

## THE SPATIAL DYNAMICS OF A ZEBRA MUSSEL MODEL IN RIVER ENVIRONMENTS

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(Dedicated to Professor Sze-Bi Hsu on the occasion of his retirement)

**ABSTRACT.** Huang et al. [10] developed a hybrid continuous/discrete-time model to describe the persistence and invasion dynamics of Zebra mussels in rivers. They used a net reproductive rate  $R_0$  to determine population persistence in a bounded domain and estimated spreading speeds by applying the linear determinacy conjecture and using the formula in [16]. Since the associated solution operator is non-monotonic and non-compact, it is nontrivial to rigorously establish these quantities. In this paper, we analyze the spatial dynamics of this model mathematically. We first solve the parabolic equation and rewrite the model into a fully discrete-time model. In a bounded domain, we show that the spectral radius  $\hat{r}$  of the linearized operator can be used to determine population persistence and that the sign of  $\hat{r} - 1$  is the same as that of  $R_0 - 1$ , which confirms that  $R_0$  defined in [10] can be used to determine population persistence. In an unbounded domain, we construct two monotonic operators to control the model operator from above and from below and obtain upper and lower bounds of the spreading speeds of the model.

**1. Introduction.** Zebra mussels have attracted researchers' attention due to their high fecundity and strong ability to influence other bivalves as well as phytoplankton and zooplankton in rivers or other aquatic environments; see, e.g., [1, 7, 10, 17]. Zebra mussels have three significant life stages: larva, juvenile, and adult. Larvae live and disperse in the flowing water before settling down to the substrate or dying in a very short time period of a year, while juveniles and adults only grow and reproduce (for adults) on the substrate. The resulted mathematical model that describes growth and dispersal of the zebra mussel population is then a hybrid model incorporating a reaction-diffusion-advection equation, an ordinary differential equation, and two discrete-time equations; see (2.1) in [10].

To investigate the long-term behavior of a population in the environment, persistence dynamics are usually analyzed for the corresponding mathematical models.

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Different quantities have been used to describe population persistence or extinction, in homogeneous environments or in spatially/temporally heterogeneous environments. The common ones are the principal eigenvalue of the Jacobian matrix at the trivial solution, the principal eigenvalue or the spectral radius of the linearized operator at the trivial solution or of the Poincaré map, or the net reproductive rate of the next generation operator, etc; see, e.g., [3, 5, 8, 15, 26]. For a discrete-time linear operator, if it is positive and compact, then the Krein-Rutman theorem implies that its spectral radius is its principal eigenvalue; see e.g., [5]. If the operator is furthermore point dissipative and ultimately bounded, then the theory of uniform persistence can guarantee that the spectral radius can be used to determine population persistence and extinction; see e.g., [14, 18, 26]. The compactness of the operator and the linearized operator is critical in applying such theories. When these operators are not compact, some type of weak compactness is usually required to accomplish the goal. Asymptotic smoothness and  $\alpha$ -contraction are two types of weak compactness that have been used to replace the compactness when conditions for persistence or extinction are established for certain models; see, e.g., [6, 13, 26].

Spreading speeds and/or the minimal wave speeds of traveling waves have been used to describe biological invasions of species in the spatial environments. If the solution (or model) operator is monotone, a systematic set of theories have been derived to establish the existence of spreading speeds and traveling wave solutions for maps or semiflows in homogeneous habitats or in spatially and/or temporally periodic habitats; see, e.g., [21, 12, 11, 22]. Under appropriate conditions, the spreading speeds are linearly determined, that is, the spreading speeds of the non-linear system or map are the same as those of the corresponding linearized system at the trivial solution, which is the so-called “linear determinacy conjecture”. For some non-monotonic solution (or model) operators, it is possible to construct two monotonic operators to control the original operator from above and below. If these two monotonic operators are associated with the same linearized operator at the trivial solution, then the spreading speeds of the non-monotonic operator can be determined by those of these monotonic operators; see, e.g., [9, 23, 25]. By applying the linear determinacy conjecture, the spreading speeds of some integro-difference systems have been formally estimated in [16].

In [10], Huang et al. defined a net reproductive rate  $R_0$  and used it to determine population persistence in a bounded domain and estimated spreading speeds by applying the linear determinacy conjecture and using the formula in [16]. In our current work, we revisit the hybrid zebra mussel model developed in [10], show that the spectral radius of the linearized operator at the trivial solution can be used to determine population persistence and extinction, verify that the net reproductive rate they defined can mathematically determine population persistence in a bounded domain, and then provide theoretical estimation for the spreading speeds in an unbounded domain. We first rewrite the model into an equivalent discrete-time system. Unfortunately, this system is non-monotone and non-compact. In the scenario of a bounded domain, we prove that the operator has  $\alpha$ -contraction property with respect to the non-compactness measure so that a generalized Krein-Rutman theorem (see [13, Lemma 2.3]) can be used to show that its spectral radius determines the persistence dynamics of the population. In the scenario of an unbounded domain, we construct two monotonic operators to control the original operator from above and from below, and then use the spreading speeds of these two operators for upper and low bounds of the spreading speeds of the original system.

This paper is organized as follows. In Section 2, we present the zebra mussel model derived in [10]. In Section 3, we establish a threshold type result on the global dynamics of the model in a bounded river environment. In Section 4, we derive upper and lower estimations of the spreading speeds for the zebra mussel population in an unbounded river environment. A brief discussion then completes the paper.

**2. The model.** Assume that there are three stages of the zebra mussel (*Dreissena polymorpha*): larva, juvenile, and adult. Larvae live in the water column with the ability to disperse; they disperse in water, settle down to the bottom, and die in the time interval  $t \in [0, \tau]$  in each year, where  $\tau$ , usually a few days or a few weeks, is the maximal dispersal time of larvae. Larvae die if they cannot attach to the substrates after time  $\tau$ ; but they become juveniles after time  $\tau$  if they can successfully settle down to the bottom during the interval  $[0, \tau]$ . Juveniles become adults when they are sexually mature. Juveniles and adults live on the bottom and they do not disperse. Based on its life cycle, the following model was derived in [10] to describe the dynamics of the zebra mussel in a one-dimensional river:

$$\begin{aligned} u_t &= \frac{1}{S(x)}(D(x)S(x)u_x)_x - \frac{P}{S(x)}u_x - m(x)u - \sigma(x)u, & x \in \Omega, t \in (0, \tau], \\ w_t &= h(x)\sigma(x)u, & x \in \Omega, t \in (0, \tau], \\ u(x, 0) &= \frac{r(x)}{h(x)}A(x, n), w(x, 0) = 0, & x \in \Omega, \\ J(x, n+1) &= \varphi(x, n)s_l(x, T)w(x, \tau), & x \in \Omega, n = 0, 1, 2, \dots, \\ A(x, n+1) &= \varphi(x, n)[s_j(x, T)J(x, n) + s_a(x, T)A(x, n)], & x \in \Omega, n = 0, 1, 2, \dots, \\ J(x, 0) &= J_0(x), A(x, 0) = A_0(x), & x \in \Omega. \end{aligned} \tag{1}$$

In system (1),  $\Omega$  represents the one-dimensional river,  $u(x, t)$  and  $w(x, t)$  are the density of dispersing larvae in the drifting water (number of larvae per unit water volume) and the density of settled larvae on the benthos (number of larvae per unit benthic area), respectively, at location  $x \in \Omega$  and time  $t$  in the dispersal period  $[0, \tau]$  of the  $n$ -th year,  $J(x, n)$  and  $A(x, n)$  are the density of juveniles (number per area) and the density of adults (number per area), respectively, at the beginning of the breeding season in year  $n$  ( $n = 1, 2, \dots$ ),  $S(x) > 0$  is the cross-sectional area of the river,  $D(x) > 0$  is the diffusion rate of larvae,  $P > 0$  is the constant water discharge,  $m(x) > 0$  is the larval mortality rate,  $\sigma(x) > 0$  is the settling rate,  $h(x) > 0$  is the spatially variable water depth,  $r(x)$  is the reproduction rate of adults,  $s_l$ ,  $s_j$ , and  $s_a$ , satisfying  $0 < s_l(x, T), s_j(x, T), s_a(x, T) < 1$  for all  $x \in \Omega$ , are the basal survival rates depending on the spatial location  $x$  and temperature  $T$  for larvae, juveniles, and adults, respectively,  $\varphi(x, n)$  is the density-dependent survival of the population due to competition for limiting resources such as nutrients space, and it can be expressed as

$$\varphi(x, n) = \frac{1}{1 + \gamma[l_l(T)w(x, \tau) + l_j(T)J(x, n) + l_a(T)A(x, n)]}, \tag{2}$$

where  $\gamma$  is the competition coefficient that relates competitive ability to a phenotypic trait, and  $l_l(T)$ ,  $l_j(T)$ , and  $l_a(T)$  are taken as the shell lengths, depending on the temperature  $T$ , of larvae, juveniles, and adults, respectively,  $J_0$  and  $A_0$  are initial distributions of juveniles and adults, respectively. See [10] for more details of the model. Moreover, all the parameters are assumed to be continuous and bounded. For notational simplicity, in the rest of the paper, we will just write  $s_l(x, T)$ ,  $s_j(x, T)$ ,

and  $s_a(x, T)$  as  $s_l(x)$ ,  $s_j(x)$ , and  $s_a(x)$ , respectively, and  $l_l(T)$ ,  $l_j(T)$ , and  $l_a(T)$  as  $l_l$ ,  $l_j$ , and  $l_a$ , respectively, as we will not specifically study the effect of temperature  $T$ .

**3. Persistence dynamics in a bounded habitat.** In this section, we study the persistence dynamics of model (1) in a bounded river with length  $L$ . When  $\Omega = [0, L]$ , model (1), together with boundary conditions, becomes

$$\begin{aligned} u_t &= \frac{1}{S(x)}(D(x)S(x)u_x)_x - \frac{P}{S(x)}u_x - m(x)u - \sigma(x)u, & x \in (0, L), t \in (0, \tau], \\ w_t &= h(x)\sigma(x)u, & x \in (0, L), t \in (0, \tau], \\ \alpha_1 u(0, t) - \alpha_2 u_x(0, t) &= 0, \beta_1 u(L, t) + \beta_2 u_x(L, t) = 0, & t \in (0, \tau], \\ u(x, 0) &= \frac{r(x)}{h(x)}A(x, n), w(x, 0) = 0, & x \in (0, L), \\ J(x, n+1) &= \varphi(x, n)s_l(x)w(x, \tau), & x \in [0, L], n = 0, 1, 2, \dots, \\ A(x, n+1) &= \varphi(x, n)[s_j(x)J(x, n) + s_a(x)A(x, n)], & x \in [0, L], n = 0, 1, 2, \dots, \\ J(x, 0) &= J_0(x), A(x, 0) = A_0(x), & x \in [0, L], \end{aligned} \quad (3)$$

where  $\alpha_i \geq 0$  and  $\beta_i \geq 0$  for  $i = 1, 2$ ,  $\alpha_1 + \alpha_2 > 0$ ,  $\beta_1 + \beta_2 > 0$ .

For mathematical simplicity, we do not consider the cases where one of the boundary conditions is Dirichlet. That is, we assume that  $\alpha_2 > 0$  and  $\beta_2 > 0$ . Let  $X = C([0, L], \mathbb{R})$  denote the Banach space of continuous functions on  $[0, L]$  with the supremum norm  $\|u\|_\infty = \max_{x \in [0, L]} |u(x)|$  for  $u \in X$ . The set of nonnegative functions forms a solid cone  $X_+$  in  $X$  with interior  $\text{Int}(X_+) = \{u \in X : u(x) > 0, \forall x \in [0, L]\}$ .

