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PERSISTENCE AND EXTINCTION OF POPULATION IN REACTION-DIFFUSION-ADVECTION MODEL WITH WEAK ALLEE EFFECT GROWTH*

YAN WANG† AND JUNPING SHI‡

Abstract. The dynamical behavior of a reaction-diffusion-advection model of a stream population with weak Allee effect type growth is studied. Under the open environment, it is shown that the persistence or extinction of population depends on the diffusion coefficient, advection rate, and type of boundary condition, and the existence of multiple positive steady states is proved for intermediate advection rate using bifurcation theory. On the other hand, for closed environment, the stream population always persists for all diffusion coefficients and advection rates.

Key words. reaction-diffusion-advection, stream population, weak Allee effect, bifurcation

AMS subject classifications. 92D25, 35K57, 35K58, 92D40

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1. Introduction.

The survival of a biological population in a river or stream depends on both the natural environment and the intrinsic growth pattern of the species. Reaction-diffusion equations have been used to model the spatiotemporal distribution and population size under passive diffusion. With the addition of the advection term for the stream flow, they can describe the population distribution under directed movement that is from sensing and following the gradient of resource distribution (taxis) or a directional fluid/wind flow [2, 12, 19, 20]. A typical form of reaction-diffusion-advection population model in a river/stream environment is

$$u_t = du_{xx} - qu_x + ug(x,u), \qquad 0 < x < L,\ t > 0, \tag{1.1}$$

where $u(x,t)$ is the population density function at the location x and time t, $d > 0$ is the diffusion coefficient, $q \geq 0$ is the advection rate (flow from left to right), L is the length of the river/stream, and $g(x,u)$ is the growth rate per capita that is affected by the heterogeneous environment.

The reaction-diffusion-advection model (1.1) has been used to describe various spatiotemporal phenomena under advective environment. The question of how populations resist washout in such environment and persist over large temporal scales has been called the "drift paradox" [15, 16, 24]. It is shown that the species have a low probability to survive if all the populations are washed down to the downstream. It is suggested that the diffusion coefficient of the species is the key for survival, and the intermediate diffusion coefficient is preferred for the population persistence [24].

Typically a logistic type growth rate has been used in population dynamics of (1.1) to model the crowding effect and competition for limited resource, and the corresponding growth rate per capital $g(x,u)$ is a decreasing function with respect to the

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†Department of Applied Science, Department of Mathematics, College of William and Mary, Williamsburg, Virginia 23187-8795 (ywang36@email.wm.edu).
‡Department of Mathematics, College of William and Mary, Williamsburg, Virginia 23187-8795 (jxshix@wm.edu).

population density u. Under the assumption of the logistic growth, there often exists a critical parameter value (diffusion coefficient, advection rate, domain size, growth rate) for the population persistence or extinction in (1.1) [2, 8, 13, 17], and in the persistence case there is a unique positive steady state which is globally asymptotically stable [2].

However in many empirical studies, it is found that the growth rate per capital $g(x,u)$ reaches the peak value at a positive population density instead of at zero, which is called Allee effect [1, 3, 7, 11, 25]. The Allee effect is strong if the growth rate per capital is negative for low population density, and if the growth rate per capital is positive and increasing with respect to u at low population density, it is called weak Allee effect. In [28], the dynamic behavior of (1.1) with a strong Allee effect growth rate was investigated. Compared to the well-studied logistic growth rate, the extinction state in the strong Allee effect case is always locally stable. It is shown that when both the diffusion coefficient and the advection rate are small, there exist multiple positive steady state solutions hence the dynamics is bistable so that different initial conditions lead to different asymptotic behavior. On the other hand, when the advection rate is large, the population becomes extinct regardless of initial condition under most boundary conditions.

In this paper, we consider the dynamical behavior of the model (1.1) with weak Allee effect growth and open or closed environment boundary conditions. Our main findings on the dynamics of reaction-diffusion-advection model (1.1) with weak Allee effect type growth are the following.

1. In a closed river environment, the population always persists for all diffusion coefficients and advection rates.
2. In an open river environment with nonhostile boundary condition, the population persists for all diffusion coefficients if the advection rate is not large, and it becomes extinct for large advection rate; in the intermediate advection rate, there exist multiple positive steady state solutions; hence the system can tend to alternative stable states asymptotically.
3. In an open river environment with even partially hostile boundary condition, the population persists when both the diffusion coefficient and advection rate are not large, and either a large diffusion coefficient or a large advection rate leads to population extinction; the bistable dynamics occurs when both the diffusion coefficient and advection rate are in the intermediate ranges.

Note that if the river population has a loss on the boundary ends due to movement, then the river is an open environment and otherwise it is a closed environment. These results are rigorously proved by using the theory of dynamical systems, comparison methods, and bifurcation theory. Global bifurcation diagrams of (1.1) with the advection rate q as the bifurcation parameter are obtained for different types of boundary conditions. Bifurcation theory is applied in this paper for the weak Allee effect and also logistic cases, while it is not applicable to the strong Allee effect case since the extinction state is always stable in that case.

Our study for the weak Allee effect case of the dynamical behavior of the system (1.1) in this paper complements the one in [28] for the strong Allee effect case, and the ones in [8, 13] for the logistic case. It reveals that in open environment, for different parameter regimes (diffusion coefficient or advection rate), the dynamical behavior of the system (1.1) with weak Allee effect growth rate can be one of "extinction" (all solutions converge to zero), "bistable" (multiple stable steady states) or "monostable" (all solutions converge to a positive steady state); see Figure 9 for a numerical demonstration. Note that in the "monostable" case, the uniqueness of positive steady state is not proved as the logistic case, as the usual subhomogeneous or sublinear algebraic condition implying uniqueness does not hold here. But numerical simulation indicates that the all solutions converge to the same positive steady state. In comparison, the dynamical behavior of the system (1.1) with strong Allee effect growth rate can only be "extinction" or "bistable" [28], while the one for logistic case can only be "extinction" or "monostable" (here the uniqueness of positive steady state is well known) [8, 13]. Similar to the analytical or numerical findings in [8, 13, 28], the transition from one dynamical behavior to another is often monotonic in the advection rate q but not so in the diffusion coefficient d (see Figure 9 lower panel). The weak Allee effect case is the most complex one with all three dynamical behavior, and the bistable regime is always in between the extinction and monostable regimes.

Dynamics of reaction-diffusion population models with weak Allee effect growth rate and without the effect of advection has been considered in [6, 22]; in [10, 18], the role of weak Allee effect in the ideal free dispersal was considered; and the effect of weak Allee effect on the population spreading/invasion has been investigated in [26].

Our paper is organized as follows. In section 2, we recall the reaction-diffusion-advection model with various growth rate functions and the boundary conditions, as well as some basic results from [28]. The main results on the persistence/extinction dynamics are presented in section 3. Some concluding remarks are given in section 4.

2. Preliminaries.

2.1. Model. Following [28], the density function of a stream population satisfies the following initial-boundary value problem of a reaction-diffusion-advection equation:

$$\begin{cases} u_t = du_{xx} - qu_x + ug(x,u), & 0 < x < L,\ t > 0, \\ du_x(0,t) - qu(0,t) = b_u qu(0,t), & t > 0, \\ du_x(L,t) - qu(L,t) = -b_d qu(L,t), & t > 0, \\ u(x,0) = u_0(x) \geq 0, & 0 < x < L. \end{cases} \tag{2.1}$$

Here $u(x,t)$ is the population density at location $x \in [0,L]$ and time $t \geq 0$, and the river environment is modeled by a one-dimensional interval $[0,L] \subset \mathbb{R}$; the upstream endpoint is $x = 0$, and the downstream endpoint is $x = L$, and L is the length of the river; the parameter d is the diffusion coefficient, q is the advection coefficient (flow rate), and $du_x(x,t) - qu(x,t)$ is the flow flux at x; in the boundary condition, the parameters $b_u \geq 0$ and $b_d \geq 0$ indicate the severity of the population loss at the upstream end $x = 0$ and the downstream end $x = L$, respectively; and the function $g(x,u)$ is the growth rate per capita that will be specified below. This form of boundary condition was proposed in [9]. Typically a no-flux (NF) boundary condition with $b_u = 0$ is imposed at the upstream end, and the downstream boundary condition can be hostile (H) which is equivalent to $b_d = \infty$, or free-flow one (FF) with $b_d = 1$, or NF one with $b_d = 0$. More discussions and biological interpretations of these boundary conditions were given in [13]. The boundary condition in (2.1) with smaller (b_u, b_d) is more favorable for population persistence (see [28, Proposition 3.3]).

We recall the assumptions on the growth rate per capita $g(x,u)$ as in [28] (see also [2, 22]):

- (g1) For any $u \geq 0$, $g(\cdot,u) \in C^\alpha[0,L]$, for some $0 < \alpha < 1$, and for any $x \in [0,L]$, $g(x,\cdot) \in C^1(\mathbb{R})$.
- (g2) For any $x \in [0,L]$, there exists $r(x) \geq 0$, where $0 < r(x) < M$ and $M > 0$ is a constant, such that $g(x,u(x)) \leq 0$ for $u > r(x)$.

(g3) For any $x \in [0, L]$, there exists $s(x) \in [0, r(x)]$ such that $g(x, \cdot)$ is increasing in $[0, s(x)]$ and decreasing in $[s(x), \infty]$; and there also exists $N > 0$ such that $g(x, s(x)) \leq N$.

Here $r(x)$ is the local carrying capacity at x that has a uniform upper bound M; $u = s(x)$ is where $g(x, \cdot)$ reaches the maximum value, and the number N is a uniform bound for $g(x, u)$ at all (x, u). Moreover we assume that $g(x, u)$ takes one of the following three forms: (see [22, 28])

(g4a) Logistic: $s(x) = 0$, $g(x, 0) > 0$, and $g(x, \cdot)$ is decreasing in $[0, \infty)$;

(g4b) Weak Allee effect: $s(x) > 0$, $g(x, 0) > 0$ and $g(x, \cdot)$ is increasing in $[0, s(x)]$, decreasing in $[s(x), \infty)$; or

(g4c) Strong Allee effect: $s(x) > 0$, $g(x, 0) < 0$, $g(x, s(x)) > 0$ and $g(x, \cdot)$ is increasing in $[0, s(x)]$, decreasing in $[s(x), \infty)$. In this case there exists a unique $h(x) \in (0, s(x))$ such that $g(x, h(x)) = 0$.

The dynamical behavior of solutions to (2.1) with logistic growth rate is well known (see [8, 13, 17]), and the one with strong Allee effect growth rate has been studied in [28]. The goal of this paper is to consider the dynamical behavior of solutions to (2.1) with weak Allee effect growth rate, and the effect of dispersal parameters q and d on the dynamics.

