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SPATIAL DYNAMICS OF AN AGE-STRUCTURED POPULATION MODEL OF ASIAN CLAMS[*]

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Abstract. Asian clam (Corbicula fluminea) is one of the most important nonnative aquatic invasive species in the freshwater ecosystem of North America, rapidly spreading in lakes, canals, streams, and rivers. This species has remarkably distinct mobility patterns in different phases of its life cycle. We formulate a novel mathematical model, in the form of nonlocal delayed partial differential equations, to calculate and characterize the invasion speed, and show that the invasion speed coincides with the minimal speed of traveling wave fronts.

Key words. Corbicula fluminea, Asian clam, invasion speed, traveling wave, delayed reaction-diffusion-advection system, nonlocal response, semiflow

AMS subject classifications. Primary, 92D25; Secondary, 37N25, 37L05, 35B51, 35C07

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1. Introduction.

Asian clam, *Corbicula fluminea* (Müller, 1774), is a small bivalve native to Southeast Asia, Australia, Africa, Indonesia, and Turkey. Asian clam was first observed in North America in the Columbia River, Washington in 1938, and in Vancouver Island [10], and the Québec side of the St. Lawrence River [24]. It has spread rapidly in lakes, canals, streams, and rivers throughout North America.

It is recognized as one of the most important nonnative aquatic invasive species in the freshwater ecosystem of North America due to the economic and ecological impact [1, 14, 15, 17, 18, 28]. Asian clam can clog waterways, canals, and pipes and result in millions of dollars of damage each year. It also impacts aesthetic and recreational values of public areas. Asian clam's excretions encourage algal growth which reduces water quality. Its intensive filtering activity and ability to reproduce rapidly can outcompete native species for food and space and alter benthic habitats. Adult Asian clam can grow up to 50 mm in length and it usually sticks to the benthic compartment. The mobility of adults is so small that it is negligible, compared to the mobility of juveniles and the rapid invasion speed.

There are substantial studies about the ecology and spread of Asian clam (see, for instance, [1, 3, 28]), but to the best of our knowledge there is no mathematical

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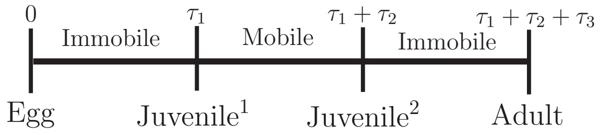

Fig. 1. *Asian clam's age structure with structure-dependent mobilities.*

model describing the mechanism for the rapid spread. In this paper, we establish a mathematical model that describes the invasion and propagation of Asian clam in an unbounded one-dimensional habitat. Asian clam has a clear age structure and different mobility patterns in different age stages. Adult clams are hermaphroditic, meaning that an adult produces sperm which in part become eggs in the shell directly and the rest discharged into the water can also become eggs by contacting other adult clams. The eggs are incubated within the parent's shell and released about 4–5 days later when becoming juveniles. The discharged juveniles are capable of dispersing via stream transport or water current and then sink into the benthic compartment to wait for maturation (see Figure 1). Thus, the mobility of juveniles seems to be a major ecological factor contributing to the rapid spread of the Asian clam.

To take the above facts into account for modeling, we start with an age-structured population formulation and derive a reduced time-delayed reaction-diffusion-advection system with nonlocal response that has a weak regularity caused by the zero diffusion in one component. Time delay, playing an important role in the modeling, naturally arises due to the maturation process. The interaction of time delay and the spatial movement of the juveniles leads to the nonlocal response. In particular, the system contains five partial differential equations (PDEs) arising from the populations in mobile and immobile stages and the sperm population, and we show that this system can be reduced to the following:

$$\frac{\partial u}{\partial t} = -d_m u + \alpha \int_{\mathbb{R}} k(x-y)[\gamma b(u(t-\tau,y)) + \beta w(t-\tau,y)u(t-\tau,y)]dy, \tag{1.1a}$$

$$\frac{\partial w}{\partial t} = D_s \frac{\partial^2 w}{\partial x^2} - v_s \frac{\partial w}{\partial x} + (1-\gamma)b(u(t,x)) - d_s w, \tag{1.1b}$$

where $u(t,x)$ and $w(t,x)$ denote the populations of adult clams and sperm at time t and location x, b is the birth function, and k is a suitable kernel to be specified later. All the parameters are positive and $\alpha, \beta, \gamma \in (0,1]$. The hermaphroditic nature of adult clams is reflected by the interaction term $\beta w(t-\tau,y)u(t-\tau,y)$, which makes the reduced model distinct from most nonlocal reaction-diffusion equations studied in the existing literature. In the absence of this nature (either $\beta = 0$ or $\gamma = 1$), the model reduces to the one in [32] which is a special case of the model derived in [27].

There is a long history in modeling biological invasion using reaction-diffusion equations. The Fisher and Fitzhugh–Nagumo equations were proposed to model the wave of advance of an advantageous gene and the impulses traveling along nerve axons, respectively. Rapid development has been made since the publication of a number of textbooks in mathematical biology such as Murray [19, 20] and Shigesada and Kawasaki [23]. Asymptotic speed of spread (sometimes called invasion or spreading speed) and traveling waves are two fundamental mathematical tools that have been shown to be useful for the description of the biological invasion process. For example, it has been shown in [2] that for the Fisher equation $\partial_t u = \partial_{xx} u + u(1-u)$, its invasion speed denoted by c^* is 2, that is, the solution of the Fisher equation u

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satisfies $\lim_{t\to\infty,\ |x|\le ct} u(t,x) = 1$ for $c < c^*$ and $\lim_{t\to\infty,\ |x|\ge ct} u(t,x) = 0$ for $c > c^*$, whenever the initial value $u(0,x)$ is compactly supported. In [5], it was shown that c^* is the minimal wave speed of leftward/rightward traveling waves that are special solutions in the form $u(t,x) = U(x \pm ct)$, where c is the wave speed and $\pm$ denote the left/right direction of traveling. These results, together with the convergence of solutions to traveling waves, characterize the evolution of a solution: it asymptotically has a wavefront-like leading edge with a certain speed $c \ge 2$ depending on the decay rate of initial values at infinity. We refer to [7] and references therein for more details.

There have been an increasing interest and progress in the study of invasion speed and traveling waves for delayed nonlocal reaction-diffusion systems, as summarized in the survey article [6]. However, the previous techniques cannot be applied directly to our reduced model (2.7) due to the hermaphroditic nature of adult clams. In particular, it is not clear whether the invasion speed of the proposed model is linearly determinate. It is also not trivial to tackle the problem by extending the well-known upper and lower solutions techniques based on the eigenvalues of the linearized systems for the study of the invasion speed and traveling waves. In this paper, we first apply some recent results on infinite dimensional dynamical systems in [11, 12] to obtain the existence of invasion speed in a weak sense, and we study the existence of traveling waves by employing the ideas involving weaker compactness developed in [4]. We then show that the invasion speed coincides with the minimal wave speed and is the practical invasion speed as in [2]. We also provide a lower bound for the established invasion speed in the weak sense and an upper bound under certain biologically reasonable assumptions, and establish the characterization and dependence on parameters of the upper bound.

This paper is organized as follows. Section 2 is devoted to the model derivation and simplification, and in section 3, the well posedness of the model is established. In sections 4 and 5, we study the invasion speed including the existence and characterization as well as its coincidence with the minimal speed of traveling wave.

2. Model formation. Let $p(t,a,x)$ be the density of the Asian clam at time $t \ge 0$, age $a \ge 0$, and location $x \in \mathbb{R}$. The total number of clams in each of the stages, egg E, mobile/immobile juvenile J_1/J_2, and adult M, at time t and location x, can be expressed as $E(t,x) = \int_0^{\tau_1} p(t,a,x)da$, $J_1(t,x) = \int_{\tau_1}^{\tau_1+\tau_2} p(t,a,x)da$, $J_2(t,x) = \int_{\tau_1+\tau_2}^{\tau} p(t,a,x)da$, and $M(t,x) = \int_{\tau}^{\infty} p(t,a,x)da$, where $\tau := \tau_1 + \tau_2 + \tau_3$ is the maturation period.

To construct a simple mathematical model that describes the life cycle and invasion process of the Asian clam, we make the following assumptions:

(i) all individuals in each stage have the same dynamic behavior and mobility pattern;
(ii) the population behavior in a given stage is homogeneous in time and location;
(iii) eggs (E) are incubated within the parents' shell and released τ_1 days later, the discharged juveniles (J_1) disperse long distances via stream transport or water current for τ_2 days, the juveniles sinking into the benthic compartment (J_2) reach maturity approximately τ_3 days later;
(iv) sperms (S) are discharged into water and become eggs by contacting adults (M) with a rate β.

With the aforementioned assumptions, we derive the model following the growth law of age-structured population,

$$\frac{\partial p}{\partial t} + \frac{\partial p}{\partial a} = D(a)\frac{\partial^2 p}{\partial x^2} - v(a)\frac{\partial p}{\partial x} - d(a)p \quad \text{for } t > 0,\ a > 0, \text{ and } x \in \mathbb{R},$$

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TABLE 1
Meaning of parameters in (2.1) *and* (2.2).