Let  $\Phi_t : X \rightarrow X$  be the solution map of

$$\begin{cases} \bar{u}_t = \frac{1}{S(x)}(D(x)S(x)\bar{u}_x)_x - \frac{P}{S(x)}\bar{u}_x - m(x)\bar{u} - \sigma(x)\bar{u}, & x \in (0, L), t > 0, \\ \alpha_1 \bar{u}(0, t) - \alpha_2 \bar{u}_x(0, t) = 0, \beta_1 \bar{u}(L, t) + \beta_2 \bar{u}_x(L, t) = 0, & t > 0. \end{cases} \quad (4)$$

Since the  $\bar{u}$ -equation in (4) is linear,  $\Phi_t$  is a linear operator for all  $t \geq 0$ . Moreover, by the standard theory of parabolic equations,  $\Phi_t$  is strongly positive and compact for each  $t > 0$  (see, e.g., [8]). Then model (3) gives rise to

$$\begin{cases} u(x, t) = \left[ \Phi_t \left( \frac{r(\cdot)}{h(\cdot)} A(\cdot, n) \right) \right] (x), & x \in (0, L), t \in (0, \tau], \\ w(x, t) = h(x)\sigma(x) \int_0^t \left[ \Phi_{\bar{t}} \left( \frac{r(\cdot)}{h(\cdot)} A(\cdot, n) \right) \right] (x) d\bar{t}, & x \in (0, L), t \in (0, \tau]. \end{cases}$$

Furthermore,  $J$  and  $A$  satisfy the following discrete system:

$$\begin{cases} J(x, n+1) = \frac{s_l(x)h(x)\sigma(x) \int_0^\tau \left[ \Phi_{\bar{t}} \left( \frac{r(\cdot)}{h(\cdot)} A(\cdot, n) \right) \right] (x) d\bar{t}}{1 + \gamma \left[ l_l h(x)\sigma(x) \int_0^\tau \left[ \Phi_{\bar{t}} \left( \frac{r(\cdot)}{h(\cdot)} A(\cdot, n) \right) \right] (x) d\bar{t} + l_j J(x, n) + l_a A(x, n) \right]}, \\ A(x, n+1) = \frac{s_j(x)J(x, n) + s_a(x)A(x, n)}{1 + \gamma \left[ l_l h(x)\sigma(x) \int_0^\tau \left[ \Phi_{\bar{t}} \left( \frac{r(\cdot)}{h(\cdot)} A(\cdot, n) \right) \right] (x) d\bar{t} + l_j J(x, n) + l_a A(x, n) \right]}, \\ J(x, 0) = J_0(x), A(x, 0) = A_0(x), \end{cases} \quad (5)$$

for  $x \in [0, L]$  and  $n = 0, 1, 2, \dots$ . Let  $V_n(x) = (J(x, n), A(x, n))$ . Then system (5) can be written as

$$V_{n+1}(x) = [Q(V_n)](x), \quad \forall x \in [0, L], n = 0, 1, 2, \dots,$$

where the operator  $Q : X \times X \rightarrow X \times X$  is defined by the right-hand side of (5). That is, for  $\psi = (\psi_1, \psi_2) \in X \times X$ ,

$$Q(\psi) = \begin{pmatrix} \frac{s_l(x)h(x)\sigma(x) \int_0^\tau \left[ \Phi_{\bar{t}} \left( \frac{r(\cdot)}{h(\cdot)} \psi_2(\cdot) \right) \right] (x) d\bar{t}}{1 + \gamma \left[ l_l h(x)\sigma(x) \int_0^\tau \left[ \Phi_{\bar{t}} \left( \frac{r(\cdot)}{h(\cdot)} \psi_2(\cdot) \right) \right] (x) d\bar{t} + l_j \psi_1(x) + l_a \psi_2(x)} \\ \frac{s_j(x)\psi_1(x) + s_a(x)\psi_2(x)}{1 + \gamma \left[ l_l h(x)\sigma(x) \int_0^\tau \left[ \Phi_{\bar{t}} \left( \frac{r(\cdot)}{h(\cdot)} \psi_2(\cdot) \right) \right] (x) d\bar{t} + l_j \psi_1(x) + l_a \psi_2(x)} \end{pmatrix}. \quad (6)$$

We first notice that any orbit of  $Q$  in  $X_+ \times X_+$  is bounded.

**Lemma 3.1.**  $Q$  is point dissipative and ultimately bounded on  $X_+ \times X_+$ .

*Proof.* For any  $\psi = (\psi_1, \psi_2) \in X_+ \times X_+$ , let  $Q(\psi) = ((Q(\psi))_1, (Q(\psi))_2)$ . For any  $x \in [0, L]$ , we have

$$\begin{aligned} 0 \leq (Q(\psi))_1(x) &\leq \frac{s_l(x)h(x)\sigma(x) \int_0^\tau \left[ \Phi_{\bar{t}} \left( \frac{r(\cdot)}{h(\cdot)} \psi_2(\cdot) \right) \right] (x) d\bar{t}}{\gamma \left[ l_l h(x)\sigma(x) \int_0^\tau \left[ \Phi_{\bar{t}} \left( \frac{r(\cdot)}{h(\cdot)} \psi_2(\cdot) \right) \right] (x) d\bar{t} \right]} \\ &\leq \frac{\max_{x \in [0, L]} \{s_l(x)\}}{\gamma l_l}, \\ 0 \leq (Q(\psi))_2(x) &\leq \frac{s_j(x)\psi_1(x) + s_a(x)\psi_2(x)}{\gamma [l_j \psi_1(x) + l_a \psi_2(x)]} \\ &\leq \frac{\max_{x \in [0, L]} \{s_j(x), s_a(x)\} (\psi_1(x) + \psi_2(x))}{\gamma \min\{l_j, l_a\} (\psi_1(x) + \psi_2(x))} \\ &= \frac{\max_{x \in [0, L]} \{s_j(x), s_a(x)\}}{\gamma \min\{l_j, l_a\}}. \end{aligned}$$

Therefore,  $Q : X_+ \times X_+ \rightarrow [\mathbf{0}, \mathbf{M}]$ , where

$$\mathbf{M} = \left( \frac{\max_{x \in [0, L]} \{s_l(x)\}}{\gamma l_l}, \frac{\max_{x \in [0, L]} \{s_j(x), s_a(x)\}}{\gamma \min\{l_j, l_a\}} \right) \quad (7)$$

and  $[\mathbf{0}, \mathbf{M}]$  contains all functions in  $X_+ \times X_+$  with values between  $\mathbf{0}$  and  $\mathbf{M}$ . Moreover, for any  $\psi \in X_+ \times X_+$ ,  $Q^n(\psi) \in [\mathbf{0}, \mathbf{M}]$  for all  $n = 1, 2, \dots$ . That is,  $Q$  is point dissipative and ultimately bounded on  $X_+ \times X_+$ .  $\square$

Note that  $Q(\mathbf{0}) = \mathbf{0}$  and the Fréchet derivative

$$\mathcal{L} := DQ(\mathbf{0}) \quad (8)$$

can be expressed as

$$[\mathcal{L}(\psi)](x) = \begin{pmatrix} s_l(x)h(x)\sigma(x) \int_0^\tau \left[ \Phi_{\bar{t}} \left( \frac{r(\cdot)}{h(\cdot)} \psi_2(\cdot) \right) \right] (x) d\bar{t} \\ s_j(x)\psi_1(x) + s_a(x)\psi_2(x) \end{pmatrix}, \quad \forall \psi = (\psi_1, \psi_2) \in X \times X. \quad (9)$$

Clearly,  $\mathcal{L}$  is positive in the sense that for any  $\psi \in X$  with  $\psi > \mathbf{0}$ , we have  $\mathcal{L}(\psi) > \mathbf{0}$ . Moreover, we have the following result.

**Lemma 3.2.**  $\mathcal{L}$  is an  $\alpha$ -contraction with respect to the non-compactness measure on  $X \times X$ .

*Proof.* For any  $\psi = (\psi_1, \psi_2) \in X \times X$ , let

$$\begin{aligned}\mathcal{L}_1(\psi)(x) &= \begin{pmatrix} s_l(x)h(x)\sigma(x) \int_0^\tau \left[ \Phi_{\bar{t}} \left( \frac{r(\cdot)}{h(\cdot)} \psi_2(\cdot) \right) \right] (x) d\bar{t} \\ 0 \end{pmatrix}, \\ \mathcal{L}_2(\psi)(x) &= \begin{pmatrix} 0 \\ s_j(x)\psi_1(x) + s_a(x)\psi_2(x) \end{pmatrix}.\end{aligned}\quad (10)$$

Then

$$[\mathcal{L}(\psi)](x) = \mathcal{L}_1(\psi)(x) + \mathcal{L}_2(\psi)(x).$$

Since  $\Phi_{\bar{t}}$  is compact for all  $\bar{t} \in [0, \tau]$ , we have  $\mathcal{L}_1$  is compact. Note that  $\mathcal{L}_2$  is a linear operator on  $X \times X$ . Then for any bounded set  $B$  in  $X \times X$ , we have  $\alpha(\mathcal{L}_2(B)) \leq \|\mathcal{L}_2\|\alpha(B)$ , where  $\alpha(B)$  is the Kuratowski measure of  $B$  defined as

$$\alpha(B) := \inf\{d > 0 : \text{there exist finitely many sets of diameter at most } d \text{ which cover } B\} \quad (11)$$

and  $\|\mathcal{L}_2\|$  is the operator norm of  $\mathcal{L}_2$  on  $X \times X$ . Since

$$\mathcal{L}_2(\psi)(x) \leq \begin{pmatrix} 0 & 0 \\ \max_{x \in [0, L]} \{s_j(x)\} & \max_{x \in [0, L]} \{s_a(x)\} \end{pmatrix} \begin{pmatrix} \psi_1(x) \\ \psi_2(x) \end{pmatrix},$$

we have  $\|\mathcal{L}_2\| \leq \max\{\max_{x \in [0, L]} \{s_j(x)\}, \max_{x \in [0, L]} \{s_a(x)\}\} < 1$ . Therefore, there exists  $\hat{k} \in (0, 1)$  such that  $\alpha(\mathcal{L}_2(B)) < \hat{k}\alpha(B)$ , which implies that  $\mathcal{L}_2$  is an  $\alpha$ -contraction. Hence  $\alpha([\mathcal{L}](B)) \leq \alpha(\mathcal{L}_1(B)) + \alpha(\mathcal{L}_2(B)) < \hat{k}\alpha(B)$ . This shows that  $\mathcal{L}$  is an  $\alpha$ -contraction.  $\square$

**Lemma 3.3.** *Let  $\mathbf{M}$  be defined in (7) and*

$$\begin{aligned}M_0 &= \|\mathbf{M}\| = \max \left\{ \frac{\max_{x \in [0, L]} \{s_l(x)\}}{\gamma l_l}, \frac{\max_{x \in [0, L]} \{s_j(x), s_a(x)\}}{\gamma \min\{l_j, l_a\}} \right\}, \\ M_1 &= l_l \max_{x \in [0, L]} \left\{ h(x)\sigma(x) \int_0^\tau \left[ \Phi_{\bar{t}} \left( \frac{r(\cdot)}{h(\cdot)} \right) \right] (x) d\bar{t} \right\} + l_j + l_a, \\ M_2 &= \max_{x \in [0, L]} \left\{ s_l(x)h(x)\sigma(x) \int_0^\tau \left[ \Phi_{\bar{t}} \left( \frac{r(\cdot)}{h(\cdot)} \right) \right] (x) d\bar{t} \right\}, \\ M_3 &= \max \left\{ \max_{x \in [0, L]} \{s_j(x)\}, \max_{x \in [0, L]} \{s_a(x)\} \right\}.\end{aligned}$$

If

$$\gamma M_0 M_1 (M_2 + M_3) < 1 - M_3, \quad (12)$$

then  $Q : [\mathbf{0}, \mathbf{M}] \rightarrow [\mathbf{0}, \mathbf{M}]$  is an  $\alpha$ -contraction with respect to the non-compactness measure.