2.2. Basic dynamics. We recall the following results from [28] (see Proposition 4.1, Theorem 4.2, and Propositions 4.7, 4.8), which show that the long time dynamic behavior of solutions of (2.1) is determined by the nonnegative steady state solutions of (2.1), and some properties of positive steady state solutions hold regardless of assumption (g4a, b, c).

THEOREM 2.1. *Suppose that $g(x, u)$ satisfies* (g1)–(g2).

1. *Equation* (2.1) *has a unique positive solution $u(x, t)$ defined for $(x, t) \in [0, L] \times (0, \infty)$, and the solutions of* (2.1) *generates a dynamical system in X_2, where*

$$X_2 = \{\phi \in W^{2,2}(0, L) : \phi(x) \geq 0,\ d\phi'(0) - q\phi(0) = b_u q\phi(0), \\ d\phi'(L) - q\phi(L) = -b_d q\phi(L)\}. \tag{2.2}$$

2. *For any $u_0 \in X_2$ and $u_0 \not\equiv 0$, the ω-limit set $\omega(u_0) \subset S$, where S is the set of nonnegative steady state solutions.*
3. *Let $u(x)$ be a positive steady state solution of* (2.1)*; then for $x \in [0, L]$,*

$$u(x) \leq e^{\alpha x} \max_{y \in [0,L]} (e^{-\alpha y} r(y)),$$

where $r(x)$ is defined in (g2) *and $\alpha = \dfrac{q}{d}$. Moreover, if $b_d \geq 1$, then $u(x) \leq M = \max_{y \in [0,L]} r(y)$ for $x \in [0, L]$.*

4. *If in addition $g(x, u)$ also satisfies* (g3)*, and there exists a positive steady state solution of* (2.1)*, then there exists a maximal steady state solution $u_{max}(x)$ such that for any positive steady state $u(x)$ of* (2.1)*, we have $u_{max}(x) \geq u(x)$. Moreover if $b_u \geq 0$ and $0 \leq b_d < 1$, then $u_{max}(x)$ is strictly increasing in $[0, L]$.*

For (2.1), there is always an extinction steady state $u = 0$ for any $d > 0$ and $q \geq 0$. The local asymptotical stability of the extinction state can be determined by the principal eigenvalue of an associated eigenvalue problem as follows.

PROPOSITION 2.2. *Suppose that $g(x, u)$ satisfy* (g1)–(g3)*, $d > 0$, and $q \geq 0$. Let $\lambda_1(q)$ be the principal eigenvalue of the eigenvalue problem:*

$$\begin{cases} d\phi'' - q\phi' + g(x,0)\phi = \lambda\phi, & 0 < x < L, \\ d\phi'(0) - q\phi(0) = b_u q\phi(0), \\ d\phi'(L) - q\phi(L) = -b_d q\phi(L). \end{cases} \tag{2.3}$$

1. *If* $\lambda_1(q) < 0$, *then* $u = 0$ *is locally asymptotically stable for* (2.1)*; and if* $\lambda_1(q) > 0$, *then* $u = 0$ *is unstable and there exists a positive steady state of* (2.1)*.*
2. *If in addition* $g(x,u)$ *also satisfies* (g4a) *or* (g4b)*, then*
   (a) *(open environment) when* $b_d > 0$ *and* $b_u \geq 0$, *there exist* $q_2 \geq q_1 > 0$ *such that* $\lambda_1(q) > 0$ *for* $0 \leq q < q_1$, $\lambda_1(q_1) = \lambda_1(q_2) = 0$, *and* $\lambda_1(q) < 0$ *for* $q > q_2$*; moreover if* $b_d > 1/2$, *then* $\lambda_1(q)$ *is strictly decreasing and* $q_1 = q_2$*.*
   (b) *(closed environment) when* $b_u = b_d = 0$, *then* $\lambda_1(q) > 0$ *for all* $q > 0$*.*
3. *If in addition* $g(x,u)$ *also satisfies* (g4a)*, then* $u = 0$ *is globally asymptotically stable for* (2.1) *when* $u = 0$ *is locally asymptotically stable, and when* $u = 0$ *is unstable, then there exists a unique positive steady state of* (2.1) *that is globally asymptotically stable.*

Proof. For part 1, the stability/instability of the extinction state follows from standard theory of semilinear parabolic equations [5]. For part 2, from the variational characterization of λ_1 in part 1 of [28, Proposition 3.1], $\lambda_1(q) > 0$ for $0 \leq q < q_1$ in the open environment case, and $\lambda_1(q) > 0$ for any $q \geq 0$ in the close environment case. Also from part 3 of [28, Proposition 3.1], $\lambda(q) \to -\infty$ as $q \to \infty$ in the open environment case, so there exists $q_2 > q_1$ such that $\lambda_1(q) < 0$ for $q > q_2$. We can choose $q_2 \geq q_1 > 0$ so that q_1 is the smallest positive root of $\lambda_1(q) = 0$ and q_2 is the largest. The strict decreasing property of $\lambda_1(q)$ when $b_d > 1/2$ is proved in Theorem 2.1 of [14]. Part 3 is from [28, Proposition 3.2]. ∎

Proposition 2.2 shows that for the logistic or weak Allee effect case, the stability of the extinction state is similar, but the global dynamics for the two cases may be different as the positive steady state may not be unique for the weak Allee effect case (see Theorem 3.5).

2.3. Nonadvective case. For reaction-diffusion-advection equation (2.1) with no advection, there have been several previous works on the existence and multiplicity of positive steady state solutions, and we recall these results here. Here the dispersal and evolution of a species are on a bounded heterogeneous habitat Ω in $\mathbb{R}^n$ with $n \geq 1$, and the inhomogeneous growth rate $g(x,u)$ is either logistic or of weak Allee effect type. In this subsection, we assume that the conditions (g1)–(g3) and (g4a)–(g4c) are defined for $x \in \overline{\Omega}$ instead of $x \in [0,L]$. If the environment is with a hostile boundary condition, then the equation is in form of

$$\begin{cases} u_t = d\Delta u + ug(x,u), & x \in \Omega,\ t > 0, \\ u(x,t) = 0, & x \in \partial\Omega,\ t > 0. \end{cases} \tag{2.4}$$

The steady state solution satisfies

$$\begin{cases} d\Delta u + ug(x,u) = 0, & x \in \Omega, \\ u(x) = 0, & x \in \partial\Omega. \end{cases} \tag{2.5}$$

Let $X = W^{2,p}(\Omega) \cap W_0^{1,p}(\Omega)$ and $Y = L^p(\Omega)$, where $p > n$. Then $F : \mathbb{R} \times X \to Y$ defined by $F(d,u) = d\Delta u + ug(x,u)$ is a continuously differentiable mapping. Denote the set of nonnegative solutions of (2.5) by $\Gamma=\{(d,u)\in\mathbb{R}^+\times X: u\ge 0, F(d,u)=0\}$. Then from the strong maximum principle, $\Gamma=\Gamma_0\cup\Gamma_+$, where $\Gamma_0=\{(d,0):d>0\}$ is the line of trivial solutions and $\Gamma_+=\{(d,u)\in\Gamma: u>0\}$ is the set of positive solutions. Define

$$d_1(g,\Omega)=\inf_{\phi\in W_0^{1,2}(\Omega)}\left\{\int_\Omega g(x,0)\phi^2(x)dx : \int_\Omega |\nabla\phi(x)|^2dx=1\right\}. \tag{2.6}$$

Then $d_1=d_1(g,\Omega)$ is a bifurcation point where nontrivial solutions of system (2.5) bifurcate from the line of trivial solutions Γ_0. Refering to [22, Theorems 1–3], we have the following result when $g(x,u)$ is of weak Allee effect type.

THEOREM 2.3. *Suppose that $g(x,u)$ satisfies* (g1)–(g3) *and* (g4b). *Then*

1. *the extinction state $u=0$ is locally asymptotically stable with respect to* (2.4) *when $d>d_1$, and it is unstable when $0<d<d_1$;*
2. *$d=d_1$ is a bifurcation point for system* (2.5)*, and there is a connected component Γ_+^1 of Γ_+ whose closure includes the point $(d,u)=(d_1,0)$ and the bifurcation at $(d_1,0)$ is subcritical; near $(d_1,0)$, Γ_+^1 can be written as a curve $(d(s),u(s))$ with $s\in(0,\delta)$, $d(s)\to d_1$ and $u(s)=s\phi_1+o(s)$ as $s\to 0^+$, where $\phi_1(x)$ is the positive eigenfunction satisfying $d_1\Delta\phi_1+g(x,0)\phi_1=0$ in Ω and $\phi_1=0$ on $\partial\Omega$;*
3. *there exists $d_*\equiv d_*(g,\Omega)$ satisfying $d_*>d_1>0$ such that* (2.5) *has no positive solution when $d>d_*$, and when $d\le d_*$,* (2.5) *has a maximal solution $u_m(d,x)$ such that for any solution $u(d,x)$ of* (2.5)*, $u_m(d,x)\ge u(d,x)$ for $x\in\Omega$, and $u_m(d,x)$ is semistable;*
4. *for $d<d_*$, $u_m(d,x)$ is decreasing with respect to d, the map $d\mapsto u_m(d,\cdot)$ is left continuous for $d\in(0,d_*)$, i.e.,*
$$\lim_{\eta\to d^-}|u_m(\eta,\cdot)-u_m(d,\cdot)|_X=0,$$
and all $u_m(d,\cdot)$ are on the global branch Γ_+^1;
5. (2.5) *has at least two positive solutions when $d\in(d_1,d_*)$.*

Note that when $g(x,u)$ satisfies (g4a) instead of (g4b), then $d=d_1$ is still a bifurcation point and the bifurcation is supercritical, and for any $0<d<d_1$, there is a unique positive solution of (2.5), and for $d\ge d_1$, there is no positive solution of (2.5). So a main distinction of weak Allee effect growth rate is to allow an intermediate range of diffusion coefficient (d_1,d_*) so that the model possesses a bistability of two nonnegative locally asymptotically stable states (one of them is zero).

On the other hand, if the habitat is a closed environment and there is no advection effect, then the population is described by the following model with a NF boundary condition:

$$\begin{cases}\dfrac{\partial u}{\partial t}=d\triangle u+ug(x,u), & x\in\Omega,\ t>0,\\ \dfrac{\partial}{\partial n}u(x,t)=0, & x\in\partial\Omega,\ t>0.\end{cases} \tag{2.7}$$

We have the following results regarding the dynamics of (2.7) when the growth rate is of weak Allee effect.

THEOREM 2.4. *Suppose that $g(x,u)$ satisfies* (g1)–(g3) *and* (g4b).

