n \rightarrow \infty} \delta_n(x) = \delta(x)$ as $n \rightarrow \infty$. In the numerical simulation, to approximate the initial function $u_0\delta(x)$ used above for (2.5), we assume the initial function as

$$u(0, x) = \begin{cases} \frac{u_0}{\Delta x}, & \text{if } x = 0, \\ 0, & \text{otherwise,} \end{cases} \quad (2.9)$$

where Δx is the spatial space step size. The extents x_t^\pm and the approximate speeds x_t^\pm/t as functions of t are also shown in Figure 3. It clearly indicates that if the dispersal kernel does not have the moment generating function but has finite moments, then the population spreads to the downstream and upstream at accelerating speeds. This verifies Theorem 2.4. Comparing x_t^\pm and x_t^\pm/t for (2.5) from the exact solutions and the approximation (2.6), we also see from Figure 3 that (2.6) underestimates the speeds of spread for the population, but at least it provides a lower bound for the spread.

3 Spreading speeds in a two-season environment

In this section, we give approximation for upstream and downstream spreading speeds of a population in a two-season environment, and study the combined influences of the flow velocity and the transfer rate, the diffusion coefficient and the settling rate on the spreading speeds in upstream and downstream directions. By a two-season environment, we mean a habitat, which has two significant seasons in a year, such as summer and winter, in either of which the population has distinct dispersal and growth function. In the following analysis, we simply assume that a year length is ω with summer length about ω_0 and winter length about $\omega - \omega_0$ ($0 < \omega_0 < \omega$).

3.1 Approximations for spreading speeds

We would like to consider upstream and downstream spreading speeds in a two-season environment with dispersal kernel k_1 and transfer rate a_1 in summer and dispersal kernel k_2 and transfer rate a_2 in winter. An abrupt change between seasons will violate the assumption (H1) (i)-(ii) and (H2) (ii) that a and k are continuous functions of time t . Hence, we need to approach the discontinuous dispersal kernel and transfer rate carefully as limits of sequences of continuous (in time) kernels and transfer rates, respectively.

First, we give a theoretical result for the approximation of spreading speeds. Assume that $k_1(x)$ and $k_2(x)$ are two dispersal kernels and the maximal interval over which both moment generating functions $M_1(\alpha) = \int_{\mathbb{R}} k_1(x)e^{\alpha x} dx$ and $M_2(\alpha) = \int_{\mathbb{R}} k_2(x)e^{\alpha x} dx$ exist is $(-\Delta_-, \Delta_+)$. Let $\{k^{(n)}(t, x)\}_{n \in \mathbb{N}}$ be a sequence of dispersal kernels which are periodic in t and defined on $[0, \omega]$ as

$$k^{(n)}(t, x) = \begin{cases} k_1(x) & 0 \leq t < \omega_0 - \frac{1}{n}, x \in \mathbb{R}, \\ k_1^{(n)}(t, x) & \omega_0 - \frac{1}{n} \leq t < \omega_0, x \in \mathbb{R}, \\ k_2(x) & \omega_0 \leq t < \omega - \frac{1}{n}, x \in \mathbb{R}, \\ k_2^{(n)}(t, x) & \omega - \frac{1}{n} \leq t < \omega, x \in \mathbb{R}, \end{cases} \quad (3.1)$$

where $k_1^{(n)}$ and $k_2^{(n)}$ are functions that patch together k_1 and k_2 over the transitive seasons of length under $1/n$ so as to ensure that $k^{(n)}$ varies continuously with time as well as satisfying all other

assumptions given in (H2). Moreover, as $k^{(n)}(t, x)$ is continuous in t uniformly for x in any bounded interval on \mathbb{R} , without loss of generality, we assume that

$$\min\{k_1(x), k_2(x)\} \leq k_i^{(n)}(t, x) \leq \max\{k_1(x), k_2(x)\} \quad (3.2)$$

for all $i = 1, 2$, $t \in [0, \omega]$ and $x \in \mathbb{R}$. Similarly, let $\{a^{(n)}(t)\}_{n \in \mathbb{N}}$ be a sequence of transfer rates, which are periodic in t and defined in $[0, \omega]$ as

$$a^{(n)}(t) = \begin{cases} a_1 & 0 \leq t < \omega_0 - \frac{1}{n}, \\ a_1^{(n)}(t) & \omega_0 - \frac{1}{n} \leq t < \omega_0, \\ a_2 & \omega_0 \leq t < \omega - \frac{1}{n}, \\ a_2^{(n)}(t) & \omega - \frac{1}{n} \leq t < \omega, \end{cases} \quad (3.3)$$

where $a_1^{(n)}(t)$ and $a_2^{(n)}(t)$ are such that $a^{(n)}(t)$ is continuous in time t for each $n \in \mathbb{N}$. We then have the following result with proof in Appendix D.

Theorem 3.1 *Assume that (H1) and (H2) hold for (1.3) with dispersal kernel $k^{(n)}(t, x)$ defined in (3.1) and transfer rate $a^{(n)}(t)$ defined in (3.3) and that c_n^\pm are the downstream and upstream spreading speeds for (1.3), respectively, for each $n \in \mathbb{N}$. Then the following approximations are valid.*

$$\begin{aligned} c_n^+ &\rightarrow \inf_{0 < \alpha < \Delta_+} \frac{\int_0^\omega g(s, 0) ds + a_1 \omega_0 (M_1(\alpha) - 1) + a_2 (\omega - \omega_0) (M_2(\alpha) - 1)}{\alpha \omega}, \\ c_n^- &\rightarrow \inf_{0 < \alpha < \Delta_-} \frac{\int_0^\omega g(s, 0) ds + a_1 \omega_0 (M_1(-\alpha) - 1) + a_2 (\omega - \omega_0) (M_2(-\alpha) - 1)}{\alpha \omega} \end{aligned} \quad (3.4)$$

as $n \rightarrow \infty$.

Thus, downstream and upstream spreading speeds in the two-season environment can be approximated by the simple formulae given in equation (3.4).

Remark 1. From the proof of Theorem 3.1 (Appendix D) we see that condition (3.2) can be relaxed to any condition such that

$$M^{(n)}(t, \alpha) = \int_{\mathbb{R}} k^{(n)}(t, x) e^{\alpha x} dx$$

has a uniform bound for $t \in [0, \omega]$, $\alpha \in (-\Delta_-, \Delta_+)$ and all $n \in \mathbb{N}$.

Remark 2. In fact, we can further show that the two limits in (3.4) are the downstream and upstream spreading speeds, respectively, of the system (1.3) with k and a defined as

$$k(t, x) = \begin{cases} k_1(x) & 0 \leq t < \omega_0, x \in \mathbb{R}, \\ k_2(x) & \omega_0 \leq t < \omega, x \in \mathbb{R}, \end{cases} \quad \text{and} \quad a(t) = \begin{cases} a_1 & 0 \leq t < \omega_0, \\ a_2 & \omega_0 \leq t < \omega. \end{cases}$$

In this case, the periodic semiflow $\{Q_t\}_{t \geq 0}$ and Poincarè map Q_ω associated with (1.3) are also well defined and continuous. Then we can still apply the theories in [14, 15, 30] and follow a similar derivation as in [9] to obtain the existence of the spreading speeds of Q_ω and hence the spreading speeds of the periodic semiflow. The linear operator approach in [15] can still be applied as in [9], so the formulae of the spreading speeds in the downstream and upstream directions can be obtained. They are exactly the two limits in (3.4). All the arguments are similar to those in [9] and Section 2 in this paper.

Now we consider a stream species in a two-season environment. The population growth rate and dispersal patterns are typically different in summer and winter due to very different temperature, food sources, flow discharge, and some other seasonal varying features, while they experience small perturbations around the summer or winter states in spring or fall. As the spring and fall time are assumed to be very short compared to the other two seasons, the spreading speeds of the species in the upstream and downstream directions can be approximated from the population dynamics and dispersal in summer and winter time, via the approximations in Theorem 3.1. That is, we may use (3.4) to approximate the spreading speeds for (1.3) rather than calculating them via (2.1)-(2.3), if the dispersal kernel $k(t, x)$ and the transfer rate $a(t)$ in (1.3) take the form of $k^{(n)}(t, x)$ (defined in (3.1)) and $a^{(n)}(t)$ (defined in (3.3)), respectively.

We now consider the class of exponential kernels of the form given in equation (1.1). In the following text, for all parameters except $g(t, x)$, we use subscript $i = 1$ to represent summer and $i = 2$ to represent winter. Let the summer and winter dispersal kernels k_i 's be in the form

$$k_i(x) = \begin{cases} A_i \exp(b_i^{(1)} x), & x \leq 0, \\ A_i \exp(b_i^{(2)} x), & x \geq 0, \end{cases}$$

with

$$b_i^{(1),(2)} = \frac{v_i}{2D_i} \pm \sqrt{\frac{v_i^2}{4D_i^2} + \frac{\beta_i}{D_i}}$$

and

$$A_i = \frac{b_i^{(1)} b_i^{(2)}}{b_i^{(2)} - b_i^{(1)}},$$

where D_i , v_i and β_i are the diffusion coefficient, the water flow velocity, and the settling rate of a species in a stream environment. These constants are nonnegative and can be considered as the averages of the related variables in summer or winter. For $i = 1$ or 2 , the moment generating function of k_i

$$M_i(\alpha) = \int_{\mathbb{R}} k_i(y) e^{\alpha y} dy = \frac{\beta_i}{\beta_i - \alpha v_i - \alpha^2 D_i}$$

exists provided that $-b_i^{(1)} < \alpha < -b_i^{(2)}$. Let $\Delta_- = \min\{b_1^{(1)}, b_2^{(1)}\}$ and $\Delta_+ = \min\{-b_1^{(2)}, -b_2^{(2)}\}$. Then $(-\Delta_-, \Delta_+)$ is the largest interval where both $M_1(\alpha)$ and $M_2(\alpha)$ exist. Moreover, we assume that the transfer rate is a_1 in summer and a_2 in winter where a_i 's are nonnegative and may represent the average of the transfer rate in summer or winter. It follows from Theorem 3.1 that the downstream and upstream spreading speeds can be approximated by

$$c^+ \approx \inf_{0 < \alpha < \Delta_+} \frac{\int_0^\omega g(s, 0) ds + a_1 \omega_0 (M_1(\alpha) - 1) + a_2 (\omega - \omega_0) (M_2(\alpha) - 1)}{\alpha \omega} \quad (3.5)$$

and

$$c^- \approx \inf_{0 < \alpha < \Delta_-} \frac{\int_0^\omega g(s, 0) ds + a_1 \omega_0 (M_1(-\alpha) - 1) + a_2 (\omega - \omega_0) (M_2(-\alpha) - 1)}{\alpha \omega} \quad (3.6)$$

respectively.