*Proof.* Let  $g : X \times X \rightarrow X$  and  $G : X \times X \rightarrow X$  be defined as

$$\begin{aligned}g(\psi)(x) &= 1 + \gamma \left[ l_l h(x)\sigma(x) \int_0^\tau \left[ \Phi_{\bar{t}} \left( \frac{r(\cdot)}{h(\cdot)} \psi_2(\cdot) \right) \right] (x) d\bar{t} + l_j \psi_1(x) + l_a \psi_2(x) \right], \\ G(\psi)(x) &= \frac{1}{g(\psi)(x)},\end{aligned}$$

for  $\psi = (\psi_1, \psi_2) \in X \times X$  and  $x \in [0, L]$ . Then  $Q(\psi) = G(\psi)(x) \cdot \mathcal{L}(\psi)(x)$ . Moreover, the Fréchet derivative of  $G$  is defined as

$$\begin{aligned}DG(\psi)(\chi)(x) &= \frac{d}{ds} G(\psi + s\chi)|_{s=0} \\ &= - \frac{\gamma [l_l h(x)\sigma(x) \int_0^\tau \left[ \Phi_{\bar{t}} \left( \frac{r(\cdot)}{h(\cdot)} \chi_2(\cdot) \right) \right] (x) d\bar{t} + l_j \chi_1(x) + l_a \chi_2(x)]}{(g(\psi)(x))^2},\end{aligned}$$

for all  $\psi, \chi \in X \times X$ .

Note that  $Q : [\mathbf{0}, \mathbf{M}] \rightarrow [\mathbf{0}, \mathbf{M}]$ . For any  $\psi \in X \times X$ ,  $\psi \in [\mathbf{0}, \mathbf{M}]$ , we have  $\|\psi\| \leq M_0$ . Let  $B$  be a bounded set in  $[\mathbf{0}, \mathbf{M}]$ . For any  $\hat{\psi}, \psi \in B$ ,  $x \in [0, L]$ ,

$$\begin{aligned} & |Q(\hat{\psi})(x) - Q(\psi)(x)| \\ &= |G(\hat{\psi})(x) \cdot \mathcal{L}(\hat{\psi})(x) - G(\psi)(x) \cdot \mathcal{L}(\psi)(x)| \\ &\leq |G(\hat{\psi})(x) \cdot \mathcal{L}(\hat{\psi})(x) - G(\hat{\psi})(x) \cdot \mathcal{L}(\psi)(x)| \\ &\quad + |G(\hat{\psi})(x) \cdot L(\psi)(x) - G(\psi)(x) \cdot L(\psi)(x)| \\ &\leq |G(\hat{\psi})(x)| \cdot \|\mathcal{L}(\hat{\psi})(x) - \mathcal{L}(\psi)(x)\| + |G(\hat{\psi})(x) - G(\psi)(x)| \cdot \|\mathcal{L}(\psi)(x)\| \\ &\leq \|\mathcal{L}(\hat{\psi})(x) - \mathcal{L}(\psi)(x)\| + \|DG(\bar{\psi})\| \cdot \|\hat{\psi} - \psi\| \cdot \|\mathcal{L}\| \cdot \|\psi\| \\ &\leq \|\mathcal{L}(\hat{\psi})(x) - \mathcal{L}(\psi)(x)\| + \|DG(\bar{\psi})\| \cdot \|\hat{\psi} - \psi\| \cdot \|\mathcal{L}\| \cdot M_0 \end{aligned}$$

for some  $\bar{\psi} \in B$ . This implies that

$$\begin{aligned} \alpha(Q(B)) &\leq \alpha(\mathcal{L}(B)) + \|DG(\bar{\psi})\| \cdot \|\mathcal{L}\| \cdot M_0 \cdot \alpha(B) \\ &\leq (\|\mathcal{L}_2\| + \|DG(\bar{\psi})\| \cdot \|\mathcal{L}\| \cdot M_0) \alpha(B) \\ &\leq (\|\mathcal{L}_2\| + \sup_{\tilde{\psi} \in B} \|DG(\tilde{\psi})\| \cdot \|\mathcal{L}\| \cdot M_0) \alpha(B). \end{aligned}$$

Note that

$$\begin{aligned} \|\mathcal{L}_1\| &\leq \max_{x \in [0, L]} \left\{ s_l(x) h(x) \sigma(x) \int_0^\tau \left[ \Phi_{\bar{t}} \left( \frac{r(\cdot)}{h(\cdot)} \right) \right] (x) d\bar{t} \right\} = M_2, \\ \|\mathcal{L}_2\| &\leq \max \left\{ \max_{x \in [0, L]} \{s_j(x)\}, \max_{x \in [0, L]} \{s_a(x)\} \right\} = M_3 < 1. \end{aligned}$$

Moreover, for  $\psi, \chi \in B$ , we have

$$\|DG(\psi)(\chi)\| \leq \gamma \max_{x \in [0, L]} (G(\psi)(x))^2 \cdot M_1 \|\chi\|,$$

and hence,

$$\|DG(\psi)\| \leq \gamma \max_{x \in [0, L]} (G(\psi)(x))^2 \cdot M_1.$$

It then follows that

$$\begin{aligned} \alpha(Q(B)) &\leq (\|\mathcal{L}_2\| + \sup_{\tilde{\psi} \in B} \|DG(\tilde{\psi})\| \cdot \|\mathcal{L}\| \cdot M_0) \alpha(B) \\ &\leq \alpha(B) \cdot \left( M_3 + \gamma \max_{\tilde{\psi} \in [\mathbf{0}, \mathbf{M}], x \in [0, L]} \{(G(\tilde{\psi})(x))^2\} \cdot M_0 M_1 \cdot (M_3 + M_2) \right), \\ &\leq \alpha(B) \cdot (M_3 + \gamma \cdot M_0 M_1 \cdot (M_3 + M_2)) \\ &= \alpha(B) \cdot k_{\mathbf{M}}, \end{aligned}$$

where  $k_{\mathbf{M}} = M_3 + \gamma \cdot M_0 M_1 \cdot (M_3 + M_2)$ . By (12), we obtain  $0 < k_{\mathbf{M}} < 1$ . Thus,  $Q : [\mathbf{0}, \mathbf{M}] \rightarrow [\mathbf{0}, \mathbf{M}]$  is an  $\alpha$ -contraction.  $\square$

**Remark 1.** In the case where  $\sigma = 0$ , the condition in (12) becomes

$$\max \left\{ \frac{\max_{x \in [0, L]} \{s_l(x)\}}{l_l}, \frac{\max_{x \in [0, L]} \{s_j(x), s_a(x)\}}{\min\{l_j, l_a\}} \right\} < \frac{1 - \max_{x \in [0, L]} \{s_j(x), s_a(x)\}}{(l_l + l_a) \cdot \left( \max_{x \in [0, L]} \{s_j(x), s_a(x)\} \right)}.$$

A sufficient condition that makes this happen is

$$\frac{(l_l + l_a)}{\min\{l_l, l_j, l_a\}} < \frac{1 - \max_{x \in [0, L]} \{s_j(x), s_a(x)\}}{\left( \max_{x \in [0, L]} \{s_j(x), s_a(x)\} \right) \max_{x \in [0, L]} \{s_j(x), s_a(x), s_l(x)\}}.$$

Our main result about persistence of (3) or (5) is as follows.

**Theorem 3.4.** *Let  $\hat{r}$  be the spectral radius of  $\mathcal{L}$ , that is,  $\hat{r} = \text{spr}(\mathcal{L})$ . Then the following statements are valid:*

- (i) *If  $0 < \hat{r} < 1$ , then for any  $V_0(\cdot) = (J_0(\cdot), A_0(\cdot)) \in X_+ \times X_+$ ,  $V_n(x) = [Q^n(V_0)](x)$  converges to  $\mathbf{0}$  uniformly for all  $x \in [0, L]$  as  $n \rightarrow \infty$ .*
- (ii) *If  $\hat{r} > 1$ , then (5) is weakly persistent in the sense that there exists  $\delta > 0$  such that*

$$\limsup_{n \rightarrow \infty} \|Q^n(V_0)\| > \delta$$

*for any initial data  $V_0 \in X_+ \times X_+ \setminus \{\mathbf{0}\}$ . If, in addition, (12) holds, then (5) is uniformly persistent in the sense that there exists  $\xi > 0$  such that for any initial data  $V_0 \in X_+ \times X_+ \setminus \{\mathbf{0}\}$ , the solution of (5) through  $V_0$  satisfies*

$$\liminf_{n \rightarrow \infty} (J(x, n), A(x, n)) \geq (\xi, \xi) \text{ uniformly for } x \in [0, L]$$

*and there exists  $V^* \in X_+ \times X_+ \setminus \{\mathbf{0}\}$  such that  $Q(V^*) = V^*$ .*

*Proof.* The spectrum of  $\mathcal{L}$  is non-empty as  $\mathcal{L}$  is linear and bounded (see, e.g., [2, Theorem 1.2.11]), so we have  $\hat{r} > 0$ .

(i). Note that  $Q \leq \mathcal{L}$  on  $X_+ \times X_+$ . Since  $\hat{r} < 1$ , there exists  $\bar{k} \in (0, 1)$  such that  $0 < \hat{r} < \bar{k} < 1$ . Then  $\hat{r} = \lim_{n \rightarrow \infty} \|\mathcal{L}^n\|^{\frac{1}{n}} < \bar{k}$ . This implies that there exists  $N_0 > 0$  such that  $\|\mathcal{L}^n\| < \bar{k}^n$  for all  $n \geq N_0$ . Hence  $\|\mathcal{L}^n\| < \bar{k}^n \rightarrow 0$  as  $n \rightarrow \infty$  since  $0 < \bar{k} < 1$ , that is,  $\lim_{n \rightarrow \infty} \|\mathcal{L}^n\| = 0$ . Then

$$\|Q^n(\phi)\| \leq \|\mathcal{L}^n(\phi)\| \leq \|\mathcal{L}^n\| \cdot \|\phi\| \rightarrow 0, \text{ as } n \rightarrow \infty$$

for all  $\phi \in X_+ \times X_+$ .