1. *The extinction state $u=0$ is unstable for any $d>0$, and for any $d>0$,* (2.7) *has a maximal steady state solution $u_m(d,x)$ such that for any solution $u(d,x)$ of* (2.7)*, $u_m(d,x)\ge u(d,x)$ for $x\in\Omega$, and $u_m(d,x)$ is semistable;*

2. *for $d > 0$, $u_m(d,x)$ is decreasing with respect to d, the map $d \mapsto u_m(d,\cdot)$ is left continuous for $d \in (0,\infty)$, i.e.,*

$$\lim_{\eta \to d^-} |u_m(\eta,\cdot) - u_m(d,\cdot)|_{X'} = 0,$$

and all $u_m(d,\cdot)$ are on a global branch Γ^1_+, where $X' = \{u \in W^{2,p}(\Omega) : \partial u/\partial n = 0$ on $\partial\Omega\}$.

Proof. When the advection is absent, Proposition 2.2 part 1 and part 3(b) still hold true for $\Omega \subset \mathbb{R}^n$ with $n \geq 1$. So the instability of $u = 0$ in part 1 follows from Proposition 2.2. The existence of a positive steady state follows from the upper-lower solution method, with the upper solution $\overline{u}(x) = M$, where M is defined in (g2), and the lower solution $\underline{u}(x) = \varepsilon\varphi_1(x)$, where $\varphi_1(x)$ is the positive eigenfunction corresponding to

$$\begin{cases} d\Delta\phi + g(x,0)\phi = \lambda_1\phi, & x \in \Omega, \\ \dfrac{\partial\phi}{\partial n} = 0, & x \in \partial\Omega. \end{cases} \tag{2.8}$$

Here $\varepsilon > 0$ is sufficiently small so that $\underline{v}(x) < \overline{v}(x)$. And there is a maximal steady state in this case as $\overline{u}$ is an upper bound of all nonnegative steady states (similar to Theorem 2.1 part 3). For part 2, let $d_1 > d_2$ and assume that $u_m(d_1,x)$ and $u_m(d_2,x)$ are the maximal steady state solutions of (2.7) with diffusion coefficients d_1 and d_2, respectively. Then we have $\Delta u_m(d_2,x) + d_1^{-1}ug(x,u_m(d_2,x)) \geq \Delta u_m(d_2,x) + d_2^{-1}ug(x,u_m(d_2,x)) = 0$. Therefore $u_m(d_2,x)$ is a lower solution of (2.7) with diffusion coefficient d_1, which implies $u_m(d_1,x) \geq u_m(d_2,x)$ as u_m are the maximal solutions. So for $d > 0$, $u_m(d,x)$ is decreasing with respect to d. Other conclusions in part 2 follow from similar arguments in [22, Theorem 3]. ∎

3. Persistence/Extinction dynamics. From subsection 2.3, we know that the persistence or extinction of a diffusive population with weak Allee effect growth rate is determined by the boundary condition and the diffusion coefficient d. Under Neumann boundary (NF) condition, there always exists a semistable positive steady state solution so the population always persists if the initial population is large enough. Under zero Dirichlet (H) boundary condition, there are three possible scenarios: unconditional persistence when $0 < d < d_1$, conditional persistence and bistability when $d_1 < d < d_*$, and extinction when $d > d_*$. In this section, we consider the effect of advection on the persistence or extinction of population through comparison method and bifurcation approach.

3.1. Comparison with logistic models. If $g(x,u)$ satisfies (g1)–(g3) and (g4a) (logistic growth), then the persistence or extinction of population in (2.1) is completely determined by the stability of the extinction state as shown in Proposition 2.2. When $g(x,u)$ satisfies (g1)–(g3) and (g4b) (weak Allee effect), the persistence or extinction could depend on the initial condition. But here we show that the solutions of (2.7) with weak Allee effect growth rate can be compared with the ones of two related equations with comparable logistic growth rates. For that purpose, we define the "upper growth function" $\overline{g}(x,u)$ and the "lower growth function" $\underline{g}(x,u)$ as follows,

$$\overline{g}(x,u) = \begin{cases} g(x,s(x)), & 0 < u < s(x), \\ g(x,u), & u > s(x), \end{cases} \tag{3.1}$$

where $s(x)$ is defined in (g3) to be the maximum point of $g(x,\cdot)$; and

$$\underline{g}(x,u) = \begin{cases} g(x,0), & 0 < u < \xi(x), \\ g(x,u), & u > \xi(x), \end{cases} \tag{3.2}$$

where, for $x \in \Omega$, $\xi(x) > s(x)$ satisfies $g(x,\xi(x)) = g(x,0)$ (see Figure 1). Thus $\overline{g}(x,u)$ and $\underline{g}(x,u)$ are both continuous functions of logistic type and satisfy $\overline{g}(x,u) \geq g(x,u) \geq \underline{g}(x,u)$. Then we have the following results regarding persistence/extinction of population in (2.1) by comparing with the ones with the two logistic growth rates $\overline{g}(x,u)$ and $\underline{g}(x,u)$, as the persistence/extinction of population under logistic growth rate is known (Proposition 2.2).

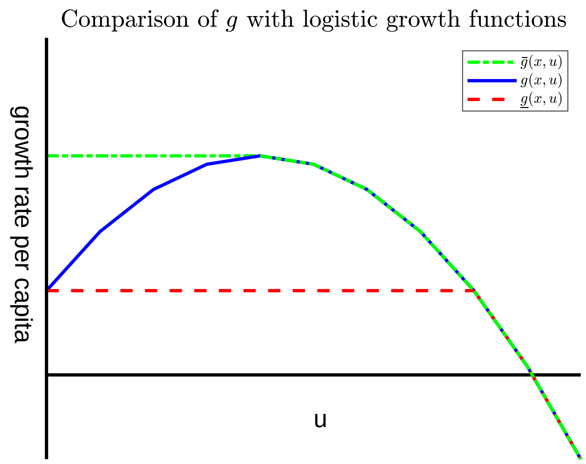

FIG. 1. *The graphs of* $g(x,u)$, $\bar{g}(x,u)$, *and* $\underline{g}(x,u)$ *for fixed* $x \in \Omega$.

THEOREM 3.1. *Suppose that* $g(x,u)$ *satisfies* (g1)–(g3) *and* (g4b), *and* $\overline{g}(x,u)$ *and* $\underline{g}(x,u)$ *are defined as in* (3.1) *and* (3.2). *Let* $u(x,t)$ *be the solution of* (2.1), *and let* $\underline{u}_m(x)$ *and* $\overline{u}_m(x)$ *be the maximal nonnegative steady state solution of* (2.1) *with growth function* $\underline{g}(x,u)$ *and* $\overline{g}(x,u)$, *respectively.*

1. *(open environment) When* $b_d > 0$ *and* $b_u \geq 0$, *then there exists constants* $\underline{q}_1$ *and* $\overline{q}_1$ *satisfying* $0 < \underline{q}_1 < \overline{q}_1$ *such that*
   (a) *if* $0 \leq q < \underline{q}_1$, (2.1) *has at least one positive steady state solution, and*
   $$\overline{u}_m(x) \geq \limsup_{t\to\infty} u(x,t) \geq \liminf_{t\to\infty} u(x,t) \geq \underline{u}_m(x) > 0; \tag{3.3}$$
   (b) *if* $q > \overline{q}_1$, (2.1) *has no positive steady state solution, and* $\lim_{t\to\infty} u(x,t) = 0$.
2. *(closed environment) When* $b_u = b_d = 0$, *then for all* $q \geq 0$, (2.1) *has a positive steady state solution and* (3.3) *holds.*

Proof. First we consider the open environment case ($b_d > 0$ and $b_u \geq 0$). From Proposition 2.2 part 3(a), for (2.1) with $\underline{g}(x,u)$, we define $\underline{q}_1$ to be the value such that $\lambda_1(\underline{q}_1, \underline{g}(x,0)) = 0$ and $\lambda_1(q, \underline{g}(x,0)) > 0$ for $0 < q < \underline{q}_1$, and for (2.1) with $\overline{g}(x,u)$, we define $\overline{q}_1$ to be the value such that $\lambda_1(\overline{q}_1, \overline{g}(x,0)) = 0$ and $\lambda_1(q, \overline{g}(x,0)) < 0$ for $q > \overline{q}_1$. Since $\overline{g}(x,u) \geq g(x,u) \geq \underline{g}(x,u)$, from the comparison principle of parabolic equations, we have $\overline{u}(x,t) \geq u(x,t) \geq \underline{u}(x,t)$ for any $x \in \overline{\Omega}$ and $t > 0$, where $\overline{u}(x,t)$ and $\underline{u}(x,t)$ are the solutions of (2.1) with growth rates $\overline{g}(x,u)$ and $\underline{g}(x,u)$ and same initial condition as in (2.1). From Proposition 2.2, if $0 \leq q < \underline{q}_1$, we obtain (3.3) as $\lim_{t\to\infty} \overline{u}(x,t) = \overline{u}_m(x)$ and $\lim_{t\to\infty} \underline{u}(x,t) = \underline{u}_m(x)$. In this case, (2.1) has at least one positive steady state solution, as $u(x,t)$ converges to a nonnegative steady state from Theorem 2.1, and the steady state is positive from (3.3). If $q > \overline{q}_1$, then $\lim_{t\to\infty} u(x,t) = 0$ as $\lim_{t\to\infty} \overline{u}(x,t) = 0$ and $\lim_{t\to\infty} \underline{u}(x,t) = 0$. The close environment case can be proved in a similar way. ∎

Theorem 3.1 shows that the stream population model (2.1) with weak Allee effect growth rate is similar to the one with logistic growth rate in small ($0 \le q < \underline{q}_1$) or large ($q > \overline{q}_1$) advection cases, but it does not provide any information for the intermediate ($\underline{q}_1 < q < \overline{q}_1$) advection rate. In the next subsection, we use bifurcation theory to explore the dynamic behavior of (2.1) in that case. In Figure 2, solutions of (2.1) with weak Allee effect growth $g(x,u) = (1-u)(u+h)$ and the ones with corresponding upper and lower logistic growth rates

$$\overline{g}(x,u) = \begin{cases} \dfrac{(1+h)^2}{4}, & 0 < u < \dfrac{1-h}{2}, \\ (1-u)(u+h), & u \ge \dfrac{1-h}{2}, \end{cases}$$

and

$$\underline{g}(x,u) = \begin{cases} h, & 0 < u < 1-h, \\ (1-u)(u+h), & u \ge 1-h, \end{cases}$$

are shown. One can observe that when the advection rate is smaller than $\underline{q}_1$, the three solutions are almost identical in their maximum values, which is due to the fact that the three functions $\overline{g}(x,u)$, $g(x,u)$, and $\underline{g}(x,u)$ have same values for large population density u. But the growth rates for small population density u are more important when the advection rate q is in an intermediate range. Figure 3 shows a comparison of profiles of maximal steady state solutions of three growth rates $\overline{g}(x,u)$, $g(x,u)$, and $\underline{g}(x,u)$.

