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SEASONAL INFLUENCES ON POPULATION SPREAD AND PERSISTENCE IN STREAMS: CRITICAL DOMAIN SIZE*

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Abstract. The critical domain size problem determines the size of the region of habitat needed to ensure population persistence. In this paper we address the critical domain size problem for seasonally fluctuating stream environments and determine how large a reach of suitable stream habitat is needed to ensure population persistence of a stream-dwelling species. Two key factors, not typically found in critical domain size problems, are fundamental in determining whether population can persist. These are the unidirectional nature of stream flow and seasonal fluctuations in the stream environment. We characterize the fluctuating environments in terms of seasonal correlations among the flow, transfer rates, diffusion, and settling rates, and we investigate the effect of such correlations on the critical domain size problem. We show how results for the seasonally fluctuating stream can formally be connected to those for autonomous integro-differential equations, through the appropriate weighted averaging methods.

Key words. seasonality, population, stream, integro-differential equations, critical domain size

AMS subject classifications. 37N25, 45C05, 92B05

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1. Introduction.

How a species invades or persists in a stream or river with a unidirectional flow is an important problem in stream ecology (see e.g., [13, 17]). While reaction-diffusion-advection equations are classic equations to describe the population dynamics in streams (see, e.g., [11, 18, 20]), integro-differential and difference equations have been attracting interest recently because they can better address the long distance dispersal via a dispersal kernel; see e.g., [7, 8, 10, 13, 14, 21] and references therein. As water discharges greatly vary between seasons, the flow velocity in a stream or river varies accordingly. The population dynamics also fluctuate with seasonal changes of temperature and other habitat conditions. As a result, any realistic investigation of persistence or invasions of a stream species must take into account the seasonal variations of stream dynamics and population dynamics.

Realistically, all natural streams or rivers are bounded and cannot be infinitely long. As a result, introduction and spread of a species into a stream does not necessarily mean that the species can persist indefinitely if there is loss over the boundaries of the stream. Thus it is meaningful to study whether the species can persist in a stream with finite length or in a bounded area in a seasonally varying environment. In this work, we study the seasonal influences on population's persistence in a bounded stream. Our model is a periodic integro-differential equation, which takes the population's long distance dispersal into the dispersal kernel, and puts the seasonality

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influences into the time-periodic functions for growth, immigration or emigration, and dispersal. This is written as

$$(1.1)\quad \frac{\partial u(t,x)}{\partial t} = \underbrace{ug(t,u(t,x))}_{\text{growth}} - \underbrace{a(t)u(t,x)}_{\text{emigration}} + \underbrace{a(t)\int_\Omega k(t,x,y)u(t,y)dy}_{\text{immigration}},\ t \geq 0,\ x \in \Omega,$$

where $\Omega = [0, L] \subset \mathbb{R}$ represents a stream with length L 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 time t that governs birth and death, $a(t)$ is the time-dependent transfer rate at which an individual leaves its current location and moves into the flowing stream, and $k(t, x, y)$ is the periodic time-dependent dispersal kernel that describes the proportion of individuals that moves from point y to point x. Equation (1.1) is the time-periodic version of (3.1) in [13]. As described in [13], this dispersal kernel can be derived from first principles from a submodel that includes the river flow rate, diffusion, and settling rate. Moreover, we assume that g, a, and k are ω-periodic in t for some $\omega > 0$. In the context of seasonal variation, ω can be considered as the length of one year. Finally, we assume hostile surroundings, so $u(t, x) = 0$ outside the domain $0 \leq x \leq L$.

The focus of this work is the critical domain size problem for (1.1). The critical domain size is a fundamental ecological quantity that describes the minimal size of the habitat needed for a species to persist. In particular, for a stream population model, it provides the minimal length of the stream such that a species can persist in the stream. If the stream length is less than the critical domain size, then the individuals will finally leave the stream and be washed out into the hostile surroundings; if the stream length is larger than the critical domain size, then the individuals can grow, reproduce, and disperse in the stream without being washed out.

The first studies of the critical domain size were in [6, 19] for reaction-diffusion models in one or more dimensional spaces. The analysis has been extended to multispecies reaction-diffusion equations [1, 2, 3, 15] and to integro-difference equations [8, 9, 10, 21] as well as stream environments [13, 18, 20]. The critical domain size for an autonomous integro-differential equivalent of (1.1) was obtained in [13]. For a specific dispersal kernel, the critical domain size was explicitly expressed, and the dependence of the critical domain size on the flow velocity was investigated.

In this paper, we will find the critical domain size for (1.1), which also leads to conditions for a stream species to persist. To generate the biological insight, we will approximate the critical domain size in a two-season environment, which represents a habitat having two main seasons, e.g., summer and winter, and hence resulting in two main forms or states of population dispersal and transfer. Through numerical examples, we obtain interesting results about the influences of coeffects (in the sense of normalized covariances) of the flow velocity, the transfer rate, the diffusion rate, and the settling rate on the critical domain size. We will show that the critical domain size of (1.1) is actually related to that of an associated autonomous model with appropriately time-averaged growth and dispersal.

The paper is organized as follows. In section 2, the critical domain size of (1.1) is obtained. In section 3, the approximation for the critical domain size in a two-season environment is established. The effects of the normalized covariances between the flow velocity and the transfer rate, the diffusion rate and the settling rate, on the critical domain size, are also obtained. The last section contains a comparison of the critical domain size for the periodic models and that for associated weighted time-averaged models.

2. Critical domain size. In this section, we study the critical domain size for (1.1); that is, the minimal length of the stream for the population to persist, by virtue of the stability of the zero solution to (1.1).

The assumptions regarding population growth and transfer are as follows.

(H1) (i) The transfer rate $a(t) > 0$ and $a(t)$ is continuous in $t \geq 0$.

(ii) $g \in C(\mathbb{R}_+^2, \mathbb{R})$ and $\partial g(t,u)/\partial u < 0$ for all $(t,u) \in \mathbb{R}_+^2$; that is, the per capita growth rate $g(t,u)$ decreases with respect to the population density. This indicates that $ug(t,u) \leq g(t,0)u$ for all $t \geq 0$ and $u \geq 0$; that is, the reproductive rate of the population is bounded above by its linearization at zero. Moreover, there exists $\hat{u} > 0$ such that $g(t,\hat{u}) \leq 0$ for all $t \geq 0$, which implies that the population growth is density dependent and is negative if the density is over $\hat{u}$, and hence, the population will not explode.

(iii) There exists $\bar{L} > 0$ such that $|u_1[g(t,u_1) - a(t)] - u_2[g(t,u_2) - a(t)]| \leq \bar{L}|u_1 - u_2|$ for all $t \geq 0, u_1, u_2 \in W$ with

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

which implies that the local dynamics $u[g(t,u) - a(t)]$ is uniformly Lipschitz continuous in $u \in W$ for all $t \geq 0$, and hence, at any time $t \geq 0$, the change rate of the local population with respect to the density is uniformly bounded provided the population density is below $\hat{u}$.

The assumptions regarding dispersal are as follows.

(H2) (i) $k(t,x,y) \geq 0$ for all $t \geq 0$, $x, y \in \mathbb{R}$, which means that the proportion of individuals that moves from one point to another point is nonnegative. All dispersing individuals move to some location so that $\int_{\mathbb{R}} k(t,x,y)dx = 1$. Lastly, there exists a constant $K_+ > 0$ such that $\sup_{x \in \mathbb{R}} \int_{\mathbb{R}} k(t,x,y)dy \leq K_+$; that is, redistribution of individuals via the dispersal kernel results in bounded density (see discussion below).

(ii) For any $t \geq 0$, $x \in [0,L]$, $k(t,x,y)$ is positive almost everywhere at $y \in [0,L]$; that is, at any location x in the stream, individuals move in from almost all the other locations in the stream.

(iii) $k(t,x,y)$ is continuous in $t \geq 0$ at any $(x,y) \in [0,L]^2$; that is, the dispersal between any two points changes continuously with respect to time. Also $k(t,x,y)$ is continuous in $x \in [0,L]$ uniformly for $y \in [0,L]$ for all $t \geq 0$; that is, individuals moving out from any location y continuously distribute in the stream.

(iv) The dispersal kernel is independent of the stream length L—it is taken as the truncation (on $[0,L]$) of the dispersal kernel $k(t,x,y)$ derived on the infinite domain [21]. This indicates that dispersing individuals do not perceive domain boundaries or, at least, do not alter their movement behavior there.

To understand (H2)(i) further we define the redistribution function (see, e.g., section 5 in [10]) as

$$K(t,x) := \int_0^L k(t,x,y)dy, \quad t \geq 0, \quad x \in [0,L].$$

(H2)(i) and (iv) imply that

$$0 \leq K(t,x) \leq K_+ \quad \forall t \geq 0, \quad x \in [0,L].$$

Biologically, this indicates that if a uniform initial distribution with $u \equiv 1$ is introduced into a habitat interval $[0, L]$, then the redistribution of these individuals is uniformly bounded by 0 and K_+ in the habitat, where the redistribution at any point x is calculated by $\int_0^L k(t,x,y)u(y)dy$ for the initial distribution u. When the dispersal kernel is a difference kernel so that $k(t,x,y) = k(t,x-y)$, $K_+ = 1$ because $\int_{\mathbb{R}} k(t,x-y)dy = \int_{\mathbb{R}} k(t,x-y)dx = 1$.

2.1. Stability of $u = 0$ in (1.1). By assumptions (H1) and (H2), we can follow a similar process as we did for [4, (1.6)] to establish the well-posedness and comparison theorem for (1.1) on $C([0,L], W)$, where

$$C([0,L],W) := \{u : u \text{ is continuous on } [0,L] \text{ and } 0 \le u(x) \le \hat{u} \text{ for all } x \in [0,L]\},$$

with W defined in (H1)(iii). Note that $u = 0$ is an equilibrium solution to (1.1). We will study the stability of the zero solution to (1.1).

