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Persistence and extinction dynamics in reaction-diffusion-advection stream population model with Allee effect growth

Yan Wang

Harbin, China

Master of Mathematics, Harbin Institute of Technology, China, 2013
Bachelor of Science, Harbin Institute of Technology, China, 2011

A Dissertation presented to the Graduate Faculty
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Doctor of Philosophy

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APPROVAL PAGE

This Dissertation is submitted in partial fulfillment of the requirements for the degree of

Doctor of Philosophy

Yan Wang

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Committee Chair
Professor Junping Shi, Mathematics/Applied Science
College of William & Mary

Associate Professor Leah B. Shaw, Mathematics/Applied Science
College of William & Mary

Professor Gregory D. Smith, Applied Science
College of William & Mary

Assistant Professor Mainak Patel, Mathematics
College of William & Mary

ABSTRACT

The question how aquatic populations persist in rivers when individuals are constantly lost due to downstream drift has been termed the "drift paradox." Reaction-diffusion-advection models have been used to describe the spatial-temporal dynamics of stream population and they provide some qualitative explanations to the paradox. Here random undirected movement of individuals in the environment is described by passive diffusion, and an advective term is used to describe the directed movement in a river caused by the flow. In this work, the effect of spatially varying Allee effect growth rate on the dynamics of reaction-diffusion-advection models for the stream population is studied.

In the first part, a reaction-diffusion-advection equation with strong Allee effect growth rate is proposed to model a single species stream population in a unidirectional flow. Under biologically reasonable boundary conditions, the existence of multiple positive steady states is shown when both the diffusion coefficient and the advection rate are small, which lead to different asymptotic behavior for different initial conditions. On the other hand, when the advection rate is large, the population becomes extinct regardless of initial condition under most boundary conditions. It is shown that the population persistence or extinction depends on Allee threshold, advection rate, diffusion coefficient and initial conditions, and there is also rich transient dynamical behavior before the eventual population persistence or extinction.

The dynamical behavior of a reaction-diffusion-advection model of a stream population with weak Allee effect type growth is studied in the second part. 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.

In the last part, the dynamics of a reaction-diffusion-advection benthic-drift population model that links changes in the flow regime and habitat availability with population dynamics is studied. In the model, the stream is divided into drift zone and benthic zone, and the population is divided into two interacting compartments, individuals residing in the benthic zone and individuals dispersing in the drift zone. The benthic population growth is assumed to be of strong Allee effect type. The influence of flow speed and individual transfer rates between zones on the population persistence and extinction is considered, and the criteria of population persistence or extinction are formulated and proved.

All results are proved rigorously using the theory of partial differential equation, dynamical systems. Various mathematical tools such as bifurcation methods, variational methods, and monotone methods are applied to show the existence of multiple steady state solutions of models.

CONTENTS

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Chapter 1

Introduction

Streams and rivers are characterized by a variety of physical, chemical and geomorphological features such as unidirectional flow, pools and riffles, bends and waterfalls, floodplains, lateral inflow and network structure and many more. These complex structures provide a wide range of qualitatively different habitat for aquatic species and organisms such as zooplankton, invertebrates, aquatic plant and fish. In [71], Müller proposed an important issue in stream ecology, termed the “drift paradox”, which asks how stream dwelling organisms can persist in a river/stream environment when continuously subjected to a unidirectional water flow. The growth of a biological population is affected by both the environmental factors and the population density. The spatial structure of the natural environment influences the movement pattern of the individuals in the population, and that in turn affects the population dynamics. Individual movement can be undirected or directed. Random undirected movement of individuals in the environment is often described by a passive diffusion of a density function in continuum following the classical approach in physics. Combining with the density-dependent growth of the population, we obtain reaction-diffusion models, which have been widely used to describe spatiotemporal behavior in both chemical [25, 81] and biological fields [9, 75, 76].

In some situations, in addition to the random dispersal, individuals in a population also make advective movement which is from sensing and following the gradient of resource distribution (taxis) or a directional fluid/wind flow. Some examples are marine living species flowing in rivers, lakes or oceans, benthic marine species along coastlines with dominant long-shore currents, or phytoplankton species in water column experiencing gravitational downward pull [38, 93]. The addition of advection to reaction-diffusion models may change the long term outcome (persistence/extinction) of the population [34, 42, 54, 63, 65].

Mathematical models of populations can be used to accurately describe changes occurring in a population and, importantly, to predict future changes. Population ecologists use a variety of mathematical methods to model population dynamics (how populations change in size and composition over time). Some of these models represent growth without environmental constraints, while others include "ceilings" determined by limited resources. In Charles Darwin's description of "struggle for existence", he recognized the fact that individuals will compete (with members of their own or other species) for limited resources. The successful ones will survive to pass on their own characteristics and traits (which we know now are transferred by genes) to the next generation at a greater rate: a process known as natural selection. To model the reality of limited resources, population ecologists developed the logistic growth model. In logistic growth, the growth rate decreases as the population reaches carrying capacity. Carrying capacity is the maximum number of individuals in a population that the environment can support. When the population follows a typical logistic growth, there often exists a critical parameter value (diffusion coefficient, advection coefficient, domain size, growth rate) for the population persistence or extinction [53, 59, 70], and it is well known that the model has a unique positive steady state solution which is globally asymptotically stable when population persists [9].

Despite the universal acceptance of logistic growth as the most reasonable one, since Allee's pioneer work [3] in 1931, ecologists have found that in many cases, the population growth could depend on the density positively instead of negative dependence as in the logistic one. When the population density is low, individual may have difficulty in finding mates or defending against predators, which will lead to low birth rate and high death rate. For high population density, population size is still restricted by the environment limits.

Thus either excessive sparsity or excessive crowding can inhibit the population growth, which means such species have an optimum intermediate range for the population growth. This phenomenon has been frequently termed as the Allee effect. 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 at low population density, it is called weak Allee effect. Allee effect has been the focus of increasing interest over the past three decades [18, 57, 94]. For instance, due to the severe harvesting, the west Atlantic cod (*Ganus morhus*) population stayed below the Allee threshold in the past few decades [22, 85]. Although many management strategies have been implemented to reduce fishing mortality after a collapse, the cod population does not show an increase of size and such a lack of recovery indicates a reduced capacity to rebound from low densities. Another example is the case of Vancouver Island marmot (*Marmota vancouverensis*) whose population has declined by 80% since the 1980s. The studies in [8] shows a growth rate of strong Allee effect type for the marmot due to the longer distance traveled when finding mates and change of social behavior. Overall more and more evidences of Allee effect in wild species populations have been found in recent studies [18, 50], especially for marine species such as blue crab, oyster whose growth rate strongly depends on the river/ocean flow [28, 29, 46].

Mathematical models, such as reaction-diffusion-advection equations and integro-differential equations have been established to study the population dynamic in advective environment. For species following logistic type growth, a "critical flow speed" has been identified, below which can ensure the persistence of the stream population [42, 53, 54, 59, 63, 65, 70, 93]. On the other hand, when the species following Allee effect type growth, population persistence for all initial conditions becomes not possible as the extinction state is always a stable state, and more delicate conditions are needed to ensure the population persistence [89, 107, 108]. The solution of stream population persistence/extinction not only leads to a better understanding of population dynamics in a stream environment, but also provides strategies for how to keep a native species persistent.

Stream hydraulic characteristics is another important factor in the ecology of stream populations. Of great importance is the presence of storage zones (zones of zero or near-zero flow) in stream channels. These zones are refuges for many organisms not adapted to high water velocity. And for some aquatic species, the individuals spend a proportion of their time immobile and a proportion of their time in an environment with a unidirectional current and do not reproduce there. Following [7, 23], the river can be partitioned into two zones, drift zone and benthic zone, and the population is also split into two interacting compartments: individuals residing in the benthic zone and the ones dispersing in the drift zone. Assuming that longitudinal movement occurs only in the drift zone, a system of coupled reaction-diffusion-advection equation of drift population and equation of benthic population can be used to model the dynamic evolution of aquatic species that reproduce on the bottom of the river and release their larval stages into the water column, such as sedentary water plant, oyster and coral [63, 78].

In this paper, reaction-diffusion-advection models for stream population in both single channel setting and benthic-drift setting are established, and the dynamical behavior of models are analyzed and simulated. In particular our focus is on the effect of Allee effect growth rate on the population dynamics.

1.1 Mathematical models

1.1.1 Equation

Following [9, 59], we first consider a reaction-diffusion-advection equation on a one-dimensional bounded habitat $(0, L)$:

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

Here $u(x,t)$ is the population density of a biological species 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; and the function $g(x,u)$ is the growth rate per capita which may depend on the location and population density. We assume that the growth rate $f(x,u) = ug(x,u)$ satisfies the following basic technical assumptions, which are similar to the ones in [9, 89]:

(g1) For any $u \geq 0$, $g(\cdot, u) \in C[0,L]$, and for any $x \in [0,L]$, $g(x,\cdot) \in C^1[0,L]$.

(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 $g(x,r(x)) = 0$, and $g(x,u) < 0$ 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 non-increasing in $[s(x),\infty]$; and there also exists $N > 0$ such that $g(x,s(x)) \leq N$.

Here $g(x,u)$ is the growth rate per capita at x; $r(x)$ is a local carrying capacity at x which 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). Typically the behavior of $g(x,\cdot)$ defined in (g3) can be one of the following three cases: (see [89])

(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 $[0,s(x)]$, non-increasing 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 $[0,s(x)]$, non-increasing in $[s(x),\infty)$. Hence there exists a unique $h(x) \in (0,s(x))$ such that $g(x,h(x)) = 0$ for all $0 < x < L$.

In (g4c), the quantity $h(x)$ is the local threshold value for the extinction/persistence of the population, which is also known as the sparsity constant. Figure 1.1 shows typical graphs of $f(x,u)$ and $g(x,u)$ for these three cases.

Typical examples of growth rate functions satisfying (g4a) is

$$f(x,u) = u(r(x) - u), \tag{1.2}$$

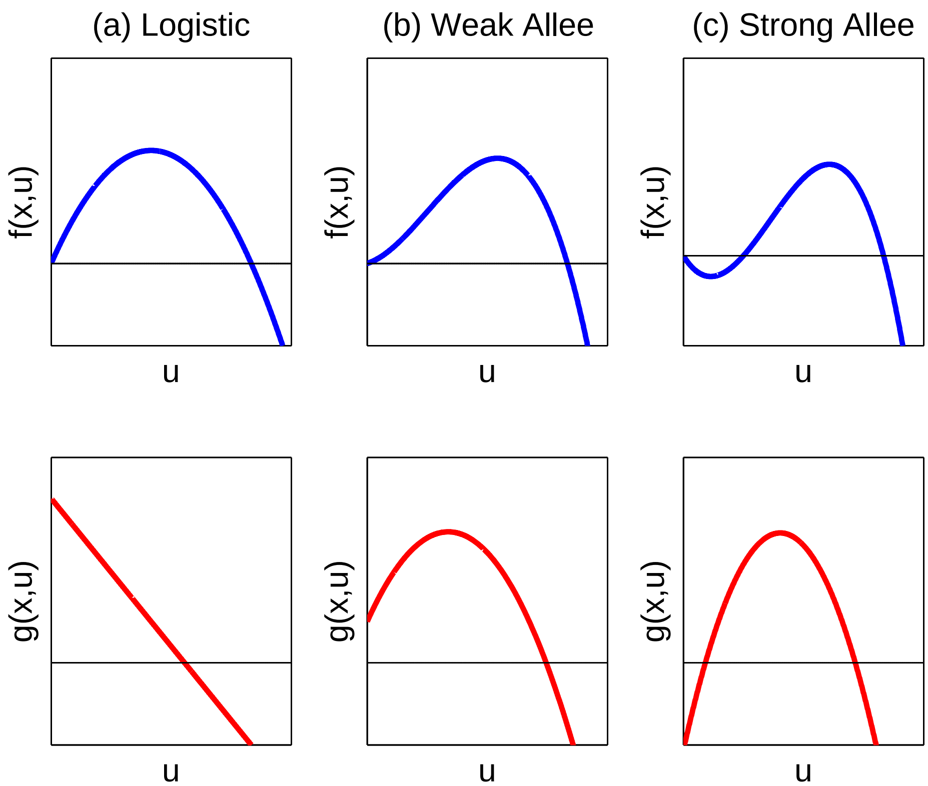

Figure 1.1: (a) logistic; (b) weak Allee effect; (c) strong Allee effect; the graphs on top row are growth rate $f(u)$, and the ones on lower row are growth rate per capita $g(u)$.

while the one for Allee effect is

$$f(x, u) = u(u - h(x))(r(x) - u), \tag{1.3}$$

where $0 < h(x) < r(x)$ represents the strong Allee effect case, and $-r(x) < h(x) < 0$ represents the weak Allee effect case. The nonlinear function $f(x, u)$ with a strong Allee effect growth rate is also called the bistable type as $u = 0$ and $u = r(x)$ are both stable solutions to the ordinary differential equation (ODE) $u' = f(x, u)$. Summarizing the above discussions, we will consider the following reaction-diffusion-advection equation with a general

Danckwerts boundary condition at the upstream ($x = 0$) and downstream ($x = L$) ends:

$$\begin{cases} u_t = du_{xx} - qu_x + ug(x,u), & 0 < x < L,\ t > 0, \\ du_x(0,t) - qu(0,t) = b_u qu(0,t), & t > 0, \\ du_x(L,t) - qu(L,t) = -b_d qu(L,t), & t > 0, \\ u(x,0) = u_0(x) \geq 0, & x \in (0,L), \end{cases} \tag{1.4}$$

where $b_u \geq 0$ 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. In chapter 2, we will investigate equation (1.4) with strong Allee effect population growth, i.e., $g(x,u)$ satisfies (g1)-(g3) and (g4c). In chapter 3, we will investigate equation (1.4) with weak Allee effect population growth, i.e., $g(x,u)$ satisfies (g1)-(g3) and (g4b).

1.1.2 Boundary conditions

The boundary condition at $x = 0$ or $x = L$ can take one of the following forms (see [59] for ecological interpretation of each boundary condition):

$$\text{No Flux (NF)} \qquad du_x(x,t) - qu(x,t) = 0, \tag{1.5}$$

$$\text{Free Flow (FF)} \qquad u_x(x,t) = 0, \tag{1.6}$$

$$\text{Hostile (H)} \qquad u(x,t) = 0. \tag{1.7}$$

Often at the upstream end $x = 0$ a no flux boundary condition is imposed, and at the downstream end $x = L$ a free flow boundary condition is used to indicate that there is a population loss due to the advective movement, or a hostile boundary condition is used which means no individuals can return to the habitat after leaving. The no-flux boundary condition can be interpreted as there is no loss of individuals at $x = 0$ or $x = L$. Following

[54, 59], we impose boundary conditions in a general form

$$du_x(0,t) - qu(0,t) = b_u qu(0,t), \quad du_x(L,t) - qu(L,t) = -b_d qu(L,t), \tag{1.8}$$

where $b_u \geq 0$ and $b_d \geq 0$. Here the parameters b_u and b_d determine the magnitude of population loss at the upstream end $x = 0$ and the downstream end $x = L$, respectively. This form of boundary condition was proposed in [54]. Typically a no-flux boundary (NF) 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 no-flux one (NF) with $b_d = 0$. More discussions and biological interpretations of these boundary conditions were given in [59]. As discussed in [59], (1.4) can be used to describe plankton growth in river flows, periphyton dynamics in the lake water column, or biological species in water flow from stream to ocean or lake. Note that (1.8) with $b_u \geq 0$ and $b_d \geq 0$ implies that

$$[du_x(x,t) - qu(x,t)]\Big|_0^L = -q[b_d u(L,t) + b_u u(0,t)] \leq 0. \tag{1.9}$$

When $b_u = b_d = 0$, we have a no-flux boundary condition at both ends of the stream:

$$\text{(NF/NF)} \qquad du_x(0,t) - qu(0,t) = 0, \quad du_x(L,t) - qu(L,t) = 0, \tag{1.10}$$

which represents a closed environment as there is no loss of the population due to the movement. On the other hand, if $b_u > 0$ or $b_d > 0$, then the total population has a loss over the region $[0, L]$ due to the movement and (1.8) depicts an open flowing environment. For example,

$$\text{(NF/FF)} \qquad du_x(0,t) - qu(0,t) = 0, \quad u_x(L,t) = 0, \tag{1.11}$$

In this paper, we consider the persistence and extinction of population $u(x,t)$ under the general boundary conditions (1.8) with $b_u \geq 0$ and $b_d \geq 0$. But hostile boundary condition will also be studied some time as a comparison, such as (H/H), (NF/H) or (H/NF). For example,

$$\text{(NF/H)} \qquad du_x(0,t) - qu(0,t) = 0, \;\; u(L,t) = 0. \tag{1.12}$$

1.1.3 Benthic-drift model

Consider a population in which individuals live and reproduce in the storage zone, and occasionally enter the water column to drift until they settle on the benthos again. We assume that advective and diffusive transport occur only in the main flowing zone, not the storage zone. So we neglect the movement in the benthic zone. While in the drifting water, we consider the individual's movement as a combination of passive diffusion movement and advective movement which is from sensing and following the gradient of resource distribution (taxis) or a directional fluid/wind flow. Let $u(x,t)$ be the population density in the drift zone and let $v(x,t)$ be the population density in the benthic zone. 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 $x = L$, where L is the length of the river. A mathematical model that describes the dynamics of the population in a river is given by [37, 63] (see Figure 1.2):

$$\begin{cases} u_t = du_{xx} - qu_x + \dfrac{A_b(x)}{A_d(x)}\mu v - \sigma u - m_1 u, & 0 < x < L, \; t > 0, \\ v_t = vg(x,v) - m_2 v - \mu v + \dfrac{A_d(x)}{A_b(x)}\sigma u, & 0 \le x \le L, \; t > 0, \\ du_x(0,t) - qu(0,t) = b_u qu(0,t), & t > 0, \\ du_x(L,t) - qu(L,t) = -b_d qu(L,t), & t > 0, \\ u(x,0) = u_0(x) \ge 0, \; v(x,0) = v_0(x) \ge 0, & x \in (0,L), \end{cases} \tag{1.13}$$

where d and q are the diffusion rate and advection rate of the population in the drifting zone, respectively; $A_b(x)$ and $A_d(x)$ are the cross-sectional areas of the benthic zone and drift zone, respectively; σ is the the transfer rate of the drift population to the benthic one and μ is the transfer rate of the benthic population to the drifting one; m_1 and m_2 are the mortality rates of the drift and benthic population, respectively. The growth rate per capita $g(x, v)$ satisfies the general conditions in subsection 1.1.1. In chapter 4, we will investigate the population persistence/extinction dynamics of system (1.13) with strong Allee effect type growth function. [1]

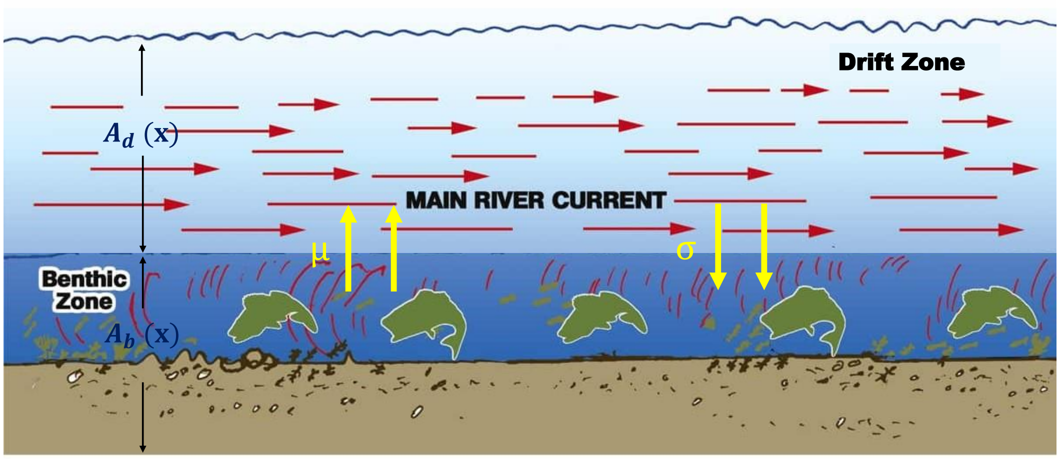

Figure 1.2: Illustration of drift-benthic habitat.

1.2 Related work

The question of dynamics of a spatially distributed species, moving passively in a stream or river, have been proposed to explore population persistence and the so-called "drift paradox" [64, 78, 93]. The drift paradox asks how stream-dwelling organisms can persist, without being washed out, when they are continuously subject to the unidirectional stream flow. With assumption of logistic population growth, the existence/persistence of a stream population in a constant environment have been considered in the framework of reaction-diffusion-advection in [53, 54, 59, 62, 70, 93, 97], and the effect of seasonal variations in environmental and climatic conditions on the stream population were considered in [41, 42, 43]. [54] studied

[1] Figure 1.2 modified from: https://midwestoutdoors.com/fishing/update-river-zones-creates-hydro-zones/.

the asymptotic profile of the steady state of a reaction-diffusion-advection model proposed in [78]. They show the existence of one or more internal transition layers and determine their locations. Such locations can be understood as the upstream invasion limits of the species. It turns out that these invasion limits are connected to the upstream spreading speed of the species and are sometimes subject to the effect of migration from upstream source patches. In [62], the authors focused on the effect of boundary conditions on evolution of dispersal in advective homogeneous environment. To assess the effect of water flow on population persistence, [70] derive three measures of persistence, among which the net reproductive rate R_0 can be used as a measure of global population persistence. [41] focused on how flow patterns affect population survival. They presented a hybrid modeling approach to couple hydrodynamic and biological processes, focusing on the combined impact of spatial heterogeneity and temporal variability on population dynamics. They considered periodically alternating pool-riffle rivers that are subjected to seasonally varying flows, established the existence of spreading speeds and the invasion ratchet phenomenon. [42] addressed the critical domain size problem for seasonally fluctuating stream environments and determine how large a reach of suitable stream habitat is needed to ensure population persistence of a stream-dwelling species. [42] established upstream and downstream spreading speeds under the assumption of periodically fluctuating environments, and also showed the existence of periodic traveling waves.