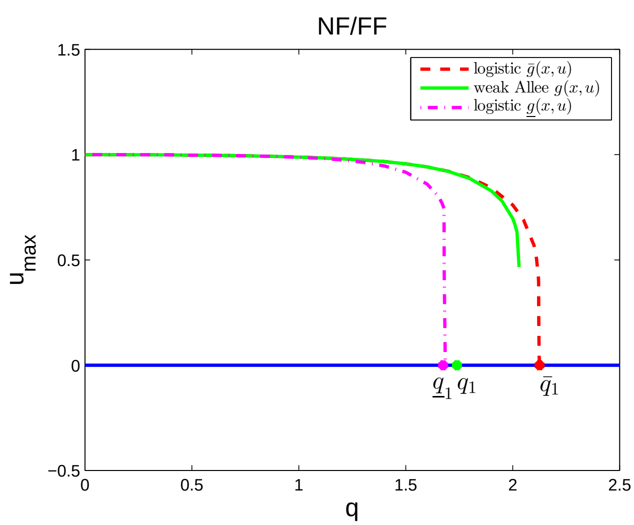

FIG. 2. *Comparison of maximal steady state solutions of* (2.1) *with growth rates* $\overline{g}(x,u)$*,* $g(x,u) = (1-u)(u+h)$*, and* $\underline{g}(x,u)$*. Here the horizontal axis is the advection rate* q*, and the vertical axis is the maximum value of the maximal steady state solutions; the parameters used are* $d = 4$*,* $h = 0.3$*,* $L = 10$*,* $b_u = 0$*, and* $b_d = 1$*.*

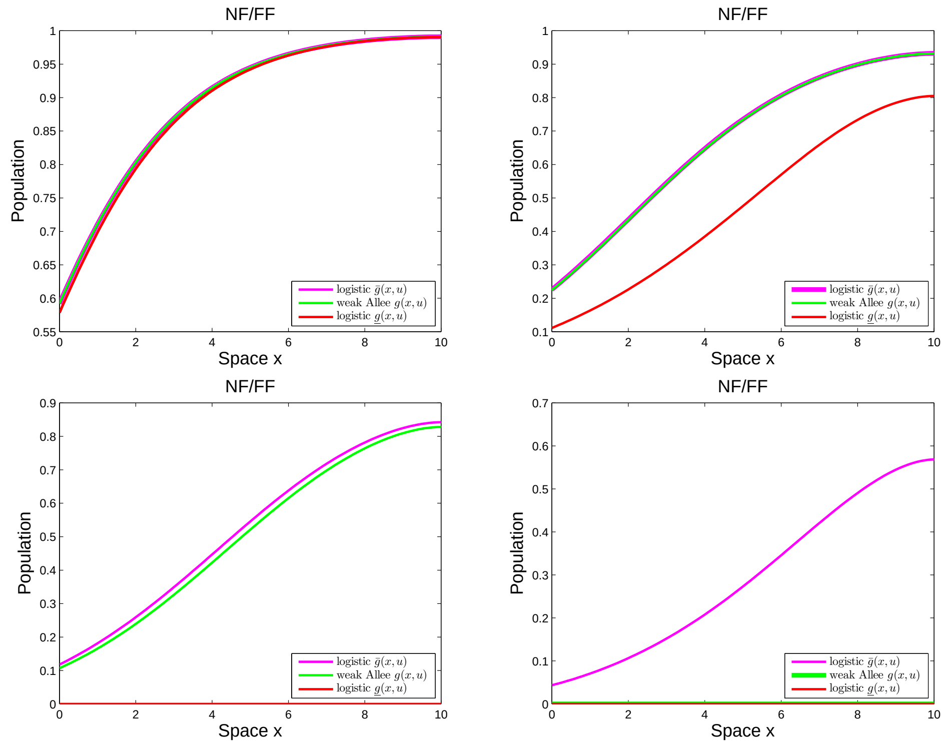

FIG. 3. *Comparison of the maximal steady state solutions to* (2.1) *of different growth rates. Here* $g(x,u) = (r-u)(u+h)$*,* $r = 1$*,* $d = 4$*,* $h = 0.3$*,* $L = 10$*,* $b_u = 0$ *and* $b_d = 1$*. Upper left:* $q = 0.9$*; Upper right:* $q = 1.65$*; Lower left:* $q = 1.9$*; Lower right:* $q = 2.1$.

3.2. Bifurcation: Open environment. In this subsection, we consider the structure of the set of positive steady state solutions of (2.1) using the advection rate q as a bifurcation parameter. The steady state equation of system (2.1) is

$$\begin{cases} du_{xx}(x) - qu_x(x) + u(x)g(x,u(x)) = 0, & 0 < x < L, \\ du_x(0) - qu(0) = b_u qu(0), \\ du_x(L) - qu(L) = -b_d qu(L). \end{cases} \tag{3.4}$$

Define $X_3 = W^{2,2}(0,L)$ and $Y = L^2(0,L)$ and a nonlinear mapping $G : \mathbb{R}^+ \times X_3 \to Y \times \mathbb{R}^2$ as

$$G(q,u) := \begin{pmatrix} du_{xx} - qu_x + ug(x,u) \\ du_x(0) - (1+b_u)qu(0) \\ du_x(L) - (1-b_d)qu(L) \end{pmatrix}. \tag{3.5}$$

We denote the set of nonnegative solutions of the equation by $\Gamma = \{(q,u) \in \mathbb{R}^+ \times X_3 : u \geq 0, G(q,u) = 0\}$. Then from the strong maximum principle, $\Gamma = \Gamma_0 \cup \Gamma_+$, where $\Gamma_0 = \{(q,0) : q > 0\}$ is the set of trivial solutions and $\Gamma_+ = \{(q,u) \in \Gamma : u > 0\}$. We consider the bifurcation of nontrivial solutions of (2.1) from the zero steady state at some bifurcation point $q = q_1$, which is identified in Proposition 2.2 part 3(a).

THEOREM 3.2. *Suppose that* $g(x,u)$ *satisfies* (g1)–(g3) *and* (g4a) *or* (g4b)*,* g *is twice differentiable in* u*,* $b_u \geq 0$*,* $b_d \geq \frac{1}{2}$*, and* $\Omega_+ = \{x \in [0,L] : g(x,0) > 0\}$ *is a set* *with positive Lebesgue measure. Recall q_1 is the unique positive number such that the principal eigenvalue of* (2.3) $\lambda_1(q) = 0$. *Then*

1. $q = q_1$ *is a bifurcation point for* (3.4), *and there is a connected component* Γ_+^1 *of the set* Γ_+ *of positive solutions to* (3.4) *whose closure includes the point* $(q, u) = (q_1, 0)$ *and the projection of* Γ_+^1 *onto* $\mathbb{R}^+$ *via* $(q, u) \mapsto q$ *contains the interval* $[0, q_1)$;
2. *near* $(q_1, 0)$, $\Gamma_+^1 = \{(q(s), u(s)) : 0 < s < \delta\}$, $q(0) = q_1$, $u(0) = 0$ *and* $u(s) = s\phi + sz(s)$, $z(0) = 0$, $z : [0, \delta) \to X_4$, $q(s), z(s)$ *are differentiable functions, where* ϕ *is the positive eigenfunction of* (2.3) *with* $q = q_1$ *and* $\lambda = \lambda_1(q_1) = 0$, *and* $X_4 = \{\varphi \in X_3 : \int_0^L \phi\varphi dx = 0\}$ *is a subspace of* X_3 *complement to* $\mathrm{Span}\{\phi\}$;
3. *when* $g(x, u)$ *satisfies* (g4a) *(logistic growth), then the bifurcation at* $(q_1, 0)$ *is forward, i.e.,* $q(s) < q_1$ *for* $s \in (0, \delta)$;
4. *when* $g(x, u)$ *satisfies* (g4b) *(weak Allee effect growth), then the bifurcation at* $(q_1, 0)$ *is backward, i.e.,* $q(s) > q_1$ *for* $s \in (0, \delta)$.

The proof of Theorem 3.2 is given in the Appendix.

Remark 3.3.

1. When $b_u = b_d = 0$ (closed environment), the trivial steady state is always unstable and there exists a stable positive steady state solution (see Theorem 3.1 part 2). Then, no bifurcation occurs from the branch of the trivial steady state solution.
2. Theorem 3.2 is proved under the assumptions of $b_u \geq 0$ and $b_d \geq 1/2$. For the case of $b_u \geq 0$, $0 < b_d < 1/2$, there always exists a critical advection rate q_1 that destabilizes the zero steady state solution, but it is not known whether it is unique in general situation. If the environment is spatially homogeneous, then such q_1 is unique for all $b_u \geq 0$ and $b_d > 0$ ([14, Theorem 2.1]). The bifurcation structure of positive solutions of (3.4) for $0 < b_d < 1/2$ is an interesting open question.

For more specific types of growth rate function, logistic or weak Allee effect, more detailed information on the global bifurcation of solutions of (3.4) can be obtained.

THEOREM 3.4. *Suppose that* $g(x, u)$ *satisfies* (g1)–(g3) *and* (g4a) *(logistic growth),* $b_u \geq 0$, $b_d \geq \frac{1}{2}$. *Then in addition to Theorem* 3.2,

1. *for each* $0 \leq q < q_1$, *there exists a unique positive solution* $u_q(x)$ *of* (3.4) *and it is linearly stable; moreover for any initial value* $u_0(x) \geq (\not\equiv) 0$, $\lim_{t\to\infty} u(x, t) = u_q(x)$ *in* X_3, *where* $u(x, t)$ *is the solution of* (2.1) *with initial condition* u_0;
2. Γ_+^1 *can be parameterized as* $\Gamma_+^1 = \{(q, u_q(x)) : 0 \leq q < q_1\}$, $\lim_{q\to q_1} u_q(\cdot) = 0$, *and the map* $q \mapsto u_q(q, \cdot)$ *is continuously differentiable.*

The proof of this result is omitted, as the uniqueness of the positive solution $u_q(x)$ is well known (see [2, 13]), and the rest parts follow from similar results about logistic type growth functions (see [2]). Figure 4 (left panel) shows a bifurcation diagram in this case.

THEOREM 3.5. *Suppose that* $g(x, u)$ *satisfies* (g1)–(g3) *and* (g4b) *(weak Allee effect growth),* $b_u \geq 0$, $b_d \geq \frac{1}{2}$. *Then in addition to Theorem* 3.2,

1. *there exists* $q_* > q_1 > 0$ *such that* (3.4) *when* $q \leq q_*$, (3.4) *has a maximal solution* $u_m(q, x)$ *such that for any positive solution* $u(q, x)$ *of* (3.4), $u_m(q, x) \geq u(q, x)$ *for* $x \in [0, L]$;
2. (3.4) *has at least two positive solutions when* $q \in (q_1, q_*)$.