Parameter	Meaning
β	contact rate between sperms and adult clams
γ	rate of becoming eggs directly in the shell
D_s	diffusion coefficient for the sperm
D_1	diffusion coefficient for the discharged juvenile
v_s	advection velocity of the sperm
v_1	advection velocity of the discharged juvenile
d_s	mortality rate of the sperm
d_ϵ	mortality rate of the egg
d_m	mortality rate of the adult
d_1	mortality rate of the discharged juvenile
d_2	mortality rate of the juveniles in the immobile state

where $D(a), v(a)$, and $d(a)$ represent diffusivity, advection, and death rates at age a, respectively. These coefficients are assumed to be step functions given by

$$D(a) = \begin{cases} 0, & a \in [0, \tau_1) \cup [\tau_1 + \tau_2, \infty), \\ D_1, & a \in [\tau_1, \tau_1 + \tau_2), \end{cases} \qquad v(a) = \begin{cases} 0, & a \in [0, \tau_1) \cup [\tau_1 + \tau_2, \infty), \\ v_1, & a \in [\tau_1, \tau_1 + \tau_2), \end{cases}$$

and

$$d(a) = \begin{cases} d_\epsilon, & a \in [0, \tau_1), \\ d_1, & a \in [\tau_1, \tau_1 + \tau_2), \\ d_2, & a \in [\tau_1 + \tau_2, \tau), \\ d_m, & a \in [\tau, \infty). \end{cases}$$

The resulting model is classified into two stages.

Mobile stage:

$$\frac{\partial J_1}{\partial t} = D_1 \frac{\partial^2 J_1}{\partial x^2} - v_1 \frac{\partial J_1}{\partial x} - d_1 J_1 + p(t, \tau_1, x) - p(t, \tau_1 + \tau_2, x); \tag{2.1}$$

Immobile stage:

$$\frac{\partial E}{\partial t} = p(t, 0, x) - d_\varepsilon E - p(t, \tau_1, x), \tag{2.2a}$$

$$\frac{\partial J_2}{\partial t} = p(t, \tau_1 + \tau_2, x) - p(t, \tau, x) - d_2 J_2, \tag{2.2b}$$

$$\frac{\partial M}{\partial t} = p(t, \tau, x) - d_m M. \tag{2.2c}$$

See Table 1 for descriptions of the coefficients involved throughout the section.

Following the method of integration along characteristics [26], the terms $p(t, \tau_1, x)$, $p(t, \tau_1 + \tau_2, x)$, and $p(t, \tau, x)$ can be expressed in terms of $p(t, 0, x)$ in a functional way. The explicit forms are given as follows:

$$p(t, \tau_1, x) = T_1(\tau_1)[p(t - \tau_1, 0, \cdot)](x), \tag{2.3a}$$

$$p(t, \tau_1 + \tau_2, x) = T_2(\tau_2) T_1(\tau_1)[p(t - \tau_1 - \tau_2, 0, \cdot)](x), \tag{2.3b}$$

$$p(t, \tau, x) = T_3(\tau_3) T_2(\tau_2) T_1(\tau_1)[p(t - \tau, 0, \cdot)](x), \tag{2.3c}$$

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where $T_i(s), i = 1, 2, 3$, are the time-s solution maps of the following linear systems $u'(s) = -d_\varepsilon u(s), \partial_s u = D_1 \partial_{xx} u - v_1 u - d_1 u, u'(s) = -d_2 u(s)$, respectively. Hence,

$$T_1(\tau_1)\phi = e^{-d_\varepsilon \tau_1}\phi, \quad T_2(\tau_2)\phi = e^{-d_1\tau_2} k * \phi, \quad T_3(\tau_3)\phi = e^{-d_2\tau_3}\phi,$$

where

$$k(y) = \frac{1}{\sqrt{4\pi D_1 \tau_2}} \exp\left(-\frac{(y - v_1\tau_2)^2}{4D_1\tau_2}\right). \tag{2.4}$$

To derive an explicit form of the model, we find the expression of $p(t, 0, x)$, the newborn eggs. As assumed, adult clams reproduce sperm, part (with fraction γ) of which become eggs directly in the parents' shell and the rest discharged into water can also become eggs when they sink to the benthic compartment by contacting with adult clams. Thus, if we assume that b is the birth function of sperm, then

$$p(t, 0, x) = \gamma b(M(t, x)) + \beta M(t, x)S(t, x). \tag{2.5}$$

Since $p(t, 0, x)$ involves sperm S, we introduce the S equation to obtain a closed system.

Sperm equation:

$$\frac{\partial S}{\partial t} = D_s \frac{\partial^2 S}{\partial x^2} - v_s \frac{\partial S}{\partial x} + (1 - \gamma)b(M(t, x)) - d_s S. \tag{2.6}$$

By (2.3c) and (2.5), the term $p(t, \tau, x)$ in (2.2c) can be expressed by M and S. It follows that the subsystem of adult equation (2.2c) and sperm equation (2.6) is uncoupled from the remaining part of the whole system. For simplification, we define

$$\alpha := e^{-d_\varepsilon \tau_1 - d_1\tau_2 - d_2\tau_3}$$

and replace $M(t, x)$ and $S(t, x)$ by $u(t, x)$ and $w(t, x)$, respectively. Hence we will focus on the following reduced system that describes the dynamic interaction of adult and sperm populations:

$$\frac{\partial u}{\partial t} = -d_m u + \alpha \int_{\mathbb{R}} k(x - y)[\gamma b(u(t - \tau, y)) + \beta w(t - \tau, y)u(t - \tau, y)]dy, \tag{2.7a}$$

$$\frac{\partial w}{\partial t} = D_s \frac{\partial^2 w}{\partial x^2} - v_s \frac{\partial w}{\partial x} + (1 - \gamma)b(u(t, x)) - d_s w. \tag{2.7b}$$

3. Preliminary.

In this section, we first study the kinetic dynamics of system (2.7) to find the conditions for the species to survive or go to extinction. Then we establish the well posedness and comparison principle for (2.7) under appropriate conditions so that the species can survive.

3.1. Kinetic dynamics.

The kinetic dynamics of (2.7) is of the form

$$\frac{du}{dt} = -d_m u + \alpha\left[\gamma b\left(u\left(t - \tau\right)\right) + \beta w\left(t - \tau\right) u\left(t - \tau\right)\right], \tag{3.1a}$$

$$\frac{dw}{dt} = (1 - \gamma)\, b(u) - d_s w. \tag{3.1b}$$

It is easy to verify that (u, w) is an equilibrium of (3.1) if and only if (u, w) satisfies

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the following system of equations:

$$b(u) = \frac{d_s d_m u}{\alpha\left[d_s\gamma + \beta(1-\gamma)u\right]} := f(u), \quad (1-\gamma)b(u) = d_s w. \tag{3.2}$$

It is clear that $E^0 := (0, 0)$ is an equilibrium of (3.1) since $b(0) = 0$. The following result shows nonexistence of positive equilibria.

Proposition 3.1. *If* $b : \mathbb{R}_+ \to \mathbb{R}_+$ *is continuous and satisfies* $b(u) < f(u)$ *for* $u > 0$*, then* (3.1) *has no positive equilibria, and the equilibrium* $E^0 := (0, 0)$ *attracts all solutions of* (3.1) *with nonnegative initial values.*

Proof. The first result follows from the first equation of (3.2) and the condition $b(u) < f(u)$ for $u > 0$. Since $f(u)$ is strictly increasing, there exists a smooth strictly increasing function b_1 such that $b(u) \le b_1(u) < f(u)$ for $u > 0$. Thus, (3.1) with b replaced by b_1 is a monotone system and any constant vector $(\bar{u}, \bar{w})$ satisfying $(1-\gamma)b_1(\bar{u}) = d_s\bar{w}$ is a superequilibrium of this monotone system. Then the corresponding solution starting from $(\bar{u}, \bar{w})$ will go to an equilibrium, which must be E^0 due to the uniqueness (see [25, Lemma 2.5.1]). From the second equation of (3.1), we see that $w(t) < \frac{1-\gamma}{d_s}b_1(+\infty)$ when t is sufficiently large. Thus, any solution of (3.1) with bounded nonnegative initial values is eventually bounded above by some constant $(\bar{u}, \bar{w})$ satisfying $(1-\gamma)b_1(\bar{u}) = d_s\bar{w}$, where $(\bar{u}, \bar{w})$ can be arbitrarily close to $(+\infty, \frac{1-\gamma}{d_s}b_1(+\infty))$. The last result follows from the comparison principle [25]. ☐

Remark 3.1. The condition: $b(u) < f(u)$ for $u > 0$ used in Proposition 3.1 can be rewritten as

$$\alpha\left[\gamma b(u) + \beta\frac{(1-\gamma)b(u)}{d_s}u\right] < d_m u, \tag{3.3}$$

where $\gamma b(u)$ and $\beta\frac{(1-\gamma)b(u)}{d_s}u$ represent two sources of the birth of eggs and α is the survival rate from eggs to adults. Thus, $b(u) < f(u)$ implies that the recruitment is less than the death for the adult clams, under which equilibrium E^0 is a global attractor of (3.1).

To study existence of positive equilibria and instability of E^0, we assume that

(H1) b is Lipschitz continuous with $b(0) = 0$ and $b'(0) > d_m(\alpha\gamma)^{-1}$;
(H2) there exists the smallest positive solution u^* of equation $b(u) = f(u)$;
(H3) b is nondecreasing in the interval $[0, u^*]$.

Assumption (H1) implies instability of E^0 and (H2) ensures that the positive equilibrium $E^* := (u^*, w^*)$ with $w^* = (1-\gamma)b(u^*)/d_s$ exists and is globally attractive under the quasi-monotone condition (H3). Due to limited resources for reproduction, the birth function b is usually assumed to be decreasing and converges to zero. As such, (H2) is easily satisfied under (H1). In what follows, we always assume that (H1)–(H3) hold. Thus, (3.1) admits the monostability and monotonicity.

Remark 3.2. An appropriate birth function is the Ricker function $b(u) = pue^{-qu}$, which is derived from assuming that per capita fecundity decreases exponentially with density, where p is the maximum per capita reproduction rate and q controls the density-dependent mortality near the equilibrium abundance [21, 22]. In such a case, although the positive equilibrium cannot be calculated explicitly due to the hermaphroditic nature ($\beta > 0, \gamma \in (0, 1)$), one can obtain the following explicit conditions equivalent to (H1)–(H3):

$$\frac{1}{\gamma} < \frac{\alpha p}{d_m} \le \frac{q d_s e}{q d_s \gamma + \beta(1-\gamma)}.$$

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In particular, if $\gamma = 1$, that is, there is no hermaphroditicity, then the condition becomes $1 < \alpha p d_m^{-1} \le e$. Such a case has been studied in [32].