The competition of two species in stream environment have also been studied in [53, 59, 60, 99, 110, 112, 114]. [59] investigated a two-species competition model in a open advective environment. In the case of non-advective environments, it is well known that lower diffusion rates are favored by selection in spatially varying but temporally constant environments. In [59], for homogeneous advective environments with free-flow and hostile boundary conditions, they show that unidirectional flow can put slow dispersers at a disadvantage and higher dispersal rate can evolve. In [53], they studied a two-species competition model in a closed advective environment, and in contrast to the case without advection, slow dispersal is generally selected against in closed advective environments. In [60], a two-species Lotka-

Volterra competition model in an advective homogeneous environment has been investigated. They show that if one competitor disperses by random diffusion only and the other assumes both random and directed movements, then the one without advection prevails. This implies that the movement without advection in homogeneous environment is evolutionary stable, as advection tends to move more individuals to the boundary of the habitat and thus cause the distribution of species mismatch with the resources which are evenly distributed in space.

To study the influence of the drift-benthic structure, the single reaction-diffusion-advection equation has been extended into a benthic-drift model, which links changes in the flow regime and habitat availability with population dynamics. Assuming logistic growth for the benthic population, the population spreading, invasion and the propagation speed were studied in [63, 78]; the population persistence criteria on a finite length river based on the net reproductive rate was investigated in [37]; and the population dynamics of two competitive species in the river was studied in [45]. All these works assume logistic growth for the benthic population so the population persistence/extinction or spreading can be completely determined by a sharp threshold which is often expressed by a basic reproduction number or a critical advection rate. Benthic-drift models of algae and nutrient population have also been considered [30, 35, 36, 100].

Several extended studies also consider the effect of river network structure [84, 86] and meandering structure [44]. On the other hand, integrodifferential and integrodifference models equations have also been used to describe the diffusion and advection but also long-distance dispersal, and comparable results with logistic growth on extinction, persistence and spreading of population have been obtained [39, 40, 65, 78]. In most of the literature mentioned above and also the present dissertation, advection is a constant and unidirectional movement. Note that in other literature, the term "advection" was used for movement towards gradient of resource function for better quality habitat [6, 10, 11, 13, 14, 15, 17, 51, 52, 56, 113]. The role of the Allee effect in population spreading and invasion in reaction-diffusion or integrodifferential models has been investigated in [47, 49, 57, 66, 95, 103, 104], and the effect of Allee effect in population persistence on a bounded habitat has been considered in [58, 77, 89].

The rest of this dissertation is structured as follows. In Chapter 2, the dynamic behavior of (1.4) with a strong Allee effect growth rate is 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. Chapter 2 was accepted by Journal of Mathematical Biology. In Chapter 3, we consider the dynamical behavior of the model (1.4) with weak Allee effect growth and open or closed environment boundary conditions. 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. Chapter 3 was submitted. In Chapter 4, by extending the single compartment reaction-diffusion-advection equation into a benthic-drift model, we studied the aquatic species that reproduce on the bottom of the river and release their larval stages into the water column. We assume that advective and diffusive transport occur only in the main flowing zone, not the storage zone. So we neglect the movement in the benthic zone. While in the drifting water, we consider the individual's movement as a combination of passive diffusion movement and advective movement. Unlike the single compartment reaction-diffusion-advection equation with a strong Allee effect growth rate, in which the advection rate q plays a important role in the persistence/extinction dynamics, the benthic-drift model dynamics with strong Allee effect relies more critically on the strength of interacting between zones, especially the transfer rate μ from the benthic zone to the drift zone. With large transfer rate μ, extinction occurs regardless of the initial conditions, the boundary condition, the diffusive and advective movement and the transfer rate from the drift zone to the benthic zone. With small transfer rate μ, a bistable structure exists also independent of the boundary condition, the diffusive and advective movement and the transfer rate from the drift zone to the benthic zone. When the transfer rate μ is in the intermediate range, the persistence or extinction depends on the diffusive and advective movement.

Chapter 2

Reaction-diffusion-advection model with strong Allee effect [1]

2.1 Introduction

In this chapter, we study the dynamic behavior of a reaction-diffusion-advection model of the density of a biological species in an open or closed river environment with a strong Allee effect population growth rate. If the river population suffers a loss on the boundary ends due to movement, then the river is an open environment and otherwise it is a closed environment. Compared to the well-studied reaction-diffusion-advection model with logistic growth rate [9, 53, 59], the model with strong Allee effect growth possesses multiple steady state solutions, and the extinction state is always locally stable. Here we set up a framework of reaction-diffusion-advection model in a one-dimensional habitat with general growth rate functions and general boundary conditions, but focus on the strong Allee effect type growth and open or closed environment boundary conditions.

Our main results on the dynamics of reaction-diffusion-advection model with strong Allee effect type growth on a bounded habitat include:

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1. The solution asymptotically always converges to a nonnegative steady state solution, and there is no temporal oscillatory behavior.

2. The population goes to extinction when the initial condition is small, or the advection rate is large and under an open environment.

3. When the initial population is sufficiently large, the population persists if the advection rate is small and the boundary condition is favorable. In that case, bistability exists in the system so different outcomes can be reached with different initial settings.

4. In a closed environment river system, when the advection rate is large, the population either becomes extinct or it only concentrates at the downstream end. Numerical results indicate that extinction or concentration at downstream depends on the relative position of the Allee effect threshold value.

5. The traveling wave speed of the associated problem is determined by the diffusion coefficient, advection rate, baseline growth rate and the Allee effect threshold, and the traveling-wave-like transient dynamics facilitates the merging of population persistence/extinction patches.

Most of the above results are rigorously proved using theory of dynamical systems, partial differential equations, and upper-lower solution methods, and various numerical simulations are also included to verify or demonstrate theoretical results. Our focus is on the influence of various system parameters (diffusion coefficient, advection rate, Allee effect threshold, boundary condition parameters) and initial conditions on the asymptotic and transient dynamical behavior.

This chapter is organized as follows: Some mathematical preliminaries regarding eigenvalue problem, comparison of the boundary conditions, previous results on the non-advective case and the upper-lower methods are prepared in Section 2.2. Our main results on the dynamic properties of the model are stated and proved in Section 2.3. By using comparison method and variational method, we investigate the existence and multiplicity of positive nontrivial steady states and derive various sufficient conditions for the population persistence and extinction under an open or closed environment. We also use numerical simulation to explore the rich transient and wave-like dynamical behaviors. Some concluding remarks are made in Section 2.4.

2.2 Preliminaries

2.2.1 Eigenvalue problem and logistic model

In this section we first recall some results on the following eigenvalue problem:

$$\begin{cases} d\phi''(x) - q\phi'(x) + p(x)\phi(x) = \lambda\phi(x), & 0 < x < L, \\ d\phi'(0) - q\phi(0) = b_u q\phi(0), \\ d\phi'(L) - q\phi(L) = -b_d q\phi(L). \end{cases} \tag{2.1}$$

Here $d > 0$, $q \geq 0$, $p(x) \in L^\infty(0, L)$, and the boundary conditions are the ones introduced in subsection 1.1.2. Then we have the following properties for the eigenvalues.

Proposition 2.1. *Suppose that $d > 0$, $L > 0$, $q \geq 0$, and $p(x) \in L^\infty(0, L)$. Then*

1. The eigenvalue problem (2.1) *has a sequence of eigenvalues*

$$\lambda_1 > \lambda_2 > \cdots > \lambda_n \to -\infty, \tag{2.2}$$

and the principal eigenvalue λ_1 has the variational characterization

$$-\lambda_1 = \inf_{\psi \in X_1, \psi \neq 0} R(\psi),$$

where $R(\psi)$ is the Rayleigh quotient

$$R(\psi) = \frac{\displaystyle\int_0^L e^{\alpha x}[d(\psi')^2(x) - p(x)\psi^2(x)]dx + qb_u\psi^2(0) + qb_d e^{\alpha L}\psi^2(L)}{\displaystyle\int_0^L e^{\alpha x}\psi^2(x)dx}, \tag{2.3}$$

$\alpha = q/d$ and $X_1 = H^1(0, L)$.

2. *The principal eigenvalue $\lambda_1 = \lambda_1(p, d, q, b_u, b_d)$ is continuously differentiable in d, q, b_u, b_d and is decreasing with respect to b_u and b_d; if $p_1(x) \geq p_2(x)$, then $\lambda_1(p_1) \geq \lambda_1(p_2)$.*

3. *If $b_d > 0$ and $b_u \geq 0$, then $\lambda_1(q) \to -\infty$ as $q \to +\infty$; moreover if $b_d > 1/2$, then $\lambda_1(q)$ is strictly decreasing in q.*

4. *If $\int_0^L e^{\alpha x}p(x)dx > 0$ and $b_d = b_u = 0$, then there always holds $\lambda_1(q) > 0$, where $\alpha = q/d$.*

5. *If $p(x) < 0$ and $b_d, b_u \geq 0$, for $x \in [0, L]$, then $\lambda_1(q) < 0$.*

Proof. We use the transform $\phi = e^{\alpha x}\psi$. Then system (2.1) becomes

$$\begin{cases} d\psi''(x) + q\psi'(x) + p(x)\psi(x) = \lambda\psi(x), & 0 < x < L, \\ d\psi'(0) = b_u q\psi(0), \quad d\psi'(L) = -b_d q\psi(L). \end{cases} \tag{2.4}$$

Part 1 is well-known as (2.4) can be written as a self-adjoint eigenvalue problem:

$$\begin{cases} (P\psi')' + (Q - \lambda S)\psi = 0, & x \in (0, L), \\ P(0)\sin\beta\psi'(0) - \cos\beta\psi(0) = 0, \quad P(L)\sin\gamma\psi'(L) - \cos\gamma\psi(L) = 0. \end{cases}$$

with

$$P(x) = de^{\alpha x},\ Q(x) = p(x)e^{\alpha x},\ S(x) = e^{\alpha x},\ \beta = \operatorname{arccot}(b_u q),\ \gamma = \operatorname{arccot}(-b_d q e^{\alpha L}).$$

Then the existence of eigenvalues follows from [16, Theorem 8.2.1]. From the definition of Rayleigh quotient (2.3), it is clear that λ_1 is decreasing in b_d or b_u and if $p_1(x) \geq p_2(x)$, then

$\lambda_1(p_1) \geq \lambda_1(p_2)$, that proves part 2. For part 3, the result that $\lambda_1(q)$ is strictly decreasing and $\lim_{q\to\infty} \lambda_1(q) = -\infty$ when $b_d > 1/2$ and $b_u \geq 0$ are proved in [59, Lemma 4.8, Lemma 4.9, Remark 4.10], and for $0 < b_d \leq 1/2$ and $b_u \geq 0$, we still have $\lim_{q\to\infty} \lambda_1(q) = -\infty$ following [62, Proposition 2.1] for the case of $b_u = 0$ and that $\lambda_1(q)$ is decreasing with respect to b_u in part 2. For part 4, since $b_d = b_u = 0$, then $\lambda_1(q) = -\inf_{\psi\in X_1,\psi\neq 0} R(\psi) \geq -R(1) > 0$, and from the definition of Rayleigh quotient (2.3), we obtain part 5. □

If $g(x, u)$ satisfies (g1)-(g3) and (g4a), then the population has a logistic type growth and the dynamics of system (1.4) in this case is well-known, see for example [9, 53, 59]. We recall the following result:

Proposition 2.2. *Suppose that $f(x, u) = ug(x, u)$ satisfy (g1)-(g3) and (g4a), $d > 0$ and $q \geq 0$. Let $\lambda_1(q)$ be the principal eigenvalue of the eigenvalue problem* (2.1) *with $p(x) = g(x, 0)$.*

1. *If $\lambda_1(q) \leq 0$, then $u = 0$ is globally asymptotically stable for* (1.4)*; if $\lambda_1(q) > 0$, there exists a unique positive steady state of* (1.4) *which is globally asymptotically stable.*

2. *If $b_d > 0$ and $b_u \geq 0$, then there exists $q_1 > 0$ such that for $q > q_1$, $\lambda_1(q) < 0$; moreover if $b_d > 1/2$ and $b_u \geq 0$, then $\lambda_1(q) < 0$ for all $q \geq 0$ if $\lambda_1(0) < 0$, and if $\lambda_1(0) > 0$, there exists $q_2 > 0$ such that $\lambda_1(q) > 0$ for $0 < q < q_2$ and $\lambda_1(q) < 0$ for $q > q_2$.*

3. *If $b_u = b_d = 0$, then $\lambda_1(q) > 0$ for all $q > 0$.*

Proof. The proof of the uniqueness and global stability of positive steady state for diffusive logistic type equation in part 1 is well known, see for example [9, Proposition 3.3]. Then parts 2 and 3 follow from Proposition 2.1 as $g(x, 0) > 0$ from the condition (g4a). □

Eq. (1.4) with $f(x, u) = u(r(x) - u)$ has been considered in [53, 54, 59], and results in Proposition 2.2 for that special case can be found in [54, Theorem 3.1, 3.2] and [59, Theorem 4.1]. Results in this section hold for $b_u, b_d \geq 0$, and they can also be adapted to hostile boundary condition by considering the limiting case when b_u or $b_d \to \infty$.

2.2.2 Comparison of boundary conditions

The dynamics of reaction-diffusion-advection system (1.4) is highly dependent on the boundary conditions. As shown in Propositions 2.1 and 2.2, since the principal eigenvalue of system (1.4) decreases with respect to b_u or b_d, then the population with larger b_u or b_d is more likely to be extinct. This monotone property for the principal eigenvalue actually also holds for nonlinear system as shown in the following result:

Proposition 2.3. *Suppose $g(x,u)$ satisfies (g1)-(g2), $0 \le b_u \le b'_u \le \infty$ and $0 \le b_d \le b'_d \le \infty$. Let $u_1(x,t)$ be the solution of (1.4), and let $u_2(x,t)$ be the solution of*

$$\begin{cases} u_t = du_{xx} - qu_x + f(x,u), & 0 < x < L, t > 0, \\ du_x(0,t) - qu(0,t) = b'_u qu(0,t), & t > 0, \\ du_x(L,t) - qu(L,t) = -b'_d qu(L,t), & t > 0, \\ u(x,0) = u_0(x) \ge 0, & 0 \le x \le L. \end{cases} \tag{2.5}$$

Then $u_1(x,t) \ge u_2(x,t) \ge 0$ for $t \in (0,\infty)$, $x \in \overline{\Omega}$. In particular, if $\lim_{t\to\infty} u_1(x,t) = 0$, then $\lim_{t\to\infty} u_2(x,t) = 0$; and if $\liminf_{t\to\infty} u_2(x,t) \ge \delta > 0$ for some positive constant $\delta > 0$, $\liminf_{t\to\infty} u_1(x,t) \ge \delta > 0$.

The proof of Proposition 2.3 follows from the maximum principle of nonlinear parabolic equations (see for example, [92, Theorem 10.1]), and we omit the details here. Note that here $b'_u = \infty$ or $b'_d = \infty$ is interpreted as the hostile boundary condition (H). The result implies the following comparison between two boundary conditions: if $b'_u \ge b_u$ and $b'_d \ge b_d$, and with identical initial condition, then the extinction in the system with parameter (b_u, b_d) implies the extinction of the system with parameter (b'_u, b'_d), and vice versa, the persistence for the system with (b'_u, b'_d) would imply the persistence for the one with (b_u, b_d).

Among all the boundary conditions, the no-flux boundary condition at $x = L$ ($b_d = 0$) is the most "friendly" for the population to persist, while the hostile boundary condition at $x = L$ ($b_d = \infty$) is the most vulnerable environment for the population. And the free flow

($b_d = 1$) is in between these two.

2.2.3 Non-advective case

For reaction-diffusion-advection equation (1.4) with the strong Allee effect growth rate in a non-advective environment, there have been several earlier papers on the existence and multiplicity of positive steady state solutions, and we recall these results here. In the environment with a hostile boundary condition, the non-advection equation in a higher dimensional domain Ω has the form

$$\begin{cases} u_t = d\Delta u + u(u-h)(r-u), & x \in \Omega,\ t > 0, \\ u(x,t) = 0, & x \in \partial\Omega,\ t > 0. \end{cases} \tag{2.6}$$

Proposition 2.4. *Suppose that Ω is a bounded smooth domain in $\mathbb{R}^n$ with $n \geq 1$, $d > 0$, and the constants h, r satisfy $0 < h < r$.*

1. *If $h > r/2$, then for any $d > 0$, the only nonnegative steady state solution of (2.6) is $u = 0$.*

2. *If $0 < h < r/2$, then there exists $d_0 > 0$ such that (2.6) has at least two positive steady state solutions for $0 < d < d_0$.*

3. *If $0 < h < r/2$ and Ω is a unit ball, then (2.6) has exactly two positive steady state solutions for $0 < d < d_0$, and has only the zero steady state when $d > d_0$.*

The nonexistence of positive steady state solution in part 1 is proven in [21], and the existence of two positive steady state solutions in part 2 can be proven using variational methods (see [58, 82]). The exact multiplicity of positive steady state solutions in part 3 is proved in [77]. The conditions of $h \leq r/2$ or $h > r/2$ in Proposition 2.4 are equivalent to $F(r) = \displaystyle\int_0^r u(u-h)(r-u)du \leq 0$ or > 0.

On the other hand, if the non-advective environment is with a free-flow (equivalent to no-flux) boundary condition, then the boundary value problem in a higher dimensional domain Ω has the form

$$\begin{cases} u_t = d\Delta u + u(u-h)(r-u), & x \in \Omega,\ t > 0, \\ \dfrac{\partial u}{\partial n}(x,t) = 0, & x \in \partial\Omega,\ t > 0. \end{cases} \tag{2.7}$$

The following results are proved in [102, Theorem 3.3, 3.4]:

Proposition 2.5. *Suppose that Ω is a bounded smooth domain in $\mathbb{R}^n$ with $n \geq 1$, $d > 0$, and the constants h, r satisfy $0 < h < r$. Let μ_m be the eigenvalues of the operator $-\Delta$ under Neumann boundary condition on Ω.*

1. *There exist three nonnegative constant steady state solutions $u = 0$, $u = h$, $u = r$ of (2.7), and all positive nonconstant steady solutions of (2.7) satisfy $0 < u(x) < r$;*

2. *Let $d_* = \dfrac{2(h+r)}{h\mu_1}$. Then for $d > d_*$, the only nonnegative steady state solutions to (2.7) are $u = 0$, $u = h$ and $u = r$.*

3. *Let $d_m = \dfrac{r-h}{\mu_m}$ with $m \geq 1$, then $d = d_m$ is a bifurcation point for the positive steady state solutions of (2.7), where a connected component Σ_m of the set of positive nonconstant steady state solutions of (2.7) bifurcates from the line of constant steady state $\{(d, u = h) : d > 0\}$.*

4. *If $n = 1$ and $\Omega = (0, L)$, then $\Sigma_m = \{(d, u_m^{\pm}(d, x)) : 0 < d < d_m\}$, the solution $u_m^{\pm}(d, \cdot) - h$ changes sign exactly m times in $(0, L)$, $u_m^{+}(d, 0) > h$ and $u_m^{-}(d, 0) < h$. In particular, (2.7) has exactly $2m$ nonconstant positive steady state solutions if $d_{m+1} < d < d_m$, and all of them are unstable.*

In particular Proposition 2.5 shows that when the diffusion coefficient d is large, the equation (2.7) has only the constant steady states, while for the small diffusion coefficient d case, (2.7) has a large number of positive steady states.