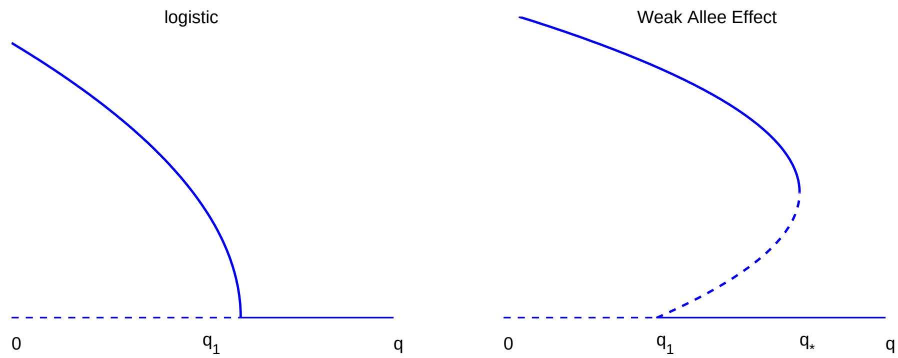

FIG. 4. *Illustrative bifurcation diagrams of nonnegative solutions to* (3.4)*. Left:* $g(x, u)$ *follows logistic type growth. Right:* $g(x, u)$ *follows weak Allee effect type growth. Here the horizontal axis is* q*, and the vertical axis is* $||u||_\infty$.

The proof of Theorem 3.5 is given in the Appendix. Figure 4 and Figure 5 show the numerical bifurcation diagrams of maximal solutions for (3.4) under the NF/FF and NF/H boundary conditions, which also reveals that the bifurcation points q_1 and q_* are smaller for NF/H boundary condition than the ones for NF/FF boundary condition. In general the bifurcation points appear to be decreasing in b_u and b_d. Note that NF/H is not covered by Theorem 3.5 but a similar proof also holds in that case (see the next subsection).

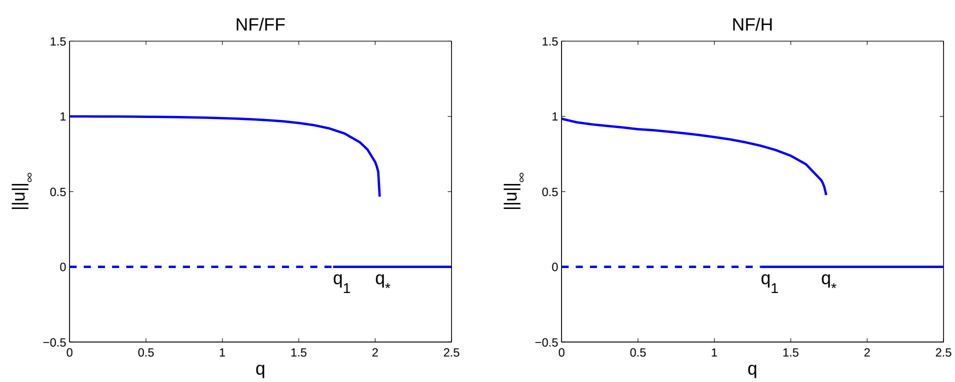

FIG. 5. *Numerical bifurcation diagrams of nonnegative solutions to* (3.4) *when* $g(x, u) = u(1 - u)(u + h)$*, and only the trivial solutions and maximal solutions are plotted. Left: the NF/FF boundary condition. Right: the NF/H boundary condition. Here* $d = 4$*,* $h = 0.3$*, and* $L = 10$*. Here the horizontal axis is* q*, and the vertical axis is* $||u||_\infty$.

3.3. Hostile boundary condition. In the boundary condition of (2.1), when $b_u \to \infty$, $b_d \to \infty$, all the individuals of the species die on the boundary so the boundary is hostile, and it can be written as $u(0) = u(L) = 0$. The dynamical behavior of the system (2.1) can still be described by Theorem 2.1 with some small modification. In particular the dynamics is determined by the nonnegative steady state solutions. In subsection 3.2, it is shown that bifurcation of positive solutions of (3.4) with respect to q follows Figure 5 for any diffusion coefficient $d > 0$. Here we show that for the hostile boundary condition, the bifurcation diagrams are different for different range of $d > 0$. The steady state equation of system (2.1) with hostile boundary condition becomes

$$\begin{cases} du_{xx}(x) - qu_x(x) + u(x)g(x, u(x)) = 0, & 0 < x < L, \\ u(0) = u(L) = 0. \end{cases} \tag{3.6}$$

THEOREM 3.6. *Suppose that* $g(x, u)$ *satisfies* (g1)–(g3) *and* (g4b) *(weak Allee effect growth). Recall the critical diffusion coefficients* d_1 *and* d_* *when* $q = 0$ *in Theorem* 2.3.

1. *If* $0 < d < d_1$*, there is a connected component* Γ_+^1 *of the set of positive solutions to* (3.6) *in the space* $\mathbb{R}^+ \times X_5$ *that connects* $(q, u) = (0, u_m)$ *and* $(q, u) = (q_1, 0)$*, where* $q_1 > 0$ *is the bifurcation point for* (3.6) *on the branch* Γ_0 *of trivial solutions, and* $X_5 = W^{2,2}(0, L) \cap W_0^{1,2}(0, L)$*; there exists* $q_* > q_1$ *such that* (3.6) *has at least two positive solutions on* Γ_+^1 *for any* $q_1 < q < q_*$*, at least one positive solution on* Γ_+^1 *for any* $0 \le q \le q_1$*, and any* $0 \le q < q_*$ *one of the solutions is the maximal solution* $u_m(q, x)$*. (See Figures* 6 *and* 7 *(left).)*

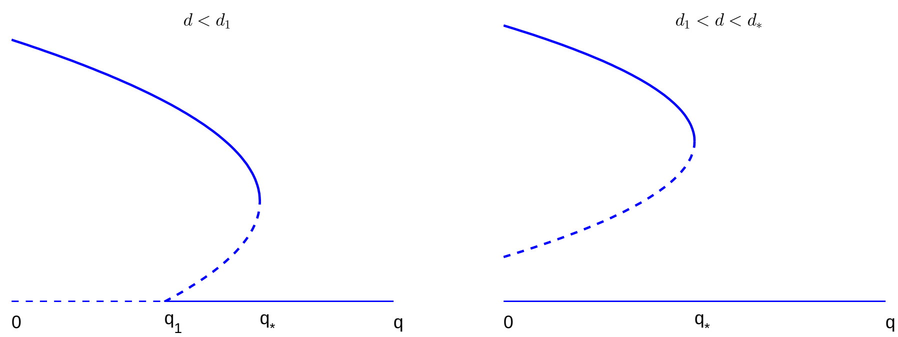

FIG. 6. *Illustrative bifurcation diagrams of nonnegative solutions to* (3.6)*. Left:* $0 < d < d_1$*. Right:* $d_1 < d < d_*$*. Here the horizontal axis is* q*, and the vertical axis is* $||u||_\infty$*.*

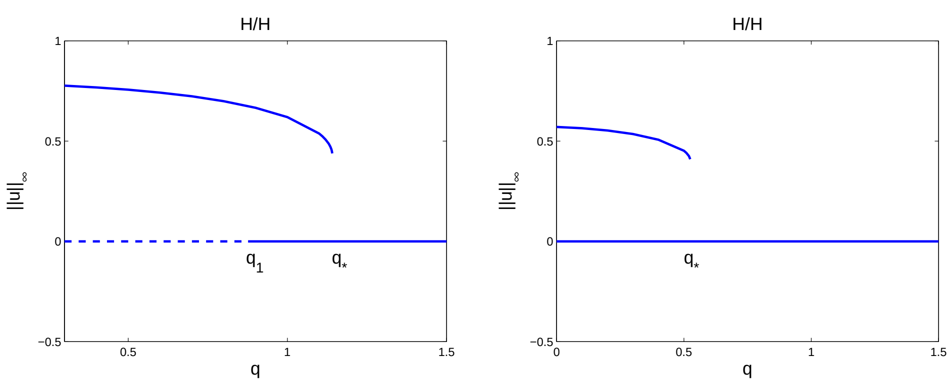

FIG. 7. *Numerical bifurcation diagrams of nonnegative solutions to* (3.6) *when* $g(x, u) = u(1 - u)(u + h)$*, and only the trivial solutions and maximal solutions are plotted. Here* $h = 0.3$*,* $L = 10$*, the horizontal axis is* q*, and the vertical axis is* $||u||_\infty$*. Left:* $d = 3$*. Right:* $d = 4$*.*

2. *If* $d_1 < d < d_*$*, there is a connected component* Γ_+^1 *of the set of positive solutions to* (3.6) *in* $\mathbb{R}^+ \times X_5$ *which connects* $(q,u) = (0,u_m)$ *and* $(q,u) = (0,u_2)$*,* u_m *is the maximal solution of* (3.6) *when* $q = 0$*, and* u_2 *is another positive solution of* (3.6) *when* $q = 0$*; there exists* $q_* > 0$ *such that* (3.6) *has at least two positive solutions on* Γ_+^1 *for any* $0 \le q < q_*$*, and one of these two solutions is the maximal solution* $u_m(q,x)$*. (See Figures* 6 *and* 7 *(right).)*

The proof of Theorem 3.6 is given in the Appendix.

Figure 6 and Figure 7 show the numerical bifurcation diagrams of maximal steady state solutions for (3.6) in the cases of $0 < d < d_1$ and $d_1 < d < d_*$.

Remark 3.7. 1. The results in Theorem 3.6 also hold when only one of the boundary condition is hostile, for example, NF/H boundary condition. In these cases, there exists a critical diffusion coefficient $d_1 > 0$ so that the bifurcation diagrams with parameter q are different when $d < d_1$ and $d > d_1$ as in Figures 6 and 7. As shown in Theorem 3.5, the qualitative bifurcation diagrams for all $d > 0$ are same for the boundary open environment boundary conditions with $b_u \in [0,\infty)$ and $b_d \in (0,\infty)$.

2. If $d > d_*$ (defined in Theorem 2.3), (3.6) has no positive solutions when $q = 0$ from Theorem 2.3. But it is not known whether (3.6) has positive solutions for some positive $q > 0$. Since it is known that there is no solutions for large $q > 0$, the set Γ_1^+ of positive solutions will be an isola, which is not connected to $q = 0$ or $u = 0$ if it is not empty.
3. The critical advection rate q_* defined in Theorems 3.5 or 3.6 is the largest advection rate for the existence of positive steady states of (2.1) on the connected component Γ_1^+, which either emerges from a bifurcation point $(q,u) = (q_1,0)$ or $(q,u) = (0,u_m)$. Theoretically we do not exclude the possibility of another connected component $\tilde{\Gamma}_1^+$ which is an isola for larger q. But numerical simulations in Figures 5 and 7 show that the set of positive solutions of (3.4) or (3.6) is connected.