3.2 Influences of parameters on spreading speeds

In the following, we will study the combined influences of the flow velocity and the transfer rate, the diffusion coefficient and the settling rate on the spreading speeds in upstream and downstream directions via the approximations (3.5) and (3.6).

First, assume that the diffusion constant and settling rate in a year are constants, i.e., $D_2 = D_1 \equiv D$ and $\beta_2 = \beta_1 \equiv \beta$, and consider how the transfer rate a_i 's and the flow velocity v_i 's influence the spreading speeds. Here D and β can be taken as the average over a year. In reality, we may expect higher flow velocity in summer and lower flow velocity in winter (i.e., $v_1 > v_2 \geq 0$) according to the variation of water discharge, but we will not restrict our analysis to this assumption. An example of a and v is shown in Figure 4.

Note that although the transfer rate $a(t)$ varies in summer and winter, in a long run, its yearly mean value may oscillate around some constant quantity. So does the water flow velocity $v(t)$. Therefore, we fix the mean values

$$\bar{a} = \frac{1}{\omega} \int_0^\omega a(s) ds = \frac{a_1 \omega_0 + a_2 (\omega - \omega_0)}{\omega}, \quad (3.7)$$

and

$$\bar{v} = \frac{1}{\omega} \int_0^\omega v(s) ds = \frac{v_1 \omega_0 + v_2 (\omega - \omega_0)}{\omega}, \quad (3.8)$$

of the transfer rate $a(t)$ and the flow velocity $v(t)$ and vary a_i 's and v_i 's to see how the variations of them influence the spreading speeds. We assume, unless stated otherwise, that $a_2 \neq a_1$ and $v_2 \neq v_1$.

To investigate the cross-effects of transfer rate $a(t)$ and water flow velocity $v(t)$ on the spreading speeds c^\pm , we define the covariance between the normalized transfer rate a/\bar{a} and flow velocity v/\bar{v}

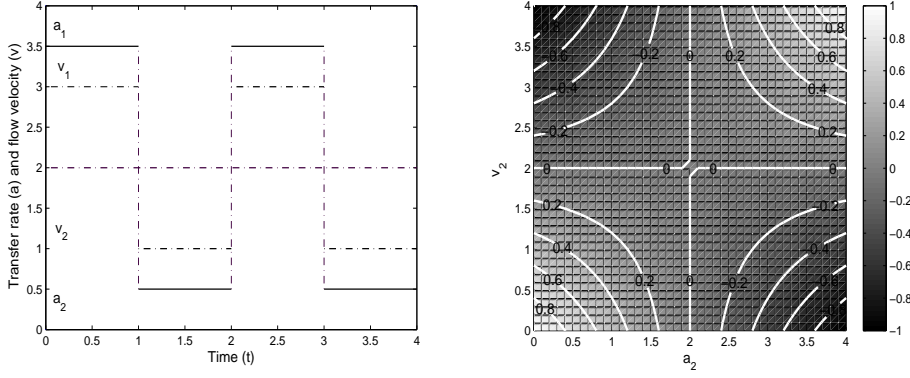


Figure 4: Left: An example of the transfer rate $a(t)$ and flow speed $v(t)$ in a two season environment, where a year length is $\omega = 2$, summer length is $\omega_0 = 1$, the annual mean of transfer rate is $\bar{a} = 2$ and the annual mean of flow speed is $\bar{v} = 2$. The solid line represents $a(t)$ and the dash line represents $v(t)$. Right: The projection of the normalized covariance $\chi_{a,v}$ between the transfer rate a and flow velocity v on the $a - v$ plane, where $\bar{a} = 2$, $\bar{v} = 2$, a_2 is the winter transfer rate and v_2 is the winter flow velocity. The contour lines show the value levels of $\chi_{a,v}$.

over a year as

$$\chi_{a,v} = \text{cov}\left(\frac{a}{\bar{a}}, \frac{v}{\bar{v}}\right) = \frac{1}{\bar{a}\bar{v}\omega} \int_0^\omega (a(s) - \bar{a})(v(s) - \bar{v})ds \quad (3.9)$$

where $\text{cov}(a, v)$ is the covariance between a and v defined as

$$\text{cov}(a, v) = \frac{1}{\omega} \int_0^\omega (a(s) - \bar{a})(v(s) - \bar{v})ds.$$

Note that $\chi_{a,v}$ is a dimensionless quantity but has the same sign as the covariance $\text{cov}(a, v)$ between a and v . Moreover, calculations show that

$$\chi_{a,v} = \frac{\omega_0(\omega - \omega_0)(v_2 - v_1)(a_2 - a_1)}{\omega^2 \bar{a}\bar{v}}, \quad (3.10)$$

which implies that $\chi_{a,v}$ is positive provided that $a_2 - a_1$ and $v_2 - v_1$ have the same sign and negative if they have opposite signs. For fixed \bar{a} and \bar{v} , the relationship between a_2 , v_2 and $\chi_{a,v}$ is shown in Figure 4. In the following, without confusion, we also call $\chi_{a,v}$ the *normalized covariance* between the transfer rate a and the flow velocity v , as the mean values \bar{a} and \bar{v} are kept as constants. This is also true for the other covariances we will introduce later.

It follows from (3.5), (3.7) and (3.10) that

$$\begin{aligned}
& c^+ \\
& \approx \inf_{0 < \alpha < \Delta_+} \frac{\int_0^\omega g(s, 0) ds + a_1 \omega_0 (M_1(\alpha) - 1) + a_2 (\omega - \omega_0) (M_2(\alpha) - 1)}{\alpha \omega} \\
& = \inf_{0 < \alpha < \Delta_+} \frac{\int_0^\omega g(s, 0) ds - \bar{a} \omega + (\bar{a} \omega - a_2 (\omega - \omega_0)) M_1(\alpha) + a_2 (\omega - \omega_0) M_2(\alpha)}{\alpha \omega} \\
& = \inf_{0 < \alpha < \Delta_+} \frac{\int_0^\omega g(s, 0) ds - \bar{a} \omega + \bar{a} \omega M_1(\alpha) + a_2 (\omega - \omega_0) (M_2(\alpha) - M_1(\alpha))}{\alpha \omega} \\
& = \inf_{0 < \alpha < \Delta_+} \frac{\int_0^\omega g(s, 0) ds + \bar{a} \omega (M_1(\alpha) - 1) + \left(\bar{a} (\omega - \omega_0) + \frac{\chi_{a,v} \bar{a} \bar{v} \omega}{(v_2 - v_1)} \right) (M_2(\alpha) - M_1(\alpha))}{\alpha \omega}.
\end{aligned} \tag{3.11}$$

For $\alpha \in (0, \Delta_+)$, let

$$c_\alpha^+ = \frac{\int_0^\omega g(s, 0) ds + a_1 \omega_0 (M_1(\alpha) - 1) + a_2 (\omega - \omega_0) (M_2(\alpha) - 1)}{\alpha \omega}. \tag{3.12}$$

Then $c^+ \approx \inf_{0 < \alpha < \Delta_+} c_\alpha^+$ and

$$\frac{dc_\alpha^+}{d\chi_{a,v}} = \frac{\bar{a} \bar{v} (M_2(\alpha) - M_1(\alpha))}{\alpha (v_2 - v_1)} > 0$$

for $0 < \alpha < \Delta_+$ since $M_2(\alpha) - M_1(\alpha)$ and $v_2 - v_1$ have the same sign for $0 < \alpha < \Delta_+$ and all the other quantities are positive. Therefore, the downstream spreading speed c^+ is an increasing function of the normalized covariance $\chi_{a,v}$ between the transfer rate a and flow velocity v , provided that summer flow velocity v_1 , the winter flow velocity v_2 and the mean value \bar{a} of the transfer rate $a(t)$ over a year are fixed. Similarly, we can approximate the upstream spreading speed c^- as

$$c^- \approx \inf_{0 < \alpha < \Delta_-} \frac{\int_0^\omega g(s, 0) ds + a_1 \omega_0 (M_1(-\alpha) - 1) + a_2 (\omega - \omega_0) (M_2(-\alpha) - 1)}{\alpha \omega} \tag{3.13}$$

and define

$$c_\alpha^- = \frac{\int_0^\omega g(s, 0) ds + a_1 \omega_0 (M_1(-\alpha) - 1) + a_2 (\omega - \omega_0) (M_2(-\alpha) - 1)}{\alpha \omega}$$

for $\alpha \in (0, \Delta_-)$. Then we obtain that c^- is a decreasing function of $\chi_{a,v}$ provided that v_1 , v_2 and \bar{a} are fixed.

Moreover, we consider a river with given summer flow velocity v_1 and winter flow velocity v_2 and assume that the annual average of a species' transfer rate \bar{a} is a constant. It follows from (3.11) that when $v_2 - v_1$ and $a_2 - a_1$ have the same sign, the smaller the absolute difference between the summer transfer rate a_1 and the winter transfer rate a_2 is, the smaller the downstream spreading speed is and the bigger the upstream spreading speed is; when $v_2 - v_1$ and $a_2 - a_1$ have the opposite signs, the smaller the absolute difference between a_1 and a_2 is, the bigger the downstream spreading speed is and the smaller the upstream spreading speed is. In other words the population has a

higher chance of persistence or spatial spread when yearly transfer rate patterns do not follow flow rate patterns and a lower chance of persistence or spatial spread when they do follow flow rate patterns.