(ii). For any bounded set  $B$  in  $X \times X$ , since  $\alpha(\mathcal{L}(B)) < \hat{k}\alpha(B)$  for some  $\hat{k} \in (0, 1)$  (see the proof of Lemma 3.2), we have  $\alpha(\mathcal{L}^n(B)) < \hat{k}^n\alpha(B)$ . Let  $r_e(\mathcal{L})$  be the essential spectral radius of  $\mathcal{L}$ . By [13, Lemma A.1] (see also [4, Theorem 9.9]), we have

$$r_e(\mathcal{L}) = \lim_{n \rightarrow \infty} (\zeta(\mathcal{L}^n))^{\frac{1}{n}} \leq \hat{k} < 1 < \hat{r} = \text{spr}(\mathcal{L}),$$

where  $\zeta(\mathcal{L}) = \inf\{k_1 > 0 : \alpha(\mathcal{L}(B)) \leq k_1\alpha(B) \text{ for any bounded } B \text{ in } X \times X\}$ . It then follows from a generalized Krein-Rutman theorem (see [13, Lemma 2.3]) that  $\hat{r}$  is an eigenvalue of  $\mathcal{L}$  associated with a positive eigenfunction  $\phi^* \in X \times X$  with  $\phi^* = (\phi_1^*, \phi_2^*) > \mathbf{0}$ . Then  $\mathcal{L}(\phi^*) = \hat{r}\phi^*$  implies

$$\begin{aligned} \hat{r}\phi_1^*(x) &= s_l(x)h(x)\sigma(x) \int_0^\tau \left[ \Phi_{\bar{t}} \left( \frac{r(\cdot)}{h(\cdot)} \phi_2^*(\cdot) \right) \right] (x) d\bar{t}, \\ \hat{r}\phi_2^*(x) &= s_j(x)\phi_1^*(x) + s_a(x)\phi_2^*(x). \end{aligned} \quad (13)$$

If  $\phi_2^* > 0$ , then by the first equation of (13) and the strong positivity of  $\Phi_t$  we have  $\phi_1^* \gg 0$ , which together with the second equation of (13) implies that  $\phi_2^* \gg 0$ . Hence,  $\phi^* \gg \mathbf{0}$ . If  $\phi_2^* \equiv 0$ , then  $s_j(x)\phi_1^*(x) = 0$  for all  $x \in [0, L]$ . By the positivity of  $s_j(x)$ , we have  $\phi_1^* \equiv 0$ , and hence  $\phi^* \equiv \mathbf{0}$ , contradicting to  $\phi^* > \mathbf{0}$ . Therefore, the eigenfunction  $\phi^*$  of  $\mathcal{L}$  corresponding to  $\hat{r}$  is strongly positive. That is,  $\phi_1^*(x) > 0$  and  $\phi_2^*(x) > 0$  for all  $x \in [0, L]$ .

Since  $\hat{r} > 1$ , there exists  $\epsilon_0 > 0$  such that for any  $0 < \epsilon < \epsilon_0$ , the spectral radius of  $\mathcal{L} - \epsilon = DQ(\mathbf{0}) - \epsilon$ , i.e.,  $\hat{r}_\epsilon = \text{spr}(\mathcal{L} - \epsilon)$ , is an eigenvalue of  $\mathcal{L} - \epsilon$  associated with a strongly positive eigenfunction  $\phi_\epsilon^*$ , and  $\hat{r}_\epsilon > 1$ . Let  $\epsilon_1 \in (0, \epsilon_0)$  and  $\phi_{\epsilon_1}^*$  be the positive eigenfunction of  $\mathcal{L} - \epsilon_1$  associated with  $\hat{r}_{\epsilon_1}$ . Since  $Q$  is a continuous operator and  $Q(\mathbf{0}) = \mathbf{0}$ , there exists  $\delta > 0$  such that  $Q(\psi) > (\mathcal{L} - \epsilon_1)(\psi)$  for all  $\psi \in X_+ \times X_+$  with  $\|\psi\| < \delta$ .



*Claim.* For any initial condition  $\phi \in X_+ \times X_+$  with  $\phi > \mathbf{0}$ ,

$$\limsup_{n \rightarrow \infty} \|Q^n(\phi)\| > \delta.$$

Indeed, if the claim is not true, then there exists  $\phi_0 > \mathbf{0}$  such that  $\limsup_{n \rightarrow \infty} \|Q^n(\phi_0)\| < \delta$ . Then there exists  $N_0 > 0$  such that  $\|Q^n(\phi_0)\| < \delta$  for all  $n \geq N_0$ . Note that when  $N_0$  is large,  $Q^{N_0}(\phi_0) \gg \mathbf{0}$ . There exists  $\theta > 0$  such that  $Q^{N_0}(\phi_0) > \theta \phi_{\epsilon_1}^*$ . Then

$$Q^n(\phi_0) = Q^{n-N_0}(Q^{N_0}(\phi_0)) > (\mathcal{L} - \epsilon_1)^{n-N_0}(\theta \phi_{\epsilon_1}^*) = \theta \hat{r}_{\epsilon_1}^{n-N_0} \phi_{\epsilon_1}^*$$

and hence,  $Q^n(\phi_0) \rightarrow \infty$  when  $n \rightarrow \infty$ , a contradiction. This proves the claim.

Define a continuous function  $p : X_+ \times X_+ \rightarrow [0, \infty)$  by

$$p(V_0) := \min\left\{\min_{x \in [0, L]} J_0(x), \min_{x \in [0, L]} A_0(x)\right\}, \forall V_0 = (J_0, A_0) \in X_+ \times X_+.$$

Then  $p^{-1}(0, \infty) \subseteq X_+ \times X_+ \setminus \{\mathbf{0}\}$  and  $p$  has the property that if  $p(V_0) > 0$  or  $p(V_0) = 0$  with  $V_0 \in X_+ \times X_+ \setminus \{\mathbf{0}\}$ , then  $p(Q^n(V_0)) > 0$  for all  $n = 1, 2, \dots$ . That is,  $p$  is a generalized distance function for the map  $Q$  (see [18]).

Note that for any  $\psi \in X_+ \times X_+$ ,  $Q^n(\psi) \in [\mathbf{0}, \mathbf{M}]$  for all  $n = 1, 2, \dots$ . By Lemma 3.3,  $Q$  is asymptotically smooth on  $[\mathbf{0}, \mathbf{M}]$ . Then [26, Theorem 1.1.2] implies that  $Q$  has a global attractor  $A \subset [\mathbf{0}, \mathbf{M}]$ . By applying [18, Theorem 3] and using the fact  $Q : X_+ \times X_+ \rightarrow [\mathbf{0}, \mathbf{M}]$ , it follows that  $Q$  is uniformly persistent in the sense that there exists an  $\xi > 0$  such that

$$\liminf_{n \rightarrow \infty} p(Q^n(V_0)) \geq \xi, \forall V_0 \in X_+ \times X_+ \setminus \{\mathbf{0}\}.$$

Thus, for any  $V_0 \in X_+ \times X_+ \setminus \{\mathbf{0}\}$ ,

$$\liminf_{n \rightarrow \infty} (J(x, n), A(x, n)) \geq (\xi, \xi)$$

uniformly for  $x \in [0, L]$ .

Since  $Q$  is uniform persistent and has a global attractor in  $X_+ \times X_+$ , it follows from [14, Theorem 3.7] that  $Q : X_+ \times X_+ \setminus \{\mathbf{0}\} \rightarrow X_+ \times X_+ \setminus \{\mathbf{0}\}$  has a global attractor  $A_0 \subset [\mathbf{0}, \mathbf{M}] \setminus \{\mathbf{0}\}$ . Since  $Q$  is  $\alpha$ -condensing on  $[\mathbf{0}, \mathbf{M}]$  (see Lemma 3.3), it then follows from [14, Theorem 4.1] that  $Q$  has a fixed point  $V^* \in [\mathbf{0}, \mathbf{M}] \setminus \{\mathbf{0}\}$ , i.e.,  $Q(V^*) = V^*$ . Further, by the definition of  $Q$ , we can easily see that  $V^* \gg \mathbf{0}$ .  $\square$

Now we establish the relation between  $\hat{r}$  and the net reproductive rate  $R_0$  defined in [10]. For  $y \in [0, L]$ , let  $k(x, y)$  represent the probability density that a larva reproduced at location  $y$  settles down at location  $x$  during the dispersal interval  $[0, \tau]$ . That is,

$$k(x, y) = h(x)\sigma(x) \int_0^\tau \Phi_{\bar{t}}\left(\frac{\delta(\cdot - y)}{h(\cdot)}\right)(x) d\bar{t}. \quad (14)$$

Then (5) can be rewritten as

$$\begin{aligned} J(x, n+1) &= \varphi(x, n) s_l(x) \int_0^L k(x, y) r(y) A(y, n) dy, & x \in (0, L), n = 0, 1, 2, \dots, \\ A(x, n+1) &= \varphi(x, n) [s_j(x) J(x, n) + s_a(x) A(x, n)], & x \in (0, L), n = 0, 1, 2, \dots, \\ J(x, 0) &= J_0(x), A(x, 0) = A_0(x), & x \in (0, L), \end{aligned} \quad (15)$$

and the linear operator  $\mathcal{L} = DQ(0)$  becomes

$$[\mathcal{L}(\psi)](x) = \begin{pmatrix} s_l(x) \int_0^L k(x, y) r(y) \psi_2(y) dy \\ s_j(x) \psi_1(x) + s_a(x) \psi_2(x) \end{pmatrix}, \forall \psi = (\psi_1, \psi_2) \in X \times X. \quad (16)$$

For an initial distribution of adults  $A_0(x)$ , the distribution of the associated next generation adults is then given as

$$(\Gamma A_0)(x) = s_l(x)s_j(x) \int_0^L \frac{r(y)}{1-s_a(y)} A_0(y)k(x,y)dy, \quad x \in [0, L], \quad (17)$$

where  $\Gamma$  is called the next generation operator. Let

$$R_0 = \text{spr}(\Gamma) \quad (18)$$

be the spectral radius of  $\Gamma$  on  $X$ . Then  $R_0$  is called the net reproductive rate and biologically represents the average number of offspring an individual may produce during its lifetime. In [10],  $R_0$  was used to be the threshold for population persistence. That is, it was assumed (without proof) that the population persists if  $R_0 > 1$  and the population will be extinct if  $R_0 < 1$ . To confirm this statement, we need the following observation.

**Lemma 3.5.**  $R_0 - 1$  and  $\hat{r} - 1$  have the same sign.

*Proof.* Define  $\mathcal{M} : X \times X \rightarrow X \times X$  and  $\mathcal{N} : X \times X \rightarrow X \times X$  by

$$(\mathcal{M}\psi)(x) = \begin{pmatrix} s_l(x) \int_0^L k(x,y)r(y)\psi_2(y)dy \\ s_j(x)\psi_1(x) \end{pmatrix}, \quad (\mathcal{N}\psi)(x) = \begin{pmatrix} 0 \\ s_a(x)\psi_2(x) \end{pmatrix},$$

for all  $\psi = (\psi_1, \psi_2) \in X \times X$ . Clearly,  $\mathcal{L} = \mathcal{M} + \mathcal{N}$  and  $\text{spr}(\mathcal{N}) < 1$ , where  $\text{spr}(\mathcal{N})$  is the spectral radius of  $\mathcal{N}$ . Note that  $(I - \mathcal{N})^{-1}(\psi)(x) = \begin{pmatrix} \psi_1(x) \\ \frac{1}{1-s_a(x)}\psi_2(x) \end{pmatrix}$  for  $\psi = (\psi_1, \psi_2) \in X \times X$ . By [19, Theorem 3.10], it follows that

$$\text{sgn}(\hat{r} - 1) = \text{sgn}(\text{spr}(\mathcal{L}) - 1) = \text{sgn}(\text{spr}(\mathcal{M}(I - \mathcal{N})^{-1}) - 1). \quad (19)$$

It is easy to see that

$$\mathcal{M}(I - \mathcal{N})^{-1}(\psi)(x) = \begin{pmatrix} s_l(x) \int_0^L k(x,y)r(y)\frac{1}{1-s_a(y)}\psi_2(y)dy \\ s_j(x)\psi_1(x) \end{pmatrix} = \begin{pmatrix} (A\psi_2)(x) \\ (B\psi_1)(x) \end{pmatrix},$$

where  $(A\psi_2)(x) = s_l(x) \int_0^L k(x,y)r(y)\frac{1}{1-s_a(y)}\psi_2(y)dy$  and  $(B\psi_1)(x) = s_j(x)\psi_1(x)$ .