Finally we compare the effect of different boundary conditions on the dynamics of (2.1). Especially we compare the different ranges of advection rate q and diffusion coefficient d that generate extinction, bistable, or monostable dynamics under different boundary conditions. Theorems 3.5 and 3.6 identify two critical advection rates q_1 and q_* that separate the ranges of advection rates of these three dynamical regimes: when $0 \le q \le q_1$, the solutions tend to the maximal steady state u_m as $t \to \infty$; when $q_1 < q < q_*$, the dynamic outcome depends on the initial conditions; most solutions either tend to the stable extinction state $u = 0$ or the stable maximal steady state u_m as $t \to \infty$, and there are also solutions on the threshold manifold that separates the basin of attractions of the two state states, and they converge to unstable steady states on the threshold manifold; and when $q > q_*$, all solutions tend to the extinction state $u = 0$. In Figure 8, we compare bifurcation points q_1, q_* and maximal solutions $u_m(q,x)$ of (2.1) for $0 \le q \le q_*$ under different boundary conditions. Here we impose the upstream boundary condition to be NF ($b_u = 0$). For open environment ($b_d \in (0,\infty]$), there always exist two bifurcation points satisfying $0 < q_1(b_d) < q_*(b_d)$. And as b_d decreases, $q_1(b_d)$ and $q_*(b_d)$ both increase. For closed environment ($b_d = 0$), there exists a (possibly unique) positive steady state solution for any $q \ge 0$ and there are no bifurcation points. One can observe from Figure 8 (left panel) that the maximum value of $u_m(q,\cdot)$ increases for small q and decreases for large q when $0 \leq b_d < 1$, while the maximum value always decreases when $b_d > 1$. On the other hand, for all boundary conditions, the total population $||u_m(q,\cdot)||_1$ decreases in q.

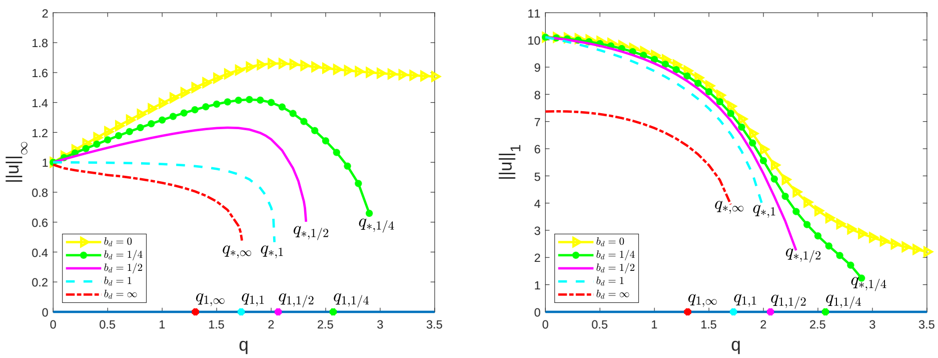

FIG. 8. *Comparison of bifurcation points q_1, q_*, and maximal steady state solutions of* (2.1) *under different boundary conditions. Here $g(x,u) = (r-u)(u+h)$, $r = 1$, $h = 0.3$, $b_u = 0$ (NF boundary condition on the upstream end), $d = 4$, $L = 10$, and the horizontal axis is q. Left: comparison of $||u||_\infty$. Right: comparison of $||u||_1$.*

In Figure 9, the parameter regions for the three dynamical behavior (monostable, bistable, and extinction) are plotted in the (d,q)-plane. For the boundary conditions that have NF on the upstream end and $b_d = 0.25$, $b_d = 0.5$, or $b_d = 1$ on the downstream end (upper panel and middle left panel), the bifurcation curves $q_1(d)$ and $q_*(d)$ increase as the diffusion coefficient d increases, and it appears that each of $q_1(d)$ and $q_*(d)$ approaches a limit as $d \to \infty$. Note that the case $b_d = 0.25$ is not included in the results of Theorem 3.5, but the behavior is similar to the one for $b_d > 0.5$. For the boundary conditions that have NF on the upstream end and $b_d = 2$, the bifurcation curves $q_1(d)$ and $q_*(d)$ are not monotone increasing but have a local maximum point in an intermediate advection rate. The curves still have asymptotic limits when $d \to \infty$. For the NF/H and H/H type boundary conditions (lower panel), not only the shape of graphs of $q_1(d)$ and $q_*(d)$ are one-hump type, each of $q_1(d)$ and $q_*(d)$ drops to zero at some $d > 0$. Indeed the value $d_1 > 0$ such that $q_1(d) = 0$ and the value $d_* > 0$ such that $q_*(d) = 0$ are exactly the critical diffusion coefficients defined in Theorem 2.3. The vanishing of the bifurcation point $q_1(d)$ and $q_*(d)$ under hostile boundary condition is shown in Theorem 3.6. When $0 < d < d_1$, the dynamics changes as "monostable-bistable-extinction" as q increases across q_1 and q_* (see Figure 6 (left)), and when $d_1 < d < d_*$, it changes to "bistable-extinction" (see Figure 6 (right)). The numerical result here also suggests that when $d > d_*$, the population does to extinction for all $q \geq 0$. Also for the NF/H and H/H type boundary conditions, if one fixes the advection rate q to be in an intermediate range and increases the diffusion coefficient d, then the dynamics varies in the sequence "extinction-bistable-monostable-bistable-extinction" (see Figure 9 (lower panel)). Note that for the logistic growth case, it is known that the dynamics changes in the sequence "extinction-monostable-extinction" [13, 24], and it was concluded that intermediate diffusion coefficient is favourable for the persistence. Here we get a similar conclusion for weak Allee effect type growth rate, but there are bistable regimes between the transition from extinction to persistence.

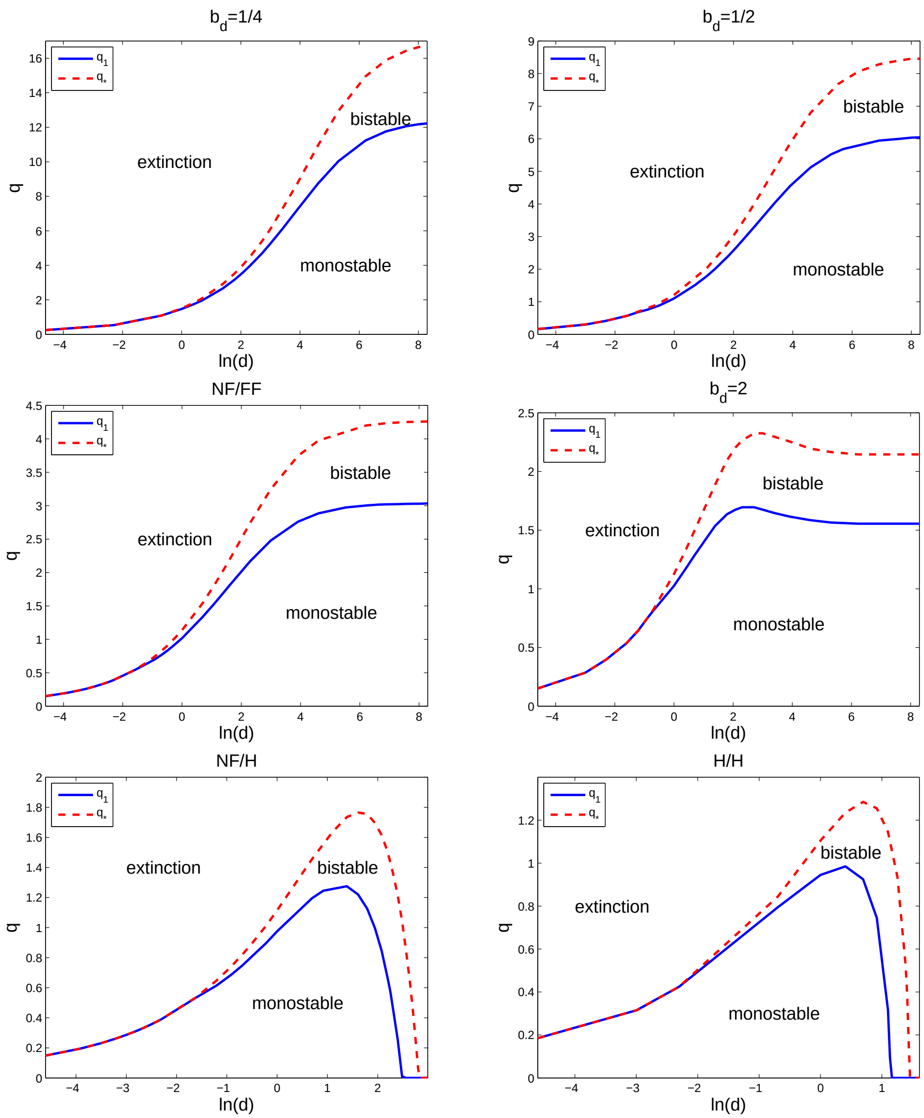

FIG. 9. *Population dynamical behavior of* (2.1) *for varying advection rate* q *and diffusion coefficient* d. *Here* $g(x,u) = (r-u)(u+h)$, $r = 1$, $h = 0.3$, $d = 4$, *and* $L = 10$. *In each graph, the horizontal axis is* d *in log scale, and the vertical axis is* q. *In all except lower right,* $b_u = 0$ *(NF). Upper left:* $b_d = 0.25$. *Upper right:* $b_d = 0.5$. *Middle left:* $b_d = 1$ *(F). Middle right:* $b_d = 2$. *Lower left: hostile boundary at* $x = L$ *(H). Lower right: hostile boundary at* $x = 0$ *and* $x = L$ *(H/H).*

4. Conclusion.

The persistence or extinction of a stream population with diffusive and advective movement is modeled by a reaction-diffusion-advection equation on an interval with boundary conditions depicting different flowing patterns at the endpoints. When the growth rate of the species is of logistic type, it is well known that the dynamics is either population extinction or convergence to a positive steady state (monostable), depending on the environment parameters (diffusion, advection, stream length) and boundary conditions [2, 8, 13, 17]. On the other hand, if the growth rate is of strong Allee effect, it was shown that either population extinction or alternative stable states (bistable) occurs, still depending on the environment parameters and boundary conditions. In this paper, the dynamics of the reaction-diffusion-advection equation with weak Allee effect growth rate is considered. Its outcome is in between the one with logistic growth and the one with strong Allee effect growth, so the extinction, bistable, and monostable dynamics all can occur for some environment parameters and boundary conditions.