Example 3.1 Assume the growth function $g(t, u) = r(1 - u/K) - \mu$ with the intrinsic growth rate $r = 1.2$, death rate $\mu = 0.5$ and carrying capacity $K > 0$, which does not influence the spreading speeds, the scaled length of a year $\omega = 2$, the summer length of a year $\omega_0 = 1$, the diffusion rate $D_2 = D_1 = 1$, the settling rate $\beta_2 = \beta_1 = 1$, the mean value of the flow velocity $\bar{v} = 2$ and the mean transfer rate $\bar{a} = 2$.

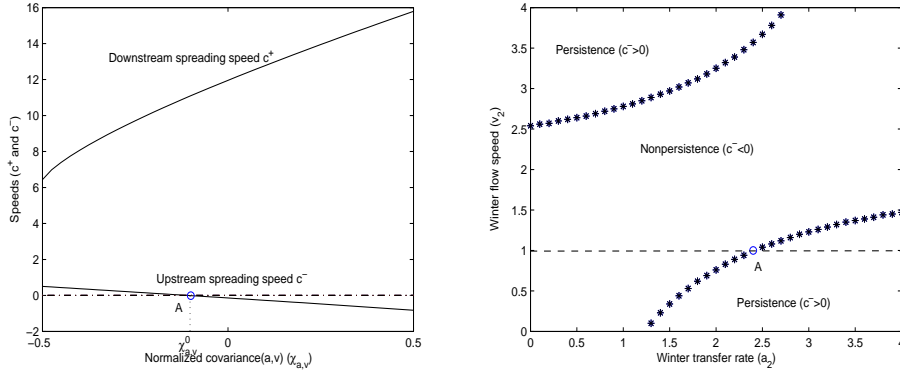


Figure 5: Left: The relationship between the spreading speeds and the normalized covariance $\chi_{a,v}$ between the transfer rate a and flow velocity v , where $g(t, u) = 1.2(1 - u/K) - 0.5$, $\beta_2 = \beta_1 = 1$, $D_2 = D_1 = 1$, $\omega = 2$, $\omega_0 = 1$, $v_1 = 3$, $v_2 = 1$, $\bar{a} = 2$, $\chi_{a,v}^0 = -0.107375$. Right: The persistence areas for the population on the $a_2 - v_2$ plane. Here, $g(t, u) = 1.2(1 - u/K) - 0.5$, $\beta_2 = \beta_1 = 1$, $D_2 = D_1 = 1$, $\omega = 2$, $\omega_0 = 1$, $\bar{v} = 2$, and $\bar{a} = 2$. The circle point “A” in the left graph corresponds to the circle point “A” in the right graph.

For summer flow velocity $v_1 = 3$ and winter velocity $v_2 = 1$, the upstream and downstream spreading speeds as a function of the normalized covariance $\chi_{a,v}$ are shown in the left graph of Figure 5. When $\chi_{a,v}$ increases, the downstream spreading speed is always positive and increases, while the upstream spreading speed decreases from positive to negative. Note that for our definition of the upstream spreading speed in this paper, positive values of the upstream spreading speed indicate population’s spreading to upstream and negative values indicate population’s spreading to downstream. We say that the larger the normalized covariance between a and v is, the easier for the population to be washed out and the harder for the population to persist in the stream.

If we describe the persistence of the population by $c^- > 0$ and nonpersistence by $c^- < 0$, then the areas for persistence and nonpersistence on the $a_2 - v_2$ plane is shown in the right graph of Figure 5. In this figure, the annual averages of the flow velocity and the population transfer rate are

fixed as $\bar{v} = 2$ and $\bar{a} = 2$. If the winter flow velocity v_2 is between 1.5 and 2.5, then the population cannot persist in the stream no matter what constant $a(t)$ is in summer or winter. When v_2 is less than 1.5 or greater than 2.5, it is possible that the population persists in the stream if $a(t)$ is the constant \bar{a} in the whole year but is washed out if $a(t)$ experiences oscillations in a year (i.e., $a(t) \not\equiv \bar{a}$) (see e.g., $v_2 = 0.5$); it is also possible that the population is washed out when $a(t) \equiv \bar{a}$ but is persistent in the stream when $a(t) \not\equiv \bar{a}$ (see e.g., $v_2 = 1$). Therefore, if the flow velocity oscillates close to its annual average, then it is easier for the population to be washed out, while if the flow velocity has big oscillation around its average, then it might be possible to adjust the population's transfer rate to help the population persist in the stream.

We also study the co-effects of the flow velocity $v(t)$ and the diffusion rate $D(t)$ or the settling rate $\beta(t)$ on the spreading speeds. Similar as in (3.7), (3.8) and (3.9), we can define mean values of $D(t)$ and $\beta(t)$ as \bar{D} and $\bar{\beta}$, the *normalized covariance* $\chi_{D,v}$ between the flow velocity v and diffusion coefficient D , and the *normalized covariance* $\chi_{\beta,v}$ between the flow velocity v and settling rate β . However, in these cases, the signs of $dc_{\alpha}^{\pm}/d\chi_{D,v}$ and $dc_{\alpha}^{\pm}/d\chi_{\beta,v}$ depend on not only the sign of $v_2 - v_1$, but also $\chi_{D,v}$ and $\chi_{\beta,v}$ themselves and the other parameter relations. They can change signs when v_0 , v_1 and \bar{D} or $\bar{\beta}$ are fixed. This can be seen from the following examples.

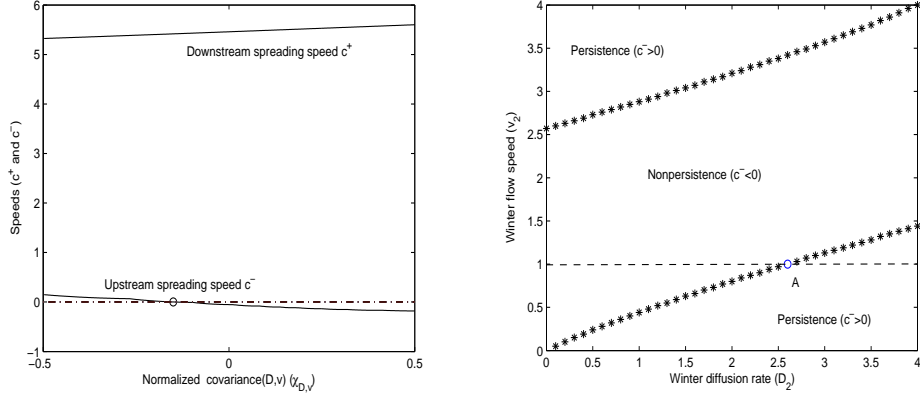


Figure 6: Left: The relationship between the spreading speeds and the normalized covariance $\chi_{D,v}$ between the flow velocity v and diffusion coefficient D . Here $g(t, u) = 0.75(1 - u/K) - 0.5$, $\beta_2 = \beta_1 = 1$, $a_2 = a_1 = 1$, $v_1 = 3$, $v_2 = 1$, $\omega = 2$, $\omega_0 = 1$, and $\bar{D} = 2$, $\chi_{D,v}^0 = -0.152525$. Right: The persistence areas for the population on the $D_2 - v_2$ plane. Here $g(t, u) = 0.75(1 - u/K) - 0.5$, $\beta_2 = \beta_1 = 1$, $a_2 = a_1 = 1$, $\omega = 2$, $\omega_0 = 1$, $\bar{v} = 2$, and $\bar{D} = 2$. The circle point “A” in the left graph corresponds to the circle point “A” in the right graph.

Example 3.2 $g(t, u) = 0.75(1 - u/K) - 0.5$, $\beta_2 = \beta_1 = 1$, $a_2 = a_1 = 1$, $\omega = 2$, $\omega_0 = 1$, $\bar{v} = 2$ and $\bar{D} = 2$. For $v_1 = 3$ and $v_2 = 1$, the relation between the spreading speeds c^{\pm} and the normalized

covariance $\chi_{D,v}$ between v and D is shown in Figure 6. For these given v_i 's, c^+ is an increasing function of $\chi_{D,v}$ and c^- decreases from positive to negative as $\chi_{D,v}$ increases. Therefore, in this case, if the normalized covariance between v and D is large and negative, the population spreads to the upstream and persists in the stream, while if it is positive, the population only spreads to the downstream and is eventually washed out.

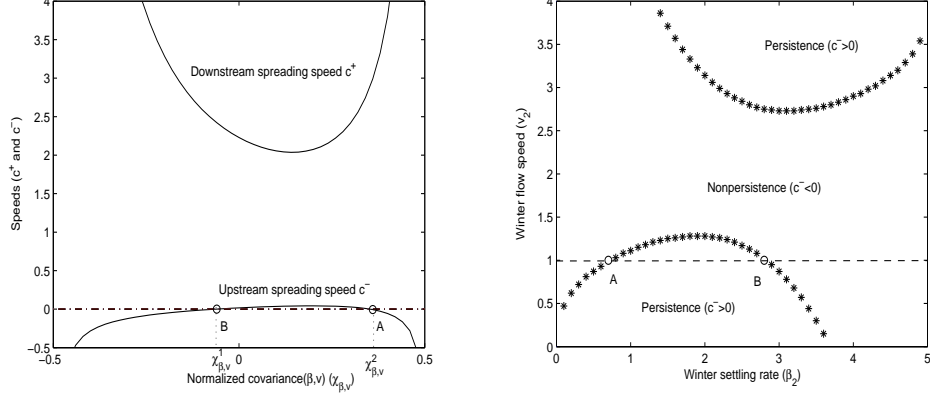


Figure 7: Left: The relation between the spreading speeds and the normalized covariance $\chi_{\beta,v}$ between the flow velocity v and settling rate β . Here $g(t, u) = 0.75(1 - u/K) - 0.5$, $a_2 = a_1 = 1$, $D_2 = D_1 = 1$, $\omega = 2$, $\omega_0 = 1$, $v_1 = 3$, $v_2 = 1$, $\bar{\beta} = 2.5$, $\chi_{\beta,v}^1 = -0.0631$, $\chi_{\beta,v}^2 = 0.35282$. $c^- < 0$ when $-0.5 < \chi_{\beta,v} < \chi_{\beta,v}^1$ or $\chi_{\beta,v}^2 < \chi_{\beta,v} < 0.5$; $c^- > 0$ when $\chi_{\beta,v}^1 < \chi_{\beta,v} < \chi_{\beta,v}^2$. Right: The persistence areas for the population on the $\beta_2 - v_2$ plane, where $g(t, u) = 0.75(1 - u/K) - 0.5$, $a_2 = a_1 = 1$, $D_2 = D_1 = 1$, $\omega = 2$, $\omega_0 = 1$, $\bar{v} = 2$, and $\bar{\beta} = 2.5$. The circle points “A” and “B” in the left graph correspond to the circle points “A” and “B” in the right graph.