This implies that  $(\mathcal{M}(I - \mathcal{N})^{-1})^2(\psi) = \begin{pmatrix} (A \circ B)(\psi_1) \\ (B \circ A)(\psi_2) \end{pmatrix}$ . Since  $\text{spr}(A \circ B) = \text{spr}(B \circ A)$  and  $\Gamma = B \circ A$ , we have

$$\begin{aligned} (\text{spr}((\mathcal{M}(I - \mathcal{N})^{-1}))^2) &= \text{spr}((\mathcal{M}(I - \mathcal{N})^{-1})^2) \\ &= \max(\text{spr}(A \circ B), \text{spr}(B \circ A)) \\ &= \text{spr}(B \circ A) \\ &= \text{spr}(\Gamma) = R_0, \end{aligned}$$

and hence,  $\text{spr}(\mathcal{M}(I - \mathcal{N})^{-1}) = R_0^{\frac{1}{2}}$ . It then follows from (19) that  $\text{sgn}(\hat{r} - 1) = \text{sgn}(R_0^{\frac{1}{2}} - 1) = \text{sgn}(R_0 - 1)$ .  $\square$

**Remark 2.** According to [20, Remark 3],  $T_{\mathcal{M}} := \text{spr}(\mathcal{M}(I - \mathcal{N})^{-1})$  is the target reproduction ratio associated with the linear operator  $\mathcal{L}$ . Thus, one can use [20, Theorem 7] and the bisection method to compute  $T_{\mathcal{M}}$  numerically, and hence  $R_0 = T_{\mathcal{M}}^2$ .

As a consequence of Theorem 3.4 and Lemma 3.5, we have the following threshold type result on the persistence dynamics in terms of  $R_0$ .

**Theorem 3.6.** Let  $R_0$  be the net reproductive rate defined in (18). Then the following statements are valid for model (5):

- (i) If  $R_0 < 1$ , then the population goes extinct for any initial distribution.
- (ii) If  $R_0 > 1$ , then the population persists for any nonzero initial distribution.

**Remark 3.** If the linear reproduction  $r(x)A(x, n)$  in (3) is replaced with a general recruitment (differentiable) function  $f(A(x, n))$  such that

$$f(0) = 0, f(u) \leq f'(0)u, |f(u) - f(v)| \leq f'(0)|u - v|, \forall u, v \geq 0,$$

then  $Q$  and  $\mathcal{L} = DQ(\mathbf{0})$ , respectively, become

$$Q(\psi)(x) = \left( \frac{s_l(x)h(x)\sigma(x) \int_0^\tau \left[ \Phi_{\bar{t}} \left( \frac{f(\psi_2(\cdot))}{h(\cdot)} \right) \right] (x) d\bar{t}}{1 + \gamma \left[ l_l h(x)\sigma(x) \int_0^\tau \left[ \Phi_{\bar{t}} \left( \frac{f(\psi_2(\cdot))}{h(\cdot)} \right) \right] (x) d\bar{t} + l_j \psi_1(x) + l_a \psi_2(x) \right]} \right. \\ \left. \frac{s_j(x)\psi_1(x) + s_a(x)\psi_2(x)}{1 + \gamma \left[ l_l h(x)\sigma(x) \int_0^\tau \left[ \Phi_{\bar{t}} \left( \frac{f(\psi_2(\cdot))}{h(\cdot)} \right) \right] (x) d\bar{t} + l_j \psi_1(x) + l_a \psi_2(x) \right]} \right) \quad (20)$$

and

$$\mathcal{L}(\psi)(x) = \left( \frac{s_l(x)h(x)\sigma(x) \int_0^\tau \left[ \Phi_{\bar{t}} \left( \frac{f'(0)}{h(\cdot)} \psi_2(\cdot) \right) \right] (x) d\bar{t}}{s_j(x)\psi_1(x) + s_a(x)\psi_2(x)} \right), \quad (21)$$

for any  $\psi = (\psi_1, \psi_2) \in X \times X$ . All the results in this section hold true if  $r(\cdot)$  is replaced with  $f'(0)$ , given slight adjustments in the proofs. In particular, if  $f$  is a logistic function, then all the results are valid.

**4. Population spread in an unbounded habitat.** In this section, we study the spatial spread of the zebra mussel in an infinitely long river (that is,  $\Omega = \mathbb{R}$  in (1)). For simplicity, assume that all parameters are spatially independent. Then model (1) becomes

$$\begin{aligned} u_t &= Du_{xx} - vu_x - mu - \sigma u, & x \in \mathbb{R}, t \in (0, \tau], \\ w_t &= h\sigma u, & x \in \mathbb{R}, t \in (0, \tau], \\ u(x, 0) &= \frac{r}{h} A(x, n), w(x, 0) = 0, & x \in \mathbb{R}, \\ J(x, n+1) &= \varphi(x, n) s_l w(x, \tau), & x \in \mathbb{R}, n = 0, 1, 2, \dots, \\ A(x, n+1) &= \varphi(x, n) [s_j J(x, n) + s_a A(x, n)], & x \in \mathbb{R}, n = 0, 1, 2, \dots, \\ J(x, 0) &= J_0(x), A(x, 0) = A_0(x), & x \in \mathbb{R}, \end{aligned} \quad (22)$$

where  $v = P/S$  represents the advection rate for larvae and

$$\varphi(x, n) = \frac{1}{1 + \gamma [l_l w(x, \tau) + l_j J(x, n) + l_a A(x, n)]}.$$

**4.1. The non-dispersal model.** In a spatially homogeneous habitat without population dispersal, model (22) becomes

$$\begin{aligned} \frac{du}{dt} &= -mu - \sigma u, & t \in (0, \tau], \\ \frac{dw}{dt} &= h\sigma u, & t \in (0, \tau], \\ u(0) &= \frac{r}{h} A(n), w(0) = 0, \\ J(n+1) &= \varphi(n) s_l w(\tau), & n = 0, 1, 2, \dots, \\ A(n+1) &= \varphi(n) [s_j J(n) + s_a A(n)], & n = 0, 1, 2, \dots, \\ J(0) &= J_0, A(0) = A_0, \end{aligned} \quad (23)$$

which leads to

$$\begin{aligned} J(n+1) &= \frac{\frac{s_l \sigma r}{m+\sigma} (1 - e^{-(m+\sigma)\tau}) A(n)}{1 + \gamma \left[ l_l \frac{\sigma r A(n)}{m+\sigma} (1 - e^{-(m+\sigma)\tau}) + l_j J(n) + l_a A(n) \right]} = \frac{a A(n)}{1 + b J(n) + c A(n)}, \\ A(n+1) &= \frac{s_j J(n) + s_a A(n)}{1 + \gamma \left[ l_l \frac{\sigma r A(n)}{m+\sigma} (1 - e^{-(m+\sigma)\tau}) + l_j J(n) + l_a A(n) \right]} = \frac{s_j J(n) + s_a A(n)}{1 + b J(n) + c A(n)}, \\ J(0) &= J_0, A(0) = A_0, \end{aligned} \quad (24)$$

where

$$a = \frac{s_l \sigma r}{m+\sigma} (1 - e^{-(m+\sigma)\tau}), b = \gamma l_j, c = \gamma l_l \frac{\sigma r}{m+\sigma} (1 - e^{-(m+\sigma)\tau}) + \gamma l_a. \quad (25)$$

Note that  $(J_0, A_0) \in \mathbb{R}_+^2$ . In the following, we use notation  $[\mathbf{0}, \eta]$  to represent all vectors between  $\mathbf{0}$  and  $\eta$  in  $\mathbb{R}_+^2$ , for  $\eta \in \mathbb{R}_+^2$ .

The linearized system of (24) at the trivial solution is

$$\begin{aligned} J(n+1) &= a A(n), \\ A(n+1) &= s_j J(n) + s_a A(n). \end{aligned} \quad (26)$$

The eigenvalues of the Jacobian matrix  $\begin{pmatrix} 0 & a \\ s_j & s_a \end{pmatrix}$  associated with (26) are

$$\lambda_1^0 = \frac{(s_a + \sqrt{s_a^2 + 4s_j a})}{2}, \lambda_2^0 = \frac{(s_a - \sqrt{s_a^2 + 4s_j a})}{2}. \quad (27)$$

Note that  $\lambda_1^0 > 0$ ,  $\lambda_2^0 < 0$  and  $0 < |\lambda_2^0| < \lambda_1^0$ . If  $\lambda_1^0 < 1$ , then  $|\lambda_2^0| < 1$  and the trivial solution is asymptotically stable for (24). If  $\lambda_1^0 > 1$ , then the trivial solution is unstable for (24). When  $\lambda_1^0 > 1$ , (24) admits a unique positive fixed point

$$\beta^* = (\beta_1^*, \beta_2^*) = \left( \frac{(\lambda_1^0 - 1)a}{ab + c\lambda_1^0}, \frac{\lambda_1^0(\lambda_1^0 - 1)}{ab + c\lambda_1^0} \right). \quad (28)$$

Let  $Q_1 : \mathbb{R}^2 \rightarrow \mathbb{R}^2$  be defined as

$$Q_1(\phi) = \begin{pmatrix} \frac{a\phi_2}{1 + b\phi_1 + c\phi_2} \\ \frac{s_j\phi_1 + s_a\phi_2}{1 + b\phi_1 + c\phi_2} \end{pmatrix}, \quad \phi = (\phi_1, \phi_2) \in \mathbb{R}^2.$$

For  $\phi, \psi \in \mathbb{R}^2$ , we have

$$Q_1(\phi) - Q_1(\psi) = \begin{pmatrix} \frac{-ab(\phi_1\psi_2 - \phi_2\psi_1) + a(\phi_2 - \psi_2)}{(1 + b\phi_1 + c\phi_2)(1 + b\psi_1 + c\psi_2)} \\ \frac{-(bs_a - cs_j)(\phi_1\psi_2 - \phi_2\psi_1) + s_a(\phi_2 - \psi_2) + s_j(\phi_1 - \psi_1)}{(1 + b\phi_1 + c\phi_2)(1 + b\psi_1 + c\psi_2)} \end{pmatrix}.$$

If  $\phi \geq \psi$ , then we cannot always obtain  $Q_1(\phi) \geq Q_1(\psi)$ . Thus,  $Q_1$  is non-monotone, and hence, (24) is a non-monotone system.