3.2. Well posedness and comparison principle. In this part, we establish the well posedness and comparison principle for the model system (2.7) in the space of continuous functions and the space of monotone functions, respectively. The properties of solutions in the two spaces will be used to calculate invasion speeds and to establish the existence of traveling waves.

Let Ω be the interval $[-\tau, 0] \subset \mathbb{R}$. Define $X = C(\Omega, \mathbb{R}^2)$ and $\mathcal{C} = C(\mathbb{R}, X)$. We equip X with the maximum norm $|\cdot|_X$ and the partial ordering induced by the positive cone $X^+ := C(\Omega, \mathbb{R}_+^2)$. For any $u, v \in X$, we write $u \ge v$ if $u - v \in X^+$, $u > v$ if $u \ge v$ but $u \ne v$, and $u \gg v$ if $u - v \in IntX^+$. Let $\mathcal{M}$ be the space consisting of all monotone functions from $\mathbb{R}$ to X. For any $u, v \in \mathcal{C}(\mathcal{M})$, we write $u \ge v$ if $u(x) \ge v(x)$ for $x \in \mathbb{R}$ and $u > v$ if $u \ge v$ but $u \ne v$. We equip both $\mathcal{C}$ and $\mathcal{M}$ with the compact open topology, which can be induced by the following norm $\|u\| = \sum_{k\in\mathbb{N}} 2^{-k} \max_{|x|\le k} |u(x)|_X$. Given $y \in \mathbb{R}$, define the translation operator T_y by $T_y[u](x) = u(x - y)$. For each $r \in X$ with $r \gg 0$, define $X_r = \{u \in X : 0 \le u \le r\}$,

$$\mathcal{C}_r = \{u \in \mathcal{C} : u(x) \in X_r, \forall x\}, \quad \mathcal{M}_r = \{u \in \mathcal{M} : u(x) \in X_r, \forall x\}. \tag{3.4}$$

For $\phi \in \mathcal{C}_r$ or $\mathcal{M}_r$, we write $\phi(\theta, x)$ instead of $\phi(x)(\theta)$, where $\theta \in \Omega$ and $x \in \mathbb{R}$.

We first show the existence and uniqueness of solutions, and positive invariance of $\mathcal{C}_r$ with $r = E^*$ relative to (2.7).

Lemma 3.2. *For initial value $\phi := (\phi_1, \phi_2) \in \mathcal{C}_{E^*}$, system* (2.7) *admits a unique solution $(u(t, x; \phi), w(t, x; \phi))$ which exists globally in time $t \ge -\tau$ such that $(u_0, w_0) = \phi$ and $(u_t, w_t) \in \mathcal{C}_{E^*}$ for $t \ge 0$, where u_t, w_t are defined by*

$$u_t(\theta, x; \phi) = u(t + \theta, x; \phi), \quad w_t(\theta, x; \phi) = w(t + \theta, x; \phi). \tag{3.5}$$

Proof. For $t \in (0, \tau]$, we solve $u(t + \theta, x; \phi)$ from (2.7a) as follows:

$$\begin{cases} u(t+\theta, x; \phi) = e^{-d_m(t+\theta)}\phi_1(0, x) + \int_0^{t+\theta} e^{-d_m(t+\theta-s)} H_1(s, x; \phi) ds & \text{if } t+\theta > 0, \\ u(t+\theta, x; \phi) = \phi_1(t+\theta, x) & \text{if } t+\theta \le 0, \end{cases} \tag{3.6}$$

where $H_1(s, x; \phi) := \alpha \int_{\mathbb{R}} k(x-y)[\gamma b(\phi_1(s-\tau, y)) + \beta\phi_2(s-\tau, y)\phi_1(s-\tau, y)]dy$. By (3.6) and (2.7b), we obtain

$$\begin{cases} w(t+\theta, x; \phi) = T(t+\theta)[\phi_2(0, \cdot)](x) + \int_0^{t+\theta} T(t+\theta-s)[H_2(s, \cdot; \phi)](x) ds \\ \qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad \text{if } \ t+\theta > 0, \\ w(t+\theta, x; \phi) = \phi_2(t+\theta, x) \qquad\qquad\qquad\qquad\qquad\quad\; \text{if } \ t+\theta \le 0, \end{cases} \tag{3.7}$$

where $T(t)$ is the solution map of the linear equation $\partial_t w = \partial_{xx} w - v_s \partial_x w - d_s w$ and $H_2(s, x; \phi) = (1-\gamma) b(u(s, x; \phi))$. Since $\phi \in \mathcal{C}_{E^*}$ and $b(u)$ is nondecreasing, we see that $0 \le F_1(s, x; \phi) \le d_m u^*$ and $F_2(s, x; \phi) \le w^*$ for $s \in [0, \tau]$; and $E^0 \le (u(t, x; \phi), w(t, x; \phi)) \le E^*$ for $t \in (0, \tau]$ and $x \in \mathbb{R}$. By the expressions (3.6) and (3.7), $(u_t, w_t) \in \mathcal{C}_{E^*}$ for $t \in (0, \tau]$. For $t \in (\tau, 2\tau]$, we employ the same arguments to obtain the solution with the same property shown above. By induction, system (2.7) admits a unique solution which exists globally in time and is positively invariant. ▯

By employing arguments similar to those in Lemma 3.2, we can obtain the well posedness on $\mathcal{M}_{E^*}$.

Lemma 3.3. *For any initial value $\phi \in \mathcal{M}_{E^*}$, system* (2.7) *admits a unique solution $(u(t, x; \phi), w(t, x; \phi))$ which exists globally in time $t \ge -\tau$ such that $(u_0, w_0) = \phi$ and $(u_t, w_t) \in \mathcal{M}_{E^*}$ for $t \ge 0$, where u_t, w_t are defined as in* (3.5).

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Next we establish the comparison principle for upper and lower solutions of (2.7). For this purpose, we introduce the following definition.

Definition 3.4. *A function* $(\bar{u}, \bar{w}) : [-\tau, \infty) \times \mathbb{R} \to \mathbb{R}^2$ *is said to be an upper solution of* (2.7) *if for* $t \geq 0$, $(u_t, w_t) \in \mathcal{C}_{E^*}(\mathcal{M}_{E^*})$ *and*

(3.8)
$$\begin{cases} \bar{u}(t,x) \geq e^{-d_m t}\bar{u}(0,x) + \alpha \int_0^t \int_{\mathbb{R}} k(x-y) e^{-d_m(t-s)} H(\bar{u}(s-\tau, y), \bar{w}(s-\tau, y)) dyds \\ \bar{w}(t,x) \geq T(t)[\bar{w}(0,\cdot)](x) + (1-\gamma) \int_0^t T(t-s)[b(\bar{u}(s,\cdot))](x) ds, \end{cases}$$

where $T(t)$ *is the solution map of the linear equation* $\partial_t w = D_s \partial_{xx} w - v_s \partial_x w - d_s w$ *and* $F : \mathbb{R}^2 \to \mathbb{R}$ *is defined by* $H(u, w) = \gamma b(u) + \beta w u$. *A lower solution can be defined similarly by reversing the inequalities in* (3.8).

Lemma 3.5. *If* $(\bar{u}, \bar{u})$ *and* $(\underline{u}, \underline{w})$ *are a pair of upper and lower solutions of* (2.7) *with* $(\bar{u}_0, \bar{u}_0) \geq (\underline{u}_0, \underline{w}_0)$, *then* $(\bar{u}_t, \bar{u}_t) \geq (\underline{u}_t, \underline{w}_t)$ *for* $t > 0$.

Proof. We only prove the conclusion for $t \in (0, \tau]$ and the rest can be proved similarly by considering the intervals $((n-1)\tau, n\tau]$ for $n \geq 2$. Indeed, from $(\bar{u}_0, \bar{u}_0) \geq (\underline{u}_0, \underline{w}_0)$ we see that

$$\bar{u}(\theta, x) \geq \underline{u}(\theta, x), \quad \bar{w}(\theta, x) \geq \underline{w}(\theta, x) \quad \text{ for } \theta \in \Omega \text{ and } x \in \mathbb{R}.$$

It follows that for $t + \theta \leq 0$,

$$\bar{u}_t(\theta, x) - \underline{u}_t(\theta, x) = \bar{u}(t+\theta, x) - \underline{u}(t+\theta, x) \geq 0 \quad \text{ for } x \in \mathbb{R}.$$

Since $H(u, w)$ is nondecreasing in u and w, for $t + \theta \leq 0$,

$$\begin{aligned} \bar{u}_t(\theta, x) - \underline{u}_t(\theta, x) &= \bar{u}(t+\theta, x) - \underline{u}(t+\theta, x) \\ &\geq e^{-d_m t}[\bar{u}(0,x) - \underline{u}(0,x)] + \alpha \int_0^t \int_{\mathbb{R}} k(x-y) e^{-d_m(t-s)} \\ &\quad \times [H(\bar{u}(s-\tau, y), \bar{w}(s-\tau, y)) - H(\underline{u}(s-\tau, y), \underline{w}(s-\tau, y))] dyds \\ &\geq 0. \end{aligned}$$

Hence, $\bar{u}_t \geq \underline{u}_t$ for $t \in (0, \tau]$. Similarly, $\bar{w}_t \geq \underline{w}_t$ for $t \in (0, \tau]$. ☐

With Lemma 3.5 and Proposition 3.1, one can see that E^0 attracts all solutions of (2.7) with initial values in $\mathcal{C}_{E^*}$ or $\mathcal{M}_{E^*}$ if $b(u) < f(u)$ for $u > 0$.