The linearized system of (1.1) at $u = 0$ is

$$\frac{\partial u(t,x)}{\partial t} = g(t,0)u(t,x) - a(t)u(t,x) + a(t)\int_0^L k(t,x,y)u(t,y)dy. \tag{2.1}$$

Let $u(t,x) = \varphi(t)\psi(x)$. Substituting $u(t,x)$ into (2.1), we have

$$\varphi'(t)\psi(x) = (g(t,0) - a(t))\varphi(t)\psi(x) + \int_0^L a(t)k(t,x,y)\varphi(t)\psi(y)dy. \tag{2.2}$$

Equation (2.2) implies that

$$\left[\frac{\varphi'(t)}{\varphi(t)} - (g(t,0) - a(t))\right]\psi(x) = \int_0^L a(t)k(t,x,y)\psi(y)dy. \tag{2.3}$$

Integrating (2.3) with respect to t from 0 to ω yields

$$\left[\int_0^\omega \frac{\varphi'(t)}{\varphi(t)}dt - \int_0^\omega (g(t,0) - a(t))dt\right]\psi(x) = \int_0^L \left(\int_0^\omega a(t)k(t,x,y)dt\right)\psi(y)dy. \tag{2.4}$$

Define

$$\mathcal{K}(x,y) := \frac{\int_0^\omega a(t)k(t,x,y)dt}{\int_0^\omega a(t)dt} \qquad \forall x,y \in \mathbb{R}. \tag{2.5}$$

Then (H2) implies

$$0 \le \int_0^L \mathcal{K}(x,y)dy = \frac{1}{\int_0^\omega a(t)dt}\int_0^L \int_0^\omega a(t)k(t,x,y)dtdy \le K_+,$$

and we see that $\mathcal{K}$ can be considered as a dispersal kernel that satisfies the autonomous version of assumption (H2). Specifically, we call $\mathcal{K}(x,y)$ the *weighted time-averaged dispersal kernel* of $k(t,x,y)$. Dividing both sides of (2.4) by $\int_0^\omega a(t)dt$, we obtain

$$\frac{\left[\ln\frac{\varphi(\omega)}{\varphi(0)} - \int_0^\omega (g(t,0) - a(t))dt\right]}{\int_0^\omega a(t)dt}\psi(x) = \int_0^L \mathcal{K}(x,y)\psi(y)dy. \tag{2.6}$$

It follows from the periodicity of $g(t,0)$, $a(t)$ and $k(t,x,y)$ that if we integrate (2.3) about t from t_0 to $t_0+\omega$ for any $t_0 \geq 0$, we still obtain

$$\frac{\left[\ln \frac{\varphi(t_0+\omega)}{\varphi(t_0)} - \int_0^\omega (g(t,0)-a(t))dt\right]}{\int_0^\omega a(t)dt}\psi(x) = \int_0^L \mathcal{K}(x,y)\psi(y)dy. \tag{2.7}$$

To further investigate this equation, we define an operator I on $C([0,L],W)$:

$$I[\psi](x) := \int_0^L \mathcal{K}(x,y)\psi(y)dy \quad \forall x\in[0,L] \quad \forall \psi \in C([0,L],W). \tag{2.8}$$

To analyze the spectra properties of I we first show that it is a compact operator.

LEMMA 2.1. *If* (H1) *and* (H2) *hold, then I is compact.*

The proof of Lemma 2.1 is in Appendix A. It follows from (H2) that for any $x \in [0,L]$, $\mathcal{K}(x,y)$ is positive at y almost everywhere in $[0,L]$, and hence, I is strongly positive on $C([0,L],W)$ in the sense that $I[\psi](x) > 0$ for all $x \in [0,L]$ and $\psi \in C([0,L],W)$ with $0 \leq \psi(x) \leq \hat{u}$ for $x \in [0,L]$ and $\psi \not\equiv 0$. The Krein–Rutman theorem implies that I has a unique simple positive principal eigenvalue with a corresponding strictly positive eigenfunction. Define

$$\lambda := \text{ the principal eigenvalue of } I.$$

Since the norm of I is bounded by K_+ (see the proof of Lemma 2.1), we have

$$0 < \lambda \leq K_+.$$

Moreover, [13, Theorem 3.1] implies that λ is a strictly increasing function of L provided that the dispersal kernel $\mathcal{K}(x,y)$ does not depend on L. However, we do not know how λ depends on the transfer rate $a(t)$ and growth rate $g(t,u)$. Let $\tilde{\psi}$ be the eigenfunction of I with $\tilde{\psi}(x) > 0$ for all $x \in [0,L]$ associated with λ. Then (2.1) admits a solution

$$\tilde{u}(t,x) = \tilde{\varphi}(t)\tilde{\psi}(x) \tag{2.9}$$

with $\tilde{u}(0,x) = \tilde{\varphi}(0)\tilde{\psi}(x)$, where $\tilde{\varphi}(t)$ is determined by (2.2) with $\psi = \tilde{\psi}$ and $\tilde{\varphi}(0) > 0$.

By the dynamics of the linearized equation (2.1) and the comparison theorem, we can obtain the following results for the stability of the zero solution to (1.1). The proof is included in Appendix B.

THEOREM 2.2. *Assume that* (H1) *and* (H2) *hold. Let λ be the principal eigenvalue of I (defined in* (2.8)*). The following results hold for* (1.1).

(i) *If $\int_0^\omega g(s,0)ds < \int_0^\omega a(s)ds$, then*

(a) *$u=0$ is unstable when*

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

(b) *$u=0$ is locally stable when*

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

(ii) *If $\int_0^\omega g(s,0)ds > \int_0^\omega a(s)ds$, then $u=0$ is unstable.*

(iii) *If $\int_0^\omega g(s,0)ds = \int_0^\omega a(s)ds$, then $u=0$ is linearly unstable; i.e., $u=0$ is unstable for* (2.1).

2.2. Critical domain size for (1.1). By the stability of $u = 0$ to (1.1), we can analyze the persistence of the population for (1.1). Theorem 2.2 (ii) and (iii) imply that the population persists in the stream no matter what its length is, provided $\int_0^\omega g(s,0)ds \geq \int_0^\omega a(s)ds$; that is, the average growth rate at low density exceeds the average transfer rate

$$\frac{1}{\omega}\int_0^\omega g(s,0)ds \geq \frac{1}{\omega}\int_0^\omega a(s,0)ds.$$

Theorem 2.2 (i) indicates that if $\int_0^\omega g(s,0)ds < \int_0^\omega a(s)ds$, then the principal eigenvalue λ of the operator I determines population persistence or extinction. When $\lambda > 1 - \frac{\int_0^\omega g(s,0)ds}{\int_0^\omega a(s)ds}$, that is, the mean per capita growth rate exceeding the mean per capita dispersal loss

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

the population is persistent in the stream, otherwise when $\lambda < 1 - \frac{\int_0^\omega g(s,0)ds}{\int_0^\omega a(s)ds}$, the population may not persist in the stream and, in particular, a small initial distribution cannot result in persistence of the population. Then

$$\lambda(L) = 1 - \frac{\int_0^\omega g(s,0)ds}{\int_0^\omega a(s)ds} \tag{2.10}$$

becomes a threshold condition for population persistence when $\int_0^\omega g(s,0)ds < \int_0^\omega a(s)ds$ although we cannot obtain a theoretical result for population persistence exactly under this condition.

Note that $0 < \lambda \leq K_+$. If $\int_0^\omega g(s,0)ds < (1-K_+)\int_0^\omega a(s)ds$, then $\lambda < 1 - \frac{\int_0^\omega g(s,0)ds}{\int_0^\omega a(s)ds}$ for all $L > 0$ and (2.10) has no solution. If $(1-K_+)\int_0^\omega a(s)ds \leq \int_0^\omega g(s,0)ds < \int_0^\omega a(s)ds$, then $1 - \frac{\int_0^\omega g(s,0)ds}{\int_0^\omega a(s)ds}$ is between 0 and K_+, and (2.10) might be solvable. Since the dispersal kernel in this paper is assumed to be independent of the stream length, it follows from [13, Theorem 3.1] that λ is a strictly increasing function of the stream length L. Consider 0 as the principal eigenvalue of I with $L = 0$. Then λ increases from 0 as L increases from 0. Thus, if the equation (2.10) admits no solution, then $\lambda < 1 - \frac{\int_0^\omega g(s,0)ds}{\int_0^\omega a(s)ds}$ for all $L > 0$. If (2.10) is solvable, then it has a unique solution L_0 with $\lambda(L_0) = 1 - \frac{\int_0^\omega g(s,0)ds}{\int_0^\omega a(s)ds}$, $\lambda(L) > 1 - \frac{\int_0^\omega g(s,0)ds}{\int_0^\omega a(s)ds}$ for $L > L_0$, and $\lambda(L) < 1 - \frac{\int_0^\omega g(s,0)ds}{\int_0^\omega a(s)ds}$ for $L < L_0$. This L_0 can be defined as the critical domain size.

We conclude all above results in the following theorem, which is the main result in this section.

THEOREM 2.3. *Assume that* (H1) *and* (H2) *hold. The following results are valid for the population model* (1.1).

- (i) *If* $\int_0^\omega g(s,0)ds \geq \int_0^\omega a(s)ds$, *then the population persists in the stream regardless of the stream length.*
- (ii) *If* $(1-K_+)\int_0^\omega a(s)ds \leq \int_0^\omega g(s,0)ds < \int_0^\omega a(s)ds$, *then the critical domain size may be determined by the threshold equation* (2.10), *where* λ *is the principal eigenvalue of the spatial operator* I *defined in* (2.8).

(a) *If* (2.10) *has a unique solution* L_0*, then* L_0 *is defined as the* **critical domain size** *and the population persists in the stream provided that the stream length is larger than the critical domain size.*

(b) *If* (2.10) *has no solution, then in any stream with a finite length, the population may not persist and, in particular, a small initial distribution cannot result in persistence of the population.*

(iii) *If* $\int_0^\omega g(s,0)ds < (1-K_+)\int_0^\omega a(s)ds$*, the population may not persist in a bounded stream and the population with a small initial distribution cannot persist in a bounded stream.*

Remark 2.1. In the cases (ii)(b) and (iii) in Theorem 2.3, we say that the critical domain size does not exist. Thus, we conclude that when $\int_0^\omega g(s,0)ds < \int_0^\omega a(s)ds$, if (2.10) admits a solution, then it is the critical domain size; otherwise, the critical domain size does not exist.