Example 3.3 $g(t, u) = 0.75(1 - u/K) - 0.5$, $D_2 = D_1 = 1$, $a_2 = a_1 = 1$, $\omega = 2$, $\omega_0 = 1$, $\bar{v} = 2$ and $\bar{\beta} = 2.5$. For $v_1 = 3$ and $v_2 = 1$, the relation between the spreading speeds c^\pm and the normalized covariance $\chi_{\beta,v}$ between v and β is shown in Figure 7. Here c^+ decreases first and then increases but is always positive, while c^- increases first and then decreases. As $\chi_{\beta,v}$ increases from negative to positive values, c^- changes from negative to positive, and to negative again. This indicates that, for the population to spread upstream and hence to persist in the stream, $\chi_{\beta,v}$ must neither be very small nor very large.

We also obtain the persistence areas for the population on the $D_2 - v_2$ and $\beta_2 - v_2$ planes, respectively, for Examples 3.2 and 3.3 (see the right graphs of Figures 6 and 7). The persistence areas on the $D_2 - v_2$ plane is similar to that on the $a_2 - v_2$ plane, so we may have similar interpretations as before. Figure 7 shows that when $\bar{v} = 2$ and $\bar{\beta} = 2.5$ are fixed, if the flow velocity in a year (mainly summer and winter) oscillates around its annual mean value \bar{v} , then it is impossible for

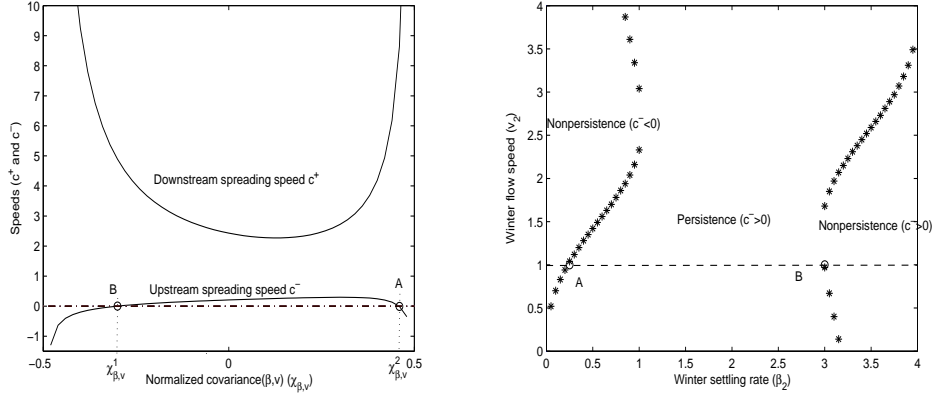


Figure 8: Left: The relation between the spreading speeds and the normalized covariance $\chi_{\beta,v}$ between the flow velocity v and settling rate β . Here $g(t, u) = 0.75(1 - u/K) - 0.5$, $a_2 = a_1 = 1$, $D_2 = D_1 = 2$, $\omega = 2$, $\omega_0 = 1$, $v_1 = 3$, $v_2 = 1$, $\bar{\beta} = 2.5$, $\chi_{\beta,v}^1 \approx -0.3$, $\chi_{\beta,v}^2 \approx 0.46$. $c^- < 0$ when $-0.5 < \chi_{\beta,v} < \chi_{\beta,v}^1$ or $\chi_{\beta,v}^2 < \chi_{\beta,v} < 0.5$; $c^- > 0$ when $\chi_{\beta,v}^1 < \chi_{\beta,v} < \chi_{\beta,v}^2$. Right: The persistence areas for the population on the $\beta_2 - v_2$ plane, where $g(t, u) = 0.75(1 - u/K) - 0.5$, $a_2 = a_1 = 1$, $D_2 = D_1 = 2$, $\omega = 2$, $\omega_0 = 1$, $\bar{v} = 2$, and $\bar{\beta} = 2.5$. The circle points “A” and “B” in the left graph correspond to the circle points “A” and “B” in the right graph.

the population to spread that for certain winter flow velocity (e.g., $v_2 = 1$), the winter settling rate should not be too small or too large so that the population can spread upstream and hence persist in the stream. We change the diffusion rate in Example 3.3 to $D_1 = D_2 = 2$ and obtain a very different graph for persistence areas on the $\beta_2 - v_2$ plane in Figure 8. It shows that for almost all possible winter flow velocity v_2 , the population can persist in the stream provided that the winter settling rate β_2 is not very large.

In summary, we investigated the effects on persistence of normalized temporal covariances between flow rate v and the following model parameters: transfer rate between growth and dispersal classes a , diffusion coefficient D , and settling rate β . On average, high flow rates have a tendency to wash resident populations down stream. Hence, a strategy that reduces transfer to the dispersal class when flow rates are high will ameliorates dispersal loss. Thus large $\chi_{a,v}$ leads to washout while small $\chi_{a,v}$ can allow for persistence (Figure 5). When it comes to random movement via diffusion, a strategy that maximizes upstream dispersal when it likely to most effective (ie., when it is not overpowered by high flow rates) will help ensure species persistence. Thus large $\chi_{D,v}$ leads to washout while small $\chi_{D,v}$ can allow for persistence (Figure 6). The pattern is the same as the one for transfer rate, given previously, although for a different reason. Finally, a low settling rate β will simultaneously enhance the effects of flow v and diffusion D whereas a high settling rate β will simultaneously diminish the effects. Persistence requires a diminishment of the effects of flow

to prevent washout, and an enhancement of the effects of diffusion to allow for upstream spread. Hence the overall impact of $\chi_{\beta,v}$ on persistence is subtle, and depends upon the diffusion levels D . However, as an overall principle, intermediate settling rates enhance the likelihood persistence, whereas high or low rates diminish the likelihood of persistence (Figures 7 and 8).

Recall that in the earlier work on critical domain size [8], we obtained the relationship between normalized covariances $\chi_{a,v}$, $\chi_{D,v}$ and $\chi_{\beta,v}$, and the critical domain size for Examples 3.1-3.3 but in a bounded stream. It was shown that the critical domain size exists for $\chi_{a,v} < \chi_{a,v}^0$ in Example 3.1, for $\chi_{D,v} < \chi_{D,v}^0$ in Example 3.2, and for $\chi_{\beta,v}^1 < \chi_{\beta,v} < \chi_{\beta,v}^2$ in Example 3.3. This indicates that the normalized covariance values ($\chi_{a,v}$, $\chi_{D,v}$ and $\chi_{\beta,v}$) such that the critical domain size (in a bounded stream) tends to infinity are exactly the values such that the upstream spreading speed (in an infinitely long stream) tends to 0 from positive values. Note that the upstream spreading speed c^- is positive if the population spreads to the upstream and c^- is negative if it spreads to the downstream (see Figure 2). The above result then provides evidence for the contention that a result given by [19] for temporally constant environments may be extended to temporally variable environments. That is, a stream species can persist in a bounded stream only if it has a positive upstream spreading speed in an infinitely long stream and, as the length of the stream becomes infinite, conditions for persistence approach those for a nonnegative upstream spreading velocity.

4 Discussion

This paper is the sequel to the paper [8], which focused on the study of the critical domain size of a periodic integro-differential equation (1.2) with $\Omega = [0, L]$ for species in a seasonally varying stream. We reconsider the model here to investigate the seasonal influences on the population spread and dispersal in streams and rivers. Again, we assume that the population dynamics and the dispersal kernel are periodic functions with respect to time t with the same period ω , which can be taken as the scaled length of a year. Moreover, the dispersal between two locations is assumed to depend on the signed distance between them, i.e., the kernel is written as $k(t, x)$ and the model becomes (1.3). We study the spreading speeds and periodic traveling waves in an infinitely long stream, and attempt to solve the drift paradox problem by finding conditions for the upstream spreading speed to be positive. It turns out that the time-varying population dynamics and movements do affect the invasions and persistence of a species in streams. However, it is not exactly the population dynamics and movements themselves ($g(t, u)$, $a(t)$ and $k(t, x)$), but the (weighted) sums ($\int_0^\omega g(t, 0)dt$, $\int_0^\omega a(t)dt$, $\int_0^\omega a(t)k(t, x)dt$), that actually play an import role in the invasions of a species. This can be seen from the formulae of the spreading speeds (see (2.1) and

2.2)). When the environment is considered to have two main seasons, e.g., summer and winter, the spreading speeds are approximated and the effects of the normalized covariances of the flow velocity and the transfer rate, the diffusion rate, and the settling rate, on the spreading speeds and population persistence have been investigated. Compared to numerical results for Examples 3.1-3.3 in [8], we see that the condition for the species to spread upstream in an infinitely long stream is exactly the same as the condition for the species to have some positive critical domain size in a bounded stream.

In the assumption (H2)(iii), we assume that the moment generating function $M(t, \alpha)$ satisfies $M(t_0, -\Delta_-) = \infty$ and $M(t_1, \Delta_+) = \infty$ for some $t_0, t_1 \geq 0$. It is used to govern that the infima in (2.1) and (2.2) are taken in the interior of $(0, \Delta_-)$ and $(0, \Delta_+)$. In fact, if $\Delta_- = \infty$ or $\Delta_+ = \infty$, this can be proved as in the proof of [9, Proposition 3.4], so this assumption is actually only applied when Δ_- or Δ_+ is finite. In the case that Δ_- or Δ_+ is finite but the infimum in (2.1) or (2.2) is taken at Δ_- or Δ_+ , we expect that the expressions for the spreading speeds are still true by adapting the process in [31] for an integro-difference equation. However, it is not addressed here in this paper.