2.2.4 Upper-lower solution method

In the following we frequently use the method of upper-lower solutions to construct steady states or study the dynamics of (1.4). We review the method in this subsection. Suppose that $u(x)$ is a steady state solution of system (1.4), then $u(x)$ satisfies

$$\begin{cases} du_{xx}(x) - qu_x(x) + f(x, u(x)) = 0, & 0 < x < L, \\ du_x(0) - qu(0) = b_u qu(0), \\ du_x(L) - qu(L) = -b_d qu(L), \end{cases} \tag{2.8}$$

where $f(x, u) = ug(x, u)$ satisfies (g1)-(g3), and $r(x)$ is defined in (g2). Using the transform $u = e^{\alpha x}v$ on system (2.8), we obtain the following system

$$\begin{cases} dv_{xx} + qv_x + e^{-\alpha x} f(x, e^{\alpha x}v) = 0, & 0 < x < L, \\ -dv_x(0) + b_u qv(0) = 0, \\ dv_x(L) + b_d qv(L) = 0. \end{cases} \tag{2.9}$$

According to [79, Definition 3.2.1], $\overline{\psi}(x)$ is said to be an upper solution if it satisfies the inequalities

$$\begin{cases} d\overline{\psi}_{xx} + q\overline{\psi}_x + e^{-\alpha x} f(x, e^{\alpha x}\overline{\psi}) \le 0, & 0 < x < L, \\ -d\overline{\psi}_x(0) + b_u q\overline{\psi}(0) \ge 0, \\ d\overline{\psi}_x(L) + b_d q\overline{\psi}(L) \ge 0. \end{cases} \tag{2.10}$$

Similarly $\underline{\psi}(x)$ is called a lower solution if it satisfies all the inequalities in (2.10) with the direction of inequalities reversed. Moreover from [79, Theorem 3.2.1], if the upper and lower solutions satisfy $\overline{\psi} \ge \underline{\psi}$, then there exists a solution $\psi(x)$ of (2.9) satisfying $\underline{\psi}(x) \le \psi(x) \le \overline{\psi}(x)$. By [79, Theorem 3.2.2], system (2.9) has a maximal solution $\psi_{max}(x)$ and a minimal solution $\psi_{min}(x)$. Similarly by using $u(x,t) = e^{\alpha x}v(x,t)$, the parabolic system (1.4) can also be converted into

$$\begin{cases} v_t = dv_{xx} + qv_x + e^{-\alpha x} f(x, e^{\alpha x} v), & 0 < x < L,\ t > 0, \\ -dv_x(0) + b_u q v(0) = 0, & t > 0, \\ dv_x(L) + b_d q v(L) = 0, & t > 0, \\ v(x,0) = v_0(x) \geq 0, & x \in (0, L), \end{cases} \tag{2.11}$$

where $v_0(x) = e^{-\alpha x} u_0(x)$. The upper and lower solutions of (2.11) can be defined in a similar fashion (see [79, Definition 2.3.1]). In particular, if $\underline{\psi}$ and $\overline{\psi}$ is a pair of upper and lower solutions of (2.9), and $\underline{\psi}(x) \leq v_0(x) \leq \overline{\psi}(x)$, then $\underline{\psi}$ and $\overline{\psi}$ is also a pair of upper and lower solutions of (2.11). According to [79, Lemma 5.4.2], system (2.11) possesses a unique solution $v(x,t)$ satisfying

$$\underline{\psi}(x) \leq v_{\underline{\psi}}(x,t) \leq v(x,t) \leq v_{\overline{\psi}}(x,t) \leq \overline{\psi}(x), \tag{2.12}$$

where $v_{\underline{\psi}}(x,t)$ (or $v_{\overline{\psi}}(x,t)$) is the solution of (2.11) with the initial value $\underline{\psi}$ (or $\overline{\psi}$), and from [79, Theorem 5.4.2], $v_{\overline{\psi}}(x,t)$ is nonincreasing in t and $\lim_{t\to+\infty} v_{\overline{\psi}}(x,t) = \psi_{max}(x)$; $v_{\underline{\psi}}(x,t)$ is nondecreasing in t and $\lim_{t\to+\infty} v_{\underline{\psi}}(x,t) = \psi_{min}(x)$.

2.3 Persistence/Extinction dynamics

In this section, we consider the dynamics of (1.4) with the growth function $f(x,u) = ug(x,u)$ satisfying (g1)-(g3) and (g4c), the strong Allee effect growth.

2.3.1 Basic dynamics

First we have the following bound for steady states of (1.4), which was proved in [53, Lemma 2.3] for $f(x,u) = r(x) - u$. We include a proof here for convenience of readers.

Proposition 2.6. *Suppose $g(x,u)$ satisfies (g1)-(g2) and $r(x)$ is defined in (g2). Let $u(x)$ be* *a positive steady state solution of system* (1.4)*, then* $u(x) \leq e^{\alpha x} \max_{y \in [0,L]} (e^{-\alpha y} r(y))$ *for* $x \in [0, L]$*. Moreover, if* $b_d \geq 1$*, then* $u(x) \leq M = \max_{y \in [0,L]} r(y)$ *for* $x \in [0, L]$*.*

Proof. Let $u = e^{\alpha x} v$. Then from (2.9), we have

$$e^{\alpha x} (dv_{xx} + qv_x) + f(x, e^{\alpha x} v(x)) = 0. \tag{2.13}$$

Let $v(x_0) = \max_{x \in [0,L]} v(x) > 0$ for $x_0 \in [0, L]$. If $x_0 = 0$, then $v'(0) \leq 0$ as $x = 0$ is the maximum point. The boundary condition implies that $bqv(0) = dv'(0) \leq 0$ which contradicts with $v(x_0) > 0$. So $x_0 \neq 0$. Similarly we have $x_0 \neq L$. Then $x_0 \in (0, L)$, and we have $v'(x_0) = 0$ and $v''(x_0) \leq 0$. Therefore (2.13) implies that $f(x_0, e^{\alpha x_0} v(x_0)) \geq 0$, and consequently,

$$g(x_0, e^{\alpha x_0} v(x_0)) \geq 0. \tag{2.14}$$

According to (g2), $e^{\alpha x_0} v(x_0) \leq r(x_0)$, which implies that

$$e^{-\alpha x} u(x) = v(x) \leq v(x_0) \leq e^{-\alpha x_0} r(x_0) \leq \max_{y \in [0,L]} (e^{-\alpha y} r(y)), \tag{2.15}$$

which implies the desired result.

Next we assume that $b_d \geq 1$. From the boundary conditions, we know that $u'(0) > 0$ and since $b_d \geq 1$, $u'(L) \leq 0$. Then there exists $x_* \in (0, L]$ such that $u'(x_*) = 0$ and $u(x_*) = \max_{x \in [0,L]} u(x)$. If $x_* \in (0, L)$ (which is the case if $b_d > 1$), then $u''(x_*) \leq 0$. According to equation in (2.8), we have $f(x_*, u(x_*)) \geq 0$. If $x_* = L$, then $b_d = 1$, we still have $u'(x_*) = 0$ then again we have $f(x_*, u(x_*)) \geq 0$. From (g2), we have $u(x) \leq u(x_*) \leq r(x_*) \leq M$. □

Now we show that the population dynamics defined by (1.4) is well-posed: the solution of (1.4) exists globally for $t \in (0, \infty)$ and it converges to a non-negative steady state solution when $t \to \infty$. Note here we only require (g1) and (g2), not (g3) and (g4), hence the results hold for both logistic and (weak or strong) Allee effect cases.

Theorem 2.7. *Suppose* $g(x, u)$ *satisfies (g1)-(g2), then* (1.4) *has a unique positive solution*

$u(x,t)$ defined for $(x,t) \in [0,L] \times (0,\infty)$, and the solutions of (1.4) generates a dynamical system in X_2, where

$$X_2 = \{\phi \in W^{2,2}(0,L) : \phi(x) \geq 0,\ d\phi'(0) - q\phi(0) = b_u q\phi(0),\\ d\phi'(L) - q\phi(L) = -b_d q\phi(L)\}. \tag{2.16}$$

Moreover, 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 non-negative steady state solutions.

Proof. Assume that $u(x,t)$ is a solution of system (1.4), then $v(x,t) = e^{-\alpha x}u(x,t)$ is a solution of system (2.11). We choose

$$M_1 = \max\left\{\max_{y\in[0,L]} e^{-\alpha y}r(y), \max_{y\in[0,L]} e^{-\alpha y}u_0(y)\right\}, \tag{2.17}$$

then M_1 is an upper solution of (2.11) and 0 is a lower solution of (2.11). Then from the discussion in subsection 2.2.4, we obtain that

$$0 \leq v(x,t) \leq v_1(x,t),$$

where $v_1(x,t)$ is the solution of (2.11) with initial condition $v_1(x,0) = M_1$. Moreover the solution $v_1(x,t)$ is nonincreasing in t and $\lim_{t\to+\infty} v_1(x,t) = v_{max}(x)$ which is maximal steady state of (2.11) not larger than M_1. From Proposition 2.6, we obtain that $u(x,t)$ exists globally for $t \in (0,\infty)$ and

$$u(x,t) \geq 0, \quad \limsup_{t\to\infty} u(x,t) \leq e^{\alpha x} \max_{y\in[0,L]} e^{-\alpha y}r(y). \tag{2.18}$$

In particular, we may assume that for any initial value u_0, the solution $u(x,t)$ of (1.4) is bounded by $M_2 := e^{\alpha L} \max_{y\in[0,L]} e^{-\alpha y}r(y) + \epsilon$ for $t > T$ and some small $\epsilon > 0$. Next we prove that the solution $u(x,t)$ is always convergent. For that purpose, we construct a Lyapunov function

$$E(u)=\int_0^L e^{-\alpha x}\left[\frac{d}{2}(u_x)^2-F(x,u)\right]dx+\frac{q}{2}(1+b_u)u^2(0)-\frac{q}{2}(1-b_d)e^{-\alpha L}u^2(L), \quad (2.19)$$

for $u\in X_2$, where $F(x,u)=\int_0^u f(x,s)ds$. Assume that $u(x,t)$ is a solution of system (1.4), we have

$$\begin{aligned}
\frac{d}{dt}E(u(\cdot,t)) &= \int_0^L e^{-\alpha x}(du_xu_{xt}-f(x,u)u_t)dx \\
&\quad + q(1+b_u)u(0,t)u_t(0,t)-q(1-b_d)e^{-\alpha L}u(L,t)u_t(L,t) \\
&= \int_0^L (de^{-\alpha x}u_x)du_t-\int_0^L e^{-\alpha x}f(x,u)u_tdx \\
&\quad + q(1+b_u)u(0,t)u_t(0,t)-q(1-b_d)e^{-\alpha L}u(L,t)u_t(L,t) \\
&= de^{-\alpha x}u_xu_t\Big|_0^L-\int_0^L[(e^{-\alpha x}du_x)_x+e^{-\alpha x}f(x,u)]u_tdx \\
&\quad + q(1+b_u)u(0,t)u_t(0,t)-q(1-b_d)e^{-\alpha L}u(L,t)u_t(L,t) \\
&= u_t(L,t)e^{-\alpha L}(du_x(L,t)-q(1-b_d)u(L,t))+ \\
&\quad u_t(0,t)(-du_x(0,t)+q(1+b_u)u(0,t))-\int_0^L e^{-\alpha x}(u_t)^2dx \\
&= -\int_0^L e^{-\alpha x}(u_t)^2dx\le 0.
\end{aligned}$$

According to (g2), $f(x,u)<0$ for $u>r(x)$ and $f(x,r(x))=0$, we have $F(x,u(x))\le F(x,r(x))$ for $u\in X_2$ and $0<r(x)\le M$. Hence when $t>T$,

$$E(u(\cdot,t))\ge-\int_0^L e^{-\alpha x}F(x,r(x))dx-\frac{q}{2}e^{-\alpha L}u^2(L,t)\ge -M_3L-\frac{qM_2^2}{2}e^{-\alpha L}, \quad (2.20)$$

where $M_3=\max_{y\in[0,L]}F(y,r(y))$. Therefore $E(u(\cdot,t)$ is bounded from below. Notice $\frac{d}{dt}E(u)=0$ holds if and only if $u_t=0$, which means that u is a steady state solution of system (1.4). Refer to [33, Theorem 4.3.4], the LaSalle's Invariance Principle, we have that for any initial condition $u_0(x)\ge 0$, the ω-limit set of u_0 is contained in the largest invariant subset of S. If every element in S is isolated, then the ω-limit set is a single steady state. □

In addition, if $f(x,u)$ satisfies (g4a) (logistic case), then from part 1 in Proposition 2.2, any solution of (1.4) either goes to zero steady state or converges to the unique positive steady state. In the following, we will focus on the case when $f(x,u)$ satisfies (g4c), for which the solutions of (1.4) have more complicated behavior.

2.3.2 Extinction

In this subsection, we consider under what condition the population goes to extinction. The zero steady state of (1.4) is always locally asymptotically stable from Proposition 2.1 part 5, and we provide some estimates of the basin of attraction of the zero steady state. Recall that $f(x,u) = ug(x,u)$ satisfies (g4c), then we have that $h(x)$ satisfies $f(x,0) = f(x,h(x)) = f(x,r(x)) = 0$ with $0 < h(x) < r(x)$ for all $x \in [0,L]$. First we note the following property of the steady state solution $u(x)$.

Proposition 2.8. *Suppose $g(x,u)$ satisfies (g1)-(g3) and (g4c). Then there is no positive solution $u(x)$ of* (2.8) *satisfying $u(x) < h(x)$ for all $x \in [0,L]$.*

Proof. Integrating both sides of (2.8), we get

$$[du_x - qu]\Big|_0^L + \int_0^L f(x,u)dx = 0. \tag{2.21}$$

According to the boundary conditions in (2.8), the first part of (2.21) is

$$-b_d qu(L) - b_u qu(0) \le 0. \tag{2.22}$$

Thus, the second part of (2.21) is non-negative,

$$\int_0^L f(x,u)dx \ge 0. \tag{2.23}$$

which does not hold if $0 < u(x) < h(x)$. Therefore, there is no positive solution $u(x)$ satisfying $u(x) < h(x)$ for all $x \in [0,L]$. □

In the following proposition, we describe the basin of attraction of the zero steady state solution of system (1.4) for different boundary conditions.

Proposition 2.9. *Suppose $g(x,u)$ satisfies (g1)-(g3) and (g4c), and let $u(x,t)$ be the solution of (1.4) with initial condition $u_0(x)$.*

1. *When $b_u \geq 0$ and $b_d \geq 0$, if $0 < u_0(x) < e^{\alpha x} \min_{y\in[0,L]} e^{-\alpha y} h(y)$, then $\lim_{t\to+\infty} u(x,t) = 0$;*

2. *When $b_u \geq 0$ and $b_d \geq 1$, if $0 < u_0(x) < \min_{y\in[0,L]} h(y)$, then $\lim_{t\to+\infty} u(x,t) = 0$.*

Proof. 1. When $b_u \geq 0$ and $b_d \geq 0$, we set $\overline{v}_1(x) = \min_{y\in[0,L]} e^{-\alpha y} h(y)$, which is a constant function. Then according to (g4c), we have

$$\begin{aligned} & d(\overline{v}_1)_{xx} + q(\overline{v}_1)_x + \overline{v}_1 \cdot g(x, e^{\alpha x}\overline{v}_1) = \min_{y\in[0,L]} e^{-\alpha y} h(y) \cdot g(x, e^{\alpha x} \min_{y\in[0,L]} e^{-\alpha y} h(y)) \\ \leq & \min_{y\in[0,L]} e^{-\alpha y} h(y) \cdot g(x, e^{\alpha x} e^{-\alpha x} h(x)) = \min_{y\in[0,L]} e^{-\alpha y} h(y) \cdot g(x, h(x)) = 0, \end{aligned} \tag{2.24}$$

and the boundary conditions $-d\overline{v}_{1x}(0) + b_u q \overline{v}_1(0) \geq 0$, $d\overline{v}_{1x}(L) + b_d q \overline{v}_1(L) \geq 0$. Thus, $\overline{v}_1(x) = \min_{y\in[0,L]} e^{-\alpha y} h(y)$ is an upper solution of system (2.9). Let $\underline{v}_1(x) = 0$ be the lower solution of system (2.9). Now assume that $0 \leq v_0(x) \leq \min_{y\in[0,L]} e^{-\alpha y} h(y)$, and let $v(x,t)$ be the solution of (2.11). From the discussion in subsection 2.2.4, there exist solutions $\overline{V}_1(x,t)$ and $\underline{V}_1(x,t)$ of system (2.11),

$$\underline{V}_1(x,t) \leq v(x,t) \leq \overline{V}_1(x,t), \tag{2.25}$$

where $\underline{V}_1(x,t)$ and $\overline{V}_1(x,t)$ are the solutions of system (2.11) with the initial condition $\underline{V}_1(x,0) = \underline{v}_1(x)$ and $\overline{V}_1(x,0) = \overline{v}_1(x)$. Moreover, $\lim_{t\to+\infty} \overline{V}_1(x,t) = v_{max}(x)$ and $\lim_{t\to+\infty} \underline{V}_1(x,t) = v_{min}(x)$, where $v_{max}(x)$, $v_{min}(x)$ are the maximal and minimal solutions of (2.9) between 0 and $\overline{v}_1(x)$. From Proposition 2.8, there is no positive solution $u(x)$ satisfying $u(x) < h(x)$ for all $x \in [0,L]$, hence $v_{min}(x) = v_{max}(x) = 0$. Therefore, if the initial value satisfies $u_0(x) < e^{\alpha x} \min_{y\in[0,L]} e^{-\alpha y} h(y)$, then $\lim_{t\to+\infty} u(x,t) = 0$.

2. When $b_u \geq 0$ and $b_d \geq 1$, we apply the upper and lower solution method directly

to (1.4), and we choose $\overline{u}_1(x) = \min_{y\in[0,L]} h(y)$ to be the upper solution and $\underline{u}_1(x) = 0$ be the lower solution. We can follow the same argument in the above paragraph to reach the conclusion. □

Proposition 2.9 only gives a partial description of the basin of attraction of the zero steady state (extinction initial values). This extinction region depends on the advection coefficient q and the boundary condition. Using a constant initial value $u_0 = K > 0$, Fig. 2.1 shows the threshold initial condition $K = K_0$ between persistence and extinction under the NF/H, NF/FF and NF/NF boundary conditions and varying advection coefficient q. The left panel corresponds to the case when the threshold h is relatively small and the right panel describes the case when threshold h is relatively large. For the NF/NF boundary conditions, the behavior of the population changes significantly due to the threshold while the other two exhibit almost the same tendency. For small threshold h and under the NF/NF boundary condition, as advection q increases, the basin of attraction of the zero steady state solution decreases. However, for large threshold h, there exists a critical $q^* > 0$, such that when the advection $q > q^*$, the population will go to extinction.

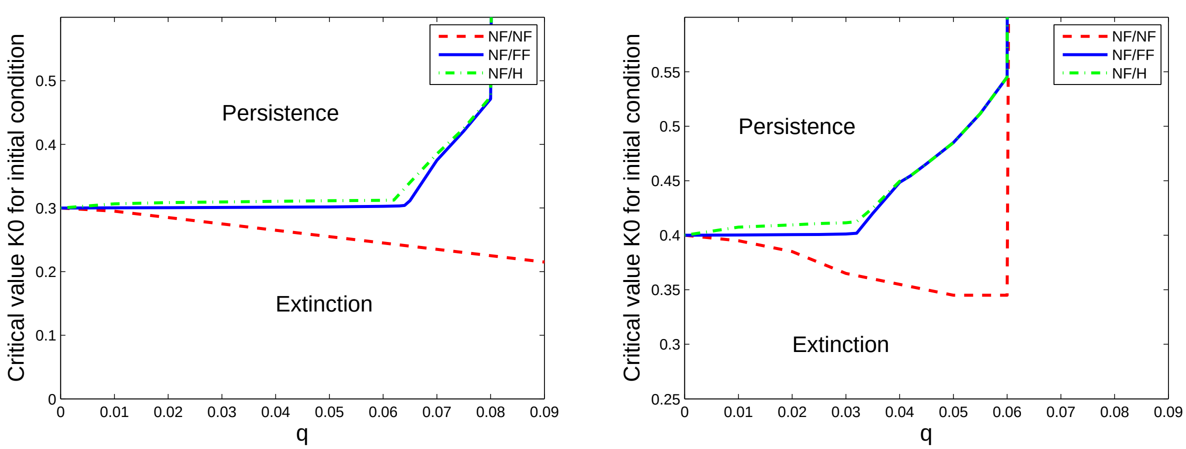

Figure 2.1: Population extinction and persistence for varying advection coefficient q and the initial condition $u_0 = K$ (constant). For each of NF/H, NF/FF and NF/NF boundary conditions, a curve is plotted to show the threshold K_0 between extinction and persistence. When $u_0 \equiv K > K_0$, the population persists; and when $u_0 \equiv K < K_0$, the population becomes extinct. Persistence/extinction is determined by the solution at $t = 3000$. Here $f(x,u) = au(1-u)(u-h)$, $a = 0.5$, $L = 10$ and $d = 0.1$. Left: $h = 0.3$; Right: $h = 0.4$.

To provide another extinction criterion, we compare the solution of (1.4) with the strong

Allee effect growth rate with the one with a comparable logistic growth rate. For that purpose, we define a function $\widetilde{f}(x,u) = u\widetilde{g}(x,u)$ as follows

$$\widetilde{g}(x,u) = \begin{cases} g(x,s(x)), & 0 < u < s(x), \\ g(x,u), & u > s(x), \end{cases} \tag{2.26}$$

where for $x \in \overline{\Omega}$, $s(x)$ is the maximum point of $g(x,u)$ defined in (g3). Thus $\widetilde{f}(x,u)$ is of logistic type and satisfies $\widetilde{f}(x,u) \geq f(x,u)$. The function $\widetilde{f}(x,u)$ is also the smallest function of logistic type which is greater than $f(x,u)$. A comparison of $\widetilde{f}$, $\widetilde{g}$ and f, g can be seen in Fig. 2.2.

Now we can define a new system with this modified growth rate:

$$\begin{cases} u_t = du_{xx} - qu_x + \widetilde{f}(x,u), & 0 < x < L, \ t > 0, \\ du_x(0,t) - qu(0,t) = b_u qu(0,t), & t > 0, \\ du_x(L,t) - qu(L,t) = -b_d qu(L,t), & t > 0. \\ u(x,0) = u_0(x) \geq 0, & 0 \leq x \leq L. \end{cases} \tag{2.27}$$

Then from the comparison principle of parabolic equations, we obtain the following comparison of solutions of (1.4) and (2.27).