Remark 2.2. If the dispersal kernel is independent of time t, then (1.1) becomes

(2.11)
$$\frac{\partial u(t,x)}{\partial t} = ug(t,u(t,x)) - a(t)u(t,x) + a(t)\int_0^L k(x,y)u(t,y)dy,\ t \geq 0,\ x \in [0,L].$$

The weighted averaged dispersal kernel $\mathcal{K}(x,y)$ (see (2.5)) is exactly $k(x,y)$, and the operator I defined in (2.8) is

$$I[\psi](x) := \int_0^L k(x,y)\psi(y)dy \qquad \forall x \in [0,L]. \tag{2.12}$$

Clearly, the above results for the critical domain size are still true for (2.11).

Example 2.1. Consider a simple case where the dispersal kernel $k(t,x,y)$ is independent of time t and depends only on the distance between two locations x and y. We write k as $k(x-y)$ and assume a special form for the function $k(x)$, $x \in \mathbb{R}$:

$$k(x) = \begin{cases} A\exp(b_1 x), & x \leq 0, \\ A\exp(b_2 x), & x \geq 0, \end{cases} \tag{2.13}$$

with

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

and

$$A = \frac{b_1 b_2}{b_2 - b_1},$$

where D is the diffusion constant, v is the water flow velocity, and β is the settling rate of aquatic insects whose larvae settle on the channel bottom and matured individuals jump into water, in a stream environment (see [13, Section 4.1] for the derivation of this kernel). The relation between the principal eigenvalue λ of the operator I (see (2.12)) and the stream length L was stated in [13, (4.6)] as

$$L(\lambda) = \frac{4\arctan\left(\sqrt{\frac{4b_1|b_2|}{\lambda(b_1-b_2)^2} - 1}\right)^{-1}}{(b_1-b_2)\sqrt{\frac{4b_1|b_2|}{\lambda(b_1-b_2)^2} - 1}}. \tag{2.14}$$

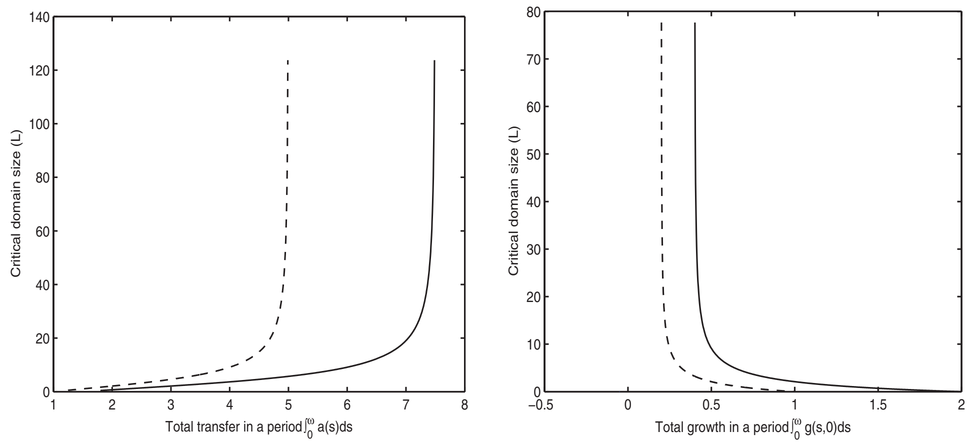

FIG. 2.1. *The critical domain size for* (2.11) *with the dispersal kernel* k *defined in* (2.13), *where the diffusion rate* $D = 1$, *the flow speed* $v = 1$, *and the settling rate* $\beta = 1$. *Left: The relationship between the critical domain size and the total transfer rate in a period* $\int_0^\omega a(s)ds$. *The solid line represents* $\int_0^\omega g(s,0)ds = 1.5$; *the dashed line represents* $\int_0^\omega g(s,0)ds = 1$. *Right: The relationship between the critical domain size and the total reproduction in a period* $\int_0^\omega g(s,0)ds$. *The solid line represents* $\int_0^\omega a(s)ds = 2$; *the dashed line represents* $\int_0^\omega a(s)ds = 1$.

By Theorem 2.3, if $\int_0^\omega g(s,0)ds \geq \int_0^\omega a(s)ds$, then the species will be persistent regardless of the stream length L; if $\int_0^\omega g(s,0)ds < \int_0^\omega a(s)ds$, then the critical domain size for the species to persist in the stream, if it exists, is

$$L\left(1 - \frac{\int_0^\omega g(s,0)ds}{\int_0^\omega a(s)ds}\right), \tag{2.15}$$

where the function L is defined in (2.14).

The relationship between the critical domain size L for the autonomous case of (2.11) and D, v, and β has been studied in [13]. From (2.15), we see that the critical domain size does not depend on the value of g or a at any specific time, but on the sums of $g(t,0)$ and $a(t)$ over a period $[0,\omega]$. Figure 2.1 shows that when the dispersal kernel is fixed, the critical domain size is an increasing function of $\int_0^\omega a(s)ds$ for a given value of $\int_0^\omega g(s,0)ds$ (see the left graph of Figure 2.1). As $a(t)$ is the transfer rate at which the population transfers from the stationary state to the mobile state, this indicates that the more population disperses, the greater the size of the stream needed for the population to persist in the stream. It is also shown in the right graph of Figure 2.1 that the critical domain size is a decreasing function of $\int_0^\omega g(s,0)ds$ for a given value of $\int_0^\omega a(s)ds$, which implies that the more reproduction the population has, the shorter the stream is required to be for the persistence of the population. These two results clearly coincide with our intuitive understanding.

3. Critical domain size in a two-season environment. In this section, we give approximation for the critical domain size for 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 critical domain size. By a two-season environment, we mean a habitat that has two significant seasons in a year, say, summer and winter. Assume that a year length is scaled as ω with summer length ω_0 and winter length $\omega - \omega_0$ $(0 < \omega_0 < \omega)$. We will show how the critical domain size can be approximately determined by a weighted combination of the population dynamics and dispersal features in summer and winter.

3.1. Approximation for critical domain size. We would like to consider the critical domain size of a stream in a two-season environment with dispersal kernel $k_1(x,y)$ and transfer rate a_1 in summer and dispersal kernel $k_2(x,y)$ and transfer rate a_2 in winter. An abrupt change between seasons will violate the assumptions (H1) (i) and (ii) and (H2) (iii) that a and k are continuous functions of time t. Hence, we need to construct the discontinuous dispersal kernel and transfer rate carefully as limits of sequences of continuous kernels and transfer rates, respectively, where the continuity is with respect to the time.

First we give a result about the convergence of the principal eigenvalues of a sequence of operators. Let $k_1(x,y)$ and $k_2(x,y)$ be two dispersal kernels and $\{k^{(n)}(t,x,y)\}_{n\in\mathbb{N}}$ be a sequence of dispersal kernels that are periodic in t with period ω and defined in $[0,\omega]$ as

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

where the $k_i^{(n)}(t,x,y)$s are functions such that for each $n \in \mathbb{N}$, $k^{(n)}(t,x,y)$ satisfies all conditions in (H2). 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

$$a^{(n)}(t) = \begin{cases} a_1 & 0, \le t < \omega_0 - \frac{1}{n}, \\ a_1^{(n)}(t), & \omega_0 - \frac{1}{n} \le t < \omega_0, \\ a_2, & \omega_0 \le t < \omega - \frac{1}{n}, \\ a_2^{(n)}(t), & \omega - \frac{1}{n} \le t < \omega, \end{cases} \tag{3.2}$$

where $a_1^{(n)}(t)$ and $a_2^{(n)}(t)$ are functions of time t such that $a^{(n)}(t)$ is continuous in t for each $n \in \mathbb{N}$. For each $k^{(n)}(t,x,y)$, define the weighted time-averaged dispersal kernel

$$\mathcal{K}_n(x,y) = \frac{1}{\int_0^\omega a^{(n)}(s)ds} \int_0^\omega a^{(n)}(s)k^{(n)}(s,x,y)ds$$

and the associated spatial operator

$$I_n[\psi](x) = \int_0^L \mathcal{K}_n(x,y)\psi(y)dy \quad \forall x \in [0,L], \quad \psi \in C([0,L],W). \tag{3.3}$$

By (2.10), the critical domain size L_n for (1.1) with dispersal kernel $k^{(n)}(t,x,y)$, transfer rate $a^{(n)}(t)$, and growth rate $g(t,u)$, can be determined by

$$\lambda_n(L_n) = 1 - \frac{\int_0^\omega g(s,0)ds}{\int_0^\omega a^{(n)}(s)ds}. \tag{3.4}$$

Moreover, define the two-season spatial operator

$$I_0[\psi](x) = \frac{a_1\omega_0 \int_0^L k_1(x,y)\psi(y)dy}{a_1\omega_0 + a_2(\omega-\omega_0)} + \frac{a_2(\omega-\omega_0)\int_0^L k_2(x,y)\psi(y)dy}{a_1\omega_0 + a_2(\omega-\omega_0)}, \tag{3.5}$$

for $\psi \in C([0,L],W)$, $x \in [0,L]$. We have the following result whose proof is in Appendix C.

LEMMA 3.1. *The principal eigenvalue of I_n converges to the principal eigenvalue of I_0 as n tends to infinity.*

Now we consider a stream species in a two-season environment. Suppose that the dispersal kernel $k(t,x,y)$ for (1.1) takes the form of $k^{(n)}(t,x,y)$ defined in (3.1), and that the transfer rate $a(t)$ takes the form of $a^{(n)}(t)$, defined in (3.2). It follows from Lemma 3.1 that, in application, for simplicity, we may use the principal eigenvalue of I_0 (defined in (3.5)) to approximate the principal eigenvalue of I (defined in (2.8)), since the operator I here takes the form of I_n, defined in (3.4). Note that $\int_0^\omega a^{(n)}(s)ds \to a_1\omega_0 + a_2(\omega-\omega_0)$ as $n \to \infty$. By Theorem 2.3, we can obtain the following result about the approximation of the critical domain size in a two-season environment.