4. Invasion speed.

To show the existence of invasion speeds for the model system (2.7), we first present a dynamical system result, which is a combination of some theories developed recently in [11, 12]. Then we apply the result to (2.7) and weaken the general conditions on initial functions imposed in [11, 12] when applying it to the specific model. Finally, under certain conditions we estimate the established invasion speeds that in general are nonlinearly determinate.

4.1. Invasion speeds for monotone semiflows.

We begin with the definition of the continuous-time semiflow.

Definition 4.1. *A family of mappings* $\{Q_t\}_{t \geq 0}$ *is said to be a semiflow on* $\mathcal{C}_{E^*}$ *if the following three properties hold:* (i) $Q_0 = I$, *where* I *is the identity mapping;* (ii) $Q_t Q_s = Q_{t+s}$ *for* $t, s \geq 0$; (iii) $Q_t[u]$ *is continuous in* $(t, u) \in [0, \infty) \times \mathcal{C}_r$.

For each $y \in \mathbb{R}$, define the translation operator T_y by $T_y[u](x) = u(x-y)$. Let $Q : \mathcal{C}_{E^*} \to \mathcal{C}_{E^*}$ be a given map. The following assumptions on map Q will be referred to:

(A1) (translation invariance) $T_y Q = Q T_y$ for $y \in \mathbb{R}$;

(A2) (continuity) $Q : \mathcal{C}_{E^*} \to \mathcal{C}_{E^*}$ is continuous with respect to the compact open topology;

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(A3) (compactness) the set $\{Q[u](x) : u \in \mathcal{C}_{E^*}, x \in \mathbb{R}\} \subset X$ is precompact;

(A4) (monotonicity) $Q : \mathcal{C}_{E^*} \to \mathcal{C}_{E^*}$ is monotone (order preserving) in the sense that $Q[u] \geq Q[v]$ whenever $u \geq v$ in $\mathcal{C}_{E^*}$;

(A5) (monostability) $Q : X_{E^*} \to X_{E^*}$ admits exactly two fixed points 0 and E^*, and $\lim_{n\to\infty} Q^n[\varpi] = r$ for $\varpi \in X_{E^*}$ with $\varpi \gg 0$.

The following lemma is a combination of [11, Theorems 2.11, 2.15, and 2.17] and [12, Theorems 3.1–3.4]. In both papers, the authors first define the numbers $c^*_\pm$ using the time-one map Q_1, and then show they are the spreading speeds and the minimal wave speeds for both continuous and discrete-time semiflows. The reflection invariance was imposed in [11] so that $c^*_- = c^*_+$, and it was removed later in [12] under a more general setting. A stronger version of the monostability assumption used in [11] was weakened to the standing one in [12].

Lemma 4.2 (see [11, 12]). *Assume that* $\{Q_t\}_{t\geq 0}$ *is a semiflow on* $\mathcal{C}_{E^*}$ *and* $Q = Q_1$ *satisfies all the hypotheses* (A1)–(A5). *Then the semiflow admits the rightward/leftward invasion speeds* $c^*_\pm$ *in the following sense:*

(i) *For* $c > c^*_+$ *and* $c' > c^*_-$, *if* $v \in \mathcal{C}_{E^*}$ *with* $0 \leq v \leq \varpi$ *for some* $\varpi \in X$ *and* $\varpi \ll E^*$, *and* $v(x) = 0$ *for* x *outside a bounded interval, then*

$$\lim_{t\to\infty, x\geq tc} Q_t[v](x) = 0 \quad \textit{and} \quad \lim_{t\to\infty, x\leq -tc'} Q_t[v](x) = 0 \quad \textit{in } X;$$

(ii) *assume that* $c^*_+ + c^*_- > 0$. *For* $c < c^*_+, c' < c^*_-$ *with* $c + c' > 0$, *and* $\sigma \in X$ *with* $\sigma \gg 0$, *there is a positive number* $l_\sigma \in \mathbb{R}$ *such that if* $v \in \mathcal{C}_{E^*}$ *and* $v(x) \geq \sigma$ *for* x *on an interval of length* $2l_\sigma$, *then*

$$\lim_{t\to\infty, -tc'\leq x\leq tc} Q_t[v](x) = E^* \quad \textit{in } X.$$

In addition, if Q_1 *is subhomogeneous, then* l_σ *can be chosen to be independent of* $\sigma \gg 0$.

In the following section, we see that the conditions in Lemma 4.2(ii) can be weakened since the solutions have certain lower bounds.

4.2. Existence of invasion speeds.

Using Lemma 4.2 we obtain the invasion speeds and weaken the conditions in Lemma 4.2(ii) by finding a lower estimate of solutions.

Let $(u(t, x; \phi), w(t, x; \phi))$ be the solution of (2.7) with initial value $\phi \in \mathcal{C}_{E^*}$. Define $Q_t : \mathcal{C}_{E^*} \to \mathcal{C}_{E^*}$ by

$$Q_t[\phi](x) = (u_t(x; \phi), w_t(x; \phi)). \tag{4.1}$$

Lemma 4.3. $\{Q_t\}_{t\geq 0}$ *is a solution semiflow on* $\mathcal{C}_{E^*}$ *with the time-one map* Q_1 *satisfying* (A1)–(A5) *with* $Q = Q_1$ *in section* 4.1.

Proof. According to Definition 4.1, we need to show that $Q_t[\phi]$ is jointly continuous in (t, ϕ). Indeed, for $t, t_n \in [0, \tau)$ and $\phi, \phi_n \in \mathcal{C}_{E^*}$ with $t_n \to t$ and $\phi_n \to \phi$, one can see from the expressions (3.6) and (3.7) that when $t_n + \theta \leq 0$,

$$|Q_{t_n}[\phi_n](\theta, x) - Q_{t_n}[\phi](\theta, x)| \leq \max_{\theta\in\Omega} |\phi_n(\theta, x) - \phi(\theta, x)|, \tag{4.2}$$

and when $t_n + \theta > 0$,

$$\begin{aligned} &|Q_{t_n}[\phi_n](\theta, x) - Q_{t_n}[\phi](\theta, x)| \\ &\leq L_1 \max_{\theta\in\Omega} |\phi_n(\theta, x) - \phi(\theta, x)| + \int_{\mathbb{R}} P(x - y) \left(\max_{\theta\in\Omega} |\phi_n(\theta, y) - \phi(\theta, y)| \right) dy, \end{aligned} \tag{4.3}$$

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where $L_1 > 0$ and P is a 2×2 nonnegative matrix with entries $p_{ij} \in L^1(\mathbb{R})$. Since $\phi_n \to \phi$, for $\epsilon > 0$ and $[a,b] \subset \mathbb{R}$ we can find $N_1, N_2 > 0$ such that

$$\int_{\mathbb{R}\setminus[-N_1,N_1]} P(y)E^* dy < \epsilon/4 \tag{4.4}$$

and for $n \geq N_2$,

$$L_1 \max_{\theta\in\Omega, x\in[a,b]} |\phi_n(\theta,x) - \phi(\theta,x)| < \epsilon/4, \qquad \max_{\theta\in\Omega, x\in[a-N_1,b-N_1]} |\phi_n(\theta,x) - \phi(\theta,x)| < \epsilon/4. \tag{4.5}$$

Combining (4.2)–(4.5), we see that for $\epsilon > 0$ and interval $[a,b] \subset \mathbb{R}$, there exists $N_2 > 0$ such that

$$\max_{\theta\in\Omega, x\in[a,b]} |Q_{t_n}[\phi_n](\theta,x) - Q_{t_n}[\phi](\theta,x)| < \epsilon \quad \text{ for } n \geq N_2$$

and $\|Q_{t_n}[\phi_n] - Q_{t_n}[\phi]\| \to 0$. By similar arguments, we can prove $\|Q_{t_n}[\phi] - Q_t[\phi]\| \to 0$. It follows from the triangle inequality that

$$\|Q_{t_n}[\phi_n] - Q_t[\phi]\| \leq \|Q_{t_n}[\phi_n] - Q_{t_n}[\phi]\| + \|Q_{t_n}[\phi] - Q_t[\phi]\| \to 0.$$

Next we prove that the time-one map Q_1 satisfies (A1)–(A5) with $Q = Q_1$. Clearly, (A2) and (A4) are satisfied. It suffices to show that (A1), (A3), and (A5) are satisfied. Indeed, note that for $y \in \mathbb{R}$, $(u(t, x-y; \phi), w(t, x-y; \phi))$ is a solution with initial value $\psi := T_y[\phi] = \phi(\cdot - y)$. It follows from the uniqueness of solutions that

$$(u(t, x-y; \phi), w(t, x-y; \phi)) = (u(t,x;\psi), w(t,x;\psi)) \quad \text{ for } t \geq 0$$

and the map Q satisfies (A1). Without loss of generality, we may assume that $\tau < 1/2$. Then we have $1 + \theta > 1/2$ for $\theta \in [-\tau, 0]$. Hence,

$$\partial_\theta Q_1[\phi](\theta,x) = (\partial_t u(1+\theta, x; \phi), \partial_t w(1+\theta, x; \phi))$$

is uniformly bounded in $x \in \mathbb{R}$, $\theta \in [-\tau, 0]$, and $\phi \in \mathcal{C}_{E^*}$. It follows that the set $\{Q[\mathcal{C}_{E^*}](x) : x \in \mathbb{R}\} \subset X_{E^*}$ is precompact and (A3) holds. Note that the restriction of $\{Q_t\}_{t\geq 0}$ on X_{E^*} is the solution semiflow of the kinetic system (3.1), which is a cooperative and irreducible delayed differential system. By [25, Corollary 5.3.5], for any $\phi \in X_{E^*}$ with $\phi \gg 0$ the solution converges to E^* and (A5) holds. ☐

From Lemmas 4.3 and 4.2, we see that for $\beta \geq 0$, system (2.7) admits the leftward and rightward invasion speeds in the sense of Lemma 4.2. For the sake of convenience, we use $c^*_\pm(\beta)$ to denote the invasion speeds for (2.7) since we will use the dependence of invasion speeds on parameter $\beta \geq 0$. When $\beta = 0$, the model system (2.7) becomes the following uncoupled system:

$$\begin{cases} \frac{\partial u}{\partial t} = -d_m u + \alpha\gamma \int_{\mathbb{R}} k(x-y) b(u(t-\tau, y)) dy, \\ \frac{\partial w}{\partial t} = D_s w_{xx} - v_s w_x + (1-\gamma) b(u) - d_s w, \end{cases} \tag{4.6}$$

which provides a lower bound for the dynamics of system (2.7) due to the monotonicity. Clearly, $c^*_\pm(\beta)$ is nonincreasing in $\beta \geq 0$ according to Lemma 3.5 and in particular, $c^*_\pm(\beta) \geq c^*_\pm(0)$.