Proposition 2.10. *Suppose $g(x,u)$ satisfies (g1)-(g3) and (g4c), and $\widetilde{f}(x,u)$ is defined as in* (2.26)*. Let $u_3(x,t)$ be the solution of* (1.4)*, and let $u_4(x,t)$ be the solution of* (2.27) *with the same initial value. Then $0 \leq u_3(x,t) < u_4(x,t)$ for $t \in (0,\infty)$ and $x \in \overline{\Omega}$. In particular, if $\lim_{t\to\infty} u_4(x,t) = 0$, then $\lim_{t\to\infty} u_3(x,t) = 0$; and if $\liminf_{t\to\infty} u_3(x,t) \geq \delta > 0$ for some positive constant $\delta > 0$, then $\liminf_{t\to\infty} u_4(x,t) \geq \delta > 0$.*

Now by using the previously known results for the logistic equation, we have the following result for population extinction with the strong Allee effect growth rate.

Theorem 2.11. *Suppose that $g(x,u)$ satisfies (g1)-(g3) and (g4c). If $b_u \geq 0$ and $b_d > 0$, then* *there exists $q_1 > 0$ such that when $q > q_1$, there is no positive steady state solution of* (1.4)*; and for any initial condition $u_0(x) \geq 0$, the solution $u(x,t)$ of* (1.4) *satisfies* $\lim_{t\to+\infty} u(x,t) = 0$.

Proof. This is a direct consequence of Proposition 2.2 and Proposition 2.10. □

Here it is shown that under an open river environment, when the advection rate q is large and there is a population loss at the downstream, then the population becomes extinct no matter what initial condition is, which is the same as the case of logistic growth [59]. This result confirms the numerical result shown in Fig. 2.1 for NF/H and NF/FF cases, but it does not include the case of NF/NF boundary condition which corresponds to the case $b_u = b_d = 0$.

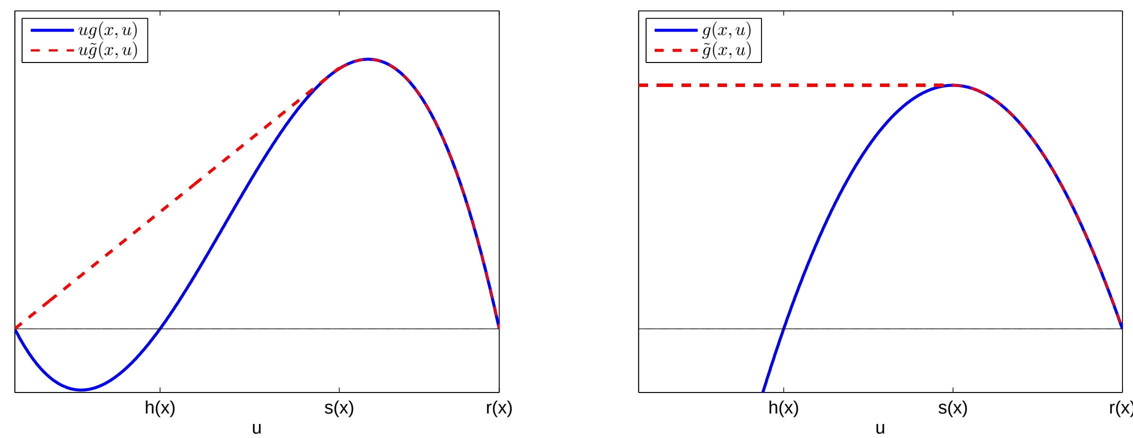

Figure 2.2: Left: The graphs of $f(\cdot,u)$ and $\widetilde{f}(\cdot,u)$ for fixed $x \in [0,L]$; Right: The graphs of $g(\cdot,u)$ and $\widetilde{g}(\cdot,u)$ for fixed $x \in [0,L]$.

In Fig. 2.3, the solutions of (1.4) with the strong Allee effect growth $f(x,u) = u(1-u)(u-h)$ and the ones of (2.27) with corresponding logistic growth rate

$$\widetilde{f}(x,u) = \begin{cases} \dfrac{(1-h)^2 u}{4}, & 0 < u < \dfrac{1+h}{2}, \\ u(1-u)(u-h), & u > \dfrac{1+h}{2}, \end{cases} \tag{2.28}$$

are shown. The results in Fig. 2.3 confirm the comparison stated in Proposition 2.10: the solution of logistic growth model is an upper solution for the case with the strong Allee effect growth. When the advection rate is small (Fig. 2.3 upper left), the two solutions are

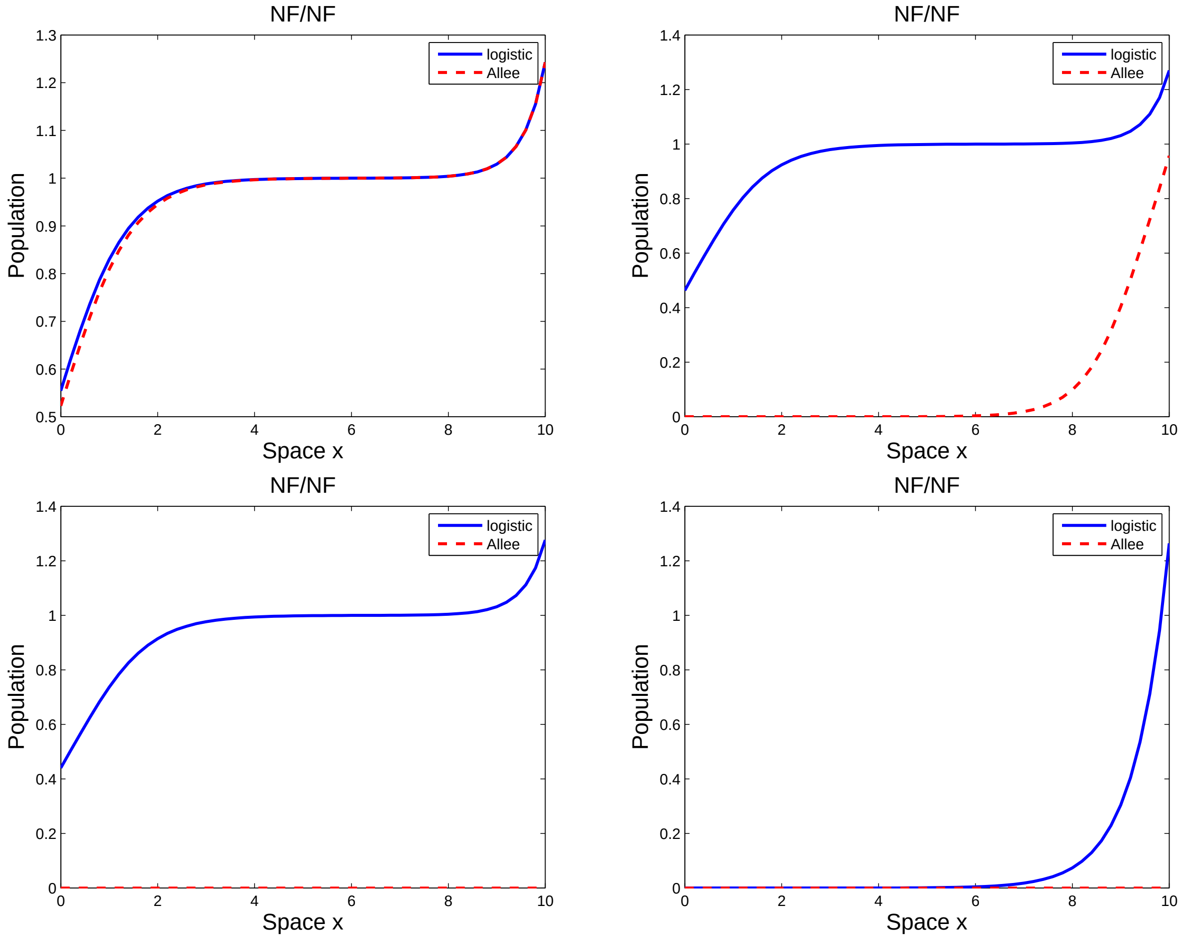

Figure 2.3: Comparison of solutions of (1.4) with strong Allee effect growth $f(x,u) = u(1-u)(u-h)$ and the one of (2.27) with corresponding logistic growth rate given in (2.28). Here $d = 0.1$, $h = 0.4$, $L = 10$, NF/NF boundary condition is used, the initial condition is $u_0 = 0.6$, and the solutions at $t = 3000$ are shown. Upper left: $q = 0.006$; Upper right: $q = 0.0068$; Lower left: $q = 0.007$; Lower right: $q = 0.2$.

almost identical despite of different growth rates; but for large advection rates, the strong Allee effect growth rate leads to extinction while the logistic one supports persistence. This clearly shows the importance of the growth rate at low population density as the two growth rates are the same in high densities.

2.3.3 Persistence

In this subsection, we provide some criteria for the population persistence of (1.4) with the strong Allee effect growth rate. Note that in the logistic case, the persistence and extinction of population is completely determined by the stability of the extinction steady state $u = 0$ (see Proposition 2.2), but in the strong Allee effect case, the extinction state $u = 0$ is always locally stable.

We first show some properties of the set of positive steady state solutions of (1.4) if there exists any.

Proposition 2.12. *Suppose $g(x,u)$ satisfies (g1)-(g3). If there exists a positive steady state solution of* (1.4)*, then there exists a maximal steady state solution $u_{max}(x)$ such that for any positive steady state $u(x)$ of system* (1.4)*, $u_{max}(x) \geq u(x)$.*

Proof. We consider the equivalent steady state equation (2.9).

Set $\overline{v}_2(x) = \max_{y\in[0,L]} e^{-\alpha y} r(y)$, which is a constant function. From (g3), we have $f_u(x,u) \leq 0$ for $u \geq r(x)$. Therefore,

$$f(x, e^{\alpha x}\overline{v}_2) = f(x, e^{\alpha x} \max_{y\in[0,L]} e^{-\alpha y} r(y)) \leq f(x, e^{\alpha x} e^{-\alpha x} r(x)) = f(x, r(x)) = 0.$$

Substituting $\overline{v}_2(x)$ into system (2.9), we have

$$\begin{cases} d\overline{v}_2'' + q\overline{v}_2' + e^{-\alpha x} f(x, e^{\alpha x}\overline{v}_2) \leq 0, & 0 < x < L, \\ -d\overline{v}_2'(0) + b_u q\overline{v}_2(0) \geq 0, \\ d\overline{v}_2'(L) + b_d q\overline{v}_2(L) \geq 0. \end{cases} \tag{2.29}$$

Thus $\overline{v}_2(x)$ is an upper solution of system (2.9). Moreover from Proposition 2.6, any positive steady state solution v of (2.9) satisfies $v(x) \leq \overline{v}_2(x)$. Since $u(x)$ is a positive steady state of (1.4), we can set the lower solution of (2.9) to be $\underline{v}_2(x) = e^{-\alpha x}u(x)$. Then from the results in subsection 3.4, there exists a maximal solution $v_{max}(x)$ of (2.9) satisfying $\underline{v}_2(x) \leq v_{max}(x)$. Since $v_{max}(x)$ is obtained through the monotone iteration process (see [4, 79]) from the upper solution $\overline{v}_2(x)$ and any positive steady state solution v of (2.9) satisfying $v(x) \leq \overline{v}_2(x)$, we conclude that $v_{max}(x)$ is the maximal steady state solution of (2.9), which implies the desired result. □

Next we show a monotonicity result for the maximal steady state solution $u_{max}(x)$.

Proposition 2.13. *Suppose $g(x,u)$ satisfies (g1)-(g3), and $b_u \geq 0$ and $0 \leq b_d \leq 1$. Then the maximal steady state solution $u_{max}(x)$ of equation (1.4) is strictly increasing in $[0, L]$ if one of the following conditions is satisfied:*

1. *$f(x,u) \equiv f(u)$, that is f is spatially homogeneous; or*

2. *$g(x,u)$ is also differentiable in x, $g_u(x,u) \leq 0$ and $g_x(x,u) \geq 0$ for $x \in [0, L]$ and $u \geq 0$.*

Proof. For part 1, we prove it by contradiction. Assuming that the maximal solution $u_{max}(x)$ is not increasing for all $x \in [0, L]$. From boundary conditions in (1.4) and the condition $b_u \geq 0$, $0 \leq b_d \leq 1$, we have

$$(u_{max})_x(0) = \alpha(b_u + 1)u_{max}(0) > 0,$$
$$(u_{max})_x(L) = \alpha(-b_d + 1)u_{max}(L) \geq 0.$$

Then $(u_{max})_x(x)$ has at least two zero points in $(0, L)$. We choose the two smallest zero points $x_1, x_2 \in (0, L)$ $(x_1 < x_2)$ such that $(u_{max})_x(x_1) = (u_{max})_x(x_2) = 0$, $(u_{max})_x(x) < 0$ on (x_1, x_2). We claim that $(u_{max})_{xx}(x_1) < 0$ and $(u_{max})_{xx}(x_2) > 0$. Indeed differentiating the equation in (2.8) with respect to x, we have

$$d(u_{max})_{xxx} - q(u_{max})_{xx} + f_u(x, u_{max})(u_{max})_x = 0. \tag{2.30}$$

Since $(u_{max})_x(x) < 0$ on (x_1, x_2), then $(u_{max})_{xx}(x_1) \leq 0$ and $(u_{max})_{xx}(x_2) \geq 0$. If $(u_{max})_{xx}(x_1) = 0$, then from (2.30) and $(u_{max})_x(x_1) = 0$, we conclude that $(u_{max})_x(x) \equiv 0$ near $x = x_1$ from the uniqueness of solution of ordinary differential equation, which contradicts with the assumption that $(u_{max})_x(x) < 0$ on (x_1, x_2). Hence we have $(u_{max})_{xx}(x_1) < 0$, and similarly we can show that $(u_{max})_{xx}(x_2) > 0$.

According to [87, Page 992], the maximal solution u_{max} is semistable. The corresponding eigenvalue problem is (2.1) with $p(x) = f_u(u_{max}(x))$:

$$\begin{cases} d\phi_{xx} - q\phi_x + f_u(u_{max})\phi = \lambda\phi, & 0 < x < L, \\ d\phi_x(0) - q\phi(0) = b_u q\phi(0), \\ d\phi_x(L) - q\phi(L) = -b_d q\phi(L), \end{cases} \tag{2.31}$$

and the corresponding principal eigenvalue $\lambda_1(f_u(u_{max})) \leq 0$ with eigenfunction $\phi > 0$. Multiplying equation (2.30) by $e^{-\alpha x}\phi$ and multiplying the equation in (2.31) by $e^{-\alpha x}(u_{max})_x$, then subtracting, we obtain

$$\begin{aligned} &de^{-\alpha x}((u_{max})_x\phi_{xx} - (u_{max})_{xxx}\phi) + qe^{-\alpha x}((u_{max})_{xx}\phi - (u_{max})_x\phi_x) \\ =&\lambda_1(f_u(u_{max}))e^{-\alpha x}\phi(u_{max})_x. \end{aligned} \tag{2.32}$$

Integrating the above equation on $[x_1, x_2]$, the right hand side of (2.32) becomes

$$\int_{x_1}^{x_2} e^{-\alpha x}\lambda_1(f_u(u_{max}))\phi(u_{max})_x dx \geq 0.$$

Since $(u_{max})_{xx}(x_1) < 0$ and $(u_{max})_{xx}(x_2) > 0$, the left hand side of (2.32) becomes

$$\begin{aligned} &d\int_{x_1}^{x_2} [(e^{-\alpha x}\phi_x)_x(u_{max})_x - (e^{-\alpha x}(u_{max})_{xx})_x\phi]dx \\ =&de^{-\alpha x}(\phi_x(u_{max})_x - \phi(u_{max})_{xx}) \mid_{x_1}^{x_2} - d\int_{x_1}^{x_2} e^{-\alpha x}(\phi_x(u_{max})_{xx} - \phi_x(u_{max})_{xx})dx \\ =&de^{-\alpha x_1}\phi(x_1)(u_{max})_{xx}(x_1) - de^{-\alpha x_2}\phi(x_2)(u_{max})_{xx}(x_2) < 0, \end{aligned}$$

which is a contradiction. Thus, the maximal solution $u_{max}(x)$ of (2.8) is increasing on $x \in (0, L)$. Moreover the strong maximum principle implies that u_{max} must be strictly increasing.

For part 2, we employ some ideas from [61, Lemma 4.2] (thanks to an anonymous reviewer for this suggestion). Let $w(x) = (u_{max})_x(x)/u_{max}(x)$. Then by some straightforward computation, we find that $w(x)$ satisfies

$$\begin{cases} -dw_{xx} + (q - 2dw)w_x - u_{max} g_u(x, u_{max})w = g_x(x, u_{max}), & 0 < x < L, \\ dw(0) = (1 + b_u)q > 0, \\ dw(L) = (1 - b_d)q \geq 0. \end{cases} \tag{2.33}$$

From the assumptions that $g_u(x, u) \leq 0$ and $g_x(x, u) \geq 0$ for $x \in [0, L]$ and $u \geq 0$ and the maximum principle, we conclude that $w(x) > 0$ for $x \in (0, L)$, which implies that $u_{max}(x)$ is strictly increasing for $x \in (0, L)$. □

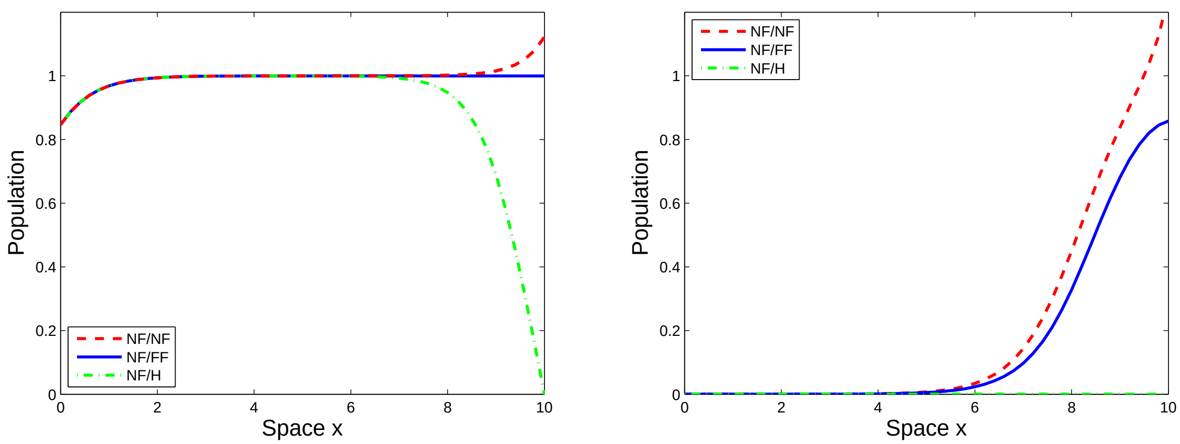

Figure 2.4: The maximal steady state solution $u_{max}(x)$ of system (1.4) with $f(x, u) = u(1 - u)(u - h)$ under different boundary conditions. Here $d = 0.1$, $h = 0.3$, $L = 10$, $q = 0.03$ (Left) and $q = 0.082$ (Right). The solutions are simulated with initial condition $u_0 = e^{qx/d}$ and the solution at $t = 3000$ is shown.

The condition $b_u \geq 0$, $0 \leq b_d \leq 1$ in Proposition 2.13 is optimal as $u'_{max}(L) = \alpha(1 - b_d)u_{max}(L) < 0$ if $b_d > 1$. Fig. 2.4 shows the maximal positive steady solutions under different boundary conditions. We can see that the maximal solution $u_{max}(x)$ is increasing for the NF/FF and NF/NF cases and is decreasing near $x = L$ for the NF/H case since $b_d > 1$ under this situation. Fig. 2.5 shows the dependence of the maximal solution $u_{max}(x)$ on the advection coefficient q. It appears that the maximum value of the maximal solution $\|u_{max}\|_\infty$ decreases in q in the NF/FF and NF/H cases, and when $q \geq q_1$ for some $q_1 > 0$, $\|u_{max}\|_\infty = 0$ which implies there is no positive steady state for such q. This verifies the extinction result proved in Theorem 2.11 for $b_d > 0$. However in the NF/NF case, $\|u_{max}\|_\infty$ is not monotone in q, and $\|u_{max}\|_\infty$ achieves the maximum at an intermediate $q_m > 0$. This suggests that an intermediate advection rate q may increase the maximum population density. Indeed under intermediate advection, the river flow pushes the population to the downstream so that the downstream end has a higher density and the upstream density is lower; but when the advection rate is high, then the population will be washed out before it can establish at the downstream. On the other hand, a larger advection always leads to a lower total steady state population (see Fig. 2.7). It is not clear whether the population can still persist for a large q under NF/NF boundary condition (see subsection 4.4), but from Fig. 2.5, the persistence range of advection q for NF/NF boundary condition is much larger than the ones for NF/FF and NF/H cases.