In the following two subsections, we give two further observations based on the results in this paper and [8].

4.1 Spreading speeds for the periodic model (1.3) and associated autonomous models

We find an interesting relationship between the periodic model (1.3) and the associated autonomous models. It follows from Theorem 2.1 that for the autonomous case of (1.3) with asymmetric dispersal kernel

$$\frac{\partial u(t, x)}{\partial t} = u(t, x)f(u(t, x)) - \varsigma u(t, x) + \varsigma \int_{\mathbb{R}} k(x - y)u(t, y)dy, \quad (4.1)$$

if f , ς and k satisfy corresponding conditions for g , a and k in (H1) and (H2), then the spreading speeds for (4.1) in the downstream and upstream directions are, respectively,

$$c_0^+ = \inf_{0 < \alpha < \Delta_+} \frac{f(0) - \varsigma + \varsigma \int_{\mathbb{R}} k(y)e^{\alpha y} dy}{\alpha} \quad (4.2)$$

and

$$c_0^- = \inf_{0 < \alpha < \Delta_-} \frac{f(0) - \varsigma + \varsigma \int_{\mathbb{R}} k(y)e^{-\alpha y} dy}{\alpha}. \quad (4.3)$$

Similarly, for the model (2.4) where the dynamics are time-periodic but the dispersal kernel does not vary with time, the spreading speeds are

$$c^+ = \frac{1}{\omega} \inf_{\alpha \in (0, \Delta_+)} \frac{\int_0^\omega (g(s, 0) - a(s))ds + \int_0^\omega a(s)ds \int_{\mathbb{R}} k(y)e^{\alpha y} dy}{\alpha} \quad (4.4)$$

and

$$c^- = \frac{1}{\omega} \inf_{\alpha \in (0, \Delta_-)} \frac{\int_0^\omega (g(s, 0) - a(s)) ds + \int_0^\omega a(s) ds \int_{\mathbb{R}} k(y) e^{-\alpha y} dy}{\alpha}, \quad (4.5)$$

in the downstream and upstream directions, respectively. Define an autonomous model associated with (2.4) as

$$\frac{\partial u(t, x)}{\partial t} = u(t, x) \frac{\int_0^\omega g(s, u) ds}{\omega} - \frac{\int_0^\omega a(s) ds}{\omega} u(t, x) + \frac{\int_0^\omega a(s) ds}{\omega} \int_{\mathbb{R}} k(x - y) u(t, y) dy. \quad (4.6)$$

Comparing the equations (4.1) and (4.6), we can easily write the spreading speeds for (4.6) and then find that the spreading speeds for the periodic model (2.4) are equal to those for the autonomous model (4.6), in the downstream and upstream directions, respectively. Define a weighted time-averaged dispersal kernel $\mathcal{K}(x - y)$ for the dispersal kernel $k(t, x - y)$ as

$$\mathcal{K}(x - y) := \int_0^\omega \frac{a(s)}{\int_0^\omega a(\xi) d\xi} k(s, x - y) ds, \quad \forall x, y \in \mathbb{R}. \quad (4.7)$$

Here the weighting is given by the normalized transfer rate. We rewrite the expressions of c^+ and c^- in (2.1)-(2.3) for (1.3) in the form of $\mathcal{K}(x - y)$ as

$$c^+ = \inf_{0 < \alpha < \Delta_+} \frac{\frac{1}{\omega} \int_0^\omega (g(s, 0) - a(s)) ds + \frac{1}{\omega} \int_0^\omega a(s) ds \int_{\mathbb{R}} \mathcal{K}(y) e^{\alpha y} dy}{\alpha} \quad (4.8)$$

and

$$c^- = \inf_{0 < \alpha < \Delta_-} \frac{\frac{1}{\omega} \int_0^\omega (g(s, 0) - a(s)) ds + \frac{1}{\omega} \int_0^\omega a(s) ds \int_{\mathbb{R}} \mathcal{K}(y) e^{-\alpha y} dy}{\alpha}. \quad (4.9)$$

Comparing (4.8) and (4.9) with (4.4) and (4.5), we see that the spreading speeds for (1.3) are the same as those for (2.4) with the time-averaged weighted dispersal kernel \mathcal{K} , in the downstream and upstream directions, respectively.

It follows from above analysis that, to study the spreading speeds for (1.3), it suffices to study those for (2.4) with the weighted time-averaged dispersal kernel \mathcal{K} , for which it only suffices to study the spreading speeds for the time-averaged model (4.6) with \mathcal{K} . Then we conclude that when studying the spreading speeds for a periodic integro-differential equation, a periodic dispersal kernel $k(t, x - y)$ has the same effect as its associated weighted time-averaged dispersal kernel $\mathcal{K}(x - y)$; moreover, the study of spreading speeds for a periodic integro-differential equation can be reduced to the study of spreading speeds for its weighted time-averaged autonomous integro-differential equation. However, it is important to note that this simplification can only be applied for the estimation of spreading speeds. There is no hint that local or global dynamics of these models are the same.

Therefore, the influences of the time-variations of population dynamics and dispersal features on the invasions can be time-averaged providing the averaging uses the appropriate weighting.

Significant changes of population dynamics or dispersal features ($g(t, u)$, $a(t)$, and $k(t, x - y)$) at a few times may not influence the long-term invasions of a species as long as the changes of their totals ($\int_0^\omega g(t, 0)dt$, $\int_0^\omega a(t)dt$ and $\mathcal{K}(x - y)$) can be neglected. In more details, if the dispersal kernel is independent of time, then it is the sums of population dynamics and transfer rate over a period, other than their values at specific times, besides the kernel, that influence the spreading speeds; if the dispersal kernel is a time-periodic function, then besides the sums of population dynamics and transfer rate over a period, the time-averaged weighted dispersal kernel plays an important role for the spreading speeds. Note that this averaged kernel is not just the average of the original kernel over a period, but the weighted average of the original kernel and the transfer rate. Thus, when the dispersal kernel is time-dependent, it is not as intuitive as it might seem to see the effects of the kernel and the transfer rate on the spreading of the population.

4.2 Population persistence in bounded and infinitely long streams

As both this paper and the paper [8] focus on the invasions of a population in streams whether infinitely long or bounded in different perspectives, we are interested in the connection between the results in these two papers. In particular, we hope to build relationship between the persistence of a population in a bounded stream and the upstream spreading speed of the population in an infinitely long stream.

Consider (1.3) in a bounded stream, i.e.,

$$\frac{\partial u(t, x)}{\partial t} = u(t, x)g(t, u(t, x)) - a(t)u(t, x) + a(t) \int_{\Omega} k(t, x - y)u(t, y)dy \quad (4.10)$$

with $\Omega = [0, L]$ where $L > 0$. [8, Theorem 2.3] implies that if $\int_0^\omega g(s, 0)ds \geq \int_0^\omega a(s)ds$, then the population persists in the stream no matter what the length of the stream is; if $\int_0^\omega g(s, 0)ds < \int_0^\omega a(s)ds$, then the critical domain size L can be obtained by solving the threshold condition

$$\lambda(L) = 1 - \frac{\int_0^\omega g(s, 0)ds}{\int_0^\omega a(s)ds},$$

where λ is the principal eigenvalue of the operator I defined as

$$I[\psi](x) := \int_0^L \mathcal{K}(x - y)\psi(y)dy, \forall x \in [0, L], \forall \psi \in C([0, L], W)$$

with \mathcal{K} defined in (4.7), and hence, the population can persist in the stream provided that the stream length is larger than the critical domain size.

Clearly, it follows from (2.2) that if $\int_0^\omega g(s, 0)ds > \int_0^\omega a(s)ds$, then the upstream spreading speed c^- for (1.3) is positive and that if $\int_0^\omega g(s, 0)ds = \int_0^\omega a(s)ds$, then c^- is nonnegative. If

$\int_0^\omega g(s, 0)ds < \int_0^\omega a(s)ds$, it is not intuitive to see the sign of c^- . However, we can determine its sign in the case where the dispersal is described by a diffusion-advection plus settling process. For (1.3) with the dispersal kernel (1.1) and constant β , v and D , the upstream spreading speed is given as

$$c^- = \inf_{0 < \alpha < b_1} \frac{\int_0^\omega (g(s, 0) - a(s))ds + \int_0^\omega a(s)ds \frac{\beta}{\beta + \alpha v - \alpha^2 D}}{\alpha \omega}. \quad (4.11)$$

The critical domain size for (4.10) with the same kernel is

$$L(\lambda) = \frac{4 \arctan \left(\sqrt{\frac{4b_1|b_2|}{\lambda(b_1-b_2)^2} - 1} \right)^{-1}}{(b_1 - b_2) \sqrt{\frac{4b_1|b_2|}{\lambda(b_1-b_2)^2} - 1}},$$

where $\lambda = 1 - \int_0^\omega g(s, 0)ds / \int_0^\omega a(s)ds$ (see (2.14) in [8]). We then obtain

$$L \left(1 - \frac{\int_0^\omega g(s, 0)ds}{\int_0^\omega a(s)ds} \right) = \infty$$

if and only if

$$1 - \frac{\int_0^\omega g(s, 0)ds}{\int_0^\omega a(s)ds} = \frac{4b_1|b_2|}{(b_1 - b_2)^2}. \quad (4.12)$$

Substituting (4.12) into (4.11), we obtain $c^- = 0$ with the infimum attained at $\alpha = v/(2D) \in (0, b_1)$. Moreover, we can show that

$$L \left(1 - \frac{\int_0^\omega g(s, 0)ds}{\int_0^\omega a(s)ds} \right) < \infty \Leftrightarrow c^- > 0.$$

Therefore, the condition for the critical domain size for (4.10) to tend to infinity is exactly the one for which the upstream spreading speed for (1.3) tends to 0 (from positive values). We then conclude that a population can persist in a bounded stream (i.e., the critical domain size is finite) if and only if it has a nonnegative upstream spreading speed in an infinitely long stream, which has been illustrated in the numerical examples in section 3. This allows us to use the condition of the upstream spreading speed $c^- \geq 0$ to represent persistence for the population in an infinitely long stream.