THEOREM 3.2. *In a two-season environment, where the summer and winter population dispersal kernels are $k_1(x,y)$ and $k_2(x,y)$ and summer and winter transfer rates are a_1 and a_2, respectively, the critical domain size for* (1.1) *can be approximated by solving*

$$\lambda_0(L) = 1 - \frac{\int_0^\omega g(s,0)ds}{a_1\omega_0 + a_2(\omega-\omega_0)} \tag{3.6}$$

(see (2.10)*), where λ_0 is the principal eigenvalue of I_0 defined in* (3.5) *and depends on the stream length L.*

We now choose specific dispersal kernels to show how to find the principal eigenvalue λ_0 for I_0. Further assume that the summer dispersal kernel $k_1(x,y)$ and the winter dispersal kernels $k_2(x,y)$ depend only on the distance between x and y and write them as $k_1(x)$ and $k_2(x)$. For all parameters in the rest of this section, we use subscript $i=1$ to represent summer and $i=2$ to represent winter. For $i=1,2$, define

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

with

$$b_i^{(1),(2)} = \frac{v_i}{2D_i} \pm \sqrt{\frac{v_i^2}{4D_i^2} + \frac{\beta_i}{D_i}} \quad \text{and} \quad A_i = \frac{b_1^i b_2^i}{b_2^i - b_1^i},$$

where D_i is the diffusion coefficient, v_i is the water flow velocity, and β_i is the settling rate of the species in a stream environment. Moreover, let λ_0 be the principal eigenvalue of I_0 with positive eigenfunction $\psi \in C([0,L],W)$ with $0 < \psi(x) \le \hat{u}$ for all $x \in [0,L]$. Then

$$I_0[\psi](x) = \lambda_0\psi(x)$$

can be written as

$$P_1 \int_0^L k_1(x-y)\psi(y)dy + P_2 \int_0^L k_2(x-y)\psi(y)dy = \lambda_0\psi(x) \quad \forall x \in [0,L], \tag{3.7}$$

where

$$P_1 = \frac{a_1\omega_0}{a_1\omega_0 + a_2(\omega-\omega_0)}, \qquad P_2 = \frac{a_2(\omega-\omega_0)}{a_1\omega_0 + a_2(\omega-\omega_0)},$$

with $P_1 + P_2 = 1$. Note that for $i = 1, 2$, k_i is a Green's function for a related differential operator

$$\frac{D_i}{\beta_i} k_i''(x) - \frac{v_i}{\beta_i} k_i'(x) - k_i(x) = -\delta(x) \quad \forall x \in [0, L], \tag{3.8}$$

where $\delta(x)$ is the Dirac delta function. Let H_1 and H_2 be two operators on a dispersal kernel k defined as

$$H_i[k] := \frac{D_i}{\beta_i} k'' - \frac{v_i}{\beta_i} k' - k, \qquad i = 1, 2.$$

Applying H_1 on both sides of (3.7), we obtain

$$\begin{aligned} &P_1 \int_0^L \left(\frac{D_1}{\beta_1} k_1'' - \frac{v_1}{\beta_1} k_1' - k_1 \right) (x - y) \psi(y) dy \\ &\quad + P_2 \int_0^L \left(\frac{D_1}{\beta_1} k_2'' - \frac{v_1}{\beta_1} k_2' - k_2 \right) (x - y) \psi(y) dy = \lambda_0 \left(\frac{D_1}{\beta_1} \psi'' - \frac{v_1}{\beta_1} \psi' - \psi \right) (x). \end{aligned}$$

It follows from (3.8) that

$$-P_1 \psi(x) + P_2 \int_0^L \left(\frac{D_1}{\beta_1} k_2'' - \frac{v_1}{\beta_1} k_2' - k_2 \right) (x-y) \psi(y) dy = \lambda_0 \left(\frac{D_1}{\beta_1} \psi'' - \frac{v_1}{\beta_1} \psi' - \psi \right) (x).$$

Apply H_2 to both sides of the above equation and use (3.8) again. After calculations, we obtain

$$\begin{aligned} &\lambda_0 \frac{D_2 D_1}{\beta_2 \beta_1} \psi^{(4)}(x) - \lambda_0 \left(\frac{D_2 v_1 + D_1 v_2}{\beta_2 \beta_1} \right) \psi'''(x) \\ &\quad + \left(\frac{P_1 D_2}{\beta_2} + \frac{P_2 D_1}{\beta_1} - \lambda_0 \left(\frac{D_2}{\beta_2} - \frac{v_2 v_1}{\beta_2 \beta_1} + \frac{D_1}{\beta_1} \right) \right) \psi''(x) \\ &\quad + \left(\lambda_0 \left(\frac{v_2}{\beta_2} + \frac{v_1}{\beta_1} \right) - \frac{P_1 v_2}{\beta_2} - \frac{P_2 v_1}{\beta_1} \right) \psi'(x) + (\lambda_0 - 1) \psi(x) = 0. \end{aligned} \tag{3.9}$$

Basic differentiations of (3.7) with respect to x give four boundary conditions for (3.9):
(3.10)

$$\begin{cases} \lambda_0 \psi''(0) = [P_1 A_1 (b_1^{(2)} - b_1^{(1)}) + P_2 A_0 (b_2^{(2)} - b_2^{(1)}) - \lambda_0 b_2^{(1)} b_1^{(1)}] \psi(0) \\ \qquad + \lambda_0 (b_1^{(1)} + b_2^{(1)}) \psi'(0), \\ \lambda_0 \psi''(L) = [P_1 A_1 (b_1^{(2)} - b_1^{(1)}) + P_2 A_0 (b_2^{(2)} - b_2^{(1)}) - \lambda_0 b_2^{(2)} b_1^{(2)}] \psi(L) \\ \qquad + \lambda_0 (b_1^{(2)} + b_2^{(2)}) \psi'(L), \\ \lambda_0 \psi'''(0) = [P_1 A_1 ((b_1^{(2)})^2 - (b_1^{(1)})^2) + P_2 A_0 ((b_2^{(2)})^2 - (b_2^{(1)})^2)] \psi(0) \\ \qquad - \lambda_0 b_2^{(1)} b_1^{(1)} (b_2^{(1)} + b_1^{(1)}) \psi(0) + \lambda_0 [(b_1^{(1)})^2 + b_2^{(1)} b_1^{(1)} + (b_2^{(1)})^2] \psi'(0) \\ \qquad + [P_1 A_1 (b_1^{(2)} - b_1^{(1)}) + P_2 A_0 (b_2^{(2)} - b_2^{(1)})] \psi'(0), \\ \lambda_0 \psi'''(L) = [P_1 A_1 ((b_1^{(2)})^2 - (b_1^{(1)})^2) + P_2 A_0 ((b_2^{(2)})^2 - (b_2^{(1)})^2)] \psi(L) \\ \qquad - \lambda_0 b_2^{(2)} b_1^{(2)} (b_2^{(2)} + b_1^{(2)}) \psi(L) + \lambda_0 [(b_1^{(2)})^2 + b_2^{(2)} b_1^{(2)} + (b_2^{(2)})^2] \psi'(L) \\ \qquad + [P_1 A_1 (b_1^{(2)} - b_1^{(1)}) + P_2 A_0 (b_2^{(2)} - b_2^{(1)})] \psi'(L). \end{cases}$$

By solving (3.9)–(3.10), we expect to obtain λ_0 as a function of L, and then estimate the critical domain size by solving (3.6). However, this might not be easy since (3.9) is a fourth order differential equation and the boundary conditions (3.10) are complex. As we are interested only in the threshold of the domain size, we can set $\lambda_0 = 1 - \int_0^\omega g(s,0)ds / \int_0^\omega a(s)ds$ (see (3.6)) and solve (3.9)–(3.10). Then we should be able to obtain L as an expression of $\int_0^\omega a(s)ds$, $\int_0^\omega g(s,0)ds$, D_i's, v_i's, and β_i's, if (3.6) has a solution. This L is the approximation of the critical domain size for (1.1) with dispersal kernel $k(t,x,y)$ having the form of $k^{(n)}(t,x,y)$ defined in (3.1) and the transfer rate $a(t)$ having the form of $a^{(n)}(t)$ defined in (3.2).

Example 3.0. Let the scaled length of a year $\omega = 2$, the scaled length of summer $\omega_0 = 1$, the transfer rate $a(t) = a_1 = a_2 = 1$, the diffusion rate $D_1 = D_2 = 1$, the settling rate $\beta_1 = \beta_2 = 1$, summer flow speed $v_1 = 3$, winter flow speed $v_2 = 1$, and the growth function $g(t,u) = r(1 - u/K) - \mu$ with the intrinsic growth rate $r = 1.2$, the death rate $\mu = 0.5$, and carrying capacity $K > 0$. Then

$$\lambda_0 = 1 - \frac{\int_0^\omega g(s,0)ds}{\int_0^\omega a(s)ds} = 0.3$$

and (3.9) becomes

$$0.3\psi^{(4)}(x) - 1.2\psi'''(x) + 1.3\psi''(x) - 0.8\psi'(x) - 0.7\psi(x) = 0. \tag{3.11}$$

By solving the characteristic equation corresponding to (3.11) numerically, we can write the general solution to (3.11) as

$$\begin{aligned}\psi(x) = {} & c_1 e^{2.923060032x} + c_2 e^{.4337033617x} \\ & + e^{0.7553216649x}(c_3\cos(1.12695759x) + c_4\sin(1.12695759x)).\end{aligned}$$

Substituting $\psi(x)$ to the boundary conditions (3.10), we find that $L = 3.08269$. This is the critical domain size that we are looking for.