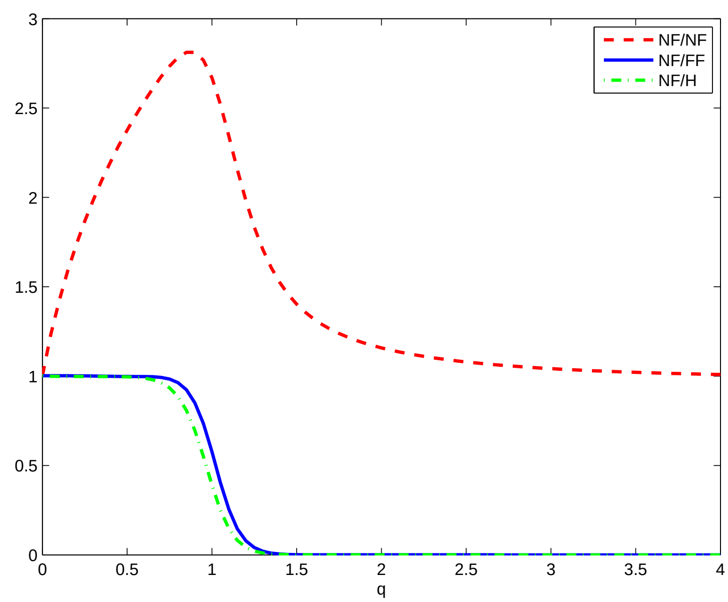

Figure 2.5: The dependence of maximal steady state solution $u_{max}(x)$ of system (1.4) with $f(x,u) = u(1-u)(u-h)$ on the advection coefficient q. The horizontal axis is q and the vertical axis is $\|u_{max}\|_\infty$. Here $d = 0.02$, $h = 0.3$, $a = 0.5$.

Next we prove the existence of positive steady state solutions of (1.4) for the NF/NF boundary condition ($b_u = b_d = 0$) case.

Theorem 2.14. *Suppose $g(x,u)$ satisfies (g1)-(g3) and (g4c), and*

$$\max_{y\in[0,L]} e^{-\alpha y}h(y) < \min_{y\in[0,L]} e^{-\alpha y}r(y). \tag{2.34}$$

Then when $b_u = b_d = 0$, (1.4) has at least two positive steady state solutions. In particular the condition (2.34) is satisfied if

$$0 < \frac{q}{d} < \frac{1}{L}\ln\left(\frac{\min_{y\in[0,L]} r(y)}{\max_{y\in[0,L]} h(y)}\right). \tag{2.35}$$

Proof. Using the transform $u = e^{\alpha x}v$, the steady state equation in this case is of the form

$$\begin{cases} dv_{xx} + qv_x + e^{-\alpha x}f(x, e^{\alpha x}v) = 0, & 0 < x < L, \\ v_x(0) = 0, \quad v_x(L) = 0. \end{cases} \tag{2.36}$$

From Proposition 2.12, $\overline{v}_2(x) = \max_{y\in[0,L]} e^{-\alpha y}r(y)$ is an upper solution of (2.36). Set $\underline{v}_2(x) = \max_{y\in[0,L]} e^{-\alpha y}h(y)$. Then from

$$e^{-\alpha x}f(x, e^{\alpha x}\underline{v}_2) = \underline{v}_2 g(x, e^{\alpha x}\max_{y\in[0,L]} e^{-\alpha y}h(y)) \geq \underline{v}_2 g(x, e^{\alpha x}e^{-\alpha x}h(x)) = g(x,h(x)) = 0,$$

we obtain that

$$\begin{cases} d\underline{v}_2'' + q\underline{v}_2' + e^{-\alpha x}f(x, e^{\alpha x}\underline{v}_2) \geq 0, & 0 < x < L, \\ \underline{v}_2'(0) = 0, \ \underline{v}_2'(L) = 0. \end{cases}$$

So $\underline{v}_2(x)$ is a lower solution of (2.36), and from (2.34), we have $\underline{v}_2(x) < \overline{v}_2(x)$. Therefore (2.36) has at least one positive solution between $\underline{v}_2$ and $\overline{v}_2$ by the results in subsection 3.4. Moreover $\underline{v}_1(x) = 0$ is a lower solution of (2.36), and from Proposition 2.9, $\overline{v}_1 = \min_{y\in[0,L]} e^{-\alpha y}h(y)$ is an upper solution of (2.36), hence we have two pairs of upper and lower solutions which satisfy

$$\underline{v}_1 < \overline{v}_1 < \underline{v}_2 < \overline{v}_2.$$

From [4, Theorem 14.2], (2.36) has at least three nonnegative solutions, which implies that there exist at least two positive solutions. The condition (2.35) can be derived from (2.34) since

$$\max_{y\in[0,L]} e^{-\alpha y}h(y) \le \max_{y\in[0,L]} h(y), \quad e^{-\alpha L}\min_{y\in[0,L]} r(y) \le \min_{y\in[0,L]} e^{-\alpha y}r(y).$$

□

Note that if $h(x) \equiv h$ and $r(x) \equiv r$, then (2.35) becomes $0 < \frac{q}{d} < \frac{1}{L}\ln(\frac{r}{h})$. Also the maximal steady state solution obtained from Theorem 2.14 is the maximal steady state solution defined in Proposition 2.12 as $\overline{v}_2$ is the bound for all positive steady states. The second positive solution in Theorem 2.14 is a saddle-type solution in between two stable solutions: the maximal one and the zero solution.

The existence result in Theorem 2.14 shows that the population is able to persist when the relative advection rate q/d is relatively small. The existence of positive steady state solution of (1.4) for other boundary conditions can also be proved along the approach in the proof of Theorem 2.14 if proper upper and lower solutions can be constructed. The numerically simulated persistence region Fig. 2.1 suggests that positive steady state solutions of (1.4) for other boundary conditions only exist when the advection q is in a more restrictive range than the one for no-flux case.

For the open environment, *i.e.* $b_u \ge 0$ and $b_d > 0$, we can also obtain the existence of multiple positive steady states, but with more restriction on the growth rate. Here we establish a persistence result for H/H boundary condition. From Proposition 2.3, we know that the persistence for the system with H/H type boundary condition would imply the persistence for the one with other boundary conditions with $b_u \ge 0$ and $b_d \ge 0$. Indeed the positive steady states under H/H type boundary condition can be used as the lower solution to obtain the existence of the positive steady states under other boundary conditions.

Theorem 2.15. *Suppose $g(x,u)$ satisfies (g1)-(g3) and (g4c), $d > 0$, $q \ge 0$ and there exists* *an interval* $(x_1, x_4) \subset [0, L]$ *and* $\delta > 0$ *such that*

$$F(x, r(x)) = \int_0^{r(x)} f(x, s)ds \geq \delta > 0, \quad x \in (x_1, x_4), \tag{2.37}$$

where $r(x)$ *is defined in (g2) and here we assume that* $r(x)$ *is continuously differentiable for* $x \in (x_1, x_4)$*. Then for any* $k > 0$*, when* $\frac{q}{d} \in [0, k]$*, there exists* $d_0(k) > 0$*, such that when* $0 < d < d_0(k)$*, the following steady state problem*

$$\begin{cases} du_{xx} - qu_x + f(x, u) = 0, \quad 0 < x < L, \\ u(0) = u(L) = 0, \end{cases} \tag{2.38}$$

has at least two positive solutions.

Proof. We prove the result following a variational approach similar to [58], see also [82]. Define an energy functional

$$E(u) = \int_0^L e^{-\alpha x} \left[\frac{d}{2}(u_x)^2 - F(x, u) \right] dx,$$

where $u \in X_3 \equiv W_0^{1,2}(0, L)$. Here we redefine $f(x, u)$ to be

$$\tilde{f}(x, u) = \begin{cases} f(x, u), & 0 \leq u \leq M, \\ 0, & u < 0 \ \text{ and } \ u > M, \end{cases} \tag{2.39}$$

where $M = \max_{y \in [0,L]} r(y)$. From Proposition 2.6, all non-negative solutions of (2.38) satisfy $0 \leq u(x) \leq M$, so this will not affect the solutions of (2.38). In the following we assume $f(x, u)$ to be $\tilde{f}(x, u)$ as defined in (2.39).

Similar to [58], we can verify that $E(u)$ satisfies the Palais-Smale condition, and similar to (2.20), we can show that $E(u)$ is bounded from below. Since any critical point of $E(u)$ is a classical solution of (2.38) and $E(u)$ satisfies the Palais-Smale condition, $\inf E(u)$ can be achieved and it is a critical value. In the following we prove that $\inf E(u) < 0 = E(0)$.

Let $[0,L]=[0,x_1]\cup(x_1,x_2]\cup(x_2,x_3)\cup[x_3,x_4)\cup[x_4,L]$ where $0<x_1<x_2<x_3<x_4<L$. Here x_2, x_3 are to be chosen and $x_3-x_2\geq(x_4-x_1)/2$. We define a test function $u_0(x)$ as follows:

$$u_0(x)=\begin{cases}0, & x\in[0,x_1],\\ \dfrac{r(x_2)}{x_2-x_1}(x-x_1), & x\in(x_1,x_2],\\ r(x), & x\in(x_2,x_3),\\ \dfrac{r(x_3)}{x_4-x_3}(x_4-x), & x\in[x_3,x_4),\\ 0, & x\in[x_4,L).\end{cases} \tag{2.40}$$

Then $u_0(x)\in X_3$. Let $v_0(x)=e^{-\alpha x}\left[\dfrac{d}{2}(u_0'(x))^2-F(x,u_0(x))\right]$. Then

$$E(u_0)=\int_{x_1}^{x_2}v_0(x)dx+\int_{x_2}^{x_3}v_0(x)dx+\int_{x_3}^{x_4}v_0(x)dx\equiv I_1+I_2+I_3.$$

Since $\alpha=\dfrac{q}{d}\in[0,k]$, we have

$$\begin{aligned}I_2&=\frac{d}{2}\int_{x_2}^{x_3}e^{-\alpha x}(r_x)^2(x)dx-\int_{x_2}^{x_3}e^{-\alpha x}F(x,r(x))dx\\ &\leq\frac{d}{2}M_4^2(x_3-x_2)-e^{-\alpha x_3}\delta(x_3-x_2)\\ &\leq\frac{d}{2}M_4^2(x_4-x_1)-\frac{1}{2}e^{-kL}\delta(x_4-x_1),\end{aligned} \tag{2.41}$$

where $M_4=\max\limits_{x_2\leq x\leq x_3}|r_x(x)|$. And

$$\begin{aligned}|I_1|+|I_3|\leq&\frac{d}{2}\frac{r(x_2)^2}{x_2-x_1}+M_5(x_2-x_1)+\frac{d}{2}\frac{r(x_3)^2}{x_4-x_3}+M_5(x_4-x_3)\\ \leq&\frac{d}{2}\frac{M^2}{x_2-x_1}+\frac{d}{2}\frac{M^2}{x_4-x_3}+M_5(x_2-x_1+x_4-x_3),\end{aligned} \tag{2.42}$$

where $M_5=\max\limits_{x_1\leq x\leq x_4}F(x,r(x))$ and recall that in (g2), $0<r(x)<M$. Now choosing x_2 sufficiently close to x_1 and x_3 sufficiently close to x_4, we can have

$$M_5(x_2-x_1+x_4-x_3)<\frac{\delta(x_4-x_1)}{8}e^{-kL}. \tag{2.43}$$

Next fixing x_2, x_3 as above, we can choose $d_0(k) > 0$ such that for $0 < d < d_0(k)$,

$$\frac{d}{2}M^2(\frac{1}{x_2 - x_1} + \frac{1}{x_4 - x_3}) < \frac{\delta(x_4 - x_1)}{8}e^{-kL}, \tag{2.44}$$

and

$$\frac{d}{2}M_4^2 < \frac{\delta}{8}e^{-kL}. \tag{2.45}$$

Now combining (2.41), (2.42), (2.43), (2.44) and (2.45), we have, for $0 < d < d_0(k)$,

$$E(u_0) \leq |I_1| + I_2 + |I_3| < -\frac{\delta(x_4 - x_1)}{8}e^{-kL} < 0. \tag{2.46}$$

Thus (2.38) has at least one positive solution $u_1(x)$ satisfying $E(u_1) = \inf E(u) < 0$ ($u_1 > 0$ follows from the definition of $f(x, u)$ in (2.39) and the strong maximum principle) from standard minimization theory in calculus of variation [83, Theorem 2.7].

Next we apply the mountain pass theorem [5] to obtain another positive solution (2.38). Note that

$$E''(u)[\varphi, \varphi] = \int_0^L de^{-\alpha x}(\varphi_x)^2 dx - \int_0^L e^{-\alpha x} f_u(x, u)\varphi^2 dx.$$

So we have

$$E''(0)[\varphi, \varphi] > e^{-\alpha L}\left(d\int_0^L (\varphi_x)^2 dx + A_1\int_0^L \varphi^2 dx\right) \geq A_2 e^{-\alpha L}||\varphi||^2, \tag{2.47}$$

where $A_1 = \min\limits_{x\in[0,L]} -f_u(x, 0) > 0$ and $A_2 = \min\{d, A_1\}$. Because $E(0) = E'(0) = 0$, and E is twice differentiable, then for any $\epsilon > 0$, there exists $\rho > 0$ such that for $||\varphi|| \leq \rho$ (here $||\cdot||$ is the norm of X_3), we have

$$\left|E(\varphi) - \frac{1}{2}E''(0)[\varphi, \varphi]\right| \leq \epsilon||\varphi||^2. \tag{2.48}$$

Now by choosing $\epsilon = \dfrac{A_2 e^{-\alpha L}}{4}$, and applying (2.47) and (2.48), we obtain that when $||\varphi|| = \rho$,

$$E(\varphi) \geq \frac{A_2 e^{-\alpha L}}{4} ||\varphi||^2 = \frac{A_2 e^{-\alpha L}}{4} \rho^2 > 0. \tag{2.49}$$

Along with the result that there exists $u_0 \in X_3$ such that $E(u_0) < 0$ and $\| u \| > \rho$, the mountain pass theorem [5] implies that $E(u)$ has another critical point u_2 such that $E(u_2) \geq \dfrac{A_2 e^{-\alpha L}}{4} \rho^2 > 0 > E(u_1)$. Therefore, u_2 is a distinct positive solution of (2.38). □

Now from the comparison of boundary condition in Proposition 2.3, under the assumption of Theorem 2.15, (1.4) always has at least two positive steady state solutions as any other boundary condition is more favorable than the H/H one in Theorem 2.15.

Theorem 2.16. *Suppose $g(x,u)$ satisfies (g1)-(g3)and (g4c), $d > 0$, $q \geq 0$, $b_u, b_d \geq 0$ and there exist an interval $(x_1, x_4) \subset [0, L]$ and $\delta > 0$ such that* (2.37) *holds, and $r(x)$ is continuously differentiable for $x \in (x_1, x_4)$. Then for any $k > 0$, if $\dfrac{q}{d} \in [0, k]$, there exists $d_0(k) > 0$, such that when $0 < d < d_0(k)$,* (1.4) *has at least two positive steady state solutions.*

Proof. We use the upper-lower solution approach from subsection 3.4. From Proposition 2.6, $\overline{v}_2(x) = e^{\alpha x} \max\limits_{y \in [0,L]} (e^{-\alpha y} r(y))$ is an upper solution of (2.9), and the solution $\underline{v}_2(x)$ of (2.38) is a lower solution. Using the same $\overline{v}_1$ and $\underline{v}_1$, we can conclude the existence of at least two positive solutions of (2.9). □

Remark 2.17. *1. The growth rate condition* (2.37) *is clearly the local version of the one used in Proposition 2.4, and this condition is sharp for the H/H boundary condition (see Proposition 2.20 below for a nonexistence results). Note that for the most favorable NF/NF boundary condition, Theorem 2.14 shows the existence without any restriction on $f(x,u)$, while for the most unfavorable H/H boundary condition, condition* (2.37) *is needed to ensure the persistence state is a more stable than the extinction state in at least some part of the habitat. Note that the potential function $F(x,u)$ is a measurement of stability, and* (2.37) *implies that* 0 *and $r(x)$ are both local minimum points of F, but $r(x)$ is a global minimum point with smaller energy.*

2. *The persistence result in Theorem 2.14 under NF/NF boundary condition requires q/d is smaller than a given value, but q and d are not necessarily small. On the other hand, the existence result in Theorems 2.15 and 2.16 for open environment allows q/d to be large but d to be small. In general, it is difficult to determine the exact range of (d, q) which supports population persistence.*

Next we show that when the growth rate is in a special form, then multiple positive steady state solutions of (1.4) exist when the diffusion coefficient d and advection rate q are in certain range. Unlike Theorem 2.14, this result holds for any $b_u, b_d \geq 0$ but not hostile boundary condition.

Theorem 2.18. *Consider the steady state solution for* (1.4)

$$\begin{cases} du_{xx} - qu_x + u(r-u)(u-h) = 0, & x \in (0, L), \\ du_x(0) - qu(0) = b_u qu(0), \\ du_x(L) - qu(L) = -b_d qu(L). \end{cases} \tag{2.50}$$

Here $0 < h < r$, $d > 0$, $q \geq 0$, and $b_u, b_d \geq 0$. Let $d_m = (r-h)L^2/(m\pi)^2$ be defined as in Proposition 2.5 for $m \in \mathbb{N}$ and also define $d_0 = \infty$. Suppose that $d_{m+1} < d < d_m$ for $m \in \mathbb{N} \cup \{0\}$. Then there exists $q_m > 0$ such that when $q \in [-q_m, q_m]$, (2.50) *has exactly $2m+2$ nonconstant positive solutions.*

Proof. We prove the result with a perturbation argument using implicit function theorem. When $q = 0$, (2.50) becomes

$$\begin{cases} du_{xx} + u(r-u)(u-h) = 0, & x \in (0, L), \\ u_x(0) = u_x(L) = 0. \end{cases} \tag{2.51}$$

From Proposition 2.5, when $d_{m+1} < d < d_m$, we know that (2.51) has exactly $2m$ nontrivial positive solutions $u_k^{\pm}(d, x)$ $(1 \leq k \leq m)$ and two trivial positive solutions $u_{m+1}^{-}(x) \equiv h$,

$u_{m+1}^{+}(x) \equiv r$. Moreover all these solutions except u_{m+1}^{+} are unstable, so each of them is non-degenerate; and $u_{m+1}^{+}(x) = r$ is locally asymptotically stable. Here a solution u of (2.50) is stable (or unstable) if the principal eigenvalue λ_1 of the eigenvalue problem

$$\begin{cases} d\phi_{xx} - q\phi_x + (-3u^2 + 2(r+h)u - rh)\phi = \lambda\phi, & x \in (0, L), \\ d\phi_x(0) - q\phi(0) = b_u q\phi(0), \\ d\phi_x(L) - q\phi(L) = -b_d q\phi(L), \end{cases} \tag{2.52}$$

is negative (or positive), and u is non-degenerate if $\lambda = 0$ is not an eigenvalue of (2.52).

We use the implicit function theorem to obtain the existence of positive solutions for (2.50) when q is near 0. Define a mapping $F : \mathbb{R} \times W^{2,p}(0, L) \to L^p(0, L) \times \mathbb{R} \times \mathbb{R}$ (where $p > 2$) by

$$F(q, u) = \begin{pmatrix} du_{xx} - qu_x + u(r-u)(u-h) \\ du_x(0) - qu(0) - b_u qu(0) \\ du_x(L) - qu(L) + b_d qu(L) \end{pmatrix}.$$

Then $F(0, u_k^{\pm}) = 0$ for $1 \le k \le m+1$. The Frechét derivative of F with respect to u at $(0, u_k^{\pm})$ is

$$F_u(0, u_k^{\pm})[w] = \begin{pmatrix} dw_{xx} + (-3(u_k^{\pm})^2 + 2(r+h)u_k^{\pm} - rh)w \\ dw_x(0) \\ dw_x(L) \end{pmatrix}, \tag{2.53}$$

where $w \in W^{2,p}(0, L)$. From the non-degeneracy of $u_k^{\pm}$, $F_u(0, u_k^{\pm})$ is invertible, then from the implicit function theorem, we obtain the existence of a positive solution $u_k^{\pm}(q, x)$ of (2.50) when $q \in (-\delta_k, \delta_k)$ for some $\delta_k > 0$ and each of $1 \le k \le m+1$. One can choose $q_m = \min_{1 \le k \le m+1} \{\delta_k\} > 0$ so (2.50) has $2m+2$ positive solutions when $q \in [-q_m, q_m]$. Note that each of these solutions is nonconstant when $q \ne 0$. By making q_m possibly smaller, there are exactly $2m+2$ such solutions when $q \in [-q_m, q_m]$ as there are exactly $2m+2$ positive solutions when $q = 0$. $\square$

Remark 2.19. *1. The solution $u_{m+1}^{+}(q, x)$ of (2.50) is locally asymptotically stable as it* *is perturbed from* $u^+_{m+1}(x) = r$ *which is locally asymptotically stable, and* $u^+_{m+1}(q, x)$ *is also the maximal steady state solution in Proposition 2.12. All other positive solutions of* (2.50) *are unstable. The trivial state* $u = 0$ *remains a locally asymptotically stable steady state for all* $d > 0$ *and* $q \geq 0$.

2. *The multiplicity of positive steady state solutions in Theorem 2.18 holds for all* $b_d, b_u \geq 0$, *but the critical advection rate* q_m *is not explicitly defined and it is only for the special form growth function* $f(u) = u(r - u)(u - h)$; *while the result in Theorem 2.14 holds for more general growth function only requiring (g1)-(g3) and (g4c) and an explicit bound of the critical advection rate* (2.35), *but only for* $b_d = b_u = 0$.