For more general dispersal kernels, we expect that the result here is still true, but it is beyond the scope of this paper.

There are still many new problems in the mathematical investigation of single species models for spread and persistence in streams. Future work includes analyzing stream systems with random as opposed to time periodic fluctuations in water flow. Also the interplay between the effects of temporal and spatial variability in stream systems is a rich area for complex dynamical outcomes.

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5 Appendix

Appendix A. Derivation of model (1.2)

To understand the population dynamics and invasions of stream species, the autonomous version of (1.2)

$$\frac{\partial u(t, x)}{\partial t} = u(t, x)g(u(t, x)) - au(t, x) + a \int_{\Omega} k(x, y)u(t, y)dy, \quad t \geq 0, \quad x \in \Omega$$

has been well established and studied in, e. g., [7, 20, 24, 27], and the temporally constant but spatially heterogeneous version of (1.2)

$$\frac{\partial u(t, x)}{\partial t} = u(t, x)g(x, u(t, x)) - a(x)u(t, x) + \int_{\Omega} k(x, y)a(y)u(t, y)dy, \quad t \geq 0, \quad x \in \Omega$$

has also been derived and investigated in, e. g., [2, 4]. These models describe growth and dispersal where dispersal is effectively instantaneous when compared to the time scale for growth. The first term in the above equations describes population growth. The second term describes transfer (uptake) into the dispersing class. The third term describes the effectively instantaneous reappearance of the disperser in a new spatial location. Unlike the above models, our model (1.2)

includes temporal heterogeneity in the growth, transfer and dispersal, so for self-completeness, we derive (1.2) from first principles.

It is well known that almost all species of invertebrates in streams have a part of the population living in the benthic zone as well as the rest of the population drifting in water [1]. Drift invertebrates transfer (uptake) from the benthic zone, drift in the water column for a short time, reattach to the benthic zone, re-enter the drift once again, and so on [5, 29]. In fact, most invertebrates spend very little time in water during each drift. For example, experiments in [5] showed that, at a site in Wilfin Beck (a small stream (length 4 km) in the English Lake District), 25% of the drifting *Baetis* or *Gammarus* returned to the substratum after only 3 seconds, 1% remained in the drift for 43 seconds, and most of the other organisms drifted in water for about 3 seconds to 43 seconds. This results in organisms' settling rate (from water to the benthic zone) on the order of $2009 - 28800 \text{ day}^{-1}$. Comparing this settling rate to *Baetis*'s growth rate (e. g., $< 0.04 \text{ day}^{-1}$ in [6]) and taxa's approximate transfer rate (or uptake rate) from the benthic zone to water (e.g., $0.29 - 6 \text{ day}^{-1}$ in [4]), we can clearly conclude that for stream invertebrates, settling process is very fast relative to transfer (or uptake) process or growth. As our goal is to understand the long-term behaviors of stream invertebrates, we would like to consider their dynamics on the time scale of average uptake.

We divide the population of stream invertebrates into two classes: stationary individuals that stay in the benthic zone and mobile individuals that drift in water. We assume that birth only occurs in the stationary class in the benthic zone, but that mortality occurs in both classes. Let u (1/space²) be the density of the stationary individuals and w (1/space²) be the depth-integrated spatial density of individuals in the water column, respectively. The per capita growth rate is $g(t, u)$ (1/time); the transfer rate (or uptake rate) from the stationary class to the mobile class is $a(t)$ (1/time); the settling rate from the mobile class to the stationary class is $\beta(t)$ (1/time); the mortality rate of the mobile individuals is $\mu(t)$ (1/time); the movement for the mobile individuals is governed by a differential operator

$$G(t) = D(t) \frac{\partial^2}{\partial x^2} - v(t) \frac{\partial}{\partial x}$$

with $D(t)$ (space²/time) being the diffusion rate and $v(t)$ (space/time) being the flow speed. It follows from the conservation of the population that the population dynamics is governed by

$$\begin{cases} \frac{\partial u(t, x)}{\partial t} = u(t, x)g(t, u(t, x)) - a(t)u(t, x) + \beta(t)w(t, x), \\ \frac{\partial w(t, x)}{\partial t} = D(t) \frac{\partial^2 w(t, x)}{\partial x^2} - v(t) \frac{\partial w(t, x)}{\partial x} + a(t)u(t, x) - \beta(t)w(t, x) - \mu(t)w(t, x). \end{cases} \quad (5.1)$$

Reasonably, we assume that $a(t)$, $\beta(t)$, $\mu(t)$, $D(t)$ and $v(t)$ are all positive, continuous and

bounded functions. Furthermore, assume that g is continuous in t and u and is decreasing in u , $\lim_{T \rightarrow \infty} \frac{1}{T} \int_0^T g(t, 0) dt > 0$, and that there exists $\hat{u} > 0$ such that $g(t, \hat{u}) \leq 0$ for all $t \geq 0$. Let $\tilde{u}(t)$ be the population's carrying capacity at time $t \geq 0$, which can be defined as the largest solution $u(t)$ to $u(t)g(t, u(t)) = 0$. That is, if $g(t, 0) > 0$, then we know $\tilde{u}(t) > 0$ for some $t \geq 0$ because $g(t, \hat{u}) \leq 0$ for \hat{u} and g is continuous in u ; if $g(t, 0) \leq 0$, it may be that $\tilde{u}(t) = 0$ for some $t \geq 0$. Define \bar{a} , \bar{v} and \bar{u} as the average values attained by $a(t)$, $v(t)$, and $\tilde{u}(t)$, respectively:

$$\bar{a} = \lim_{T \rightarrow \infty} \frac{1}{T} \int_0^T a(t) dt, \quad \bar{v} = \lim_{T \rightarrow \infty} \frac{1}{T} \int_0^T v(t) dt, \quad \bar{u} = \lim_{T \rightarrow \infty} \frac{1}{T} \int_0^T \tilde{u}(t) dt.$$

By the assumptions in g it follows that $\bar{u} > 0$. Since settling is much faster than transfer, we can assume that $\frac{a(t)}{\beta(t)}$ is $O(\varepsilon)$ uniformly in time for some ε with $0 < \varepsilon \ll 1$. That is,

$$\frac{a(t)}{\beta(t)} = \varepsilon h(t),$$

where $h(t)$ is a positive bounded function of order 1. Assume that the first time $a(t)$ attains its average value \bar{a} is at time $t = \bar{t}$, i.e., $a(\bar{t}) = \bar{a}$. Let $\bar{\beta} = \beta(\bar{t})$. Without loss of generality, we further assume ε is chosen such that $h(\bar{t}) = 1$. Then $\varepsilon = \frac{a(\bar{t})}{\beta(\bar{t})} = \frac{\bar{a}}{\bar{\beta}}$.

Rescale space and time appropriately by

$$t^* = t\bar{a}, \quad x^* = \frac{x\bar{\beta}}{\bar{v}}, \quad u^* = \frac{u}{\bar{u}}, \quad w^* = \frac{w}{\bar{u}}.$$

The system (5.1) becomes

$$\begin{cases} \frac{\partial u^*}{\partial t^*} = u^* \frac{g(t, u)}{\bar{a}} - \frac{a(t)}{\bar{a}} u^* + \frac{\beta(t)}{\bar{a}} w^*, \\ \frac{\partial w^*}{\partial t^*} = \frac{D(t)\bar{\beta}^2}{\bar{v}^2 \bar{a}} \frac{\partial^2 w^*}{\partial x^{*2}} - \frac{v(t)\bar{\beta}}{\bar{v} \bar{a}} \frac{\partial w^*}{\partial x^*} + \frac{a(t)}{\bar{a}} u^* - \frac{\beta(t)}{\bar{a}} w^* - \frac{\mu(t)}{\bar{a}} w^*, \end{cases} \quad (5.2)$$

where u^* and w^* are functions of t^* and x^* . Let $g^*(t^*, u^*) = g(t, u)/\bar{a}$, $a^*(t^*) = a(t)/\bar{a}$, $\mu^*(t^*) = \mu(t)/\bar{a}$, $\beta^*(t^*) = \beta(t)/\bar{\beta}$, $D^*(t^*) = D(t)\bar{\beta}/\bar{v}^2$, and $v^*(t^*) = v(t)/\bar{v}$. Dropping asterisks for notational simplicity and substituting $\varepsilon = \frac{\bar{a}}{\bar{\beta}}$, we rewrite (5.2) as follows

$$\begin{cases} \varepsilon \frac{\partial u(t, x)}{\partial t} = \varepsilon u(t, x) g(t, u(t, x)) - \varepsilon a(t) u(t, x) + \beta(t) w(t, x), \\ \varepsilon \frac{\partial w(t, x)}{\partial t} = D(t) \frac{\partial^2 w(t, x)}{\partial x^2} - v(t) \frac{\partial w(t, x)}{\partial x} + \varepsilon a(t) u(t, x) - \beta(t) w(t, x) - \varepsilon \mu(t) w(t, x). \end{cases} \quad (5.3)$$

Next we derive (1.2) from (5.3) by singular perturbation theory (see e.g., [10]). Substituting a regular asymptotic series solution

$$\begin{aligned} u(t, x) &= u^0(t, x) + \varepsilon u^1(t, x) + \dots \\ w(t, x) &= w^0(t, x) + \varepsilon w^1(t, x) + \dots \end{aligned}$$

into (5.3) and comparing the coefficients of the orders of ε , we obtain $w^0(t, x) = 0$ at $O(1)$ and

$$\begin{cases} \frac{\partial u^0(t, x)}{\partial t} = u^0(t, x)g(t, u^0(t, x)) - a(t)u^0(t, x) + \beta(t)w^1(t, x), \\ 0 = D(t)\frac{\partial^2 w^1(t, x)}{\partial x^2} - v(t)\frac{\partial w^1(t, x)}{\partial x} + a(t)u^0(t, x) - \beta(t)w^1(t, x) \end{cases} \quad (5.4)$$

at $O(\varepsilon)$. The second equation of (5.4) is equivalent to

$$-u^0(t, x) = \frac{D(t)}{a(t)}\frac{\partial^2 w^1(t, x)}{\partial x^2} - \frac{v(t)}{a(t)}\frac{\partial w^1(t, x)}{\partial x} - \frac{\beta(t)}{a(t)}w^1(t, x)$$

at $O(\varepsilon)$. Let $k(t, x, y)$ satisfy $\int_{\mathbb{R}} k(t, x, y)dx = 1$ and

$$\frac{D(t)}{\beta(t)}\frac{\partial^2 k(t, x, y)}{\partial x^2} - \frac{v(t)}{\beta(t)}\frac{\partial k(t, x, y)}{\partial x} - k(t, x, y) = -\delta(x - y).$$

By a similar analysis as in section 4.1 in [20], the kernel $k(t, x, y)$ can be derived as in the form in (1.1). Then

$$w^1(t, x) = \frac{a(t)}{\beta(t)} \int_{\mathbb{R}} k(t, x, y)u^0(t, y)dy,$$

and hence,

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

which takes the form of (1.2) and is valid to $O(\varepsilon)$. Indeed, this is the equation describing population dynamics of stream invertebrates on the time scale of the average uptake.