For the comparison purpose, for  $\phi = (\phi_1, \phi_2) \in \mathbb{R}_+^2$ , we define

$$Q_1^+(\phi) = \begin{pmatrix} \frac{a\phi_2}{1 + c\phi_2} \\ \frac{s_j\phi_1 + s_a\phi_2}{1 + b\beta_1^* + c\beta_2^*} \end{pmatrix} \quad \text{and} \quad Q_1^-(\phi) = \begin{pmatrix} \frac{a\phi_2}{1 + b\beta_1^* + c\beta_2^*} \\ \frac{s_j\phi_1 + s_a\phi_2}{1 + b\beta_1^* + c\beta_2^*} \end{pmatrix}. \quad (29)$$

Then

$$Q_1^-(\phi) \leq Q_1(\phi), \quad \forall \phi \in [0, \beta^*]; \quad Q_1(\phi) \leq Q_1^+(\phi), \quad \forall \phi \geq 0. \quad (30)$$

Moreover, if  $\lambda_1^0 > 1$ ,  $Q_1^+$  has a unique positive fixed point

$$\beta_+^* = (\beta_{1+}^*, \beta_{2+}^*) = \left( \frac{(\lambda_1^0 - 1)(\lambda_1^0 + 1 - s_a)}{cs_j}, \frac{(\lambda_1^0 - 1)(\lambda_1^0 + 1 - s_a)}{c(1 - s_a)} \right) \quad (31)$$

and  $Q_1^-$  has a unique positive fixed point  $\beta_-^* = (\beta_{1-}^*, \beta_{2-}^*) = (\beta_1^*, \beta_2^*)$  with  $\beta_{1-}^* = \beta_1^* < \beta_{1+}^*$ ,  $\beta_{2-}^* = \beta_2^* < \beta_{2+}^*$ .

The linearized system of  $\phi_{n+1} = Q_1^+(\phi_n)$  at the trivial solution is the same as (26) and  $DQ_1^+(\mathbf{0}) = \begin{pmatrix} 0 & a \\ s_j & s_a \end{pmatrix}$ . We then have the following result for  $Q_1^+$ .

**Lemma 4.1.** *The following statements are valid:*

- (i) *If  $\lambda_1^0 \leq 1$ , then every positive orbit of  $Q_1^+$  in  $\mathbb{R}_+^2$  converges to  $\mathbf{0}$ ;*
- (ii) *If  $\lambda_1^0 > 1$ , then every positive orbit of  $Q_1^+$  in  $[\mathbf{0}, \beta_+^*] \setminus \{\mathbf{0}\}$  converges to  $\beta_+^*$ .*

*Proof.* By the definition of  $Q_1^+$ , we have

$$(Q_1^+)^2(\phi) = \begin{pmatrix} \frac{a(s_j\phi_1 + s_a\phi_2)}{1 + c(s_j\phi_1 + s_a\phi_2)} \\ s_j \frac{a\phi_2}{1 + c\phi_2} + s_a(s_j\phi_1 + s_a\phi_2) \end{pmatrix}, \phi \in \mathbb{R}_+^2.$$

For  $\phi, \psi \in \mathbb{R}_+^2$  with  $\phi > \psi$ ,

$$\begin{aligned} (Q_1^+)^2(\phi) - (Q_1^+)^2(\psi) &= \begin{pmatrix} \frac{a(s_j(\phi_1 - \psi_1) + s_a(\phi_2 - \psi_2))}{(1 + c(s_j\phi_1 + s_a\phi_2))(1 + c(s_j\psi_1 + s_a\psi_2))} \\ s_j a \frac{(\phi_2 - \psi_2)}{(1 + c\phi_2)(1 + c\psi_2)} + s_a(s_j(\phi_1 - \psi_1) + s_a(\phi_2 - \psi_2)) \end{pmatrix} \\ &\gg \mathbf{0}. \end{aligned}$$

For  $\phi \in \mathbb{R}_+^2$  with  $\phi \gg \mathbf{0}$  and  $\nu \in (0, 1)$ ,

$$\begin{aligned} &(Q_1^+)^2(\nu\phi) - \nu(Q_1^+)^2(\phi) \\ &= \begin{pmatrix} a\nu(s_j\phi_1 + s_a\phi_2) \left( \frac{1}{1 + c\nu(s_j\phi_1 + s_a\phi_2)} - \frac{1}{1 + c(s_j\phi_1 + s_a\phi_2)} \right) \\ s_j a \nu \phi_2 \left( \frac{1}{1 + c\nu\phi_2} - \frac{1}{1 + c\phi_2} \right) \end{pmatrix} \\ &\gg \mathbf{0}. \end{aligned}$$

Therefore,  $(Q_1^+)^2$  is strongly monotone and strictly subhomogeneous in  $\mathbb{R}_+^2$ . Note that  $D(Q_1^+)^2(\mathbf{0}) = (D(Q_1^+(\mathbf{0})))^2$ , and the spectral radii of these two matrices satisfy  $\text{spr}(D(Q_1^+)^2(\mathbf{0})) = \text{spr}((D(Q_1^+(\mathbf{0})))^2) = (\lambda_1^0)^2$ . Note that  $\beta_+^*$  is also a positive fixed point of  $(Q_1^+)^2$  when  $\lambda_1^0 > 1$ . By [26, Theorem 2.3.4], it follows that (1) if  $\lambda_1^0 \leq 1$ , then  $((Q_1^+)^2)^n(\phi) \rightarrow \mathbf{0}$  as  $n \rightarrow \infty$  for all  $\phi \in \mathbb{R}_+^2$ ; (2) if  $\lambda_1^0 > 1$ , then  $\beta_+^*$  is the unique positive fixed point of  $(Q_1^+)^2$  and  $((Q_1^+)^2)^n(\phi) \rightarrow \beta_+^*$  as  $n \rightarrow \infty$  for all  $\phi \in \mathbb{R}_+^2 \setminus \{\mathbf{0}\}$ . In case (1), for  $\phi \in \mathbb{R}_+^2$ , we have  $((Q_1^+)^2)^n(Q_1^+(\phi)) = (Q_1^+)^{2n+1}(\phi) \rightarrow \mathbf{0}$  as  $n \rightarrow \infty$ . It then follows that  $(Q_1^+)^n(\phi) \rightarrow \mathbf{0}$  as  $n \rightarrow \infty$  for all  $\phi \in \mathbb{R}_+^2$ . In case (2), for  $\phi \in \mathbb{R}_+^2 \setminus \{\mathbf{0}\}$ , we obtain  $Q_1^+(\phi) \in \mathbb{R}_+^2 \setminus \{\mathbf{0}\}$  and  $((Q_1^+)^2)^n(Q_1^+(\phi)) = (Q_1^+)^{2n+1}(\phi) \rightarrow \beta_+^*$  as  $n \rightarrow \infty$ . Thus,  $(Q_1^+)^n(\phi) \rightarrow \beta_+^*$  as  $n \rightarrow \infty$  for all  $\phi \in \mathbb{R}_+^2 \setminus \{\mathbf{0}\}$ .  $\square$

The linearized system of  $\phi_{n+1} = Q_1^-(\phi_n)$  at the trivial solution is

$$\begin{aligned} \phi_1(n+1) &= \frac{a\phi_2(n)}{1 + b\beta_1^*}, \\ \phi_2(n+1) &= \frac{s_j\phi_1(n) + s_a\phi_2(n)}{1 + b\beta_1^* + c\beta_2^*} \end{aligned} \quad (32)$$

and  $DQ_1^-(\mathbf{0}) = \begin{pmatrix} 0 & \frac{a}{1+b\beta_1^*} \\ \frac{s_j}{1+b\beta_1^*+c\beta_2^*} & \frac{s_a}{1+b\beta_1^*+c\beta_2^*} \end{pmatrix}$ . Let  $\lambda_{1-}^0$  and  $\lambda_{2-}^0$  be the two eigenvalues of  $DQ_1^-(\mathbf{0})$  with  $\lambda_{1-}^0 > 0$ ,  $\lambda_{2-}^0 < 0$  and  $0 < |\lambda_{2-}^0| < \lambda_{1-}^0$ . We can show that  $\lambda_{1-}^0 > 1$  if and only if  $\lambda_1^0 > 1$ . Using similar arguments as in Lemma 4.1, we have the following result for  $Q_1^-$ .

**Lemma 4.2.** *The following statements are valid:*

- (i) *If  $\lambda_1^0 \leq 1$ , then every positive orbit of  $Q_1^-$  in  $\mathbb{R}_+^2$  converges to  $\mathbf{0}$ ;*
- (ii) *If  $\lambda_1^0 > 1$ , then every positive orbit of  $Q_1^-$  in  $[\mathbf{0}, \beta^*] \setminus \{\mathbf{0}\}$  converges to  $\beta^*$ .*

By applying (30) and Lemmas 4.1 and 4.2, we have the following threshold result for system (24).

**Lemma 4.3.** *The following statements hold true for system (24):*

- (i) *If  $\lambda_1^0 \leq 1$ , then  $\lim_{n \rightarrow \infty} (J_n, A_n) = \mathbf{0}$  for any nonnegative initial condition  $(J_0, A_0) \in \mathbb{R}_+^2$ .*
- (ii) *If  $\lambda_1^0 > 1$ , then  $\beta^* \leq \liminf_{n \rightarrow \infty} (J_n, A_n) \leq \limsup_{n \rightarrow \infty} (J_n, A_n) \leq \beta_+^*$  for initial condition  $(J_0, A_0) \in [\mathbf{0}, \beta^*] \setminus \{\mathbf{0}\}$ .*

Lemma 4.3 implies that system (24) is uniformly persistent when  $\lambda_1^0 > 1$  (or equivalently, when  $as_j + s_a - 1 > 0$ ).

**4.2. The propagation dynamics.** We start with a reduction of the spatial model (22) to a discrete-time system.

As in section 2, we let  $\Psi_t : C(\mathbb{R}, \mathbb{R}) \rightarrow C(\mathbb{R}, \mathbb{R})$  be the solution map of

$$\bar{u}_t = D\bar{u}_{xx} - v\bar{u}_x - m\bar{u} - \sigma\bar{u}, \quad x \in \mathbb{R}, \quad t > 0. \quad (33)$$

Then model (22) yields

$$\begin{aligned} u(x, t) &= \left[ \Psi_t \left( \frac{r}{h} A(\cdot, n) \right) \right] (x), \\ &= \frac{1}{\sqrt{4D\pi t}} e^{(-\frac{v^2 t}{4D} - (m+\sigma)t)} \int_{-\infty}^{\infty} e^{(-\frac{(x-y)^2}{4Dt} + \frac{v(x-y)}{2D})} \frac{rA(y, n)}{h} dy, \\ w(x, t) &= h\sigma \int_0^t \left[ \Psi_{\bar{t}} \left( \frac{r}{h} A(\cdot, n) \right) \right] (x) d\bar{t}, \\ &= \int_0^t \frac{r\sigma}{\sqrt{4D\pi \bar{t}}} e^{(-\frac{v^2 \bar{t}}{4D} - (m+\sigma)\bar{t})} \int_{-\infty}^{\infty} e^{(-\frac{(x-y)^2}{4D\bar{t}} + \frac{v(x-y)}{2D})} A(y, n) dy d\bar{t}, \\ &= r\sigma \int_{-\infty}^{\infty} A(y, n) e^{\frac{v(x-y)}{2D}} \int_0^t \frac{1}{\sqrt{4D\pi \bar{t}}} e^{(-\frac{v^2 \bar{t}}{4D} - (m+\sigma)\bar{t} - \frac{(x-y)^2}{4D\bar{t}})} d\bar{t} dy, \end{aligned}$$

for  $x \in \mathbb{R}$ ,  $t \in (0, \tau]$ . Moreover,  $J$  and  $A$  satisfy the following discrete system:

$$\begin{cases} J(x, n+1) = \frac{s_l h \sigma \int_0^\tau \left[ \Psi_{\bar{t}} \left( \frac{r}{h} A(\cdot, n) \right) \right] (x) d\bar{t}}{1 + \gamma \left[ l_l h \sigma \int_0^\tau \left[ \Psi_{\bar{t}} \left( \frac{r}{h} A(\cdot, n) \right) \right] (x) d\bar{t} + l_j J(x, n) + l_a A(x, n) \right]}, \\ A(x, n+1) = \frac{s_j J(x, n) + s_a A(x, n)}{1 + \gamma \left[ l_l h \sigma \int_0^\tau \left[ \Psi_{\bar{t}} \left( \frac{r}{h} A(\cdot, n) \right) \right] (x) d\bar{t} + l_j J(x, n) + l_a A(x, n) \right]}, \\ J(x, 0) = J_0(x), \quad A(x, 0) = A_0(x), \end{cases} \quad (34)$$

for  $x \in \mathbb{R}$  and  $n = 0, 1, 2, \dots$ .