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Next we establish a lower bound for the dynamics of uncoupled system (4.6) and weaken the conditions in Lemma 4.2(ii) when applying it to (2.7).

LEMMA 4.4. *The uncoupled system* (4.6) *has the following properties:*

(i) $c^*_+(0) + c^*_-(0) > 0$*;*

(ii) *for any* $\phi := (\phi_1, \phi_2) \in \mathcal{C}_{E^*}$ *with* $\phi_1 \not\equiv 0$*, there is a* $\rho > 0$ *such that for any finite number* $K > 0$ *there exist* $t_0 > 0$ *and an interval* $I \subset \mathbb{R}$ *of length* K *such that* $\min_{\theta\in[-1,0],x\in I} Q_{t_0}[\phi](\theta, x) > \rho$.

Proof. By assumption (H1), we can find a C^1 function b_1 with

$$b_1(u) \le b(u), \quad b_1'(0) > f'(0), \quad \text{and} \quad b_1(u) \le b_1'(0)u. \tag{4.7}$$

To prove the conclusions, we need the properties of the following auxiliary equation

$$\partial_t v = -d_m v + \alpha\gamma \int_{\mathbb{R}} k(x - y)b_1(v(t - \tau, y))dy, \tag{4.8}$$

which, as we have already shown, admits the leftward/rightward spreading speeds $\hat{c}_\pm$ in the sense of Lemma 4.2.

To prove (i), we characterize $\hat{c}_\pm$ using the linearized equation under the conditions $b_1'(0) > f'(0)$ and $b_1(u) \le b_1'(0)u$. Indeed, following the approach in [11, section 3] we can show that $\hat{c}_\pm = \min_{\mu>0} \frac{\lambda_1(\pm\mu)}{\mu}$, where $\lambda_1(\mu)$ is the principle eigenvalue of

$$\lambda = -d_m + \alpha\gamma b_1'(0)e^{-\lambda\tau} \int_{\mathbb{R}} e^{\mu y}k(y)dy.$$

Here we omit the details since they are essentially similar to the proofs used in [12, section 7.1]. Suppose the minimum values of $\frac{\lambda_1(\pm\mu)}{\mu}$ are attained at $\mu = \mu_1$ and $\mu = \mu_2$, respectively. Since $\lambda_1(\mu)$ is convex in $\mu \in \mathbb{R}$, we see that

$$\begin{aligned}\hat{c}_- + \hat{c}_+ &= \frac{\lambda_1(-\mu_1)}{\mu_1} + \frac{\lambda_1(\mu_2)}{\mu_2} = \frac{\mu_1 + \mu_2}{\mu_1\mu_2}\left[\frac{\mu_2}{\mu_1 + \mu_2}\lambda_1(-\mu_1) + \frac{\mu_1}{\mu_1 + \mu_2}\lambda_1(\mu_2)\right] \\ &\ge \frac{\mu_1 + \mu_2}{\mu_1\mu_2}\lambda_1(0).\end{aligned}$$

Note that $\lambda_1(0) > 0$ since $b_1'(0) > f'(0)$. It follows that $c^*_+(0) + c^*_-(0) \ge \hat{c}_- + \hat{c}_+ > 0$.

To prove (ii), we first study the dynamics of (4.8) since its solution provides a lower estimate for (2.7). Denote the smallest positive solution of the equation $\alpha\gamma b_1(v) = d_m$ by v^*. Choose $\epsilon_0 > 0$ such that $\epsilon_0\phi_1 \le v^*$ for any $\phi = (\phi_1, \phi_2) \in \mathcal{C}_{E^*}$. Then for the solution $v(t, x; \epsilon_0\phi_1)$ of (4.8), we have the following result.

CLAIM. *If* $\phi_1 \not\equiv 0$*, then* $v(t, x; \epsilon_0\phi_1) > 0$ *for* $t \ge \tau$ *and* $x \in \mathbb{R}$.

Since $\phi_1 \not\equiv 0$, there exist a number $\delta_0 > 0$ and two intervals $[l_1, r_1] \subset [-\tau, 0]$ and $[l_2, r_2] \subset \mathbb{R}$ such that

$$\phi_1(\theta, x) \ge \delta_0 \quad \text{for } \theta \in [l_1, r_1] \text{ and } x \in [l_2, r_2]. \tag{4.9}$$

Note that for $t \in (0, \tau]$,

$$v(t, x; \epsilon_0\phi_1) \ge \alpha\gamma \int_0^t \int_{\mathbb{R}} e^{-d_m(t-s)}k(x - y)b(\phi_1(s - \tau, y))dyds.$$

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By (4.9) and monotonicity of b_1, we have for $t \in [\tau + r_1, \tau]$ and $x \in \mathbb{R}$,

$$\begin{aligned} v(t, x; \epsilon_0\phi_1) &\geq \alpha\gamma \int_{\tau+l_1}^{\tau+r_1} \int_{l_2}^{r_2} e^{-d_m(t-s)} k(x-y) b(\phi_1(s-\tau, y)) dy ds \\ &\geq \alpha\gamma \int_{\tau+l_1}^{\tau+r_1} \int_{l_2}^{r_2} e^{-d_m(t-s)} k(x-y) b(\delta_0) dy ds \ > 0. \end{aligned}$$

Hence, we obtain $v(t, x; \epsilon_0\phi_1) \geq e^{-d_m(t-\tau)} v(\tau, x; \epsilon_0\phi_1) > 0$ for $t > \tau$ and $x \in \mathbb{R}$.

Since (4.8) admits the invasion speeds in the sense of Lemma 4.2 and b_1 is subhomogenous, in Lemma 4.2(ii) we can choose the number l_σ used in Lemma 4.2(ii) to be the number l, so that $l_\sigma = l$ is independent of σ. By the claim, we can define a positive number $\sigma := \min_{\theta\in\Omega, x\in[-l,l]} v(1+\theta, x; \epsilon_0\phi_1)$. Let $\hat{Q}_t$ be the time-t solution map of (4.8). Consequently, for $c_1 < \hat{c}_+, c_2 < \hat{c}_-$ with $c_1 + c_2 > 0$, and nonzero function ϕ_1, we have $\liminf_{t\to\infty, -tc_2 \leq x \leq tc_1} \hat{Q}_t[\hat{Q}_1[\epsilon_0\phi_1]] = v^*$, which is equivalent to $\liminf_{t\to\infty, -(t-1)c_2 \leq x \leq (t-1)c_1} \hat{Q}_t[\epsilon_0\phi_1] = v^*$. For $K > 0$ there exists $t_0 > 0$ such that $(c_1 + c_2)(t_0 - 1) \geq K$ and

$$\min_{x\in I} u(t, x; \phi) \geq \min_{x\in I} \hat{Q}_t[\epsilon_0\phi_1] \geq v^*/2 := \rho \quad \text{for } I \subset [-(t-1)c_2, (t-1)c_1] \text{ and } t \geq t_0.$$

$w(t, x; \phi)$ can be expressed by $u(t, x; \phi)$ and has the same property as $u(t, x, ; \phi)$. ∎

Now we prove existence of invasion speed in the practical sense for system (2.7).

THEOREM 4.5. *System* (2.7) *admits the leftward and rightward invasion speeds, denoted by* c_-^* *and* c_+^**, respectively, satisfying* $c_-^* + c_+^* > 0$*, in the following sense:*

(i) *For* $c > c_+^*$ *and* $c' > c_-^*$*, if the initial function* $\phi \in \mathcal{C}_{E^*}$ *has compact support and* $\phi(x) \ll \varpi$ *for* $x \in \mathbb{R}$ *and some* $\varpi \in X_{E^*}$ *with* $\varpi \ll E^*$*, then the solution* (u, w) *has the property*

$$\lim_{t\to\infty, x\geq tc \, or \, x\leq -tc'} (u(t, x; \phi), w(t, x; \phi)) = E^0;$$

(ii) *for* $c < c_+^*$ *and* $c' < c_-^*$ *with* $c + c' > 0$*, if the initial function* $\phi := (\phi_1, \phi_2) \in C(\mathbb{R}, X_{E^*})$ *with* $\phi_1 \not\equiv 0$*, then the solution* (u, w) *has the property*

$$\lim_{t\to\infty, \ -tc' \leq x \leq tc} (u(t, x; \phi), w(t, x; \phi)) = E^*.$$

Proof. According to Lemma 4.3, we see that system (2.7) generates a solution semiflow on $\mathcal{C}_{E^*}$ satisfying all the conditions in Lemma 4.2. Thus, it admits the leftward and rightward invasion speeds $c_\pm^*$ in the weak sense as in Lemma 4.2. By Lemma 4.4 we can drop the condition $c_-^* + c_+^* > 0$ and weaken the condition on the initial function to be $\phi_1 \not\equiv 0$ in Lemma 4.2(ii) when applying Lemma 4.2 to (2.7). ∎

4.3. Continuity of invasion speeds at $\beta = 0$.

It is not clear whether the established invasion speeds $c_\pm^*(\beta)$ are linearly determinate. Below we give an estimation of $c_\pm^*(\beta)$ when β is close to zero, and construct an upper traveling wave solution, which provides an upper bound for the invasion speeds $c_\pm^*(\beta)$ with β close to zero. Combining the upper bound with the fact that $c_\pm^*(\beta) \geq c_\pm^*(0)$, we obtain the continuity of $c_\pm^*(\beta)$ at $\beta = 0$ and conclude that $c_\pm^*(0)$ are linearly determinate when $b(u) \leq b'(0)u$ for $u \in [0, u^*]$.