3. *The multiplicity result in Theorem 2.18 does not include the NF/H or even H/H boundary conditions. Indeed in the hostile boundary condition case, positive steady states of* (2.50) *may not exist when* $h > r/2$, *see the following Proposition 2.20.*

Finally we show a nonexistence of positive steady state solution result when the upstream boundary condition is hostile and the Allee threshold is high.

Proposition 2.20. *Suppose* $g(x, u)$ *satisfies (g1)-(g3) and (g4c), and for* $r(x) \equiv M$ *defined in (g2),*

$$F(M) = \int_0^M f(s)ds < 0, \tag{2.54}$$

Then the following steady state problem

$$\begin{cases} du_{xx} - qu_x + f(u) = 0, & x \in (0, L), \\ u(0) = 0, & \\ du_x(L) - qu(L) = -b_d qu(L), & \end{cases} \tag{2.55}$$

has no positive solution if $b_d \geq 1$.

Proof. Suppose that $u(x)$ is a positive solution of (2.55). From Proposition 2.6 and $b_d \geq 1$, we have $u(x) \leq M$. Multiplying the equation in (2.55) by u_x, and integrating over an arbitrary interval $[a, b] \subseteq [0, L]$, we obtain that

$$\left[\frac{d}{2}u_x(x)^2 + F(u(x))\right]\Bigg|_{x=a}^{x=b} - q\int_a^b u_x^2(x)dx = 0, \tag{2.56}$$

as

$$\int_a^b (du_{xx}u_x + f(u)u_x)dx = \frac{d}{2}u_x^2(x)|_{x=a}^{x=b} + \int_{u(a)}^{u(b)} f(u)du = \left[\frac{d}{2}u_x(x)^2 + F(u(x))\right]\Bigg|_{x=a}^{x=b}.$$

From the boundary condition of (2.55), $u_x(0) > 0$ and $du_x(L) = (1 - b_d)qu(L) \leq 0$. Hence there exists $x_0 \in (0, L]$ such that $u_x(x_0) = 0$. Applying (2.56) to the interval $[0, x_0]$, we obtain that

$$F(u(x_0)) - \frac{d}{2}u_x^2(0) - q\int_0^{x_0} u_x^2(x)dx = 0.$$

But (2.54) implies that $F(u) < 0$ for any $u > 0$. That is a contradiction. Therefore (2.55) has no positive solution if $b_d \geq 1$. □

The condition (2.54) is satisfied for $f(u) = u(r - u)(u - h)$ with $h > r/2$, so the result in Proposition 2.20 is partly similar to the nonexistence of solutions for Dirichlet boundary value problem in Proposition 2.4. The nonexistence of positive steady state of (1.4) when the upstream boundary is hostile and the Allee threshold is high also holds when the downstream boundary is hostile, but is not proven here though it can be observed numerically (see Fig. 2.6 lower right panel).

Theorem 2.15 and Proposition 2.20 show that the Allee effect threshold h plays an important role in the persistence/exitinction of population. In Fig. 2.6, the population persistence/extinction behavior for (1.4) with $f(u) = u(r - u)(u - h)$, varying advection rate q and strong Allee threshold h is shown under the three boundary conditions: NF/NF, NF/FF and NF/H, with an initial condition $u_0(x) = r = 1$. For the NF/FF boundary condition, the population persists under small q for all $h \in (0, 1)$, and it goes to extinction for large q. For the NF/H boundary condition, the persistence for small q only occurs for $0 < h < r/2$, while the behavior is similar for NF/FF case for large q. It is interesting

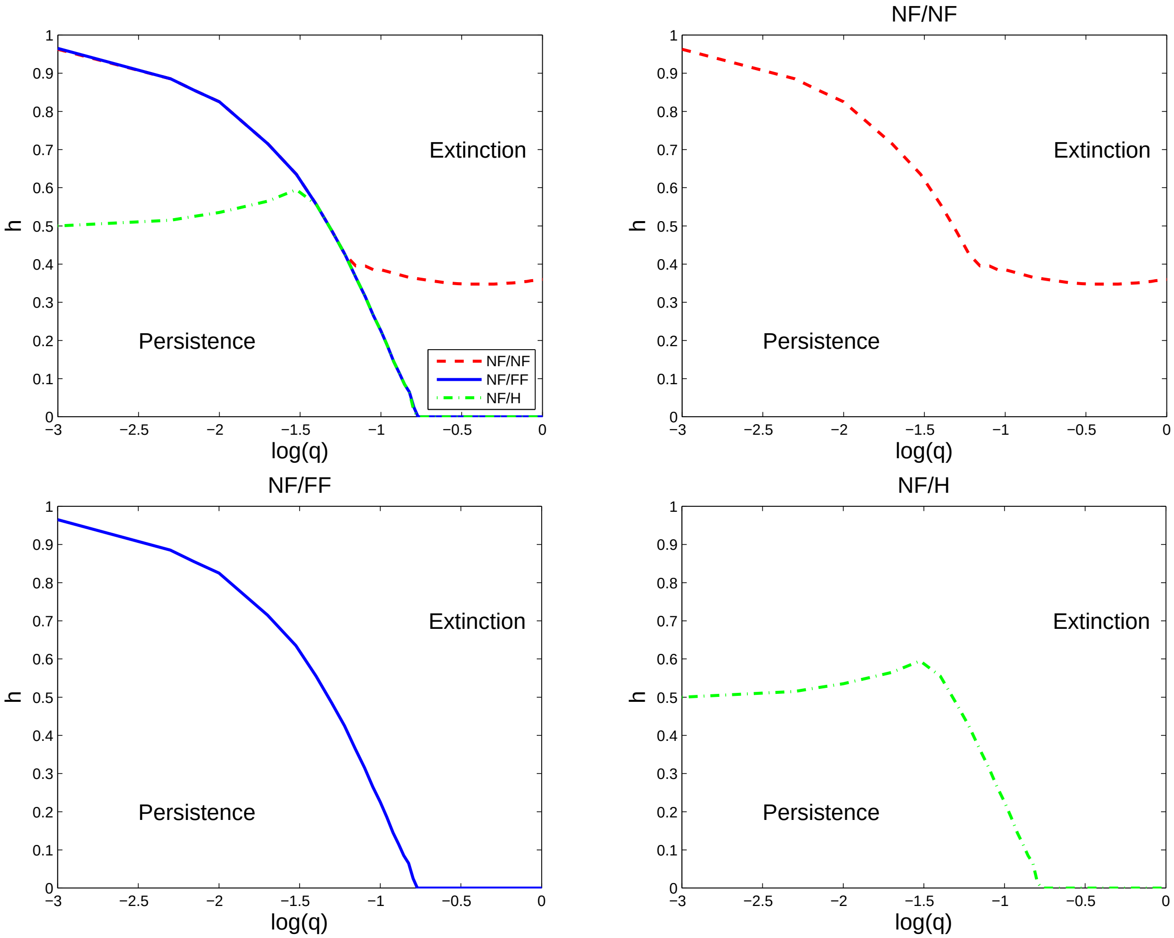

Figure 2.6: Population extinction and persistence for varying advection coefficient q (log scale) and the Allee threshold h. Here $f(x,u) = au(1-u)(u-h)$, $a = 0.5$, $d = 0.1$, $L = 10$ and the initial condition is $u_0(x) = 1$. (Upper left): comparison of NF/NF, NF/FF and NF/H boundary conditions; (Upper right): NF/NF; (Lower left): NF/FF; (Lower right): NF/H.

that for small positive $q > 0$, the threshold h_c between persistence and extinction is actually slightly higher than $r/2$.

2.3.4 Closed environment

Theorem 2.11 shows that when $b_d > 0$, i.e. when the population has a loss at the downstream, then a large advection rate q always drives the population to extinction. But the restriction of $b_u \geq 0$ and $b_d > 0$ in Theorem 2.11 excludes the NF/NF boundary condition for which the population does not have a loss at the downstream end, so under the NF/NF boundary condition, (1.4) could have a positive steady state solution for large advection rate q. In the subsection, we discuss the asymptotic profile of positive steady state under closed advective environment, so we consider this special case of (1.4) and (2.8) with $b_u = b_d = 0$:

$$\begin{cases} u_t = du_{xx} - qu_x + f(x,u), & 0 < x < L,\ t > 0, \\ du_x(0,t) - qu(0,t) = 0, & t > 0, \\ du_x(L,t) - qu(L,t) = 0, & t > 0, \\ u(x,0) = u_0(x) \geq 0, & x \in (0,L), \end{cases} \tag{2.57}$$

and

$$\begin{cases} du_{xx} - qu_x + f(x,u) = 0, & x \in (0,L), \\ du_x(0) - qu(0) = 0, \\ du_x(L) - qu(L) = 0. \end{cases} \tag{2.58}$$

First we have the following maximum principle (see [20, Lemma 3.1]).

Lemma 2.21. *Recall that* $N = \max_{y\in[0,L],u\geq 0} g(y,u)$ *from (g3). Suppose that* $g(x,u)$ *satisfies (g1)-(g3),* q, d *satisfy* $q^2/d \geq 4N$, *and* $u(x) \in C^2(0,L) \cap C[0,L]$ *satisfies*

$$\begin{cases} du_{xx} - qu_x + g(x,u(x))u \leq 0, & 0 < x < L, \\ -du_x(0) + qu(0) \geq 0, \quad u(L) \geq 0, \end{cases} \tag{2.59}$$

then either $u(x) \equiv 0$ *or* $u(x) > 0$ *in* $[0,L)$.

Proof. Using the change of variables $v(x) = e^{-\alpha x/2}u(x)$, we obtain that $v(x)$ satisfies

$$\begin{cases} dv_{xx} + v\tilde{g}(x, e^{\alpha x/2}v) \leq 0, & 0 < x < L, \\ -dv_x(0) + \dfrac{q}{2}v(0) \geq 0, \quad v(L) \geq 0, \end{cases} \tag{2.60}$$

where $\tilde{g}(x,u) = g(x,u) - q^2/4d \leq 0$. From the maximum principle, $u(x) \geq 0$ in $[0,L]$. Moreover either $u(x) \equiv 0$ or $u(x) > 0$ in $[0,L)$ according to the strong maximum principle.

□

For some results below, we also assume that $f(x,u) = ug(x,u)$ satisfies one of the following:

(g5) there exists constants $A, B > 0$ such that, $g(x,u) \leq A - Bu$ for $x \in [0,L]$ and $u \geq 0$.

(g6) there exists $P, Q > 0$ such that $g(x,u) \geq -P$ for any $x \in [0,L]$ and $u \geq 0$, and $g(x,u) \leq -Q$ for any $x \in [0,L]$ and $u \geq u_1$ where $u_1 > 2M$ and $M = \max_{y\in[0,L]} r(y)$.

For the growth function satisfying (g5), the growth function per capita can be controlled by a declining linear function. In (g6) the growth rate per capita is non-increasing but it has a lower bound $-P$. We will prove our limiting profile result under the condition (g5), but in the process of the proof, we first prove the result under the condition (g6). Note that the cubic function $f(u) = u(r-u)(u-h)$ satisfies (g5) but does not satisfy (g6), while the function

$$f(x,u) = \begin{cases} u(r-u)(u-h), & 0 \leq u \leq u_1, \\ u(r-u_1)(u_1-h), & u > u_1 \end{cases} \tag{2.61}$$

satisfies (g6) but does not satisfy (g5), where $u_1 > r > h > 0$.

Now we can obtain the following estimates for the positive solution $u(x)$ of (2.58), which is inspired by [20, Lemma 3.2].

Proposition 2.22. *Suppose $g(x,u)$ satisfies (g1)-(g3), and $u(x)$ is a positive solution of (2.58). Let $C_1 = 2 + N + P$, and assume that $q^2/d \geq C_1^2$. Then we have:*

1.

$$u(x) \leq u^+(x) := u(L)\exp((-\frac{q}{d} + \frac{C_1}{q})(L-x)), \quad x \in [0,L]. \tag{2.62}$$

2. If, in addition, we assume that $f(x,u) = ug(x,u)$ also satisfies (f6), then

$$u(x) \geq u^-(x) := u(L)\exp((-\frac{q}{d} - \frac{C_1}{q})(L-x)), \quad x \in [0,L]. \tag{2.63}$$

Proof. We denote $\alpha = q/d$ and $\beta = C_1/q$. Since $q^2/d \geq C_1^2 \geq 4N$, we have $d\beta^2 \leq 1$ and

$$\begin{aligned} & du_{xx}^+ - qu_x^+ + g(x, u(x))u^+ \\ =& [d(\alpha-\beta)^2 - q(\alpha-\beta) + g(x,u(x))]u^+ \\ \leq& [-C_1 + d\beta^2 + N]u^+ \\ \leq& [-1 + d\beta^2]u^+ \leq 0, \end{aligned} \tag{2.64}$$

and

$$-du_x^+(0) + qu^+(0) = d\beta u^+(0) \geq 0, \quad u^+(L) = u(L). \tag{2.65}$$

Applying Lemma 2.21 to $u^+(x) - u(x)$, we obtain the estimate in (2.62).

Similarly, we have

$$\begin{aligned} & du_{xx}^- - qu_x^- + g(x, u(x))u^- \\ =& [d(\alpha+\beta)^2 - q(\alpha+\beta) + g(x,u(x))]u^- \\ \geq& [C_1 + d\beta^2 - P]u^+ \geq 0, \end{aligned} \tag{2.66}$$

and

$$-du_x^-(0) + qu^-(0) = -d\beta u^-(0) \leq 0, \quad u^-(L) = u(L). \tag{2.67}$$

Now applying Lemma 2.21 to $u(x) - u^-(x)$, we obtain the estimate in (2.63). □

We note that the estimates in Proposition 2.22 does not require (g4a), (g4b) or (g4c), hence it holds not only for the Allee effect case but also for the logistic case. It shows that when the advection rate q is large, the population density exhibits a spike layer profile: the population concentrates at the downstream boundary end and the density elsewhere except $x = L$ tends to zero.

Theorem 2.23. *Suppose $g(x, u)$ satisfies (g1)-(g3), (g5) and $g_x(x, u) \geq 0$, and $u_q(x)$ is a positive solution of* (2.58)*. Recall C_1 is the constant defined in Proposition 2.22. Then*

1. *There exist positive constants C_2 and C_3, such that when $q^2/d \geq C_1^2$ and $\frac{q}{d} \geq C_2$, we have*

$$u_q(x) < C_3 \frac{q}{d} \exp((-\frac{q}{d} + \frac{C_1}{q})(L - x)). \tag{2.68}$$

2. *Let $d > 0$, $L > 0$ be fixed, then $\lim_{q \to +\infty} \int_0^L u_q(x)dx = 0$ and $\lim_{q \to +\infty} u_q(x) = 0$ for any $x \in [0, L)$.*

Proof. It is clear that if the conclusions hold for the maximal solution of (2.58), then the conclusions also hold for any other positive solutions. So without loss of generality, we assume that $u_q(x)$ is the maximal solution of (2.58). To prove (2.68) under the assumptions (g1)-(g3) and (g5), we first prove (2.68) under the assumptions (g1)-(g3) and (g6). From (g1)-(g3) and (g6), there exist positive constants A, B and Q, such that

$$g(x, u) \leq \begin{cases} A - Bu, & x \in [0, L],\ 0 \leq u \leq u_1, \\ -Q, & x \in [0, L],\ u \geq u_1. \end{cases} \tag{2.69}$$

Integrating the first equation of (2.58) over $(0, L)$ and applying the boundary condition, we have

$$\int_0^L u_q g(x, u_q) dx = 0. \tag{2.70}$$

From Proposition 2.13, $u_q(x)$ is strictly increasing over $x \in [0, L]$. We assume that $u_q(L) > u_1$ (otherwise (2.68) obviously holds). Then there exists $0 < L_1 < L$, such that $u_q(L_1) = u_1$, recalling u_1 is defined in (f6). Now (2.70) combined with (2.69) yields

$$B \int_0^{L_1} u_q^2 dx + Q \int_{L_1}^L u_q dx \leq A \int_0^{L_1} u_q dx \leq ALu_1. \tag{2.71}$$

According to Proposition 2.22, when $q^2/d \geq C_1^2$, we have $u_q^-(x) \leq u_q(x) \leq u_q^+(x)$, where $u_q^\pm = u_q(L) \exp\left((-\alpha \mp \beta)(L - x)\right)$, $\alpha = q/d$ and $\beta = C_1/q$. Now substituting u_q^- into (2.71), we obtain

$$\begin{aligned}&\frac{Bu_q^2(L)}{2(\alpha+\beta)}[\exp\left(-2(\alpha+\beta)(L-L_1)\right)-\exp\left(-2(\alpha+\beta)L\right))\\&+\frac{Qu_q(L)}{\alpha+\beta}(1-\exp\left(-(\alpha+\beta)L\right)]\leq ALu_1.\end{aligned}\tag{2.72}$$

Claim: As $\alpha\to\infty$, we have

$$\exp\left(-(\alpha+\beta)(L-L_1)\right)=\frac{u_1}{u_q(L)}(1+O(\alpha^{-1})).\tag{2.73}$$

Proof of Claim 2.3.4. Since $u_q^-(x)\leq u_q(x)\leq u_q^+(x)$, there exist $x_1,x_2\in(0,L)$ satisfying $x_1<L_1<x_2$ such that $u_q^-(x)=u_q^+(x)=u_1$, that is

$$\exp\left(-(\alpha+\beta)(L-x_1)\right)=\exp\left(-(\alpha-\beta)(L-x_2)\right)=\frac{u_1}{u_q(L)}.\tag{2.74}$$

Notice that for fixed $d>0$ when $\alpha\to\infty$, $\beta=O(\alpha^{-1})$. Thus,

$$\exp\big((-\alpha+O(\alpha^{-1}))(L-x_1)\big)=\exp\big((-\alpha+O(\alpha^{-1}))(L-x_2)\big)=\frac{u_1}{u_q(L)}.\tag{2.75}$$

Since $x_1\leq L_1\leq x_2$, we have

$$\exp\big((-\alpha+O(\alpha^{-1}))(L-L_1)\big)=\frac{u_1}{u_q(L)},\tag{2.76}$$

which implies the claim. □

Substituting (2.73) into (2.72), we have (as $\alpha\to\infty$)

$$\begin{aligned}&\frac{1}{\alpha+\beta}\left[Bu_1^2-Bu_q^2(L)\exp\big(-2(\alpha+O(\alpha^{-1}))L\big)+Qu_q(L)-Qu_1+O(\alpha^{-1})\right]\\&\leq ALu_1.\end{aligned}\tag{2.77}$$

From Proposition 2.6, $u_q(L) \le C_4 e^{\alpha L}$, where C_4 is a constant. Therefore (2.77) implies that

$$\frac{1}{\alpha+\beta}\left[Qu_q(L)+O(1)\right] \le ALu_1, \quad \text{as } \alpha \to \infty. \tag{2.78}$$

From (2.78), we conclude that there exist positive constants C_2, C_3 such that $u_q(L) \le C_3\alpha$ whenever $\alpha \ge C_2$ and $q^2/d \ge C_1^2$. Together with (2.62), we obtain (2.68). This proves (2.68) when (g1)-(g3) and (g6) are satisfied.

Now suppose that $f(x,u) = ug(x,u)$ satisfy (g1)-(g3) and (g5), then we can define a $\tilde{f}(x,u) = u\tilde{g}(x,u)$ satisfying (g1)-(g3) and (g6), and $g(x,u) \le \tilde{g}(x,u)$. Then a comparison argument implies that the solutions of (2.58) satisfy $u_q(x) \le \tilde{u}_q(x)$, where $u_q(x)$ is the solution of (2.58) with $f(x,u)$, and $\tilde{u}_q(x)$ is a solution of (2.58) with $\tilde{f}(x,u)$. Indeed this can be shown using argument as in the proof of Theorem 2.14, as $\tilde{u}_q(x)$ can be constructed with $u_q(x)$ as the lower solution and $e^{\alpha x}\max\limits_{y\in[0,L]} e^{-\alpha y} r(y)$ as the upper solution. Now the estimate (2.68) holds for $\tilde{u}_q(x)$, then it also holds for $u_q(x)$ under the conditions (g1)-(g3) and (g5). This completes the proof of part 1.