**Remark 4.** If we use  $K(x, y)$  to represent the probability that a larva reproduced at location  $y$  settles down at location  $x$  during its dispersal interval  $[0, \tau]$ , then

$$K(x, y) = \sigma e^{\frac{v(x-y)}{2D}} \int_0^\tau \frac{1}{\sqrt{4D\pi t}} e^{\left(-\frac{v^2 t}{4D} - (m+\sigma)t - \frac{(x-y)^2}{4Dt}\right)} d\bar{t}$$

and  $w(x, \tau) = r \int_{-\infty}^\infty A(y, n) K(x, y) dy$ , Hence, model (34) can be rewritten accordingly. An estimation of  $K(x, y)$  was obtained in [10] based on the assumption  $u(x, \tau) = 0$ .

In order to study the propagation dynamics of model (34), in the rest of this section we always assume that

$$(H) \quad \lambda_1^0 > 1.$$

Let  $\mathcal{C}$  be the set of all bounded and continuous functions from  $\mathbb{R}$  to  $\mathbb{R}^2$ . For  $\phi, \psi \in \mathcal{C}$ , we write  $\phi \geq (\gg) \psi$  if  $\phi(x) \geq (>) \psi(x)$  for all  $x \in \mathbb{R}$ , and  $\phi > \psi$  if  $\phi \geq \psi$  but  $\phi \neq \psi$ . Let  $\mathcal{C}_+ = \{\phi \in \mathcal{C} : \phi(x) \geq \mathbf{0}, \forall x \in \mathbb{R}\}$ . We also equip  $\mathcal{C}$  with the compact open topology in which sense  $\phi^n \rightarrow \phi$  as  $n \rightarrow \infty$  for  $\phi^n, \phi \in \mathcal{C}$  means that  $\phi^n(x)$  converges to  $\phi(x)$  as  $n$  tends to  $\infty$  uniformly in any compact set on  $\mathbb{R}$ . For any given  $\vartheta \in \mathbb{R}^2$  with  $\vartheta \gg \mathbf{0}$ , let  $\mathcal{C}_\vartheta = \{\phi \in \mathcal{C} : \mathbf{0} \leq \phi(x) \leq \vartheta, \forall x \in \mathbb{R}\}$ .

Let  $V_n(x) = (J(x, n), A(x, n))$ . Then system (34) can be written as

$$V_{n+1}(x) = [Q(V_n)](x), \quad \forall x \in \mathbb{R}, \quad n = 0, 1, 2, \dots,$$

where the operator  $Q$  is defined by the right-hand side of (34). That is,

$$Q(\phi)(x) = \begin{pmatrix} \frac{s_l h \sigma \int_0^\tau [\Psi_{\bar{t}}(\frac{r}{h} \phi_2(\cdot))] (x) d\bar{t}}{1 + \gamma [l_l h \sigma \int_0^\tau [\Psi_{\bar{t}}(\frac{r}{h} \phi_2(\cdot))] (x) d\bar{t} + l_j \phi_1(x) + l_a \phi_2(x)]} \\ \frac{s_j \phi_1(x) + s_a \phi_2(x)}{1 + \gamma [l_l h \sigma \int_0^\tau [\Psi_{\bar{t}}(\frac{r}{h} \phi_2(\cdot))] (x) d\bar{t} + l_j \phi_1(x) + l_a \phi_2(x)]} \end{pmatrix} \quad (35)$$

for  $\phi = (\phi_1, \phi_2) \in \mathcal{C}$ . Similarly as  $Q_1$  and (24), we also see that  $Q$  and (34) are non-monotone. Note that  $Q(\mathbf{0}) = \mathbf{0}$  and the Frechet derivative

$$\mathcal{L} := DQ(\mathbf{0}) \quad (36)$$

is expressed as

$$[\mathcal{L}(\phi)](x) = \begin{pmatrix} s_l h \sigma \int_0^\tau [\Psi_{\bar{t}}(\frac{r}{h} \phi_2(\cdot))] (x) d\bar{t} \\ s_j \phi_1(x) + s_a \phi_2(x) \end{pmatrix}, \quad \forall \phi = (\phi_1, \phi_2) \in \mathcal{C}.$$

Let

$$V_{n+1}^+(x) = [Q^+(V_n^+)](x), \quad \forall x \in \mathbb{R}, \quad n = 0, 1, 2, \dots, \quad (37)$$

where the operator  $Q^+$  is defined by

$$Q^+(\phi)(x) = \begin{pmatrix} \frac{s_l h \sigma \int_0^\tau [\Psi_{\bar{t}}(\frac{r}{h} \phi_2(\cdot))] (x) d\bar{t}}{1 + \gamma [l_l h \sigma \int_0^\tau [\Psi_{\bar{t}}(\frac{r}{h} \phi_2(\cdot))] (x) d\bar{t} + l_a \phi_2(x)]} \\ s_j \phi_1(x) + s_a \phi_2(x) \end{pmatrix}, \quad \forall \phi \in \mathcal{C}, \quad (38)$$

and

$$V_{n+1}^-(x) = [Q^-(V_n^-)](x), \quad \forall x \in \mathbb{R}, \quad n = 0, 1, 2, \dots, \quad (39)$$

where the operator  $Q^-$  is defined by

$$Q^-(\phi)(x) = \left( \frac{\frac{s_l h \sigma \int_0^\tau [\Psi_{\bar{t}}(\frac{r}{h} \phi_2(\cdot))] (x) d\bar{t}}{1 + \gamma [l_l h \sigma \int_0^\tau [\Psi_{\bar{t}}(\frac{r}{h} \phi_2(\cdot))] (x) d\bar{t} + l_j \beta_1^* + l_a \phi_2(x)]}}{s_j \phi_1(x) + s_a \phi_2(x)} \right) \frac{1}{1 + \gamma l_j \beta_1^* + (\gamma l_l \frac{\sigma r}{m+\sigma} (1 - e^{-(m+\sigma)\tau}) + \gamma l_a) \beta_2^*}, \quad \forall \phi \in \mathcal{C}. \quad (40)$$

Now we appeal to the theory developed in [6] and [12] to study the spreading speeds for systems (37) and (39). Accordingly, we have the following result.

**Theorem 4.4.** *System (37) has a spreading speed  $c_{down}^{+*}$  in the downstream direction and a spreading speed  $c_{up}^{+*}$  in the upstream direction in the sense that*

- (i) *if  $\phi \in \mathcal{C}_{\beta_+^*}$ , where  $\beta_+^*$  is the fixed point of  $Q_1^+$  defined in (31), has a compact support, then for any  $c > c_{down}^{+*}$ ,  $c' > c_{up}^{+*}$ , we have*

$$\lim_{n \rightarrow +\infty, x \geq cn} Q^{+n}(\phi)(x) = \mathbf{0} \text{ and } \lim_{n \rightarrow +\infty, x \leq -c'n} Q^{+n}(\phi)(x) = \mathbf{0}; \quad (41)$$

- (ii) *if  $\phi \in \mathcal{C}_{\beta_+^*}$  and  $\phi \neq \mathbf{0}$ , then for any  $c < c_{down}^{+*}$ ,  $c' < c_{up}^{+*}$ , we have*

$$\lim_{n \rightarrow +\infty, -c'n \leq x \leq cn} Q^{+n}(\phi)(x) = \beta_+^*. \quad (42)$$

Moreover,  $c_{down}^{+*}$  and  $c_{up}^{+*}$  are given by

$$c_{down}^{+*} = \inf_{\mu > 0} \frac{1}{\mu} \ln \frac{\left( s_a + \sqrt{s_a^2 + 4s_j s_l \sigma \gamma \frac{e^{(-m-\sigma+\mu v+\mu^2 D)\tau} - 1}{-m-\sigma+\mu v+\mu^2 D}} \right)}{2},$$

$$c_{up}^{+*} = \inf_{\mu > 0} \frac{1}{\mu} \ln \frac{\left( s_a + \sqrt{s_a^2 + 4s_j s_l \sigma \gamma \frac{e^{(-m-\sigma-\mu v+\mu^2 D)\tau} - 1}{-m-\sigma-\mu v+\mu^2 D}} \right)}{2}.$$

*Proof.* For any  $y \in \mathbb{R}$ , define the translation operator  $T_y$  as  $T_y(\phi)(x) = \phi(x - y)$ , for any  $\phi \in \mathcal{C}$  and  $x \in \mathbb{R}$ . By the form of (37), we have  $T_y \circ Q^+ = Q^+ \circ T_y$ , for all  $y \in \mathbb{R}$ . By following similar arguments as in [24, Lemma 3.1], we can prove that  $Q^+$  is continuous with respect to the compact open topology. Let  $k \in [0, 1)$  and  $U \subseteq \mathcal{C}_{\beta_+^*}$ . Then  $U(0)$  is a bounded set in  $\mathbb{R}^2$  and  $\alpha(U(0)) = 0$ . Moreover,  $Q^+(U)(0)$  is also a bounded set in  $\mathbb{R}^2$ . Hence,  $\alpha(Q^+(U)(0)) = \alpha(U(0)) = 0$  and the relation  $\alpha(Q^+(U)(0)) \leq k\alpha(U(0))$  is always true for  $k \in [0, 1)$  and  $U \subseteq \mathcal{C}_{\beta_+^*}$ . Let  $\phi, \psi \in \mathcal{C}_{\beta_+^*}$  with  $\phi \geq \psi$ . Then  $Q^+(\phi) \geq Q^+(\psi)$  follows from the definition of  $Q^+$ , and hence  $Q^+$  is monotone in  $\mathcal{C}_{\beta_+^*}$ . It follows from assumption (H) and Lemma 4.1 that  $Q^+ : [\mathbf{0}, \beta_+^*] \rightarrow [\mathbf{0}, \beta_+^*]$  admits two fixed points  $\mathbf{0}$  and  $\beta_+^*$  and for any  $\phi \in \mathcal{C}_{\beta_+^*}$  with  $\mathbf{0} \ll \phi \leq \beta_+^*$ , we have  $\lim_{n \rightarrow \infty} Q^{+n}(\phi)(x) = \beta_+^*$  uniformly for  $x \in \mathbb{R}$ . Then  $Q^+$  satisfies all conditions in [6, Remark 3.7], and hence the system (37) has a spreading  $c_{down}^{+*}$  in the downstream direction and a spreading speed  $c_{up}^{+*}$  in the upstream direction, satisfying (41) and (42).