3.2. Influences of parameters on critical domain size. By virtue of Theorem 3.2, we can study the combined influences of the flow velocity $v(t)$ and the transfer rate $a(t)$, the diffusion coefficient $D(t)$ and the settling rate $\beta(t)$ on the critical domain size of the stream for a species to persist in a two-season environment. The same as in the last subsection, let subscript $i = 1$ represent summer and $i = 2$ represent winter for v, a, D, and β.

First, we consider the combined influence of the flow velocity v_i's and the transfer rate a_i's on the critical domain size, while fixing the other parameters. To summarize the cross effects we define the covariance between the normalized transfer rate and normalized flow velocity, which we call the *normalized covariance* between the transfer rate and flow velocity in the rest of the paper, as

$$\chi_{a,v} = cov\left(\frac{a}{\bar{a}}, \frac{v}{\bar{v}}\right) = \frac{1}{\bar{a}\bar{v}\omega}\int_0^\omega (a(s) - \bar{a})(v(s) - \bar{v})ds, \tag{3.12}$$

where $\bar{a}$ and $\bar{v}$ are the annual averages of $a(t)$ and $v(t)$ defined as

$$\bar{a} = \frac{1}{\omega}\int_0^\omega a(s)ds = \frac{a_1\omega_0 + a_2(\omega - \omega_0)}{\omega}, \tag{3.13}$$

and

$$\bar{v} = \frac{1}{\omega}\int_0^\omega v(s)ds = \frac{v_1\omega_0 + v_2(\omega - \omega_0)}{\omega}, \tag{3.14}$$

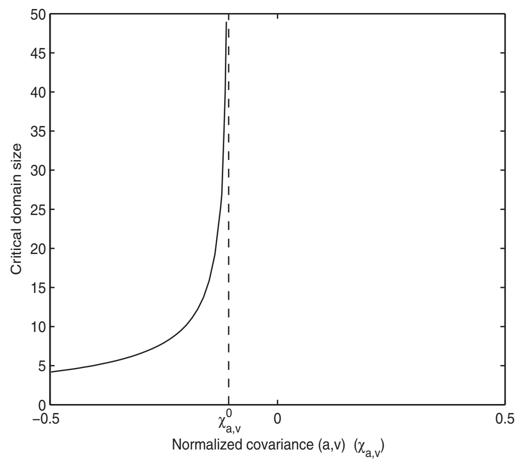

FIG. 3.1. *The relationship between the critical domain size and the normalized covariance $\chi_{a,v}$ between the transfer rate a and flow velocity v, where $g(u) = 1.2(1 - u/K) - 0.5$, $\beta_1 = \beta_2 = 1$, $D_1 = D_2 = 1$, $\omega = 2$, $\omega_0 = 1$, $v_1 = 3$, $v_2 = 1$, $\bar{a} = 2$, and $\chi^0_{a,v} = -0.107375$.*

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

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

The exact relationship between the critical domain size and the normalized covariance $\chi_{a,v}$ cannot be described as we need to solve boundary problem (3.9)–(3.10). However, we may calculate the critical domain size for some specific values of $\chi_{a,v}$ and determine the quantitative relationship between them.

Example 3.1. Assume the growth function $g(u) = r(1 - u/K) - \mu$ with the intrinsic growth rate $r = 1.2$, death rate $\mu = 0.5$ and carrying capacity $K > 0$, the scaled length of a year $\omega = 2$, the summer length of a year $\omega_0 = 1$, the diffusion rate $D_1 = D_2 = 1$, and the settling rate $\beta_1 = \beta_2 = 1$. The carrying capacity K does not influence the critical domain size. We fix the summer and winter water velocities $v_1 = 3$ and $v_2 = 1$, and the annual mean value of the transfer rate $\bar{a} = 2$. The relationship between the critical domain size and the normalized covariance $\chi_{a,v}$ is given in Figure 3.1. It is very clear that when the normalized covariance $\chi_{a,v}$ increases, the critical domain size becomes larger and larger till it approaches infinity as $\chi_{a,v}$ tends to $\chi^0_{a,v} = -0.107375$. As the critical domain size is the smallest domain size for the population to persist in the stream, this indicates that the larger the normalized covariance between a and v, the harder it is for the population to persist in the stream.

Similarly, we can define the normalized covariance between the diffusion rate and flow velocity as $\chi_{D,v} = cov(\frac{D}{\bar{D}}, \frac{v}{\bar{v}})$, and the normalized covariance between the settling rate and flow velocity as $\chi_{\beta,v} = cov(\frac{\beta}{\bar{\beta}}, \frac{v}{\bar{v}})$ as we did in (3.12), and then study how $\chi_{D,v}$ or $\chi_{\beta,v}$ influences the critical domain size while the other parameters are fixed.

Example 3.2. Let $g(u) = 0.75(1 - u/K) - 0.5$, $\beta_1 = \beta_2 = 1$, $a_1 = a_2 = 1$, $\omega = 2$, $\omega_0 = 1$, $v_1 = 3$, $v_2 = 1$, and $\bar{D} = 2$. The relationship between the critical domain size and the normalized covariance $\chi_{D,v}$ between the diffusion rate D and flow velocity v is shown in Figure 3.2. When $\chi_{D,v}$ increases, the critical domain size increases and tends to infinity as $\chi_{D,v}$ tends to $\chi^0_{D,v} = -0.152525$. The quantitative result is similar

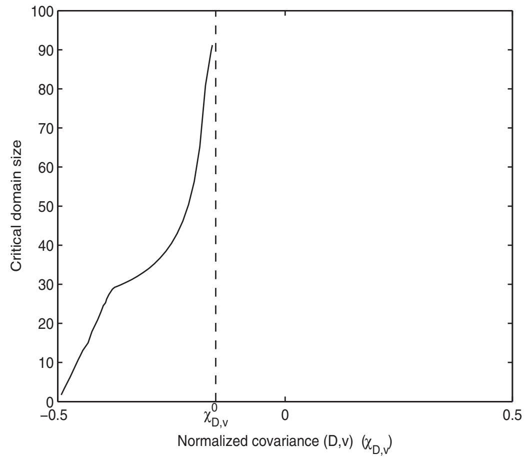

FIG. 3.2. *The relationship between the critical domain size and the normalized covariance* $\chi_{D,v}$ *between the diffusion rate* D *and the flow velocity* v*, where* $g(u) = 0.75(1-u/K)-0.5$*,* $\beta_1 = \beta_2 = 1$*,* $a_1 = a_2 = 1$*,* $\omega = 2$*,* $\omega_0 = 1$*,* $v_1 = 3$*,* $v_2 = 1$*,* $\bar{D} = 2$*, and* $\chi^0_{D,v} = -0.152525$.

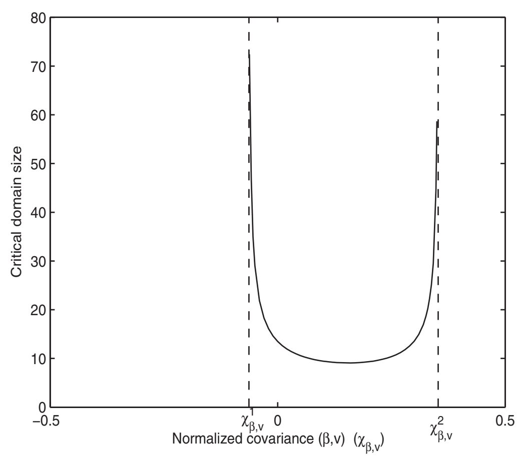

FIG. 3.3. *The relation between the critical domain size and the normalized covariance* $\chi_{\beta,v}$ *between the settling rate* β *and flow velocity* $\frac{v}{\bar{v}}$*, where* $g(u) = 0.75(1-u/K)-0.5$*,* $D_1 = D_2 = 1$*,* $a_1 = a_2 = 1$*,* $\omega = 2$*,* $\omega_0 = 1$*,* $v_1 = 3$*,* $v_2 = 1$*,* $\bar{\beta} = 2.5$*,* $\chi^1_{\beta,v} = -0.0631$*, and* $\chi^2_{\beta,v} = 0.35282$.

to that found between the transfer rate and flow velocity in Example 3.1: The larger the normalized covariance $\chi_{D,v}$ the harder it is for the population to persist.

Example 3.3. Let $g(u) = 0.75(1-u/K)-0.5$, $D_1 = D_2 = 1$, $a_1 = a_2 = 1$, $\omega = 2$, $\omega_0 = 1$, $v_1 = 3$, $v_2 = 1$, and $\bar{\beta} = 2.5$. The relationship between the critical domain size and the normalized covariance $\chi_{\beta,v}$ between the settling rate β and flow velocity v is shown in Figure 3.3. The graph is very different from those in Examples 3.1 and 3.2. The critical domain size is positive for $\chi^1_{\beta,v} < \chi_{\beta,v} < \chi^2_{\beta,v}$ and tends to infinity as $\chi_{\beta,v}$ tends to $\chi^1_{\beta,v} = -0.0631$ or $\chi^2_{\beta,v} = 0.35282$. Therefore, to help the population persist in the stream, the normalized covariance $\chi_{\beta,v}$ has to be kept at intermediate values lying in the interval $(\chi^1_{\beta,v}, \chi^2_{\beta,v})$.

4. Discussion. In this paper, we study the seasonal influences on population persistence for stream species and attempt to suggest solutions for the important *drift* *paradox* problem in stream ecology. We assume that both the population dynamics and individual movements (i.e., the dispersal kernel) are periodic with respect to time t with the same period ω, which can be taken as the scaled dimensionless length of a year. Noting that all natural streams or rivers are actually bounded, we study the periodic integro-differential equation (1.1) in a bounded spatial domain $\Omega = [0, L]$, where L is the length of the stream. As the critical domain size is an important ecological feature, which indicates the minimal length of a stream for the population to persist, and actually from another perspective provides a solution to the drift paradox problem in a bounded stream, we obtain the critical domain size for (1.1) when the population dynamics and dispersal satisfy certain conditions (H1) and (H2) (see section 2). To better understand the effects of time varying environment on the critical domain size we considered an environment with two main seasons, say, summer and winter. This allowed us to analytically approximate the critical domain size and to assess the effects of the normalized covariances of the flow velocity, transfer rate, diffusion rate, and the settling rate on the critical domain size. This analysis was supplemented with numerical examples (section 3).