Appendix B. Proof of Proposition 2.1

Case 1. $\Delta_{\pm} = \infty$. In this case, we can apply the theory of spreading speeds for monotone scalar maps in [15, 30] to (1.3) to show the existence of the spreading speeds of Q_{ω} in the downstream and upstream directions. The details are omitted here as they are similar to those in [9, Lemma 3.2]. Then we estimate the spreading speeds c_{ω}^{\pm} of Q_{ω} by using the linear approach introduced in [15] and following similar arguments as in [9, Proposition 3.4]. The formulae of downstream and upstream spreading speeds of Q_{ω} when $\Delta_{\pm} = \infty$ are given in (2.1) and (2.2), respectively.

Case 2. $\Delta_{-} < \infty$ or $\Delta_{+} < \infty$. In these cases, we follow a similar limiting argument as mentioned in the proof of Proposition 3.4 in [9] to show the existence of the spreading speeds in the associated directions. We show (2.2) when $\Delta_{-} < \infty$. If $\Delta_{+} < \infty$, (2.1) can be similarly obtained. For $t \geq 0$ and $m > 0$, define

$$k_m(t, x) = \begin{cases} k(t, x), & x \geq -m, \\ 0, & x < -m. \end{cases} \quad (5.5)$$

Let $h_m = \int_{\mathbb{R}} k_m(t, y) dy$. Then k_m/h_m satisfies (H2) with $\Delta_{\pm}(m) = \infty$ and the result in Case 1 can be applied to the period map $Q_{\omega}(m)$ of the system

$$\begin{aligned} \frac{\partial u(t, x)}{\partial t} &= u(t, x)g(t, u(t, x)) - a(t)u(t, x) + a(t) \int_{\mathbb{R}} k_m(t, x - y)u(t, y)dy, \\ &= u(t, x)g(t, u(t, x)) - a(t)u(t, x) + a(t)h_m \int_{\mathbb{R}} \frac{k_m(t, x - y)}{h_m} u(t, y)dy, \end{aligned} \quad (5.6)$$

for $m \geq m_0$ with $m_0 > 0$ being some sufficiently large number. Hence, for $m \geq m_0$, the upstream spreading speed of $Q_{\omega}(m)$ is

$$c_{\omega}^{-}(m) = \inf_{\alpha > 0} \Phi_m(\alpha), \quad (5.7)$$

where $\Phi_m(\alpha) = [\int_0^{\omega} (g(s, 0) - a(s))ds + \int_0^{\omega} a(s) \int_{\mathbb{R}} k_m(s, y)e^{-\alpha y} dy ds] / \alpha$. Define

$$\Phi(\alpha) = \frac{\int_0^{\omega} (g(s, 0) - a(s))ds + \int_0^{\omega} a(s) \int_{\mathbb{R}} k(s, y)e^{-\alpha y} dy ds}{\alpha} \quad (5.8)$$

for $\alpha \in (0, \Delta_-)$ and c_{ω}^{-} as in (2.2).

Claim: $\lim_{m \rightarrow \infty} c_{\omega}^{-}(m) = c_{\omega}^{-}$. Note that, for $m \geq m_0$, $\Phi_m(\alpha)$ is a positive continuous function of $\alpha > 0$. For each $\alpha > 0$, $\Phi_m(\alpha)$ is monotone increasing in m . For each $\alpha \in (0, \Delta_-)$, $\Phi_m(\alpha) < \Phi(\alpha)$ and $\Phi_m(\alpha) \rightarrow \Phi(\alpha)$ as $m \rightarrow \infty$. It then follows that $c_{\omega}^{-}(m) \leq c_{\omega}^{-}$. By [9, Lemma 3.2 and Proposition 3.4], $\Phi_m(\alpha) \rightarrow +\infty$ as $\alpha \rightarrow 0$ or $+\infty$. Let $\bar{\alpha}_m$ be the value of α satisfying $c_{\omega}^{-}(m) = \Phi_m(\bar{\alpha}_m)$. By the fact that $\lim_{\alpha \rightarrow 0} \Phi_m(\alpha) = +\infty$ and the monotonicity of Φ_m in m , there exists $\alpha_1 > 0$ such that $\Phi_m(\alpha) > c_{\omega}^{-}$ for $0 < \alpha < \alpha_1$ for all $m \geq m_0$. Note that (H2)(iii) implies $\Phi(\Delta_-) = \infty$. Given $K_0 > c_0$, there exists a $\delta \in (0, \Delta_-)$ such that $\Phi(\alpha) > K_0$ for $\alpha \in [\Delta_- - \delta, \Delta_-)$. Then there exists an $m_1 \geq m_0$, such that $\Phi_m(\Delta_- - \delta) > K_0$ for all $m > m_1$. It follows that $\bar{\alpha}_m \in [\alpha_1, \Delta_- - \delta]$ for all $m \geq m_1$. Thus, there is a convergent subsequence $\{\bar{\alpha}_{m_n}\}$ of $\{\bar{\alpha}_m\}_{m \geq m_1}$ and for some $\alpha^0 \in [\alpha_1, \Delta_- - \delta]$, $\bar{\alpha}_{m_n} \rightarrow \alpha^0$ as $n \rightarrow \infty$. Then $c_{\omega}^{-} \geq \limsup_{n \rightarrow \infty} c_{\omega}^{-}(m_n) \geq \liminf_{n \rightarrow \infty} \Phi_{m_n}(\bar{\alpha}_{m_n}) = \Phi(\alpha^0) \geq c_{\omega}^{-}$, and hence $\lim_{n \rightarrow \infty} c_{\omega}^{-}(m_n) = c_{\omega}^{-}$. Since $c_{\omega}^{-}(m)$ is increasing in $m \geq m_0$, we then have $\lim_{m \rightarrow \infty} c_{\omega}^{-}(m) = c_{\omega}^{-}$.

We now show that c_{ω}^{-} is the upstream spreading speed of the periodic map Q_{ω} of (1.3). For any $c > c_{\omega}^{-}/\omega$, we fix $\hat{c} \in (c_{\omega}^{-}/\omega, c)$. Then there exists $\bar{\alpha} \in (0, \Delta_-)$, such that $\hat{c}\omega \geq \Phi(\bar{\alpha}) \geq c_{\omega}^{-}$. Let $\varphi \in C_{u^*(0)}$ and $\varphi(x) = 0$ for $x < \rho$ with $\rho \in \mathbb{R}$ and $u(t, \cdot; \varphi)$ be the solution of (1.3) satisfying $u(0, \cdot; \varphi) = \varphi$. Choose $\bar{\gamma} > 0$ such that $0 \leq \varphi(x) \leq \bar{\gamma}e^{\bar{\alpha}x}$ for all $x \in \mathbb{R}$. Then we can verify that $\bar{u}(t, x) = \bar{\gamma}e^{\bar{\alpha}(\hat{c}t+x)}$ is an upper solution of the linearized system to (1.3) at $u = 0$. It then follows from the comparison principle that

$$0 \leq u(n\omega, x; \varphi) \leq \bar{u}(n\omega, x) = \bar{\gamma}e^{\bar{\alpha}(\hat{c}n\omega+x)} \leq \bar{\gamma}e^{\bar{\alpha}(\hat{c}-c)n\omega}, \quad \forall n \in \mathbb{N}, x \leq -cn\omega,$$

which implies that $\lim_{n \rightarrow \infty, x \leq -cn\omega} u(n\omega, x; \varphi) = 0$. Let $c \in (0, c_{\omega}^{-}/\omega)$ be fixed, $\varphi \in C_{u^*(0)}$, $\varphi \not\equiv 0$ and $u(t, \cdot; \varphi)$ be the solution of (1.3) satisfying $u(0, \cdot; \varphi) = \varphi$. Since $\lim_{m \rightarrow \infty} c_{\omega}^{-}(m) = c_{\omega}^{-}$ and $c_{\omega}^{-}(m) \leq c_{\omega}^{-}$,

there exists a sufficiently large number $\bar{m}_1 \geq m_0$ such that $c\omega < c_\omega^-(m) \leq c_\omega^-$, $\forall m \geq \bar{m}_1$. For any given $m \geq \bar{m}_1$, let $\varphi_1^m(x) = \min\{\varphi(x), u_m^*(0)\}$ for all $x \in \mathbb{R}$, where $u_m^*(t)$ is the periodic solution of (5.6) and its existence can be shown similarly as we do for $u^*(t)$ to (1.3). Moreover, we can show that $\lim_{m \rightarrow \infty} u_m^*(0) = u^*(0)$. Note that $u(t, \cdot; \varphi)$ is an upper solution of (5.6). Then $u(t, x; \varphi) \geq u_m(t, x; \varphi_1^m)$, for all $(t, x) \in [0, \infty) \times \mathbb{R}$ and $m \geq \bar{m}_1$, where $u_m(t, \cdot; \varphi_1^m)$ is the unique solution of (5.6) with $u_m(0, \cdot; \varphi_1^m) = \varphi_1^m$. Since $c_\omega^-(m)$ is the upstream spreading speed of $Q_\omega(m)$, we have $\lim_{n \rightarrow \infty, x \leq -cn\omega} u_m(n\omega, x; \varphi_1^m) = u_m^*(0)$. Then

$$\begin{aligned} u^*(0) &\geq \limsup_{n \rightarrow \infty, x \leq -cn\omega} u(n\omega, x; \varphi) \geq \liminf_{n \rightarrow \infty, x \leq -cn\omega} u(n\omega, x; \varphi) \\ &\geq \liminf_{n \rightarrow \infty, x \leq -cn\omega} u_m(n\omega, x; \varphi_1^m) = u_m^*(0) \end{aligned}$$

for all $m \geq \bar{m}_1$. Letting $m \rightarrow \infty$, we obtain $\lim_{n \rightarrow \infty, x \leq -cn\omega} u(n\omega, x; \varphi) = u^*(0)$. Therefore, c_ω^- is the upstream spreading speed of Q_ω .