Note that

$$DQ^+(\mathbf{0})(\phi)(x) = \left( \frac{s_l h \sigma \int_0^\tau [\Psi_{\bar{t}}(\frac{r}{h} \phi_2(\cdot))] (x) d\bar{t}}{s_j \phi_1(x) + s_a \phi_2(x)} \right), \quad \forall \phi \in \mathcal{C}_+, \forall x \in \mathbb{R}.$$



For  $\mu \in \mathbb{R}$ , we define

$$\begin{aligned} B_\mu^+ \begin{pmatrix} \varsigma_1 \\ \varsigma_2 \end{pmatrix} &:= \left[ DQ^+(\mathbf{0}) \left( \begin{pmatrix} \varsigma_1 \\ \varsigma_2 \end{pmatrix} e^{-\mu x} \right) \right] (0) \\ &= \begin{pmatrix} 0 & s_l \sigma \gamma \frac{e^{(-m-\sigma+\mu v+\mu^2 D)\tau}-1}{-m-\sigma+\mu v+\mu^2 D} \\ s_j & s_a \end{pmatrix} \begin{pmatrix} \varsigma_1 \\ \varsigma_2 \end{pmatrix}, \end{aligned}$$

for  $\begin{pmatrix} \varsigma_1 \\ \varsigma_2 \end{pmatrix} \in \mathbb{R}_+^2$ . Let  $\xi^+(\mu)$  be the principal eigenvalue of  $B_\mu^+$ . Then by [12, Proposition 3.9], the spreading speed of (37) in the downstream direction is given as

$$c_{down}^{+*} = \inf_{\mu>0} \frac{1}{\mu} \ln \xi^+(\mu) = \inf_{\mu>0} \frac{1}{\mu} \ln \frac{\left( s_a + \sqrt{s_a^2 + 4s_j s_l \sigma \gamma \frac{e^{(-m-\sigma+\mu v+\mu^2 D)\tau}-1}{-m-\sigma+\mu v+\mu^2 D}} \right)}{2}.$$

The spreading speed of (37) in the upstream direction can be similarly derived as

$$c_{up}^{+*} = \inf_{\mu>0} \frac{1}{\mu} \ln \xi^+(-\mu) = \inf_{\mu>0} \frac{1}{\mu} \ln \frac{\left( s_a + \sqrt{s_a^2 + 4s_j s_l \sigma \gamma \frac{e^{(-m-\sigma-\mu v+\mu^2 D)\tau}-1}{-m-\sigma-\mu v+\mu^2 D}} \right)}{2}.$$

□

Similarly, we have the following result for system (39).

**Theorem 4.5.** *System (39) has a spreading speed  $c_{down}^{-*}$  in the downstream direction and a spreading speed  $c_{up}^{-*}$  in the upstream direction in the sense that*

(i) *if  $\phi \in \mathcal{C}_{\beta^*}$  has a compact support, then for any  $c > c_{down}^{-*}$ ,  $c' > c_{up}^{-*}$ , we have*

$$\lim_{n \rightarrow +\infty, x \geq cn} Q^{-n}(\phi)(x) = \mathbf{0} \text{ and } \lim_{n \rightarrow +\infty, x \leq -c'n} Q^{-n}(\phi)(x) = \mathbf{0}; \quad (43)$$

(ii) *if  $\phi \in \mathcal{C}_{\beta^*}$  and  $\phi \neq \mathbf{0}$ , then for any  $c < c_{down}^{-*}$ ,  $c' < c_{up}^{-*}$ , we have*

$$\lim_{n \rightarrow +\infty, -c'n \leq x \leq cn} Q^{-n}(\phi)(x) = \beta^*. \quad (44)$$

Moreover,  $c_{down}^{-*}$  and  $c_{up}^{-*}$  are given by

$$c_{down}^{-*} = \inf_{\mu>0} \frac{1}{\mu} \ln \xi^-(\mu), \quad c_{up}^{-*} = \inf_{\mu>0} \frac{1}{\mu} \ln \xi^-(-\mu),$$

where

$$\begin{aligned} \xi^-(\mu) &= \frac{1}{\mu} \ln \left( \frac{s_a}{1+b\beta_1^*+c\beta_2^*} + \sqrt{\left( \frac{s_a}{1+b\beta_1^*+c\beta_2^*} \right)^2 + 4 \left( \frac{s_j}{1+b\beta_1^*+c\beta_2^*} \right) (s_l \sigma \gamma \frac{e^{(-m-\sigma+\mu v+\mu^2 D)\tau}-1}{(-m-\sigma+\mu v+\mu^2 D)(1+b\beta_1^*)})} \right) \end{aligned} \quad (45)$$

for  $\mu \in \mathbb{R} \setminus \{0\}$ .

*Proof.* The existence of spreading speeds  $c_{down}^{-*}$  and  $c_{up}^{-*}$  follows from similar arguments as in the proof in Theorem 4.4. Note that

$$DQ^-(\mathbf{0})(\phi)(x) = \begin{pmatrix} \frac{s_l h \sigma \int_0^\tau [\Psi_i(\frac{\tau}{h} \phi_2(\cdot))](x) d\bar{t}}{1+b\beta_1^*} \\ \frac{s_j \phi_1(x) + s_a \phi_2(x)}{1+b\beta_1^*+c\beta_2^*} \end{pmatrix}, \quad \forall \phi \in \mathcal{C}_+, \forall x \in \mathbb{R}.$$

For  $\mu \in \mathbb{R}$ , let

$$\begin{aligned} B_\mu^- \begin{pmatrix} \varsigma_1 \\ \varsigma_2 \end{pmatrix} &:= \left[ DQ^-(\mathbf{0}) \left( \begin{pmatrix} \varsigma_1 \\ \varsigma_2 \end{pmatrix} e^{-\mu x} \right) \right] (0) \\ &= \begin{pmatrix} 0 & s_l \sigma \gamma \frac{e^{(-m-\sigma+\mu v+\mu^2 D)\tau}-1}{(-m-\sigma+\mu v+\mu^2 D)(1+b\beta_1^*)} \\ \frac{s_j}{1+b\beta_1^*+c\beta_2^*} & \frac{s_a}{1+b\beta_1^*+c\beta_2^*} \end{pmatrix} \begin{pmatrix} \varsigma_1 \\ \varsigma_2 \end{pmatrix} \end{aligned}$$

for  $\begin{pmatrix} \varsigma_1 \\ \varsigma_2 \end{pmatrix} \in \mathbb{R}_+^2$ . Let  $\xi^-(\mu)$  be the principal eigenvalue of  $B_\mu^-$ . Then  $\xi^-(\mu)$  is given as in (45) and the formulae of  $c_{down}^*$  and  $c_{up}^*$  follow from the same process as in the proof of Theorem 4.4.  $\square$

Note that  $Q^-(\phi) \leq Q(\phi)$  for  $\phi \in \mathcal{C}_{\beta^*}$  and  $Q(\phi) \leq Q^+(\phi)$  for  $\phi \in \mathcal{C}_{\beta_+^*}$  and that  $c_{up}^{+*} < c_{down}^{+*}$ ,  $c_{up}^* < c_{down}^*$ ,  $c_{down}^* < c_{down}^{+*}$  and  $c_{up}^* < c_{up}^{+*}$ . By using the comparison arguments and Theorems 4.4 and 4.5, we can easily obtain the following result about the spreading of the zebra mussel population for system (34) or (22).

**Theorem 4.6.** *The following statements are valid for system (34):*

(i) *If  $\phi \in \mathcal{C}_{\beta^*}$  has a compact support, then for any  $c > c_{down}^{+*}$ ,  $c' > c_{up}^{+*}$ , we have*

$$\lim_{n \rightarrow +\infty, x \geq cn} Q^n(\phi)(x) = \mathbf{0} \text{ and } \lim_{n \rightarrow +\infty, x \leq -c'n} Q^n(\phi)(x) = \mathbf{0}.$$

(ii) *If  $\phi \in \mathcal{C}_{\beta^*} \setminus \{\mathbf{0}\}$ , then for any  $c < c_{down}^*$ ,  $c' < c_{up}^*$ , we have*

$$\beta^* \leq \liminf_{n \rightarrow +\infty, -c'n \leq x \leq cn} Q^n(\phi)(x) \leq \limsup_{n \rightarrow +\infty, -c'n \leq x \leq cn} Q^n(\phi)(x) \leq \beta_+^*.$$

(iii) *If  $\phi \in \mathcal{C}_{\beta^*} \setminus \{\mathbf{0}\}$  has a compact support, then for any  $c \in (c_{down}^*, c_{down}^{+*})$ ,  $c' \in (c_{up}^*, c_{up}^{+*})$ , we have*

$$0 \leq \liminf_{n \rightarrow +\infty, -c'n \leq x \leq cn} Q^n(\phi)(x) \leq \limsup_{n \rightarrow +\infty, -c'n \leq x \leq cn} Q^n(\phi)(x) \leq \beta_+^*.$$

**Remark 5.** By the fact that  $Q^-(\phi) \leq Q(\phi)$  for  $\phi \in \mathcal{C}_{\beta^*}$  and  $Q(\phi) \leq Q^+(\phi)$  for  $\phi \in \mathcal{C}_{\beta_+^*}$ , as well as Theorems 4.4-4.6, we see that  $c_{down}^*$  and  $c_{down}^{+*}$  are the lower bound and upper bound, respectively, of the invasion speed of the zebra mussel in the downstream direction and that  $c_{up}^*$  and  $c_{up}^{+*}$  are the lower bound and upper bound, respectively, of the invasion speed of the zebra mussel in the upstream direction.  $c_{down}^{+*}$  and  $c_{up}^{+*}$  are the spreading speeds used for (34) or (22) from linear determinacy in [10]. However, since we have not been able to construct an operator  $Q^-$  such that  $c_{down}^* = c_{down}^{+*}$  and  $c_{up}^* = c_{up}^{+*}$ , it remains an unsolved problem to verify that  $c_{down}^{+*}$  and  $c_{up}^{+*}$  are the spreading speeds of (34) or (22).

**5. Discussion.** In this paper, we revisited a zebra mussel derived in [10]. The authors there defined a net reproductive rate  $R_0$  to predict long-term population persistence or extinction and used the linear determinacy conjecture to estimate the asymptotic speed of spread of the population. Although the model operator and the associated linearized operator were non-compact, we were able to prove that they are  $\alpha$ -contractions with respect to the non-compactness measure, and hence, we can apply a generalized Krein-Rutman theorem (see [13, Lemma 2.3]) to show that the spectral radius  $\hat{r}$  of the linearized operator is also its principal eigenvalue with a positive eigenfunction if  $\hat{r} \geq 1$ . Hence,  $\hat{r}$  could be used to predict population persistence and extinction. We also established the equivalence of the sign of  $\hat{r} - 1$  and  $R_0 - 1$ , and hence, verified that  $R_0$  can be mathematically used to describe

the long-term behavior of the zebra mussel population, which has been used in [10]. When it came to the spreading speeds, as the model operator is non-monotone, we constructed two monotone operators to sandwich the model operator and then used the spreading speeds of these monotone operators for estimations of the upper bound and lower bound of the spreading speeds of the original model operator. Due to the complexity of the non-monotonicity of the model, it seems to be difficult, if not impossible, to construct a lower controlling operator with the same linearization at the trivial solution. Thus, we were unable to obtain the exact formulae of the spreading speeds but only upper and lower bounds instead, although the upper bounds match the spreading speeds from the linear determinacy. With the same reason, we have not been able to use the method of upper and lower solutions to prove the existence of traveling waves. We leave this challenging problem for future work.

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