For a closed advective environment, the dynamic behavior of the stream population with weak Allee effect growth is similar to the one with logistic growth, and the population persists for all diffusion coefficients and advection rates. For the open environment with non-hostile boundary condition, still similar to the logistic growth case, the trivial steady state in the weak Allee effect case is destabilized at a critical advection rate so it is stable for large advection and unstable for small advection. However, at the critical advection rate, unlike the logistic case, a backward bifurcation occurs so there is a range of advection rates for which the dynamics of stream population is bistable. Hence the model with weak Allee effect growth has features of the logistic model in some parameter ranges, but it also possesses the bistable dynamics that are characteristic for strong Allee effect growth in other parameter ranges. We use bifurcation theory to identify the range of advection rate for these three dynamic regimes: extinction, bistable, and monostable, and the diffusion coefficient does not affect the qualitative dynamics in this case.

For the open environment with hostile boundary condition, it is shown that both of the diffusion coefficient and the advection rate affect the dynamic outcomes. For an intermediate advection rate, when increasing the diffusion coefficient, the dynamics changes from extinction to bistable, then to monostable, then to bistable again, and back to extinction. This is more complicated than the logistic growth case but also shows that intermediate diffusion coefficient is favorable for population persistence even when the growth rate has a weak Allee effect. This extends the previous explanation of the "drift paradox" in [15, 16, 24] to the weak Allee effect growth case but with an additional possibility of bistable dynamics in two windows of diffusion coefficients.

Appendix.

Proof of Theorem 3.2. We apply a local bifurcation theorem [4, Theorem 1.7] and a global version in [23]. The nonlinear map G defined in (3.5) is differentiable and twice differentiable in u, and $G(q,0) = 0$ for all $q \geq 0$. At the bifurcation point $(q,u) = (q_1, 0)$,

$$G_u(q_1,0)[\phi] := \begin{pmatrix} d\phi_{xx} - q_1\phi_x + g(x,0)\phi \\ d\phi_x(0) - (1+b_u)q_1\phi(0) \\ d\phi_x(L) - (1-b_d)q_1\phi(L) \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \\ 0 \end{pmatrix}, \tag{4.1}$$

from Proposition 2.2, $G_u(q_1,0)$ has a one-dimensional kernel spanned by ϕ as $\lambda_1(q_1) = 0$ is the principal eigenvalue of (2.3), and the codimension of the range of $G_u(q_1,0)$ is also one from [23]. Here we make the range $R(G_u(q_1,0))$ of $G_u(q_1,0)$ more specific. Suppose there exists a $\varphi \in X_3$ such that

$$G_u(q_1,0)[\varphi] := \begin{pmatrix} d\varphi_{xx} - q_1\varphi_x + g(x,0)\varphi \\ d\varphi_x(0) - (1+b_u)q_1\varphi(0) \\ d\varphi_x(L) - (1-b_d)q_1\varphi(L) \end{pmatrix} = \begin{pmatrix} h(x) \\ a \\ b \end{pmatrix}, \tag{4.2}$$

where $(h(x), a, b) \in Y \times \mathbb{R}^2$. Notice that the first equation in (4.1) can be written as

$$d(e^{-\alpha_1 x}\phi_x)_x + g(x,0)e^{-\alpha_1 x}\phi = 0, \tag{4.3}$$

where $\alpha_1 = \frac{q_1}{d}$. Similarly, from (4.2), we have

$$d(e^{-\alpha_1 x}\varphi_x)_x + g(x,0)e^{-\alpha_1 x}\varphi = e^{-\alpha_1 x}h(x). \tag{4.4}$$

Then multiplying (4.3) by φ and (4.4) by ϕ, subtracting each other, and integrating from 0 to L, we have

$$-e^{-\alpha_1 L}b\phi(L) + a\phi(0) = -\int_0^L e^{-\alpha_1 x}\phi(x)h(x)dx. \tag{4.5}$$

Therefore we have

$$R(G_u(q_1,0)) = \{(h(x),a,b) \in Y \times \mathbb{R}^2 : l(h(x),a,b) = 0\},$$

where $l : Y \times \mathbb{R}^2 \to \mathbb{R}$ is a linear functional in $(Y \times \mathbb{R}^2)^*$ defined by

$$l(h(x),a,b) = \int_0^L e^{-\alpha_1 x}\phi(x)h(x)dx + a\phi(0) - e^{-\alpha_1 L}b\phi(L). \tag{4.6}$$

Therefore $\dim N(G_u(q_1,0)) = \operatorname{codim} R(G_u(q_1,0)) = 1$.

Next we prove that $G_{qu}(q_1,0)[\phi] \notin R(G_u(q_1,0))$, where $\phi \in N(G_u(q_1,0))$ and $\phi \neq 0$. We have

$$G_{qu}(q_1,0)[\phi] := \begin{pmatrix} -\phi_x \\ -(1+b_u)\phi(0) \\ -(1-b_d)\phi(L) \end{pmatrix}. \tag{4.7}$$

By using $b_d \geq \frac{1}{2}$ and $G_u(q_1,0)[\phi] = 0$, we have

(4.8)
$$\begin{aligned} l(G_{qu}(q_1,0)[\phi]) &= -\int_0^L e^{-\alpha_1 x}\phi(x)\phi_x(x)dx - (1+b_u)\phi^2(0) + e^{-\alpha_1 L}(1-b_d)\phi^2(L) \\ &= -\frac{1}{2}e^{-\alpha_1 x}\phi^2(x)|_0^L - \int_0^L \frac{\alpha_1}{2}e^{-\alpha_1 x}\phi^2(x)dx - (1+b_u)\phi^2(0) \\ &\quad + e^{-\alpha_1 L}(1-b_d)\phi^2(L) \\ &= -\int_0^L \frac{\alpha_1}{2}e^{-\alpha_1 x}\phi^2(x)dx - \left(\frac{1}{2}+b_u\right)\phi^2(0) + e^{-\alpha_1 L}\left(\frac{1}{2}-b_d\right)\phi^2(L); \\ &< 0, \end{aligned}$$

hence $G_{qu}(q_1,0)[\phi] \notin R(G_u(q_1,0))$.

Now from [4, Theorem 1.7], the set of positive solutions of (3.4) near the bifurcation point $(q_1,0)$ is $\Gamma^1_+ = \{(q(s),u(s)) : 0 < s < \delta\}$, $q(0) = q_1$, $u(0) = 0$ and $u(s) = s\phi + sz(s)$, $z(0) = 0$, $z : [0,\delta) \to X_4$, $q(s), z(s)$ are continuous functions, where $X_4 = \{\varphi \in X_3 : \int_0^L \phi\varphi dx = 0\}$ is a subspace of X_3 complement to $\mathrm{Span}\{\phi\}$. Since

$$G_{uu}(q_1,0)[\varphi_1,\varphi_2] := \begin{pmatrix} 2g_u(x,0)\varphi_1\varphi_2 \\ 0 \\ 0 \end{pmatrix}, \tag{4.9}$$

where $\varphi_1, \varphi_2 \in X_3$, we also obtain that (see [21])

$$\begin{aligned} q'(0) &= -\frac{\langle l, G_{uu}(q_1,0)[\phi,\phi]\rangle}{2\langle l, G_{qu}(q_1,0)[\phi]\rangle} \\ &= \frac{2\int_0^L e^{-\alpha_1 x}g_u(x,0)\phi^3(x)dx}{\alpha_1\int_0^L e^{-\alpha_1 x}\phi^2(x)dx + (2b_u+1)\phi^2(0) + (2b_d-1)e^{-\alpha_1 x}\phi^2(L)}. \end{aligned} \tag{4.10}$$

Therefore, if $g_u(x,0) < 0$ for all $x \in \Omega$, which is the logistic type growth rate, we have $q'(0) < 0$, and the bifurcation occurring at $(q_1, 0)$ is forward. And if $g_u(x,0) > 0$ for all $x \in \Omega$, which is the weak Allee type growth rate, we have $q'(0) > 0$, and the bifurcation occurring at $(q_1, 0)$ is backward.

Next we apply [23, Theorem 4.3, 4.4] to obtain a global connected component Γ_1^+ containing the local bifurcation curve which we obtain above. The conditions in [23, Theorem 4.3, 4.4] can all be verified using standard ways; see [23, 27]. Then we conclude that there exists a connected component Γ_+^1 of Γ_+ such that its closure contains $(q_1, 0)$, and there are three possibilities: (i) Γ_+^1 is unbounded in $\mathbb{R} \times X_3$; (ii) the closure of Γ_+^1 contains another $(q_i, 0)$, where q_i is another eigenvalue satisfying the kernel of $G_u(q_i, 0)$ is nontrivial and $q_i \neq q_1$; or (iii) Γ_+^1 contains a point (q, z), where $z \in X_4$. Case (ii) cannot happen since according to Lemma 3.1 all solutions on Γ_+^1 are positive, but the solutions bifurcating from $(q_i, 0)$ with $q_i \neq q_1$ are sign-changing near the bifurcation point, as 0 is a nonprincipal eigenvalue of (2.3) with $q = q_i$. Case (iii) cannot occur either as $z \in X_4$ implying that z is sign-changing but all solutions on Γ_+^1 are positive. Therefore case (i) must occur and Γ_+^1 must be unbounded in $\mathbb{R} \times X_3$. And from Proposition 2.1, we have

$$u(x) \leq e^{q_* x/d} \max_{y \in [0,L]} (e^{-q_* y/d} r(y)),$$

where $r(x)$ is defined in (g2), which gives that Γ_+^1 is bounded in $\mathbb{R}^+ \times X_3$. Thus, the projection of Γ_+ on $\mathbb{R}^+$ is bounded. On the other hand, from Lemma 3.1, we know that there exist a $\overline{q}_1 > 0$ such that positive solutions of system (3.4) only exist when $q < \overline{q}_1$. Therefore $(-\infty, \overline{q}_1) \supset \mathrm{Proj}_q \Gamma_+^1 \supset (-\infty, q_1) \supset [0, q_1)$. $\square$

Proof of Theorem 3.5. From Theorem 3.1, we know that there exists a $\overline{q}_1 > 0$, such that (3.4) has no positive solution when $q > \overline{q}_1$. For any $q \geq 0$, using the transform $u = e^{\alpha x} v$ ($\alpha = q/d$) on (3.4), we obtain the following boundary value problem for v:

$$\begin{cases} dv_{xx} + qv_x + vg(x, e^{\alpha x} v) = 0, & 0 < x < L, \\ -dv_x(0) + b_u q v(0) = 0, \\ dv_x(L) + b_d q v(L) = 0. \end{cases} \tag{4.11}$$

Set $\overline{v}(x) = \max_{y \in [0,L]} e^{-\alpha y} r(y)$. From (g3), we have $g(x, u) \leq 0$ for $u \geq r(x)$ which implies that

$$g(x, e^{\alpha x} \overline{v}) = g\left(x, e^{\alpha x} \max_{y \in [0,L]} e^{-\alpha y} r(y)\right) \leq g(x, e^{\alpha x} e^{-\alpha x} r(x)) = g(x, r(x)) = 0.$$

Hence $\overline{v}(x)$ satisfies

$$\begin{cases} d\overline{v}'' + q\overline{v}' + vg(x, e^{\alpha x} \overline{v}) \leq 0, & 0 < x < L, \\ -d\overline{v}'(0) + b_u q \overline{v}(0) \geq 0, \\ d\overline{v}'(L) + b_d q \overline{v}(L) \geq 0, \end{cases} \tag{4.12}$$

which shows that $\overline{v}(x)$ is an upper solution of (4.11) for any $q \geq 0$. For a given $0 \leq q \leq q_*$, if there exists a positive solution $v(x)$ of (4.11), then it satisfies $v(x) \leq \overline{v}(x)$ from Theorem 2.1 part 2. We can set the lower solution of (4.11) to be $\underline{v}(x) = v(x)$.