While the actual flow velocity in a specific stream can be estimated from the historical data, generally it is large in summer and small in winter, just as given in the examples in section 3. Simulations there suggest that to help the population persist in the stream easily, strategies may be made to decrease as much as possible the normalized covariance $\chi_{a,v}$, decrease the normalized covariance $\chi_{D,v}$, or keep the normalized covariance $\chi_{\beta,v}$ in a moderate level between $(\chi^1_{\beta,v}, \chi^2_{\beta,v})$, while the annual averages $\bar{a}$, $\bar{D}$, or $\bar{\beta}$ are kept as some constants and the other parameters are fixed in different situations.

Furthermore, we can analyze the critical domain sizes of (1.1) in relation to a so-called weighted dispersal kernel. Let $\mathcal{K}(x, y)$ be the weighted time-averaged dispersal kernel defined in (2.5). By the derivation of the the threshold equation (2.10), the critical domain size of (1.1) is the same as that of

(4.1)
$$\frac{\partial u(t,x)}{\partial t} = ug(t, u(t,x)) - a(t)u(t,x) + a(t)\int_0^L \mathcal{K}(x,y)u(t,y)dy,\ t \geq 0,\ x \in [0, L].$$

Define an autonomous model associated with (1.1) with time-averaged growth $\int_0^\omega ug(s,u)ds/\omega$ and dispersal $\int_0^\omega a(s)ds/\omega$:

(4.2)
$$\frac{\partial u(t,x)}{\partial t} = \frac{\int_0^\omega ug(s,u)ds}{\omega} - \frac{\int_0^\omega a(s)ds}{\omega}u(t,x) + \frac{\int_0^\omega a(s)ds}{\omega}\int_0^L \mathcal{K}(x,y)u(t,y)dy,$$

for all $t \geq 0$, $x \in [0, L]$. Recall that in [13], the critical domain size of

$$u_t(t,x) = f(u(t,x)) - \mu u(t,x) + \mu \int_0^L k(x,y)u(t,y)dy,\ t \geq 0,\ x \in [0, L] \quad (4.3)$$

is given as

$$\lambda(L) = 1 - f'(0)/\mu,$$

where λ is the principal eigenvalue of the integral operator

$$I[\psi](x) = \int_0^L k(x,y)\psi(y)dy.$$

Then by simple comparison, we see that the critical domain size of (1.1) is the same as that of (4.2). Therefore, to study the critical domain size of the periodic model (1.1) with periodic dispersal kernel $k(t,x,y)$, it suffices to study that of the periodic model with the weighted time-averaged dispersal kernel $\mathcal{K}(x,y)$ (4.1) or that of its associated autonomous model (4.2) with the time-averaged kernel $\mathcal{K}(x,y)$.

We then conclude that when studying the critical domain size for a periodic integro-differential equation, a periodic dispersal kernel $k(t,x,y)$ has the same effect as its associated appropriately weighted time-averaged dispersal kernel $\mathcal{K}(x,y)$, and that the study of the critical domain size for a periodic integro-differential equation can be reduced to the study of the critical domain size for an associated autonomous integro-differential equation. However, it is important to notice that this simplification is true only for the estimation of the critical domain size and that the dynamics of these models are very different.

Appendix A. Proof of Lemma 2.1. For any $\psi \in C([0,L],W)$, we have $0 \le ||\psi|| = \max_{x\in[0,L]} \psi(x) \le \hat{u}$ and

$$||I[\psi]|| = \max_{x\in[0,L]} \int_0^L \mathcal{K}(x,y)\psi(y)dy \le \max_{x\in[0,L]} \int_0^L \mathcal{K}(x,y)dy \cdot \max_{y\in[0,L]} \psi(y) \le K_+ \cdot ||\psi||.$$

This indicates that I is uniformly bounded by K_+.

Moreover, for any $\psi \in C([0,L],W)$ and $x_1,\ x_2 \in [0,L]$, we have

$$\begin{aligned} |I[\psi](x_1) - I[\psi](x_2)| &= \left| \int_0^L \mathcal{K}(x_1,y)\psi(y)dy - \int_0^L \mathcal{K}(x_2,y)\psi(y)dy \right| \\ &= \left| \int_0^L (\mathcal{K}(x_1,y) - \mathcal{K}(x_2,y))\psi(y)dy \right| \\ &\le \max_{x\in[0,L]} \psi(x) \cdot \left| \int_0^L (\mathcal{K}(x_1,y) - \mathcal{K}(x_2,y))dy \right| \\ &= \hat{u} \left| \int_0^L (\mathcal{K}(x_1,y) - \mathcal{K}(x_2,y))dy \right|. \end{aligned}$$

By the assumptions for $k(t,x,y)$, $\mathcal{K}(x,y)$ is continuous in $x \in [0,L]$ uniformly for $y \in [0,L]$. Therefore, I is equicontinuous.

Then the Arzelà–Ascoli theorem implies that I is compact.

Appendix B. Proof of Theorem 2.2. (i). Assume $\int_0^\omega g(s,0)ds < \int_0^\omega a(s)ds$**.**

(a) Suppose that the principal eigenvalue λ of I satisfies

$$\lambda > 1 - \frac{\int_0^\omega g(s,0)ds}{\int_0^\omega a(s)ds}. \tag{B.1}$$

CLAIM 1. *For any $u_0 \in C([0,L],W)$ with $u_0 \not\equiv 0$, the solution to* (1.1) *with $u(0,\cdot) = u_0(\cdot)$ satisfies $u(t,x) > 0$ for all $(t,x) \in (0,+\infty) \times [0,L]$.*

Let $u_0 \in C([0,L],W)$ with $u_0 \not\equiv 0$. Note that

$$ug(t,u(t,x)) - a(t)u + a(t) \int_0^L k(t,x,y)u(t,y)dy \ge ug(t,u(t,x)) - a(t)u$$

for any $u(t,\cdot) \geq 0$. Since the solution $\bar{u}(t,x)$ to

$$\frac{\partial \bar{u}(t,x)}{\partial t} = \bar{u}g(t,\bar{u}(t,x)) - a(t)\bar{u}$$

with $\bar{u}(0,\cdot) = u_0(\cdot)$ is nonnegative for all $t \geq 0$, it follows from the comparison theorem, the solution $u(t,x)$ to (1.1) with $u(0,\cdot) = u_0(\cdot)$ satisfies $u(t,x) \geq \bar{u}(t,x) \geq 0$ for all $(t,x) \in (0,+\infty) \times [0,L]$. We need to further show strict positivity of u. Let α be sufficiently large such that $\alpha u + ug(t,u) - a(t)u \geq 0$ for all $t \geq 0$ and $u \in [0,\hat{u}]$. Rewrite (1.1) as

(B.2)
$$\frac{\partial u(t,x)}{\partial t} = -\alpha u(t,x) + \alpha u(t,x) + u(g(t,u(t,x)) - a(t)) + a(t)\int_0^L k(t,x,y)u(t,y)dy.$$

Given the initial condition u_0, (B.2) is equivalent to the integral equation

$$\begin{aligned} u(t,x) &= e^{-\alpha t}u_0(x) \\ &+ \int_0^t e^{-\alpha(t-s)}\left(\alpha u(s,x) + u(g(s,u(s,x)) - a(s)) + a(s)\int_0^L k(s,x,y)u(s,y)dy\right)ds. \end{aligned}$$

By the nonnegativity of u_0 and $\alpha u + ug(t,u) - a(t)u$, we further have

$$\begin{aligned} &u(t,x) \\ &\geq \int_0^t e^{-\alpha(t-s)}\left(\alpha u(s,x) + u(g(s,u(s,x)) - a(s)) + a(s)\int_{\mathbb{R}} k(s,x,y)u(s,y)dy\right)ds \\ &\geq m_1 \int_0^t e^{-\alpha(t-s)}\int_{\mathbb{R}} k(s,x,y)u(s,y)dyds, \end{aligned}$$

where $m_1 = \min_{t\in[0,\omega]} a(t) > 0$. Since $u_0 \not\equiv 0$ and the solution $u(t,x)$ is continuous in t and x, for any $t \geq 0$, there is an open interval $B_t \subset [0,L]$ such that $u(t,x) > 0$ for all $x \in B_t$. Note that $k(t,x,y)$ is positive almost everywhere at $y \in [0,L]$ for any $t \geq 0$ and $x \in [0,L]$. We then have $u(t,x) > 0$ for all $t > 0$ and $x \in [0,L]$. This completes the proof for the claim.

Now we prove the main result. For $\varepsilon > 0$, define an operator

(B.3) $$I_\varepsilon[\psi](x) := -\frac{\varepsilon\omega}{\int_0^\omega a(s)ds}\psi(x) + \int_0^L \mathcal{K}(x,y)\psi(y)dy \quad \forall x \in [0,L]$$

for all $\psi \in C([0,L],W)$. Then $I_\varepsilon \to I$ as $\varepsilon \to 0$, where I is defined in (2.8), and $I_\varepsilon = I$ when $\varepsilon = 0$. Since the principal eigenvalue λ of I satisfies (B.1), there exists a small ε_1 such that the principal eigenvalue λ_ε of I_ε satisfies

(B.4) $$\lambda_\varepsilon > 1 - \frac{\int_0^\omega g(s,0)ds}{\int_0^\omega a(s)ds}$$

for all $\varepsilon \in (0,\varepsilon_1)$. We fix an $\varepsilon \in (0,\varepsilon_1)$. Since $\lim_{u\to 0^+} \frac{ug(t,u)}{u} = g(t,0)$ uniformly for $t \in [0,\omega]$, there exists $\delta > 0$ such that $ug(t,u) > (g(t,0) - \varepsilon)u$ for all $t \in [0,\omega]$ and $0 < u < \delta$.