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We only prove the limit $\lim_{\beta\to 0} c_+^*(\beta) = c_+^*(0)$ because the proof for $c_-^*(\beta)$ is similar. By the proof of Lemma 4.4, we see that under the condition $b(u) \le b'(0)u$, the speed $c_+^*(0)$ can be characterized by

$$c_+^*(0) = \min_{\mu>0} \frac{\lambda(\mu)}{\mu} = \frac{\lambda(\mu_1)}{\mu_1} \quad \text{for some } \mu_1 > 0, \tag{4.10}$$

where $\lambda(\mu)$ is the principle eigenvalue of

$$\lambda = -d_m + \alpha\gamma b'(0) e^{-\lambda\tau} \int_{\mathbb{R}} e^{\mu y} k(y)dy, \tag{4.11}$$

where k is defined in (2.4) and depends on parameters D_1 and v_1.

The following result gives another characterization of $c_+^*(0)$.

LEMMA 4.6. *The invasion speed* $c_+^*(0)$ *in* (4.10) *has the following properties:*

(i) $(\mu_1, c_+^*(0))$ *is the unique solution to the* (μ, c)*-system*

$$\mu > 0, \quad F(\mu, c) = 0, \quad \partial_\mu F(\mu, c) = 0, \tag{4.12}$$

where

$$F(\mu, c) := c\mu + d_m - \alpha\gamma b'(0) \int_{\mathbb{R}} k(y) e^{\mu(y-\tau c)} dy; \tag{4.13}$$

(ii) *for any* $c > c_+^*(0)$*, there exists* $\mu > 0$ *such that* $F(\mu, c) > 0$*;*

(iii) $c_+^*(0)$ *is increasing in* v_1 *and* $c_+^*(0) = 0$ *when*

$$v_1 = -2\sqrt{\frac{D_1}{\tau_2} \ln \frac{\alpha\gamma b'(0)}{d_m}}. \tag{4.14}$$

Proof.

(i) Since $F(\mu, c)$ is concave down in μ and increasing in c, we see that system (4.12) admits a unique solution, denoted by $(\bar{\mu}, \bar{c})$, and $\bar{c}$ is the smallest value of c such that $F(\mu, c)$ has a positive solution $\bar{\mu}$. Since $\partial_c F(\mu, c) > 0$, for each μ there is a unique $c = c(\mu)$ such that $F(\mu, c(\mu)) = 0$ and, hence, $\bar{c} = \min_{\mu>0} c(\mu)$. On the other hand, $\lambda(\mu)$ is the unique real solution to the μ-parameterized equation (4.11), which implies that $F(\mu, \frac{\lambda(\mu)}{\mu}) = 0$. Therefore, $c(\mu) = \frac{\lambda(\mu)}{\mu}$ and $(\bar{\mu}, \bar{c}) = (\mu_1, c_+^*(0))$.

(ii) Property (ii) follows directly from the arguments used in (i).

(iii) To study the effect of v_1 on $c_+^*(0)$, we write $F(\mu, c, v_1)$ instead of $F(\mu, c)$. Using the expression of k in (2.4), we have

$$\int_{\mathbb{R}} k(y) e^{\mu y} dy = e^{D_1\tau_2\mu^2 + v_1\tau_2\mu}. \tag{4.15}$$

Hence, $F(\mu, c, v_1)$ is decreasing in v_1 and increasing in c. This implies that $c_+^*(0)$ is increasing in v_1. Consequently, $c_+^*(0) = 0$ if and only if

$$F(\mu, 0, v_1) = 0 \quad \text{and} \quad \partial_\mu F(\mu, 0, v_1) = 0,$$

which is equivalent to

$$D_1\tau_2\mu^2 + v_1\tau_2\mu = \ln \frac{d_m}{\alpha\gamma b'(0)} \quad \text{and} \quad 2D_1\mu + v_1 = 0$$

by using the expression (4.15). The conclusion follows. ☐

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Remark 4.1. In the limiting case where both $\beta = 0$ and $\tau_2 = 0$, that is, the species does not move in all stages, spreading cannot happen. We conjecture the limit $\lim_{\tau_2 \to 0} c_+^*(0) = 0$, but unfortunately, we do not know how to prove it..

With the properties of $c_+^*(0)$ in Lemma 4.6, we construct an upper traveling wave solution which provides an upper bound for $c_+^*(\beta)$ when β is small.

LEMMA 4.7. *For $\epsilon > 0$, define $c^\epsilon := c_+^*(0) + \epsilon$. Assume $b(u) \le b'(0)u$ for $u \in [0, u^*]$. Then there exist positive numbers $\delta, \eta_1, \eta_2, \kappa$ such that $(\bar{u}, \bar{w})$ defined by*

$$\bar{u}(t,x) := \min\{\kappa e^{-\eta_1(x-c^\epsilon t)}, u^*\} \quad \text{and} \quad \bar{w}(t,x) := \min\{e^{-\eta_2(x-c^\epsilon t)}, w^*\}$$

is an upper solution when $\beta < \delta$ in the sense of Definition 3.4.

Proof. By Lemma 4.6, there exists $\eta_1 > 0$ such that $F(\eta_1, c^\epsilon) > 0$. Define

$$G(\eta, c) = c\eta - D_s\eta^2 + v_s\eta + d_s.$$

Since $G(0, c^\epsilon) = d_s$, there exists $\eta_2 \in (0, \eta_1)$ such that $G(\eta_2, c^\epsilon) > d_s/2$. We can choose small $\kappa > 0$ and small $\delta > 0$ such that $\kappa(1-\gamma)b'(0)(w^*)^{\frac{\eta_1-\eta_2}{\eta_2}} < d_s/2$ and $\alpha\gamma\delta u^* w^* < \kappa F(\eta_1, c^\epsilon)$. Let ξ_+ be the solution of the equation $e^{-\eta_2\xi} = w^*$. Then for any $x - c^\epsilon t \le \xi_+$, we have $\bar{u}(t,x) \le u^*$ and $\bar{w}(t,x) = w^*$; and for $x - c^\epsilon t > \xi_+$, we have $\bar{u}(t,x) := \kappa e^{-\eta_1(x-c^\epsilon t)}$ as well as $\bar{w}(t,x) := e^{-\eta_2(x-c^\epsilon t)}$.

Next we show that $(\bar{u}, \bar{w})$ is an upper solution of (2.7). Indeed, for $x - c^\epsilon t \ne \xi_+$ and $\beta \le \delta$,

$$\begin{aligned} & e^{\eta_1(x-c^\epsilon t)} \left\{ \bar{u}_t + d_m\bar{u} - \alpha\gamma \int_{\mathbb{R}} \left[b(\bar{u}(t-\tau, y)) + \beta\bar{w}(t-\tau, y)\bar{u}(t-\tau, y) \right] k(x-y)dy \right\} \\ & \quad \ge \kappa F(\eta_1, c^\epsilon) - \alpha\gamma\beta u^* w^* > 0. \end{aligned}$$

For $x - c^\epsilon t < \xi_+$,

$$\bar{w}_t - D_s\bar{w}_{xx} + v_s\bar{w}_x - (1-\gamma)b(\bar{u}) + d_s\bar{w} \ge d_s w^* - (1-\gamma)b(u^*) = 0$$

and for $x - c^\epsilon t > \xi_+$,

$$\begin{aligned} & e^{\eta_2(x-c^\epsilon t)}[\bar{w}_t - D_s\bar{w}_{xx} + v_s\bar{w}_x - (1-\gamma)b(\bar{u}) + d_s\bar{w}] \\ & \quad = G(\eta_2, c^\epsilon) - (1-\gamma)b(\bar{u})e^{\eta_2(x-c^\epsilon t)} \ge d_s/2 - (1-\gamma)b'(0)\bar{u}(t,x)e^{\eta_2(x-c^\epsilon t)} \\ & \quad = d_s/2 - \kappa(1-\gamma)b'(0)e^{(\eta_2-\eta_1)(x-c^\epsilon t)} \ge d_s/2 - \kappa(1-\gamma)b'(0)e^{(\eta_2-\eta_1)\xi_+} \\ & \quad = d_s/2 - \kappa(1-\gamma)b'(0)(w^*)^{\frac{\eta_1-\eta_2}{\eta_2}} > 0. \end{aligned}$$

By the same arguments as those in [29, 30], we can show that $(\bar{u}, \bar{w})$ is an upper solution in the sense of Definition 3.4. □

THEOREM 4.8. *Regard $c_\pm^*(\beta)$ as a function of β. Then the following results hold:*

(1) *Both $c_\pm^*(\beta)$ are nondecreasing in $\beta \ge 0$;*

(2) *if $b(u) \le b'(0)u$ for $u \in [0, u^*]$, then*

$$c_\pm^*(\beta) \ge \min_{\mu>0} \frac{\lambda(\pm\mu)}{\mu} \quad \text{and} \quad \lim_{\beta\to 0} c_\pm^*(\beta) = \min_{\mu>0} \frac{\lambda(\pm\mu)}{\mu},$$

where $\lambda(\mu)$ is the principle eigenvalue of (4.11).