Then there exists a maximal solution $v_m(x)$ of (4.11) satisfying $\underline{v}(x) \le v_m(x)$. Since $v_m(x)$ is obtained through iteration from $\overline{v}(x)$ and any positive solution v of (4.11) satisfies $v(x) \le \overline{v}(x)$, then $v_m(x)$ is the maximal solution of (4.11). Hence the maximal solution $v_m(x)$ always exists as long as a positive solution $v(x)$ of (4.11) exists. From Theorem 3.2, under the conditions (g1)–(g3) and (g4b), (4.11) has a positive solution $v(x)$ for $q \in (q_1, q_1+\delta)$ with some $\delta > 0$, and these solutions are on a connected component Γ_+^1 that emerges from the bifurcation point $q = q_1$. Define $q_* = \sup\{q > 0 :$ there exists a positive solution $(q, u) \in \Gamma_+^1$ of (3.4)$\}$. Then q_* is well defined and $q_1 < q_* \le \overline{q}_1$. Because of the continuity of Γ_+^1 and Theorem 3.2, (4.11) (or (3.4)) has a positive solution (q, v) (or (q, u)) for all $q \in [0, q_*)$. Then from above argument, (4.11) has a maximal solution $v_m(q, x)$ for $q \in [0, q_*)$, and consequently (3.4) has a maximal solution $u_m(q, x)$ for $q \in [0, q_*)$.

From Theorem 2.1, the solutions $\{u_m(q, x) : 0 \le q < q_*\}$ are uniformly bounded, and thus they are also bounded in X_3 from elliptic estimates. By taking a subsequence, we may assume that $u_m(q_*, x) = \lim_{q\to(q^*)^-} u_m(q, x) \ge 0$ exists, and it is a solution of (3.4). From the maximum principle, either $u_m(q_*, x) > 0$ or $u_m(q_*, x) \equiv 0$. If $u_m(q_*, x) \equiv 0$, then $q = q_*$ is also a bifurcation point for (3.4) from the trivial branch Γ_0, but $q = q_1$ is the only bifurcation point where positive solutions of (3.4) can bifurcate from Γ_0. So this is impossible as $q_* > q_1$. Therefore $u_m(q_*, x) > 0$ so (3.4) has a maximal solution $u_m(q, x)$ for $q \in [0, q_*]$. Finally the existence of two positive solutions of (3.4) when $q \in (q_1, q_*)$ follows from the same argument of [22, Theorem 3] but using the energy functional

(4.13)
$$E(u) = \int_0^L e^{-\alpha x}\left[\frac{d}{2}(u')^2 - F(x, u)\right] dx + \frac{q}{2}(1+b_u)u^2(0) - \frac{q}{2}(1-b_d)e^{-\alpha L}u^2(L),$$

for $u \in X_2$, where $F(x, u) = \displaystyle\int_0^u ug(x, s)ds$. ∎

Proof of Theorem 3.6. For the case that $0 < d < d_1$, when $q = 0$, the trivial solution $u = 0$ of (3.6) is unstable and according to Theorem 2.3, (2.5) has a maximal solution u_m. Then we can follow the same proof of Theorems 3.2 and 3.5 to prove that there is a unique bifurcation point $q_1 > 0$ for (3.6) on the branch Γ_0 of trivial solutions, the bifurcation is backward so the bifurcating branch Γ_+^1 can be extended to some $q_* > q_1$, and Γ_1^+ connects to $(0, u_m)$. Other parts can also be obtained using the same proof as the ones of Theorems 3.2 and 3.5.

For the case that $d_1 < d < d_*$, when $q = 0$, the trivial solution $u = 0$ of (3.6) is stable. From Theorem 2.3, (2.5) has a maximal solution u_m and at least another positive solution u_2. Let Γ_+^1 be the connected component of the set of positive solutions to (3.6) in $\mathbb{R}^+ \times X_3$ containing $(0, u_m)$. Then from [29, Theorem 4.2], the following alternatives hold: (i) Γ_+^1 is unbounded in $\mathbb{R}^+ \times X_5$, or (ii) Γ_+^1 contains another $(0, u_2) \in \mathbb{R} \times X_5$ with $u_2 \ne u_m$, or (iii) $\Gamma_+^1 \cap \partial(\mathbb{R}^+ \times X_5) \ne \emptyset$, where $\partial(\mathbb{R}^+ \times X_5)$ is the boundary of $\mathbb{R}^+ \times X_5$. Since the zero steady state is always stable, (iii) is not possible. From Theorem 3.1, Γ_+^1 is bounded; hence (i) is also not possible. Therefore, Γ_+^1 contains another $(0, u_2) \in \{0\} \times X_5$ with $u_2 \ne u_m$. Other parts can also be obtained using the same proof as the ones of Theorems 3.2 and 3.5. ∎

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REFERENCES

[1] W. C. Allee, *Animal aggregations. A study in general sociology*, University of Chicago Press, Chicago, 1931.

[2] R. S. Cantrell and C. Cosner, *Spatial ecology via reaction-diffusion equations*, Wiley Series in Mathematical and Computational Biology, John Wiley & Sons, Chichester, 2003.

[3] F. Courchamp, L. Berec, and J. Gascoigne, *Allee Effects in Ecology and Conservation*, Oxford University Press, Oxford, 2008.

[4] M. G. Crandall and P. H. Rabinowitz, *Bifurcation from simple eigenvalues*, J. Functional Analysis, 8 (1971), pp. 321–340.

[5] D. Henry, *Geometric theory of semilinear parabolic equations*, Lecture Notes in Mathematics 840, Springer-Verlag, New York, 1981.

[6] C.-G. Kim and J.-P. Shi, *Multiple positive solutions for p-Laplacian equation with weak Allee effect growth rate*, Differential Integral Equations, 26 (2013), pp. 707–720.

[7] A. M. Kramer, B. Dennis, A. M. Liebhold, and J. M. Drake, *The evidence for Allee effects*, Population Ecology, 51 (2009), pp. 341–354.

[8] K. Y. Lam, Y. Lou, and F. Lutscher, *Evolution of dispersal in closed advective environments*, J. Biol. Dyn., 9 (2015), pp. 188–212.

[9] K. Y. Lam, Y. Lou, and F. Lutscher, *The emergence of range limits in advective environments*, SIAM J. Appl. Math., 76 (2016), pp. 641–662.

[10] K.-Y. Lam and D. Munther, *Invading the ideal free distribution*, Discrete Contin. Dyn. Syst. Ser. B, 19 (2014), pp. 3219–3244.

[11] M. A. Lewis and P. Kareiva, *Allee dynamics and the spread of invading organisms*, Theo. Popu. Biol., 43 (1993), pp. 141–158.

[12] M. A. Lewis, S. V. Petrovskii, and J. R. Potts, *The mathematics behind biological invasions*, Interdisciplinary Applied Mathematics 44, Springer, New York, 2016.

[13] Y. Lou and F. Lutscher, *Evolution of dispersal in open advective environments*, J. Math. Biol., 69 (2014), pp. 1319–1342.

[14] Y. Lou and P. Zhou, *Evolution of dispersal in advective homogeneous environment: The effect of boundary conditions*, J. Differential Equations, 259 (2015), pp. 141–171.

[15] F. Lutscher, R. M. Nisbet, and E. Pachepsky, *Population persistence in the face of advection*, Theo. Ecol., 3 (2010), pp. 271–284.

[16] F. Lutscher, E. Pachepsky, and M. A. Lewis, *The effect of dispersal patterns on stream populations*, SIAM J. Appl. Math., 65 (2005), pp. 1305–1327.

[17] H. W. Mckenzie, Y. Jin, J. Jacobsen, and M. A. Lewis, *R_0 analysis of a spatiotemporal model for a stream population*, SIAM J. Appl. Dyn. Syst., 11 (2012), pp. 567–596.

[18] D. Munther, *The ideal free strategy with weak Allee effect*, J. Differential Equations, 254 (2013), pp. 1728–1740.

[19] W.-M. Ni, *The mathematics of diffusion*, CBMS-NSF Regional Conference Series in Applied Mathematics 82, Society for Industrial and Applied Mathematics, Philadelphia, 2011.

[20] A. Okubo and S. A. Levin, *Diffusion and ecological problems: modern perspectives*, Interdisciplinary Applied Mathematics 14, 2nd ed., Springer-Verlag, New York, 2001.

[21] J.-P. Shi, *Persistence and bifurcation of degenerate solutions*, J. Funct. Anal., 169 (1999), pp. 494–531.

[22] J.-P. Shi and R. Shivaji, *Persistence in reaction diffusion models with weak Allee effect*, J. Math. Biol., 52 (2006), pp. 807–829.

[23] J.-P. Shi and X.-F. Wang, *On global bifurcation for quasilinear elliptic systems on bounded domains*, J. Differential Equations, 246 (2009), pp. 2788–2812.

[24] D. C. Speirs and W. S. C. Gurney, *Population persistence in rivers and estuaries*, Ecology, 82 (2001), pp. 1219–1237.

[25] P. A. Stephens and W. J. Sutherland, *Consequences of the Allee effect for behaviour, ecology and conservation*, Trends Ecol. Evol., 14 (1999), pp. 401–405.

[26] M.-H. Wang and M. Kot, *Speeds of invasion in a model with strong or weak Allee effects*, Math. Biosci., 171 (2001), pp. 83–97.

[27] X. F. Wang and Q. Xu, *Spiky and transition layer steady states of chemotaxis systems via global bifurcation and Helly's compactness theorem*, J. Math. Biol., 66 (2013), pp. 1241–1266.

[28] Y. Wang, J.-P. Shi, and J.-F. Wang, *Persistence and extinction of population in reaction-diffusion-advection model with strong Allee effect growth*, J. Math. Biol., 78 (2019), pp. 2093–2140.

[29] Y.-H. Zhao, Y.-W. Wang, and J.-P. Shi, *Steady states and dynamics of an autocatalytic chemical reaction model with decay*, J. Differential Equations, 253 (2012), pp. 533–552.