Claim 2. *$\lim_{t\to\infty}\sup ||u(t,\cdot)|| \geq \delta$ for all solution $u(t,x)$ to* (1.1) *with initial function $u_0 \in C([0,L],W)$ with $u_0 \not\equiv 0$.*

We prove this claim by contradiction. Suppose that there exists $u_0 \in C([0,L],W)$ *with* $u_0 \not\equiv 0$ *such that the solution* $u(t,x)$ *to* (1.1) *with initial value* u_0 *satisfies* $\lim_{t\to\infty}\sup ||u(t,\cdot)|| < \delta$. *Then there exists* $t_0 > 0$ *such that* $u(t,x) < \delta$ *for all* $t \geq t_0$. *By Claim* 1, *we obtain that* $u(t,x)$ *satisfies*

(B.5)
$$\frac{\partial u(t,x)}{\partial t} > (g(t,0) - a(t) - \varepsilon)u(t,x) + a(t)\int_0^L k(t,x,y)u(t,y)dy \quad \forall t \geq t_0,\ x \in [0,L].$$

Let $u_\varepsilon(t,x) = \varphi_\varepsilon(t)\psi_\varepsilon(x)$ *be a solution to*

(B.6)
$$\frac{\partial u(t,x)}{\partial t} = (g(t,0) - a(t) - \varepsilon)u(t,x) + a(t)\int_0^L k(t,x,y)u(t,y)dy \quad \forall t \geq t_0,\ x \in [0,L].$$

Similarly as we do in section 2, *we can obtain*

(B.7)
$$\frac{\left[\ln \frac{\varphi_\varepsilon(t+\omega)}{\varphi_\varepsilon(t)} - \int_0^\omega (g(s,0) - a(s))ds\right]}{\int_0^\omega a(s)ds}\psi_\varepsilon(x) = -\frac{\varepsilon\omega}{\int_0^\omega a(s)ds}\psi_\varepsilon(x) + \int_0^L \mathcal{K}(x,y)\psi_\varepsilon(y)dy,$$

for all $t \geq 0$. *Let* $\tilde{\psi}_\varepsilon$ *be the positive eigenfunction of* I_ε *in* $C([0,L],W)$ *with respect to* λ_ε *and write*

$$\lambda_\varepsilon = \frac{\left[\ln \frac{\tilde{\varphi}_\varepsilon(t+\omega)}{\tilde{\varphi}_\varepsilon(t)} - \int_0^\omega (g(s,0) - a(s))ds\right]}{\int_0^\omega a(s)ds},$$

which can be used to determine $\tilde{\varphi}_\varepsilon$. *Then* $\tilde{u}_\varepsilon(t,x) = \tilde{\varphi}_\varepsilon(t)\tilde{\psi}_\varepsilon(x)$ *is a special solution to* (B.6). *Let* $\theta = \frac{\tilde{\varphi}_\varepsilon(t+\omega)}{\tilde{\varphi}_\varepsilon(t)}$ *for* $t \geq 0$. *It follows from* (B.4) *that* $\theta > 0$. *Since* $u(t_0,x) > 0$ *for all* $x \in [0,L]$, *there exists a multiple of* $\tilde{\psi}_\varepsilon$ *such that* $\tilde{\varphi}_\varepsilon(0)\tilde{\psi}_\varepsilon(x) \leq u(t_0,x)$ *for all* $x \in [0,L]$. *Then by* (B.5) *and the comparison theorem,*

$$u(t,x) \geq \tilde{u}_\varepsilon(t,x) = \tilde{\varphi}_\varepsilon(t)\tilde{\psi}_\varepsilon(x) \quad \forall t \geq t_0, \quad x \in [0,L].$$

In particular, it follows from the definition of θ *that*

$$u(t_0+n\omega,x) \geq \tilde{u}_\varepsilon(t_0+n\omega,x) = \tilde{\varphi}_\varepsilon(t_0+n\omega)\tilde{\psi}_\varepsilon(x) = e^{n\theta}\tilde{\varphi}_\varepsilon(t_0)\tilde{\psi}_\varepsilon(x) \quad \forall t \geq t_0,\ x \in [0,L],$$

and hence, $u(t_0+n\omega,x) \to \infty$ *as* $n \to \infty$ *for all* $x \in [0,L]$, *since* $\theta > 0$, *a contradiction. Therefore,* $\lim_{t\to\infty}\sup \max_{x\in[0,L]}\{u(t,x)\} \geq \delta$ *for all solutions* $u(t,x)$ *to* (1.1) *with initial function* $u_0 \in C([0,L],W)$ *with* $u_0 \not\equiv 0$.

It follows from Claim 2 that the zero solution to (1.1) is unstable.

(b). Now we consider

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

Let $\tilde{u}(t,x) = \tilde{\varphi}(t)\tilde{\psi}(x)$ be the solution to (2.1) defined in (2.9). By (2.7), the principal eigenvalue λ of the operator I defined in (2.8) satisfies

(B.8)
$$\lambda = \frac{\left[\ln \frac{\tilde{\varphi}(t+\omega)}{\tilde{\varphi}(t)} - \int_0^\omega (g(s,0) - a(s))ds\right]}{\int_0^\omega a(s)ds} \qquad \forall t \geq 0.$$

By (B.8) we have $\ln \frac{\tilde{\varphi}(t+\omega)}{\tilde{\varphi}(t)} < 0$ for all $t \geq 0$, which implies that

$$\tilde{\varphi}(t) > \tilde{\varphi}(t+\omega) > \tilde{\varphi}(t+2\omega) > \cdots \qquad \forall t \geq 0,$$

and hence, $\tilde{u}(t,x) = \tilde{\varphi}(t)\tilde{\psi}(x)$ satisfies

$$\text{(B.9)} \qquad \tilde{u}(t,x) > \tilde{u}(t+\omega,x) > \tilde{u}(t+2\omega,x) > \cdots \quad \forall t \geq 0, \quad x \in [0,L].$$

For any $\varepsilon > 0$, there exists a multiple of $\tilde{\psi}$, which we again write as $\tilde{\psi}$, such that $||\tilde{\varphi}(0)\tilde{\psi}|| = \max_{x\in[0,L]} \tilde{\varphi}(0)\tilde{\psi}(x) < \varepsilon$. Moreover, by the continuity of solutions with respect to initial values, we can restrict $\tilde{\psi}$ such that

$$||Q_t^L[\tilde{\varphi}(0)\tilde{\psi}]|| = ||\tilde{u}(t,x)|| = \max_{x\in[0,L]} \tilde{u}(t,x) = \max_{x\in[0,L]} \tilde{\varphi}(t)\tilde{\psi}(x) < \varepsilon \qquad \forall t \in [0,\omega].$$

Then (B.9) implies that

$$||\tilde{u}(t,\cdot)|| < \varepsilon \qquad \forall t \geq 0.$$

Let $m_2 = \min_{x\in[0,L]} \tilde{\psi}(x)$. It follows that $0 < \tilde{\varphi}(0)m_2 < \varepsilon$ and that for any initial function $u_0 \in C([0,L])$ with $||u_0|| \leq \tilde{\varphi}(0)m_2$, the solution $u(t,x)$ to (2.1) through u_0 satisfies

$$u(t,x) = Q_t^L[u_0](x) \leq Q_t^L[\tilde{\varphi}(0)\tilde{\psi}](x) = \tilde{u}(t,x) < \varepsilon \quad \forall t \geq 0, \quad x \in [0,L].$$

Let $\bar{\bar{u}}(t,x)$ be the solution to (1.1) with the initial function u_0 as above. Since $g(t,u) \leq g(t,0)$ for $t \geq 0$ and $u \in [0,\hat{u}]$, by the comparison theorem, $\bar{\bar{u}}(t,x)$ satisfies

$$\bar{\bar{u}}(t,x) = Q_t[u_0](x) \leq Q_t^L[u_0](x) = u(t,x) < \varepsilon \quad \forall t \geq 0, \quad x \in [0,L],$$

where Q_t is the solution map of (1.1). Therefore, we proved that for any $\varepsilon > 0$, there exists $\delta = \tilde{\varphi}(0)m_2$, such that for any initial function $u_0 \in C([0,L],W)$ with $||u_0|| \leq \delta$, the solution $\bar{\bar{u}}(t,x)$ to (1.1) through u_0 satisfies $0 \leq \bar{\bar{u}}(t,x) < \varepsilon$ for all $t \geq 0$, $x \in [0,L]$. This implies that the zero solution to (1.1) is stable. The proof is completed.

(ii) Assume that $\int_0^\omega g(s,0)ds > \int_0^\omega a(s)ds$**.**

There exists $\varepsilon_1 > 0$ such that $\int_0^\omega (g(s,0) - a(s) - \varepsilon)ds > 0$ for all $\varepsilon \in (0,\varepsilon_1)$. Fix an $\varepsilon \in (0,\varepsilon_1)$. Since $\lim_{u\to 0^+} \frac{ug(t,u)}{u} = g(t,0)$ uniformly for $t \in [0,\omega]$, there exists $\delta > 0$ such that $ug(t,u) > g(t,0) - \varepsilon)u$ for all $t \in [0,\omega]$ and $0 < u < \delta$. Note that

$$\text{(B.10)} \qquad \begin{aligned} \frac{\partial \bar{u}(t,x)}{\partial t} &= (g(t,0) - a(t) - \varepsilon)\bar{u}(t,x) + a(t)\int_0^L k(t,x,y)\bar{u}(t,y)dy \\ &\geq (g(t,0) - a(t) - \varepsilon)\bar{u}(t,x),\ t \geq 0,\ x \in [0,L] \end{aligned}$$

and the solution to

$$\text{(B.11)} \qquad \frac{\partial \bar{u}(t,x)}{\partial t} = (g(t,0) - a(t) - \varepsilon)\bar{u}(t,x),\ t \geq 0,\ x \in [0,L]$$

can be expressed as

$$\text{(B.12)} \qquad \bar{u}(t,x) = \bar{u}(0,x)e^{\int_0^t (g(s,0)-a(s)-\varepsilon)ds},\ \forall t \geq 0,\ x \in [0,L],$$

where $\bar{u}(0,\cdot) \in C([0,L])$ is the initial function for (B.11). By the periodicity of $(g(t,0) - a(t))$ and the assumption $\int_0^\omega (g(s,0) - a(s) - \varepsilon)ds > 0$, we have

$$\text{(B.13)} \qquad \bar{u}(t,x) < \bar{u}(t+\omega,x) < \bar{u}(t+2\omega,x) < \cdots \quad \forall t \geq 0, \quad x \in [0,L].$$

Then similarly as we did in the proof of **(i)(a)**, we can show that $\lim_{t\to\infty} \sup ||u(t,\cdot)|| \geq \delta$ for all solution $u(t,x)$ to (1.1) with initial function $u_0 \in C([0,L],W)$ with $u_0 \not\equiv 0$. This implies that the zero solution to (1.1) is unstable.