For part 2, we follow the proof of [53, Lemma 2.5]. From (g5), there exist constants $A, B > 0$ such that $g(x,u) \le A - Bu$ for $x \in [0,L]$ and $u \ge 0$. Then from comparison method as in the last paragraph, it is sufficient to consider the solution $u_q(x)$ of

$$\begin{cases} du_{xx} - qu_x + u(A-Bu) = 0, & x \in (0,L), \\ du_x(0) - qu(0) = 0, \\ du_x(L) - qu(L) = 0. \end{cases} \tag{2.79}$$

Integrating (2.79) on $(0,L)$ and applying the boundary condition, we obtain

$$B\int_0^L u_q^2(x)dx = A\int_0^L u_q(x)dx \le A\sqrt{L}\sqrt{\int_0^L u_q^2(x)dx}. \tag{2.80}$$

In particular, $\int_0^L u_q^2(x)dx$ is bounded by a quantity independent of q. Choosing any function

$m(x) \in C^2[0, L]$ with $m_x(0) = m_x(L) = 0$, multiplying the equation in (2.79) by $m(x)$ and integrating by parts, we obtain

$$d \int_0^L m_{xx} u_q dx + q \int_0^L m_x u_q dx + \int_0^L m u_q (A - B u_q) dx = 0. \tag{2.81}$$

Since both $\int_0^L u_q(x)dx$ and $\int_0^L u_q^2(x)dx$ are bounded and $q \to +\infty$, then (2.81) implies that $\int_0^L m_x(x)u_q(x)dx \to 0$ and consequently $\int_0^L u_q(x)dx \to 0$ as $q \to +\infty$. For the pointwise convergence, suppose it is not true. Then there exists a constant $\delta > 0$ and a $x^* \in [0, L)$, such that $\liminf_{q \to +\infty} u_q(x^*) \geq \delta > 0$. Since $u_q(x)$ is strictly increasing, we have

$$\int_0^L u_{q_n}(x)dx \geq \int_{x^*}^L u_{q_n}(x)dx \geq \delta(L - x^*) > 0,$$

for a sequence $q_n \to \infty$, which contradicts with $\int_0^L u_q dx \to 0$ as $q \to +\infty$. Therefore, we have $\lim_{q \to +\infty} u_q(x) = 0$ for any $x \in [0, L)$. □

We remark that the results of Theorem 2.23 hold under the assumption that such a steady state solution $u_q(x)$ exists for (2.58) when the advection rate q is large, and the results hold for logistic (g4a), weak Allee effect (g4b), and strong Allee effect (g4c) cases. The existence of such steady state solutions for the logistic case and any $q > 0$ has been proven in [53, Lemma 2.1], and the existence for the weak Allee effect case can also be established (see our forthcoming work). So the results of Theorem 2.23 are relevant for these two cases. However, the existence for the strong Allee effect case for large q remains an open question. Nevertheless, the properties of the solution profile established in Theorem 2.23 indicates that when q is large, then the population concentrates at the downstream end but the total biomass becomes very small regardless of the type of growth rate. In Fig. 2.7, the time series of total biomass of (2.57) for different advection rate q are plotted. It can be observed that the total biomass always decreases with respect to q. For small advection rate, the population is close to carrying capacity; but for large advection rate, the total population tends to near zero (or indeed zero) when $t \to \infty$.

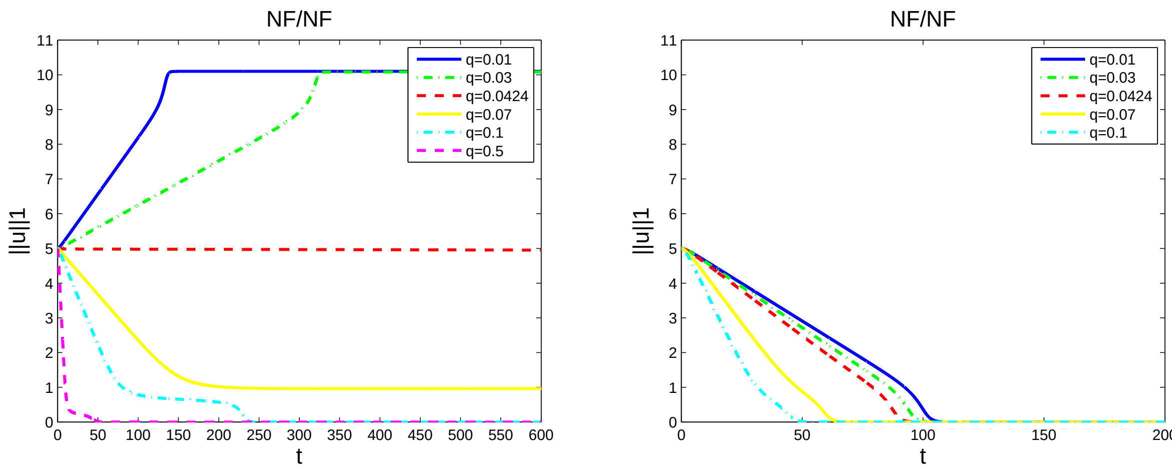

Figure 2.7: The evolution of total biomass of (2.57) with respect to time under NF/NF boundary condition and varying advection coefficient q. The horizontal axis is t and the vertical axis is $\|u(\cdot,t)\|_1 = \int_0^L u(x,t)dx$. Here $f(x,u) = u(1-u)(u-h)$, $d = 0.09$, $L = 10$ and the initial condition is $u_0(x) = 0$ for $x \in [0, L/2]$ and $u_0(x) = 1$ for $x \in [L/2, L]$. Left: $h = 0.4$; Right: $h = 0.6$.

2.3.5 Transient dynamics and traveling waves

From Fig. 2.7 left panel, the total biomass of the species increases in time t for small advection rate q, but it decreases in time t for large q; while in the right panel, the total biomass always decreases in time. Moreover, in all cases, the total biomass increases or decreases in an almost linear fashion for a long time period until it is near the equilibrium level, and the slope of linear change before the total biomass reaching the equilibrium level decreases with respect to q.

Such wave-propagating-like transient dynamics of (2.57) is closely related to the traveling wave solution of the reaction-diffusion-advection equation:

$$u_t = du_{xx} - qu_x + au(r-u)(u-h), \quad t > 0, \ x \in (-\infty, \infty), \tag{2.82}$$

where $d > 0$, $a > 0$, $q \in \mathbb{R}$, and $0 < h < r$. It is well-known [31, 57] that (2.82) has a unique

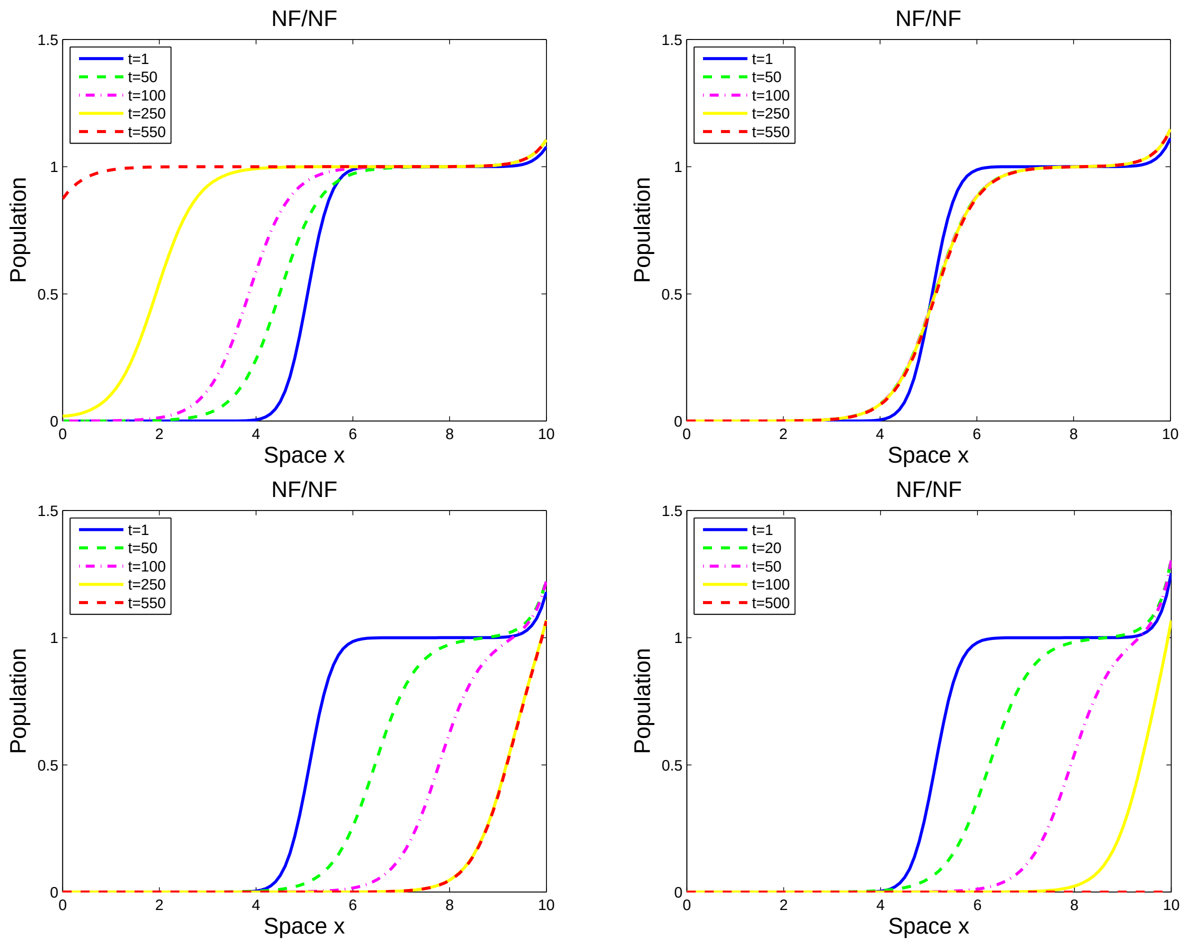

Figure 2.8: Propagation of interface and formation of boundary layer in (2.57). Here $f(x, u) = u(1-u)(u-h)$, $h = 0.4$, $d = 0.09$, $L = 10$ and the initial condition is $u_0(x) = 0$ for $x \in [0, L/2]$ and $u_0(x) = 1$ for $x \in [L/2, L]$. Upper left: $q = 0.03$; Upper right: $q = 0.043$; Lower left: $q = 0.07$; Lower right: $q = 0.1$.

pair of traveling wave solutions $U_\pm(x - c_\pm t)$ satisfying

$$\begin{cases} dU''_\pm(y) - (q - c_\pm)U'_\pm(y) + aU_\pm(y)(r - U_\pm(y))(U_\pm(y) - h) = 0, \quad y \in (-\infty, \infty), \\ c_- : \quad U_-(-\infty) = 0, \ U_-(\infty) = r, \\ c_+ : \quad U_+(-\infty) = r, \ U_+(\infty) = 0, \end{cases} \tag{2.83}$$

with

$$c_\pm = q \pm \sqrt{2ad}\left(\frac{r}{2} - h\right). \tag{2.84}$$

Indeed it can be explicitly computed that

$$U_{\pm}(y) = \frac{r}{1+e^{\pm ky}}, \quad \text{where} \quad k = \sqrt{\frac{a}{2d}}r. \tag{2.85}$$

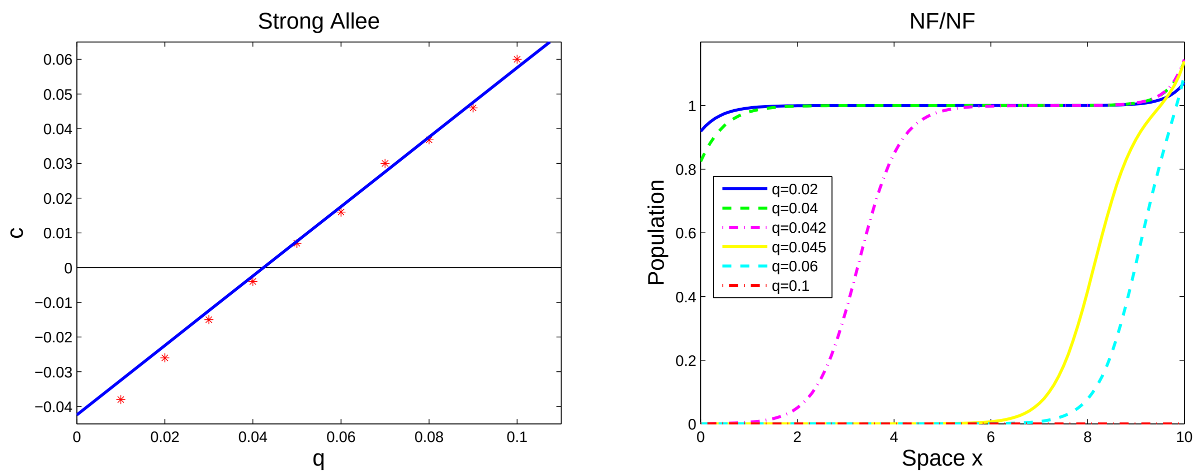

Figure 2.9: Effect of advection rate q to the population propagation in (2.57). Left: The dependence of traveling wave speed c with respect to the advection rate q; Right: The dependence of maximal steady state solution on the advection rate q. Here $f(x,u) = u(1-u)(u-h)$, $d = 0.09$, $h = 0.4$ and the initial condition is $u_0(x) = 0$ for $x \in [0, L/2]$ and $u_0(x) = 1$ for $x \in [L/2, L]$.

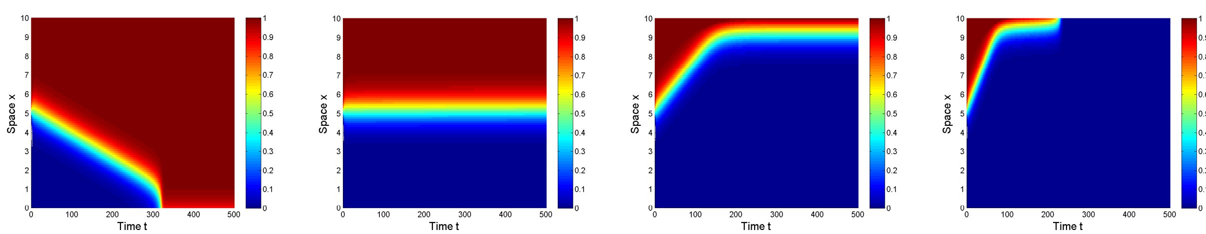

Figure 2.10: Traveling-wave-like dynamics for different advection rate q. Here $f(x,u) = u(1-u)(u-h)$, $d = 0.09$, $h = 0.4$, $L = 10$, and the initial condition is $u_0(x) = 0$ for $x \in [0, L/2]$ and $u_0(x) = 1$ for $x \in [L/2, L]$. The advection rate from left to right is $q = 0.03$, $q = 0.043$, $q = 0.07$ and $q = 0.1$.

The initial condition used in Fig. 2.7 and 2.8 is a step function, which represents that the initial population only exists over the region $[L/2, L]$. The profile of this initial condition resembles the shape of U_-. The formula for c_- in (2.84) shows that when $h < r/2$, the wave speed c_- is negative for small q, so the wave front moves upstream and the population persists in the entire river (see Fig. 2.7 left panel and Fig. 2.8 upper left panel); for large q, the wave speed is positive, the wave front moves downstream, and the population could form a boundary layer steady state at downstream end (see Fig. 2.7 left panel and Fig. 2.8

lower left panel), or the population could become extinct (see Fig. 2.7 left panel and Fig. 2.8 lower right panel). Between the waves of two opposite directions, there is a "break-even" advection rate q_0 (that is ≈ 0.042 for parameters in Fig. 2.7 and 2.8) such that the total biomass is almost unchanged for all time, and the traveling wave is a standing one with $c_- \approx 0$ (see Fig. 2.8 upper right panel). On the other hand, when $h > r/2$, the formula of c_- in (2.84) shows that the wave speed c_- is always positive, hence for any advection rate q, the population cannot invade the upstream region (see Fig. 2.7 right panel). Indeed, Fig. 2.7 right panel suggests that extinction always occurs in this case for any advection rate q when the initial condition is a step function from 0 to 1. Note that positive steady states of (2.57) still exist for small q even when $h > r/2$ (see Theorem 2.14). However, this phenomenon of population is unable to persist in the upstream region when $h > r/2$ echoes the nonexistence of positive steady states in Propositions 2.4 and 2.20 when the upstream end has Dirichlet boundary condition.

The traveling-wave-like transient dynamics of (2.57) occurs when the diffusion coefficient d and advection rate q are relatively small, the river length L is comparably large, and the interface between extinction and persistence is far away from the boundary. Fig. 2.9 left panel shows the comparison of the numerical wave speeds in Fig. 2.7 right panel and the theoretical one in (2.84); Fig. 2.9 right panel shows that the maximal steady state solution of (2.57) decreases in q, and the solution maintains a transition layer profile between the extinction and persistence states. Fig. 2.10 shows the traveling-wave-like behavior of the solutions for different q. The slope of the interface is approximately c_-: it is negative when $q = 0.03$, and it is positive when $q = 0.07$ and $q = 0.1$. It is almost zero when $q = 0.043$ (the break-even advection rate).

Fig. 2.11 shows the evolution of population profile under different q when the initial condition is a step function $u_0(x) = 1$ for $x \in [0, L/2]$ and $u_0(x) = 0$ for $x \in [L/2, L]$. That is, the population initially is at upstream end, but not downstream end. Then in all cases, the population can invade the downstream as $c_+ > 0$ in this case. The invasion is successful for small q case and the population is established in the entire river (see Fig. 2.11

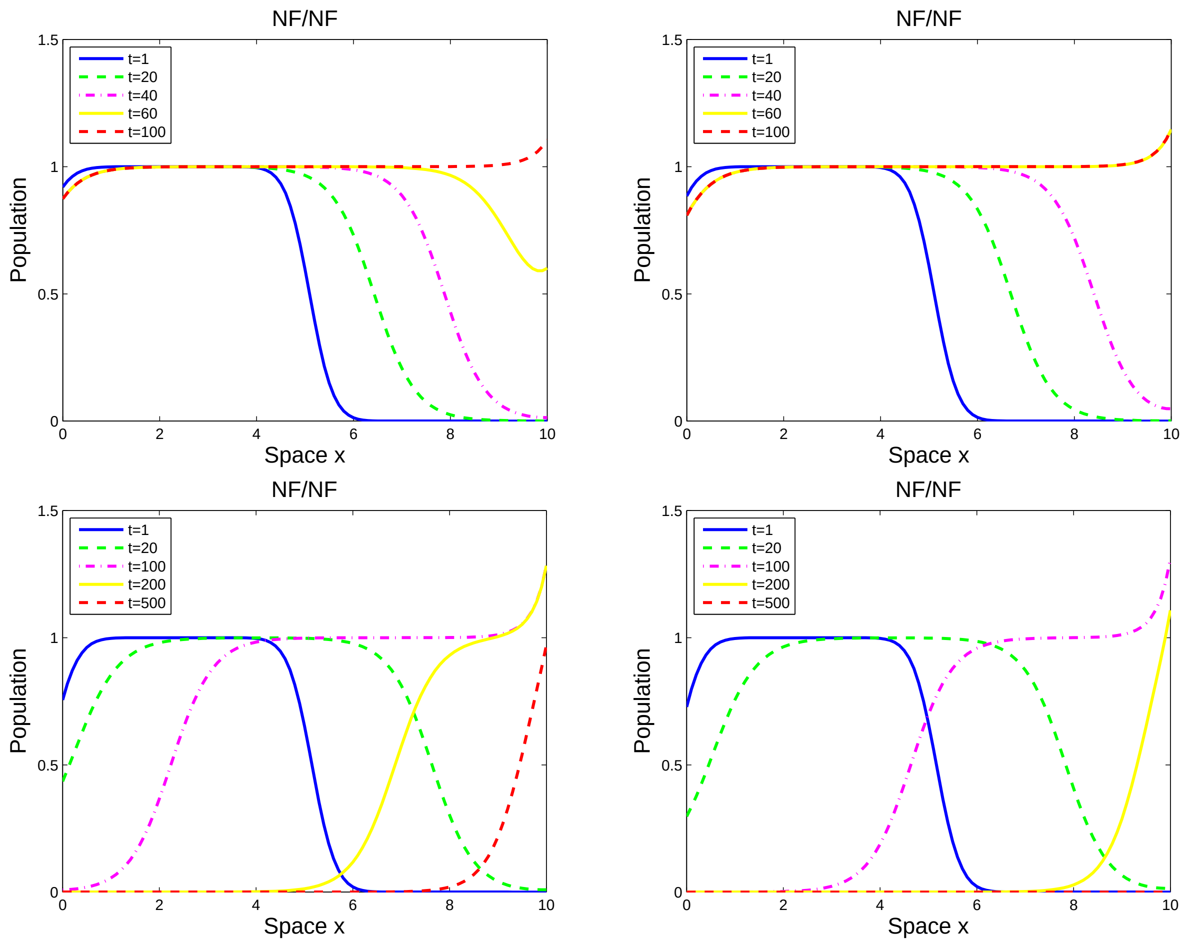

Figure 2.11: Formation of boundary layer. Here $f(x,u) = u(1-u)(u-h)$, $h = 0.4$, $d = 0.09$, $L = 10$ and the initial condition is $u_0(x) = 1$ for $x \in [0, L/2]$ and $u_0(x) = 0$ for $x \in [L/2, L]$. Upper left: $q = 0.03$; Upper right: $q = 0.043$; Lower left: $q = 0.09$; Lower right: $q = 0.1$.

upper left and upper right panels). But for large q, another wave is formed at the upstream end and propagates at $c_- > 0$ downstream. Hence for some time period, there are two wave propagating: the front invasion wave with speed c_+, and the back extinction wave with speed c_-. Although the back wave never catches up with the front wave as $c_+ > c_-$, the back extinction wave eventually wipes out the entire population in the upstream region. Either it ends at a boundary layer steady state at downstream end (see Fig. 2.11 lower left panel), or the population becomes extinct (see Fig. 2.11 lower right panel).