Proof. By Lemma 4.7, for $\phi \in \mathcal{C}_{E^*}$ with $\phi(x) \le (\bar{u}(0,x), \bar{w}(0,x))$ we have

$$u(t,x;\phi) \le \bar{u}(t,x) \quad \text{and} \quad w(t,x;\phi) \le \bar{w}(t,x).$$

It follows that $c_+^*(\beta) \le c^\epsilon = c_+^*(0) + \epsilon$ whenever $\beta < \delta$. This, together with the lower bound $c_+^*(\beta) \ge c_+^*(0)$, implies that $\lim_{\beta\to 0} c_+^*(\beta) = c_+^*(0)$. □

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5. Traveling waves.

A leftward traveling wave with speed c of system (2.7) is a special solution having the form $w(t,x) = W(x+ct)$ and $u(t,x) = U(x+ct)$. A rightward traveling wave with speed c is defined using $x - ct$.

The main result of this section reveals that the invasion speeds established in section 4 are the minimal wave speeds. To prove it, we recall the definition of a semiflow on the space $\mathcal{M}_{E^*}$ of monotone functions from $\mathbb{R}$ to the order interval X_{E^*}.

Definition 5.1. *A family of mappings* $\{Q_t\}_{t\ge 0}$ *is said to be a semiflow on* $\mathcal{M}_{E^*}$ *if the following three properties hold:* (i) $Q_0 = I$, *where* I *is the identity mapping;* (ii) $Q_t Q_s = Q_{t+s}$ *for* $t, s \ge 0$; (iii) *If* $u_n \to u$ *in* $\mathcal{M}_{E^*}$ *and* $t_n \to t$, *then both* $Q_{t_n}[u](x) \to Q_t[u](x)$ *and* $Q_t[u_n](x) \to Q_t[u](x)$ *in* X *almost everywhere.*

The abstract results on traveling waves in [11, 12] require that the semiflow has a certain compactness. It is not possessed by the model (2.7) due to zero diffusion in the first component. Instead, we apply another result established recently in [4].

For a given subset $A \subseteq \mathcal{M}$ and number $s \in \mathbb{R}$, we define $A(s) := \{u(s) : u \in A\}$. For a given operator $Q : \mathcal{M}_{E^*} \to \mathcal{M}_{E^*}$, the following assumptions will be referred to:

(B1) (translation invariance) $T_y Q = Q T_y$ for $y \in \mathbb{R}$;

(B2) (continuity) if $u_k \to u$ in $\mathcal{M}$, then $Q[u_k](x) \to Q[u](x)$ almost everywhere in X;

(B3) (weak compactness) there exists $k \in [0,1)$ such that $\alpha(Q[\mathcal{U}](0)) \le k\alpha(\mathcal{U}(0))$ for $\mathcal{U} \subseteq \mathcal{M}_{E^*}$;

(B4) (monotonicity) $Q : \mathcal{M}_{E^*} \to \mathcal{M}_{E^*}$ is monotone (order preserving) in the sense that $Q[u] \ge Q[v]$ whenever $u \ge v$ in $\mathcal{M}_{E^*}$;

(B5) (monostability) Q admits two fixed points 0 and E^* in X^+, and for $\varpi \in X^+$ with $0 \ll \varpi \le E^*$; $\lim_{n\to\infty} Q^n[\varpi] = E^*$.

The following result is the combination of [4, Theorem 4.1 and Remark 3.2].

Lemma 5.2. *Let* $c^*_\pm$ *be the invasion speeds established in Lemma* 4.2 *for the semiflow* $\{Q_t\}_{t\ge 0}$ *on* $\mathcal{C}_{E^*}$. *Assume that* $\{Q_t\}_{t\ge 0}$ *is a semiflow on* $\mathcal{M}_{E^*}$ *and for* $t > 0$, *the map* $Q := Q_t$ *satisfies* (B1)–(B5) *with fixed points of* Q *replaced by equilibria in* (B5). *Then* $c^*_\pm$ *are the minimal wave speeds for rightward/leftward traveling waves.*

Now, we prove that the invasion speeds established in section 4 and the minimal wave speeds are same.

Theorem 5.3. *Let* $c^*_\pm$ *be the invasion speeds of* (2.7) *established in Theorem* 4.5. *Then* c^*_- *is the minimal wave speed of leftward nondecreasing traveling waves connecting* E^0 *to* E^* *and* c^*_+ *is the minimal wave speed of rightward nonincreasing traveling waves connecting* E^* *to* E^0.

Proof. The nonexistence of a leftward (rightward) traveling wave with speed less than $c^*_-(c^*_+)$ follows directly from the comparison principle and the property of invasion speed. For the existence of such traveling waves, it suffices to show that (2.7) generates a solution semiflow on $\mathcal{M}_{E^*}$ in the sense of Definition 5.1 which satisfies all the conditions in Lemma 5.2. Indeed, by Lemma 3.3 and the proof of Lemma 4.3, we see that (2.7) generates a solution semiflow $\{Q_t\}_{t\ge 0}$ on $\mathcal{M}_{E^*}$ in the sense of Definition 5.1. It is easy to see that each time-t map Q_t with $t > 0$ satisfies (B1), (B2), (B4), and (B5) with $Q = Q_t$ and fixed points replaced by equilibria of the semiflow in (B5). Thus, it remains to show that each Q_t satisfies the weak compactness assumption (B3). Recall that $Q_t[\phi](\theta, x) := (u(t+\theta, x; \phi), w(t+\theta, x; \phi))$ for $t \ge 0, \theta \in [-\tau, 0], x \in \mathbb{R}$. Define

$$L_t[\phi](\theta, x) = \begin{cases} \phi(t+\theta, x) - \phi(0, x), & t+\theta < 0, \\ 0, & t+\theta \ge 0, \end{cases}$$

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and

$$S_t[\phi](\theta,x)=\begin{cases}\phi(0,x), & t+\theta<0,\\ Q_t[\phi](\theta,x), & t+\theta\geq 0.\end{cases}$$

Obviously, $Q_t = L_t + S_t$ for $t > 0$. For any bounded set $\mathcal{U}$ in $\mathcal{M}_{E^*}$, the set $S_t[\mathcal{U}](\cdot,0)$ is compact due to the uniform boundedness of the derivatives $(\partial_t u(t,0;\phi),\partial_t w(t,0;\phi))$ for $t>0$ and $\phi\in\mathcal{U}$. In view of the α-contraction property of the solution map of delay differential equations (see, for example, [8, 12]), we have $\alpha(L_t[\mathcal{U}](0))\leq e^{-\gamma t}\alpha(\mathcal{U}(0))$ for some $\gamma>0$. Thus, we obtain

$$\alpha(Q_t[\mathcal{U}](0))\leq \alpha(L_t[\mathcal{U}](0))+\alpha(S_t[\mathcal{U}](0))\leq e^{-\gamma t}\alpha(\mathcal{U}(0)),$$

which means that each time-t map satisfies (B3) with $k=e^{-\gamma t}$. ∎

6. Discussion.

There have been intensive studies about the spread of Asian clam from a biological perspective (see, for instance, [3, 9]). Our study, however, represents the first formulation of a mathematical model in terms of a time-delayed reaction-diffusion-advection system that describes the invasion of Asian clam. Using our novel mathematical model, we have mathematically studied the invasion speed.

We have shown that our system admits the rightward/leftward invasion speeds and the speeds coincide with the minimal wave speeds of traveling waves in both directions. Due to the fact that these invasion speeds may be nonlinearly dependent, there are difficulties in characterizing the invasion speeds by linearization at equilibrium E^0 (see [13] even for scalar equations). Biologically, the contact rate β between the adults and sperms released into the water, can be very small; that is, reproduction occurs mostly by self-fertilization. Mathematically, the invasion speeds continuously depend on β around $\beta=0$, so we can approximate the speeds by the special case $\beta=0$, under the sublinearity condition on the birth function. Hence, for small β, we can discuss the parameter dependence of the invasion speeds.

Most management practices to prevent the spread of invasive species rely on reducing the abundance of invasive species populations. By means of our analytic results in the case of no contact between adult clams and sperms released into the water, in Figure 2, we are able to graph the M-coordinates of positive equilibria (M^*) and rightward invasion speed $c^*_+(0)$, where $\beta=0$, as a function of mortality rate of the adults (d_m) for various times spent by the discharged juveniles in the water, τ_2. Parameter values used in the figure are based on studies that appear in most papers and reports (see, for instance, [31]). We assume that the mortality rates are relatively high [16]; we also assumed some other parameter values such as diffusivity, advection speed, and mortality rates of sperms and the discharged juveniles, which may be difficult to determine under field conditions. For our numerical studies, unless otherwise specified, we usually suppose the spatial scale is measured in kilometers and time is measured in days.

In Figure 2(a), we observe that the longer discharged juveniles spend in the mobile state, the more vulnerable the population is to extinction as we increase the mortality rate of the adult clams. In addition, Figure 2(b) shows that the invasion speed decreases as the death rate of the adult population increases and the longer discharged juveniles spend in the mobile state, the faster the invasion.

Figure 3 depicts a graph of rightward invasion speed $c^*_+(0)$ as a function of advection velocity of the discharged juveniles v_1 in the case of $\beta=0$. We see that c^* linearly increases as v_1 increases for the cases $\tau_2=3$ and $\tau_2=5$. Our numerical calculations

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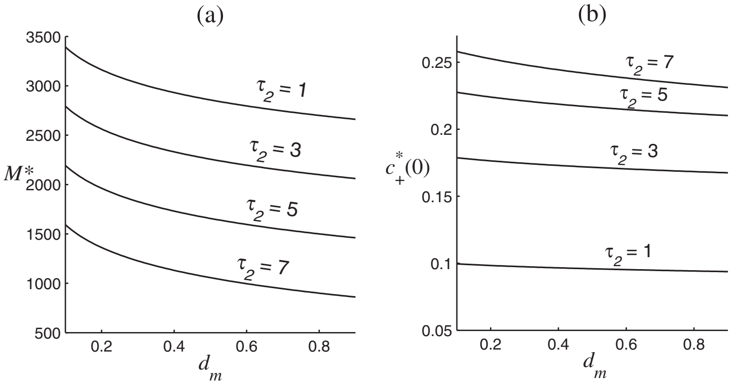

FIG. 2. *Graphs of* (a) *M-coordinates of positive equilibria* (M^*) *and* (b) *invasion speed* $c_+^*(0)$ *as a function of mortality rate of the adult* (d_m) *in the case* $\beta = 0$ *(no contact between the adult and sperms released into the water). Parameter values used for the figure are* $D_s = 0.02km^2/day$, $v_s = 0.01km/day$, $D_1 = 2km^2/day$, $v_1 = 2km/day$, $d_s = 0.9$ *per day,* $d_1 = 0.9$ *per day,* $q = 0.003$ *per adult clam,* $\tau_1 = 4.5$ *days,* $\tau_3 = 100$ *days,* $\gamma = 0.1$, *and* $\nu(= \alpha\gamma p) \approx 6482.5\ e^{-d_1\tau_2}$.