(iii) Assume that $\int_0^\omega g(s,0)ds = \int_0^\omega a(s)ds$**.**

Note that (2.1) admits a solution

$$\tilde{u}(t,x) = \tilde{\varphi}(t)\tilde{\psi}(x) \tag{B.14}$$

with $\tilde{u}(0,x) = \tilde{\varphi}(0)\tilde{\psi}(x)$, where $\tilde{\psi}$ with $\tilde{\psi}(x) > 0$ for all $x \in [0,L]$ is the eigenfunction of I corresponding to the principal eigenvalue λ of I, and $\tilde{\varphi}(t)$ is determined by (2.2) with $\psi = \tilde{\psi}$ and $\tilde{\varphi}(0) > 0$. It follows from $\int_0^\omega g(s,0)ds = \int_0^\omega a(s)ds$ and (2.7) that

$$\frac{\ln \dfrac{\tilde{\varphi}(t+\omega)}{\tilde{\varphi}(t)}}{\int_0^\omega a(s)ds} = \frac{\int_0^L \mathcal{K}(x,y)\tilde{\psi}(y)dy}{\tilde{\psi}(x)} = \frac{I[\tilde{\psi}](x)}{\tilde{\psi}(x)} = \lambda \qquad \forall t \geq 0, \tag{B.15}$$

which implies that

$$\tilde{\varphi}(t+\omega) = e^{\lambda \int_0^\omega a(s)ds}\tilde{\varphi}(t) \qquad \forall t \geq 0.$$

Let $\theta = e^{\lambda \int_0^\omega a(s)ds}$. We have $\theta > 1$ by the positivity of λ and $\int_0^\omega a(s)ds$. Then

$$\tilde{\varphi}(t) < \tilde{\varphi}(t+\omega) < \tilde{\varphi}(t+2\omega) < \cdots \qquad \forall t \geq 0,$$

and hence,

$$\tilde{u}(t,x) = \tilde{\varphi}(t)\tilde{\psi}(x) < \tilde{u}(t+\omega,x) < \tilde{u}(t+2\omega,x) < \cdots \quad \forall t \geq 0, \quad x \in [0,L],$$

which indicates that the zero solution to (2.1) is not stable, i.e., the zero solution to (1.1) is linearly unstable. This completes the proof of Theorem 2.2.

Appendix C. Proof of Lemma 3.1. For any $\psi \in C([0,L],W)$, $x \in [0,L]$,

$$\begin{aligned}
I_n[\psi](x) &= \frac{1}{\int_0^\omega a^{(n)}(s)ds} \int_0^L \int_0^\omega a^{(n)}(s)k^{(n)}(s,x,y)ds\psi(y)dy \\
&\leq \frac{1}{\int_0^\omega a^{(n)}(s)ds} \int_0^L \int_0^\omega a^{(n)}(s)k^{(n)}(s,x,y)ds \cdot \max_{y\in[0,L]} \psi(y)dy \\
&= \frac{1}{\int_0^\omega a^{(n)}(s)ds} \int_0^\omega a^{(n)}(s) \int_0^L k^{(n)}(s,x,y)dyds \cdot ||\psi|| \\
&\leq K_+||\psi||,
\end{aligned}$$

which implies that

$$||I_n|| = \sup_{||\psi||=1} ||I_n[\psi]|| = \sup_{||\psi||=1} \max_{x\in[0,L]} I_n[\psi](x) \leq K_+.$$

Similarly, we can obtain $||I_0|| \leq K_+$.

Moreover, we can show $||I_n - I_0|| \to 0$ as $n \to \infty$. In fact, for any $\psi \in C([0,L],W)$ and $x \in [0,L]$,

$$
\begin{aligned}
&\int_0^\omega a^{(n)}(s)ds \cdot |I_n[\psi](x) - I_0[\psi](x)| \\
&\quad = \left| \int_0^\omega a^{(n)}(s)ds \cdot I_n[\psi](x) - \int_0^\omega a^{(n)}(s)ds \cdot I_0[\psi](x) \right| \\
&\quad = \left| a_1 \left(\omega_0 - \frac{1}{n}\right) \int_0^L k_1(x,y)\psi(y)dy + \int_{\omega_0 - \frac{1}{n}}^{\omega_0} a_1^{(n)}(s) \int_0^L k_1^{(n)}(s,x,y)\psi(y)dyds \right. \\
&\qquad + a_2 \left(\omega - \frac{1}{n} - \omega_0\right) \int_0^L k_2(x,y)\psi(y)dy + \int_{\omega - \frac{1}{n}}^{\omega} a_2^{(n)}(s) \int_0^L k_2^{(n)}(s,x,y)\psi(y)dyds \\
&\qquad \left. - \frac{\int_0^\omega a^{(n)}(s)ds}{a_1\omega_0 + a_2(\omega - \omega_0)} \left(a_1\omega_0 \int_0^L k_1(x,y)\psi(y)dy + a_2(\omega - \omega_0) \int_0^L k_2(x,y)\psi(y)dy \right) \right| \\
&\quad = \left| \int_0^L k_1(x,y)\psi(y)dy \left(a_1 \left(\omega_0 - \frac{1}{n}\right) - \frac{\int_0^\omega a^{(n)}(s)ds}{a_1\omega_0 + a_2(\omega - \omega_0)} a_1\omega_0 \right) \right. \\
&\qquad + \int_0^L k_2(x,y)\psi(y)dy \left(a_2 \left(\omega - \frac{1}{n} - \omega_0\right) - \frac{\int_0^\omega a^{(n)}(s)ds}{a_1\omega_0 + a_2(\omega - \omega_0)} a_2(\omega - \omega_0) \right) \\
&\qquad \left. + \int_{\omega_0 - \frac{1}{n}}^{\omega_0} a_1^{(n)}(s) \int_0^L k_1^{(n)}(s,x,y)\psi(y)dyds + \int_{\omega - \frac{1}{n}}^{\omega} a_2^{(n)}(s) \int_0^L k_2^{(n)}(s,x,y)\psi(y)dyds \right| \\
&\quad \to 0
\end{aligned}
$$

as $n \to \infty$. It then follows from the boundedness of $a^{(n)}(t)$ and $\psi(x)$ and the assumption (H2) that

$$
||I_n[\psi] - I_0[\psi]|| = \max_{x \in [0,L]} |I_n[\psi](x) - I_0[\psi](x)| \to 0 \quad \text{as } n \to \infty
$$

for any $||\psi|| = \max_{x \in [0,L]} \{\psi(x)\} \leq \hat{u}$. Then

$$
||I_n - I_0|| = \sup_{||\psi|| \leq 1} ||I_n[\psi] - I_0[\psi]|| \to 0 \quad \text{as } n \to \infty.
$$

Let λ_i be the principal eigenvalue of I_i, for $i = 0, 1, 2, \ldots$. Set $\eta(I_0) = \lambda_0$. Then by the perturbation theory for linear operators in [5, Theorem 2.23, sections 4.3.4 and 4.3.5], there exists $\{\eta(I_n)\}_{n \in \mathbb{N}}$, where $\eta(I_n)$ is an eigenvalue of I_n, such that $\eta(I_n) \to \eta(I_0) = \lambda_0$ as $n \to \infty$. On the other hand, it follows from the uniform boundedness of $\{||I_n||\}_{n \in \mathbb{N}}$ that the principal eigenvalues λ_n's of I_n's are uniformly bounded by 1. Then, $\{\lambda_n\}_{n \in \mathbb{N}}$ admits a convergent subsequence $\{\lambda_{n_k}\}_{k \in \mathbb{N}}$, which satisfies $\lambda_{n_k} \to \bar{\lambda}$ as $k \to \infty$ for some $\bar{\lambda} \geq 0$. If $\bar{\lambda}$ is a resolvent value of I_0, then by [5, Theorem 2.25], $\bar{\lambda}$ is a resolvent value of I_{n_k} for sufficiently large $k \in \mathbb{N}$. Since the resolvent set of an operator is an open set, there exists an open neighborhood $U(\bar{\lambda})$ of $\bar{\lambda}$ such that any value in $U(\bar{\lambda})$ is a resolvent of I_{n_k} for large $k \in \mathbb{N}$. This contradicts the fact that eigenvalues λ_{n_k} converge to $\bar{\lambda}$. Therefore, $\bar{\lambda}$ is an eigenvalue of I_0. Moreover, since $|\eta(I_k)| \leq \lambda_{n_k}$ for all $k \in \mathbb{N}$, we have $\lambda_0 \leq \bar{\lambda}$, which indicates that $\lambda_0 = \bar{\lambda}$ as λ_0 is the principal eigenvalue of I_0. This also implies that any convergent subsequence of $\{\lambda_n\}_{n \in \mathbb{N}}$ converges to λ_0. Therefore, $\{\lambda_n\}_{n \in \mathbb{N}}$ itself converges to λ_0 (i.e., $\lambda_n \to \lambda_0$) as $n \to \infty$. That is, the principal eigenvalues of the integral operators $\{I_n\}_{n \in \mathbb{N}}$ converge to the principal eigenvalue of I_0.

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