Appendix C. Proof of Theorem 2.5

Let

$$U(t, \theta) = \int_{\mathbb{R}} u(t, x) e^{-i\theta x} dx, \quad K(\theta) = \int_{\mathbb{R}} k(x) e^{-i\theta x} dx, \quad \forall t \geq 0, \theta \in \mathbb{R}.$$

Applying the Fourier transform to both sides of (2.5) yields

$$\frac{\partial U(t, \theta)}{\partial t} = g(t, 0)U(t, \theta) - a(t)U(t, \theta) + a(t)K(\theta)U(t, \theta), \quad \forall t \geq 0, \theta \in \mathbb{R},$$

which implies that

$$U(t, \theta) = U(0, \theta) e^{\int_0^t [g(s, 0) - a(s) + K(\theta)a(s)] ds}, \quad \forall t \geq 0, \theta \in \mathbb{R}, \quad (5.9)$$

where $U(0, \theta) = \int_{\mathbb{R}} u_0 \delta(x) e^{-i\theta x} dx = u_0$. Note that $K(\theta)$ can be rewritten as

$$K(\theta) = \sum_{n=0}^{\infty} \zeta_n \frac{(i\theta)^n}{n!}$$

where

$$\zeta_n = \int_{\mathbb{R}} x^n k(x) dx$$

(see e.g., [11, 32]). Then we take the inverse Fourier transform of (5.9) and obtain

$$\begin{aligned}
& u(t, x) \\
&= \frac{1}{2\pi} \int_{\mathbb{R}} U(t, \theta) e^{i\theta x} d\theta \\
&= \frac{1}{2\pi} \int_{\mathbb{R}} U(0, \theta) e^{\int_0^t (g(s,0) - a(s)) ds} e^{\int_0^t a(s) ds} K(\theta) e^{i\theta x} d\theta \\
&= u_0 e^{\int_0^t (g(s,0) - a(s)) ds} \int_{\mathbb{R}} \frac{1}{2\pi} e^{\int_0^t a(s) ds} K(\theta) e^{i\theta x} d\theta \\
&= u_0 e^{\int_0^t (g(s,0) - a(s)) ds} \int_{\mathbb{R}} \frac{1}{2\pi} \sum_{m=0}^{\infty} \frac{1}{m!} \left\{ \left[\int_0^t a(s) ds \right]^m [K(\theta)]^m \right\} e^{i\theta x} d\theta \\
&= u_0 e^{\int_0^t (g(s,0) - a(s)) ds} \sum_{m=0}^{\infty} \frac{1}{m!} \left\{ \left[\int_0^t a(s) ds \right]^m \int_{\mathbb{R}} \frac{1}{2\pi} [K(\theta)]^m e^{i\theta x} d\theta \right\} \\
&= u_0 e^{\int_0^t (g(s,0) - a(s)) ds} \sum_{m=0}^{\infty} \frac{1}{m!} \left\{ \left[\int_0^t a(s) ds \right]^m \int_{\mathbb{R}} \frac{1}{2\pi} K(\theta) \left[\sum_{n=0}^{\infty} \zeta_n \frac{(i\theta)^n}{n!} \right]^{m-1} e^{i\theta x} d\theta \right\}.
\end{aligned}$$

Note that $(i\theta)^n K(\theta)$ is the Fourier transform of $(-1)^n d^n k(x)/dx^n$. Similarly as in [11, Appendix A], we can obtain that

$$\int_{\mathbb{R}} \frac{1}{2\pi} K(\theta) \left[\sum_{n=0}^{\infty} \zeta_n \frac{(i\theta)^n}{n!} \right]^{m-1} e^{i\theta x} d\theta \sim k(x), \quad |x| \gg 1, \quad m = 1, 2, \dots,$$

provided that

$$\lim_{|x| \rightarrow \infty} \left[\frac{1}{k(x)} \frac{d^n k(x)}{dx^n} \right] = 0$$

uniformly for all $n \geq 0$. Therefore, if the above equation is true, then we can obtain an approximation of the solution to (2.5) with an initial point source of strength u_0 :

$$u(t, x) \sim u_0 e^{\int_0^t (g(s,0) - a(s)) ds} e^{\int_0^t a(s) ds} k(x) = u_0 k(x) e^{\int_0^t [(g(s,0) - a(s)) + a(s)] ds}$$

for $|x| \gg 1, t > 0$.

Appendix D. Proof of Theorem 3.1

It follows from (3.2) that the moment generating function of $k^{(n)}(t, x)$ satisfies

$$M^{(n)}(t, \alpha) = \int_{\mathbb{R}} k^{(n)}(t, x) e^{\alpha x} dx \leq \int_{\mathbb{R}} k_2(x) e^{\alpha x} dx + \int_{\mathbb{R}} k_1(x) e^{\alpha x} dx = M_2(\alpha) + M_1(\alpha),$$

for any $n \in \mathbb{N}, t \geq 0$ and $\alpha \in (-\Delta_-, \Delta_+)$, which implies that for any $n \in \mathbb{N}$ and $t \in [0, \omega]$, $M^{(n)}(t, \alpha)$ exists for all $\alpha \in (-\Delta_-, \Delta_+)$. Let

$$I_n(\alpha) = - \int_0^\omega a^{(n)}(s) ds + \int_0^\omega a^{(n)}(s) \int_{\mathbb{R}} k^{(n)}(s, y) e^{\alpha y} dy ds,$$

for all $n \in \mathbb{N}$ and $\alpha \in (-\Delta_-, \Delta_+)$. By (3.2) again, for any $\alpha \in (-\Delta_-, \Delta_+)$ and $n \in \mathbb{N}$, we have

$$\begin{aligned}
& -a_1\left(\omega_0 - \frac{1}{n}\right) - a_2\left(\omega - \frac{1}{n} - \omega_0\right) - \int_{\omega_0 - \frac{1}{n}}^{\omega_0} a_1^{(n)}(s) ds - \int_{\omega - \frac{1}{n}}^{\omega} a_2^{(n)}(s) ds \\
& + \left(\int_{\omega_0 - \frac{1}{n}}^{\omega_0} + \int_{\omega - \frac{1}{n}}^{\omega} \right) \int_{\mathbb{R}} a^{(n)}(s) \min\{k_2(y), k_1(y)\} e^{\alpha y} dy ds \\
& + \int_0^{\omega_0 - \frac{1}{n}} \int_{\mathbb{R}} a_1 k_1(y) e^{\alpha y} dy ds + \int_{\omega_0}^{\omega - \frac{1}{n}} \int_{\mathbb{R}} a_2 k_2(y) e^{\alpha y} dy ds \\
\leq & I_n(\alpha) \\
\leq & -a_1\left(\omega_0 - \frac{1}{n}\right) - a_2\left(\omega - \frac{1}{n} - \omega_0\right) - \int_{\omega_0 - \frac{1}{n}}^{\omega_0} a_1^{(n)}(s) ds - \int_{\omega - \frac{1}{n}}^{\omega} a_2^{(n)}(s) ds \\
& + \left(\int_{\omega_0 - \frac{1}{n}}^{\omega_0} + \int_{\omega - \frac{1}{n}}^{\omega} \right) \int_{\mathbb{R}} a^{(n)}(s) \max\{k_2(y), k_1(y)\} e^{\alpha y} dy ds \\
& + \int_0^{\omega_0 - \frac{1}{n}} \int_{\mathbb{R}} a_1 k_1(y) e^{\alpha y} dy ds + \int_{\omega_0}^{\omega - \frac{1}{n}} \int_{\mathbb{R}} a_2 k_2(y) e^{\alpha y} dy ds.
\end{aligned}$$

Therefore, for any $\alpha \in (-\Delta_-, \Delta_+)$,

$$I_n(\alpha) \rightarrow -a_1\omega_0 - a_2(\omega - \omega_0) + a_1\omega_0 M_1(\alpha) + a_2(\omega - \omega_0) M_2(\alpha) \text{ as } n \rightarrow \infty.$$

By (2.1) and (2.3), the downstream spreading speed for (1.3) with dispersal kernel $k^{(n)}(t, x)$ and transfer rate $a^{(n)}(t)$ satisfies

$$\begin{aligned}
c_n^+ &= \frac{1}{\omega} \inf_{0 < \alpha < \Delta_+} \frac{\int_0^{\omega} g(s, 0) ds - \int_0^{\omega} a^{(n)}(s) ds + \int_0^{\omega} a(s) \int_{\mathbb{R}} k^{(n)}(s, y) e^{\alpha y} dy ds}{\alpha} \\
&\rightarrow \frac{1}{\omega} \inf_{0 < \alpha < \Delta_+} \frac{\int_0^{\omega} g(s, 0) ds + a_1\omega_0(M_1(\alpha) - 1) + a_2(\omega - \omega_0)(M_2(\alpha) - 1)}{\alpha}
\end{aligned} \tag{5.10}$$

as $n \rightarrow \infty$. Similarly, we obtain that the upstream spreading speed for (1.3) with dispersal kernel $k^{(n)}(t, x)$ satisfies

$$c_n^- \rightarrow \frac{1}{\omega} \inf_{0 < \alpha < \Delta_-} \frac{\int_0^{\omega} g(s, 0) ds + a_1\omega_0(M_1(-\alpha) - 1) + a_2(\omega - \omega_0)(M_2(-\alpha) - 1)}{\alpha} \tag{5.11}$$

as $n \rightarrow \infty$.