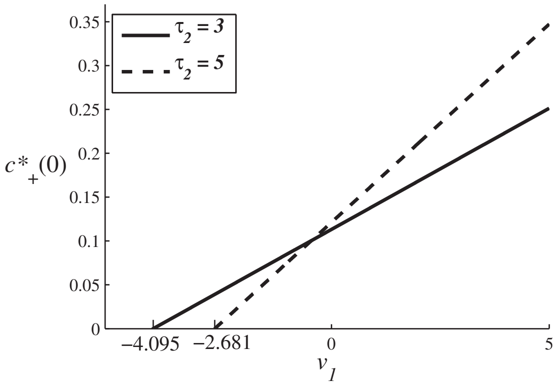

FIG. 3. *A graph of invasion speed* $c_+^*(0)$ *as a function of advection velocity of the discharged juveniles* (v_1) *in the case of* $\beta = 0$ *(no contact between the adult and sperms released into the water). Parameter values used for the figure are* $D_s = 0.02km^2/day$, $v_s = 0.01km/day$, $D_1 = 2km^2/day$, $d_1 = 0.9$ *per day,* $d_m = 0.8$ *per day,* $q = 0.003$ *per adult clam,* $\tau_1 = 4.5$ *days,* $\tau_3 = 100$ *days,* $\gamma = 0.1$, *and* $\nu(= \alpha\gamma p) \approx 6482.5\ e^{-d_1\tau_2}$.

show that $c_+^*(0) = 0$ when $v_1 \approx -4.095$ for $\tau_2 = 3$ and $v_1 \approx -2.681$ for $\tau_2 = 5$. These approximations agree with our analytic result in Lemma 4.6(iii): $v_1 \approx -4.099$ for $\tau_2 = 3$ and $v_1 \approx -2.683$ for $\tau_2 = 5$. We see that when the population experiences leftward advection (i.e., $v_1 < 0$), they cannot propagate to the right if the advection speed $|v_1|$ is greater than the critical value given in (4.14) that is decreasing in the traveling time τ_2. In the presence of the leftward advection speed, longer traveling time for the discharged juveniles has a negative effect on the rightward invasion of the species, while in the presence of the rightward advection speed, the longer traveling time has a positive effect on the rightward invasion.

We illustrate our numerical approach to calculating the invasion speed using the model itself in Appendix A. This numerical calculation can be used to study the invasion speed in the case $\beta \neq 0$.

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There are several open questions for future research. In our model, we assume all the coefficients are positive constants. With consideration for life cycle and sensitivity to sudden temperature change of Asian clam's biological activity, it is conceivable that some coefficients depend on age or seasonal temperature change. It then would be mathematically much harder to characterize the invasion speeds. Another possible project, given the actual experimental data, would be to study optimal strategies to control this invasive species.

Appendix A. Numerical studies. In this section, we numerically compute c_+^* and show it is increasing in parameter β. For our numerical studies, we set the following set of parameters for ages, measured in days, of each stage:

$$\tau_1 = 4.5, \quad \tau_3 = 165 - (\tau_1 + \tau_2),$$

where $\tau = 165$ and τ_2 can vary (we set, for instance, $\tau_2 = 10$).

To simulate the spread of the species and estimate the invasion speed, c_+^*, we use the forward difference for time and central difference for space. For convenience we write $S_j^n = S(t_n, x_j)$, where a grid in the tx-plane is a set of points $(t_n, x_j) = (n\kappa, ih)$; here $\kappa = \Delta t$ is the time step and $h = \Delta x$ is the grid spacing. The initial population density is assumed to have a compact support. In order to numerically compute the integral, we use the trapezoidal rule:

$$\int_a^b F(y)dy \approx \frac{\Delta y}{2} \sum_{i=1}^{N} [F(y_{i+1}) + F(y_i)]$$

with $a = y_1$ and $b = y_{N+1}$, where N is the number of subintervals. When considering a computational domain, the solution can only be found on a finite length domain. Thus, we take the finite sized computational domain into account, for instance, $y \in [-B, B]$, where $B \in \mathbb{R}^+$.

Equations in (2.7) are discretized as follows:

$$S_j^{n+1} = C_1 S_{j+1}^n + C_2 S_j^n + C_3 S_{j-1}^n + \kappa(1-\gamma)pM_j^n e^{-qM_j^n}, \tag{A.1a}$$

$$M_j^{n+1} = (1 - \kappa d_m) M_j^n + \alpha\kappa \int_{-B}^{B} k(y)\xi(t-\tau, x-y)dy, \tag{A.1b}$$

where

$$C_1 = D_s\frac{\kappa}{h^2} - v_s\frac{\kappa}{2h}, \quad C_2 = 1 - 2D_s\frac{\kappa}{h^2} - \kappa d_s, \quad C_3 = D_s\frac{\kappa}{h^2} + v_s\frac{\kappa}{2h},$$

and

$$\xi(t-\tau, x-y) = \gamma pM(t-\tau, x-y)e^{-qM(t-\tau,x-y)} + \beta S(t-\tau, x-y)M(t-\tau, x-y).$$

To calculate spreading speeds numerically, we hold the adult population at a certain level ($M = 10$), take a sample point location for every τ period, and estimate the slope of the resulting linear position function of time, which fits the obtained sample data (Figure 4). With the parameter set described in the figure, where $\beta = 10^{-8}$, the invasion speed is approximately 0.15431. We conduct further numerical

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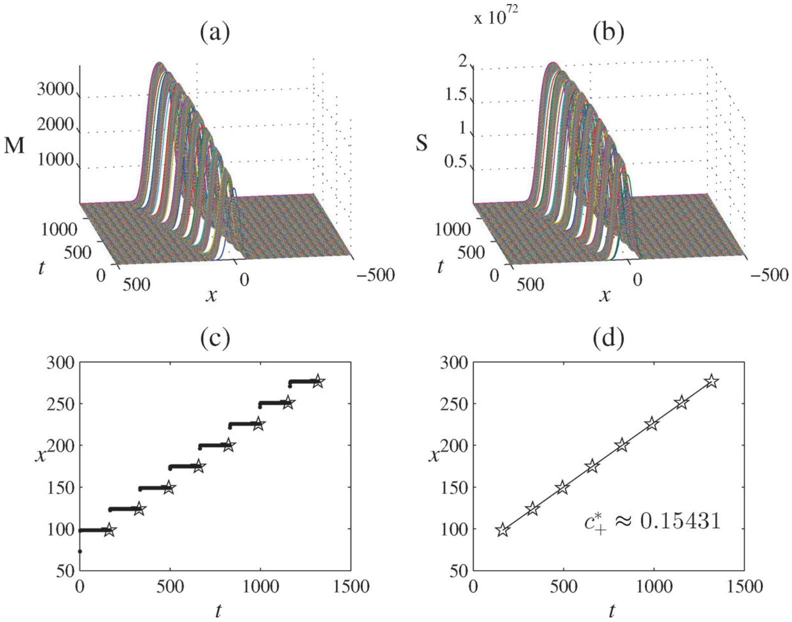

FIG. 4. *Traveling wave of invasion. The values of diffusion coefficients and advection speeds for the sperm and the discharged juveniles are* $D_s = 0.02, v_s = 0.01, D_1 = 2, v_1 = 2$*. The values of death rates are set to* $d_s = 0.9, d_m = d_\varepsilon = 0.9, d_1 = 0.9, d_2 = 0.95$*. Contact rate between the sperm* (S) *and the adult* (M) *clams* β *is* 10^{-8} *and the rate of becoming eggs* $\gamma = 0.1$*. We set* $q \approx 0.0001$ *and* $p = 1.5\ d_m/(\gamma\alpha)$ *to meet the condition* $p > d_m/(\gamma\alpha)$*. To numerically compute invasion speed* c^*_+*, we hold* $M = 10$*, take a sample point location for every* τ *period, indicated as star marks* $(\star)$*, and estimate* c^*_+ *by the slope of the resulting linear position function of time.*

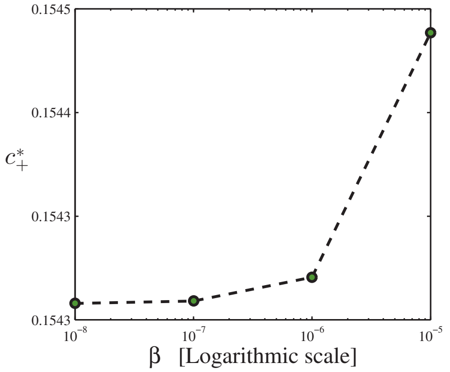

FIG. 5. *Invasion speeds with different values of* $\beta(= 10^{-8}, 10^{-7}, 10^{-6}, 10^{-5})$ *on logarithmic scale. Other parameter values are the same as those in Figure* 4.1.

studies to see how the invasion speed changes while we increase β from 10^{-8} to 10^{-5}. We observe that increasing β results in the increase in the invasion speed (Figure 5).

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