In Fig. 2.12, the dynamics of (2.57) for small diffusion coefficient $d = 0.0001$ and various q is shown with the initial condition $u_0(x) = h + 0.1\sin x$. It is known that when there is no advection present, sharp interfaces between the two stable states are generated quickly, then

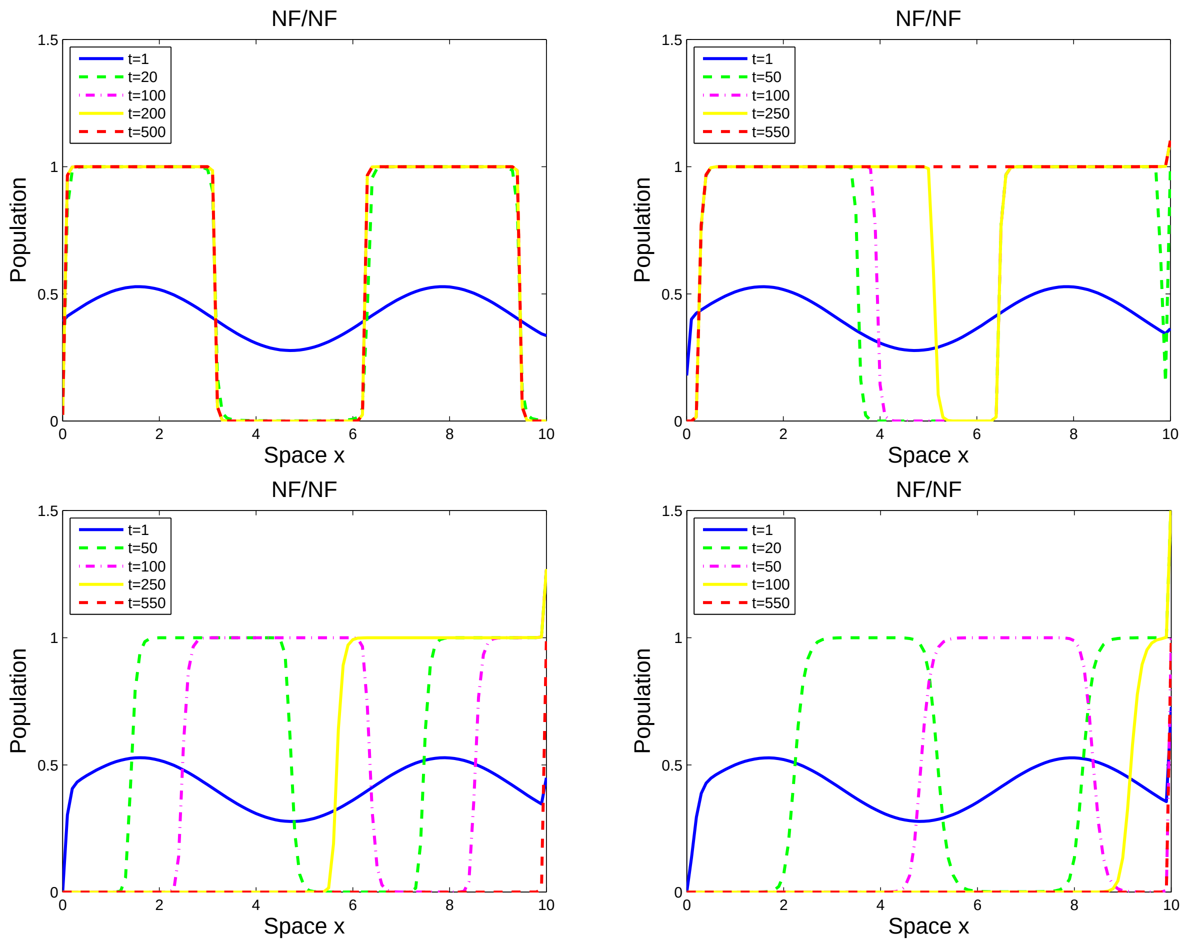

Figure 2.12: Slow interface motion, persistence and extinction with advection in (2.57). Here $f(x,u) = u(1-u)(u-h)$, $h = 0.4$, $d = 0.0001$, $L = 10$ and the initial condition is $u_0 = h + 0.1 \sin x$. Upper left: $q = 0.001$; Upper right: $q = 0.008$; Lower left: $q = 0.03$; Lower right: $q = 0.1$.

the interfaces move slowly if the bistable nonlinearity is balanced ($h = r/2$) [12, 26], or the interfaces move with traveling wave speed if it is unbalanced ($h \neq r/2$) [27]. Here we observe that the sharp interfaces between the two stable states are still formed quickly in all cases of advection rate q. Next a sufficiently small $q = 0.001$ can facilitate the slow movement of the interfaces (see Fig. 2.12 upper left panel); or a larger $q = 0.008$ can speed up the transition layer from 1 to 0 to catch the transition layer from 0 to 1, so the two transition layers merge and the two patches of high density population collide into one (see Fig. 2.12 upper right panel). However if the advection rate q increases further, then the strong flow will push all population patches downstream before they can establish in the middle sections (see Fig. 2.12 lower panel). In the large q case (Fig. 2.12 lower panel), a very sharp boundary layer appears to persist, which demonstrates that the boundary layer solution as in Theorem 2.23 exists for such q.

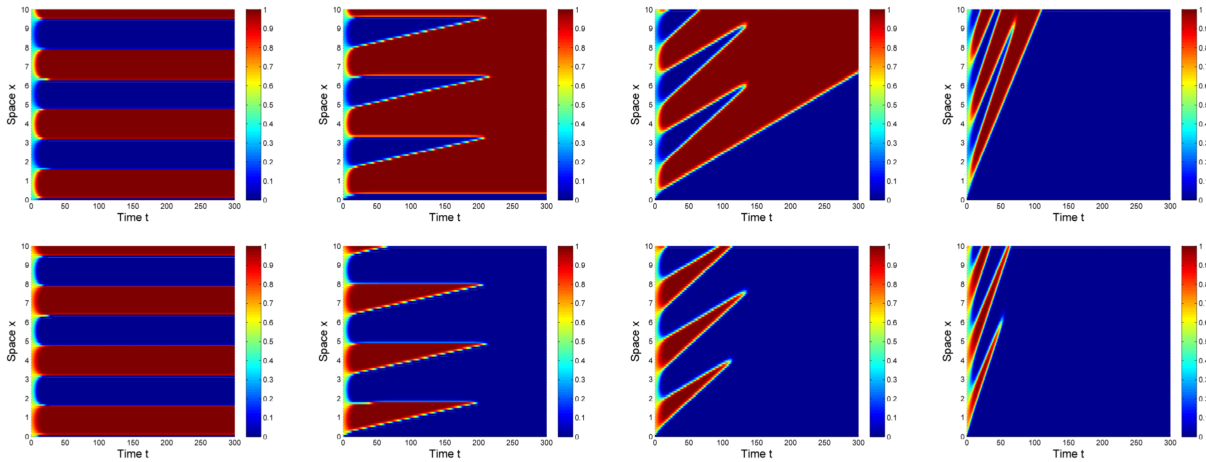

Figure 2.13: Interface merging, persistence and extinction with advection in (2.57). Here $f(x,u) = u(1-u)(u-h)$, $d = 0.0001$, $L = 10$ and the initial condition is $u_0 = h + 0.1 \sin 2x$. Upper row: $h = 0.4$; Lower row: $h = 0.6$; The advection rate from left to right: $q = 0.001$, $q = 0.008$, $q = 0.03$, and $q = 0.1$.

The merging of the interfaces and the collision of persistence/extinction patches can be clearly observed in Fig. 2.13. In the upper panel ($h = 0.4$), the persistence patches merge through coarsening as $c_+ > c_-$; and in the lower panel ($h = 0.6$), the extinction patches merge as $c_+ < c_-$. When the advection rate q is large, the extinction wave starting from the upstream end point prevails so the extinction eventually occurs despite there being a large merged persistence patch (Fig. 2.13 upper row $q = 0.03$ or $q = 0.1$). Also when the advection rate q is sufficiently small, the steady state with multiple interfaces appears to be metastable regardless of $h = 0.4$ or $h = 0.6$ (see Fig. 2.13 first column).

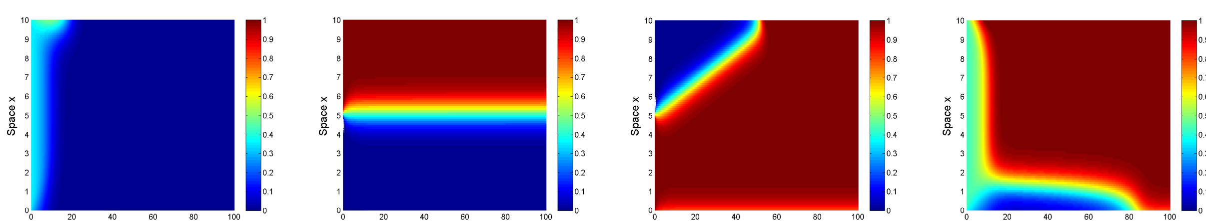

Figure 2.14: Bistable dynamics for different initial conditions. Here $f(x,u) = u(1-u)(u-h)$, $d = 0.09$, $h = 0.4$, $L = 10$, and $q = 0.043$. The initial conditions from left to right are $u_0(x) = 0.36$; $u_0(x) = 0$ for $x \in [0, L/2]$ and $u_0(x) = 1$ for $x \in [L/2, L]$; $u_0(x) = 1$ for $x \in [0, L/2]$ and $u_0(x) = 0$ for $x \in [L/2, L]$, and $u_0(x) = 0.43$.

Finally Fig. 2.14 and 2.15 demonstrate the bistable nature of (2.57) for different initial conditions. In Fig. 2.14, the population becomes extinct when starting from an initial population which is entirely smaller than the Allee threshold (first panel); and the population reaches the maximal steady state when starting from relatively large initial population (third and fourth panels). Both of the extinction and maximal steady state solutions are locally asymptotically stable (see Proposition 2.13), and we expect that there are the only stable ones. But the second panel also shows a stable pattern with a transition layer. We conjecture that the transition layer solution is unstable and metastable (with a small positive eigenvalue), so the pattern can be observed for a long time in numerical simulation. The stability of such steady states will be a question for further studies.

Fig. 2.15 shows a well-known feature of the spreading/extinction bistable structure. For bistable equation on unbounded domain ($\mathbb{R}$) (2.82) with $q = 0$, it is known that when the initial condition is a function $u_L(x) = 1$ when $|x| \leq L$ and $u_L(x) = 0$ otherwise, then there is a sharp threshold $L_0 > 0$, such that the corresponding solution converges to 0 if $L < L_0$, and the solution converges to a traveling wave if $L > L_0$ [115], and such threshold phenomenon hold for more general situations [24, 73]. Fig. 2.15 illustrates this phenomenon (bistability between extinction and maximal steady state) with $q > 0$ and no-flux boundary condition. It can be seen that here $L_0 \approx 0.07L$ where L is the length of habitat, and the value of L_0 appears to be independent of location of initial patch.

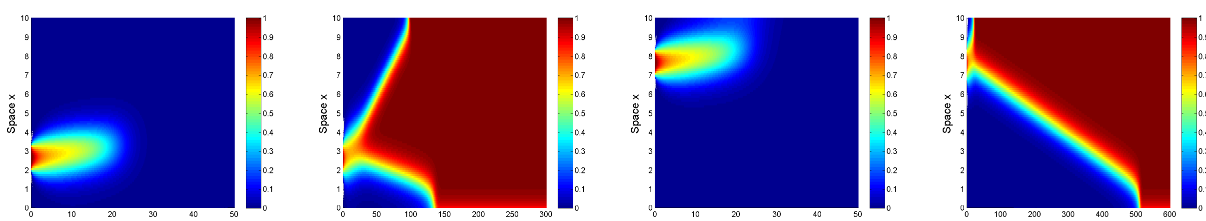

Figure 2.15: Minimal initial patch size for invasion. Here $f(x,u) = u(1-u)(u-h)$, $d = 0.09$, $h = 0.4$, $L = 10$, $q = 0.03$, and the initial condition is $u_0(x) = 1$ for $x \in [C-W, C+W]$ and $u_0(x) = 0$ otherwise. Values of (C,W) from left to right: $(C,W) = (0.25L, 0.065L)$; $(C,W) = (0.25L, 0.07L)$; $(C,W) = (0.75L, 0.065L)$; and $(C,W) = (0.75L, 0.07L)$.

2.4 Conclusion

The persistence or extinction of a stream population can be modeled by a reaction-diffusion-advection equation defined on a one-dimensional habitat (river environment). While it is typical that the growth rate exhibits logistic type, it is also common that the growth rate of the species exhibits a strong Allee effect so that the growth is negative at lower density. It is shown that other than the extinction of population due to the small initial condition, a strong advection can also drive the population to extinction in an open environment regardless of initial condition. On the other hand, in a closed environment, the population becomes extinct in the upstream region but may concentrate near the downstream end under strong flow rate. In general, a large increase of the advection rate makes the extinction more likely, but there are a few numerical simulations indicating that an intermediate advection rate may increase the population size or possibility of persistence (see Fig. 2.5 NF/NF case and Fig. 2.6 NF/H case).

The logistic growth usually leads to an unconditional persistence of the population for all initial condition, and the Allee effect growth rate causes a bistability in the population dynamics. For a species with Allee effect type growth, multiple stable states are possible and different initial conditions can lead to different asymptotic behavior, so the persistence is always conditional. The question of persistence or extinction also depends on the boundary conditions, advection rate, diffusion rate and the Allee threshold. From both analytical and numerical approaches, we can see that in general, a higher Allee threshold or a higher advection rate often lead to a wider range of the extinction region.

Our numerical results also suggest that when the Allee threshold satisfies certain condition, a global extinction for all initial conditions is possible even in a closed environment. For example, in Fig. 2.1 and Fig. 2.6, under NF/NF boundary condition and the growth function $f(x,u) = u(1-u)(u-h)$, a global extinction occurs if $h = 0.4$ for all large advection rate q, but for $h = 0.3$, the population appears to at least survive at the downstream end not in a total extinction. A theoretical verification of this phenomenon is an interesting open question. Similar global extinction when $h > 0.5$ has been observed and proved for a two-patch ODE model with strong Allee effect growth function $f(u) = u(1-u)(u-h)$ and no loss due to dispersal [96].

Most of our results in this paper allow a spatially heterogeneous nonlinear growth function $f(x, u)$ with a bistable structure. A multiplicity result for the steady state solutions with a homogeneous growth function is obtained for small advection rate (see Theorem 2.18), and the number of such solution can be large if the diffusion coefficient is sufficiently small. In the absence of advection, the existence of steady state solutions with multiple transition layers or spike layers has been proved in [1, 2, 32, 74] for one-dimensional case and many others for higher dimensional case. The existence and profile of such solutions under small diffusion and appropriate advection rate is another interesting question for future investigation.

Chapter 3

Reaction-diffusion-advection model with weak Allee effect

3.1 Introduction

In this chapter, we consider the dynamical behavior of the model (1.4) with weak Allee effect growth and open or closed environment boundary conditions. Our main findings on the dynamics of reaction-diffusion-advection model (1.4) with weak Allee effect type growth are

1. In a closed river environment, the population always persists for all diffusion coefficients and advection rates;

2. In an open river environment with non-hostile 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 (1.4) 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 (1.4) in this chaper complements the one in chaper 3 for the strong Allee effect case, and the ones in [53, 59] 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 (1.4) 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 Fig. 3.9 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 sub-homogeneous 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 (1.4) with strong Allee effect growth rate can only be "extinction" or "bistable", while the one for logistic case can only be "extinction" or "monostable" (here the uniqueness of positive steady state is well-known) [53, 59]. Similar to the analytical or numerical findings in [53, 59, 108], 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 Fig. 3.9 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 [48, 89]; in [55, 72], 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 [103].

This chapter is organized as follows: In Section 3.2, we recall the reaction-diffusion-advection model with various growth rate functions and the boundary conditions, as well as some basic results from chapter 2. The main results on the persistence/extinction dynamics are presented in Section 3.3. Some concluding remarks are given in Section 3.4.

3.2 Preliminaries

3.2.1 Basic dynamics

We recall the following results from chapter 2 (see Proposition 4.1, Theorem 4.2 and Propositions 4.7, 4.8), which show that the long time dynamic behavior of solutions of (1.4) is determined by the non-negative steady state solutions of (1.4), and some properties of positive steady state solutions hold regardless of assumption (g4a,b,c).

Theorem 3.1. *Suppose that $g(x,u)$ satisfies (g1)-(g2).*

1. (1.4) *has a unique positive solution $u(x,t)$ defined for $(x,t) \in [0,L] \times (0,\infty)$, and the solutions of* (1.4) *generates a dynamical system in X_2, where*

$$X_2 = \{\phi \in W^{2,2}(0,L) : \phi(x) \geq 0,\ d\phi'(0) - q\phi(0) = b_u q\phi(0),\\ d\phi'(L) - q\phi(L) = -b_d q\phi(L)\}. \tag{3.1}$$

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 non-negative steady state solutions.*

3. *Let $u(x)$ be a positive steady state solution of* (1.4)*, then $u(x) \leq e^{\alpha x} \max\limits_{y\in[0,L]}(e^{-\alpha y} r(y))$*

for $x \in [0, L]$, *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* (1.4), *then there exists a maximal steady state solution* $u_{max}(x)$ *such that for any positive steady state* $u(x)$ *of* (1.4), *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 (1.4), 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 3.2. *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:*

$$\begin{cases} d\phi'' - q\phi' + g(x, 0)\phi = \lambda\phi, & 0 < x < L, \\ d\phi'(0) - q\phi(0) = b_u q\phi(0), & \\ d\phi'(L) - q\phi(L) = -b_d q\phi(L). & \end{cases} \tag{3.2}$$

1. *If* $\lambda_1(q) < 0$, *then* $u = 0$ *is locally asymptotically stable for* (1.4); *and if* $\lambda_1(q) > 0$, *then* $u = 0$ *is unstable and there exists a positive steady state of* (1.4).

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* (1.4) *when* $u = 0$ *is locally asymptotically stable, and when* $u = 0$ *is unstable, then there*

exists a unique positive steady state of (1.4) *that is globally asymptotically stable.*

Proof. For part 1, the stability/instability of the extinction state follows from standard theory of semilinear parabolic equations [33]. For part 2, from the variational characterization of λ_1 in part 1 of [108, Proposition 3.1], $\lambda_1(q) > 0$ for $0 \le q < q_1$ in the open environment case, and $\lambda_1(q) > 0$ for any $q \ge 0$ in the close environment case. Also from part 3 of [108, 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 $q_2 \ge q_1 > 0$ 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 [62]. Part 3 is from [108, Proposition 3.2]. □

Proposition 3.2 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 3.9).

3.2.2 Non-advective case

For reaction-diffusion-advection equation (1.4) 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 $n \ge 1$, 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

$$\begin{cases} u_t = d\Delta u + ug(x, u), & x \in \Omega,\ t > 0, \\ u(x, t) = 0, & x \in \partial\Omega,\ t > 0. \end{cases} \tag{3.3}$$

The steady state solution satisfies

$$\begin{cases} d\Delta u + ug(x,u) = 0, & x \in \Omega, \\ u(x) = 0, & x \in \partial\Omega. \end{cases} \tag{3.4}$$

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 non-negative solutions of (3.4) by $\Gamma = \{(d,u) \in \mathbb{R}^+ \times X : u \geq 0, F(d,u) = 0\}$. 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

$$d_1(g,\Omega) = \inf_{\phi \in W_0^{1,2}(\Omega)} \left\{ \int_\Omega g(x,0)\phi^2(x)dx : \int_\Omega |\nabla\phi(x)|^2 dx = 1 \right\}. \tag{3.5}$$

then $d_1 = d_1(g,\Omega)$ is a bifurcation point where nontrivial solutions of system (3.4) bifurcate from the line of trivial solutions Γ_0. Refer to [89, Theorem 1-3], we have the following result when $g(x,u)$ is of weak Allee effect type.

Theorem 3.3. *Suppose that $g(x,u)$ satisfies (g1)-(g3) and (g4b). Then*

1. *The extinction state $u = 0$ is locally asymptotically stable with respect to* (3.3) *when $d > d_1$, and it is unstable when $0 < d < d_1$;*

2. *$d = d_1$ is a bifurcation point for system* (3.4) *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* (3.4) *has no positive solution when $d > d_*$, and when $d \leq d_*$,* (3.4) *has a maximal solution $u_m(d,x)$ such that for any solution $u(d,x)$ of* (3.4)*, $u_m(d,x) \geq u(d,x)$ for $x \in \Omega$, and $u_m(d,x)$ is semi-stable;*

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. (3.4) *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 (3.4), and for $d \geq d_1$, there is no positive solution of (3.4). 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 no-flux boundary condition:

$$\begin{cases} \dfrac{\partial u}{\partial t} = d\triangle u + ug(x, u), & x \in \Omega, \ t > 0, \\ \dfrac{\partial}{\partial n} u(x, t) = 0, & x \in \partial\Omega, \ t > 0. \end{cases} \tag{3.6}$$

We have the following results regarding the dynamics of (3.6) when the growth rate is of weak Allee effect.

Theorem 3.4. *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 $d > 0$,* (3.6) *has a maximal steady state solution $u_m(d, x)$ such that for any solution $u(d, x)$ of* (3.6)*, $u_m(d, x) \geq u(d, x)$ for $x \in \Omega$, and $u_m(d, x)$ is semi-stable;*

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 $X' = \{u \in W^{2,p}(\Omega) : \partial u / \partial n = 0 \text{ on } \partial\Omega\}$.*

Proof. When the advection is absent, Proposition 3.2 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 3.2. 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

$$\begin{cases} d\Delta\phi + g(x,0)\phi = \lambda_1\phi, & x \in \Omega, \\ \dfrac{\partial\phi}{\partial n} = 0, & x \in \partial\Omega. \end{cases} \tag{3.7}$$

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 3.1 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 (3.6) 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 (3.6) 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 [89, Theorem 3]. □

3.3 Persistence/Extinction dynamics

From subsection 3.2.2, 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 (no-flux) condition, there always exists a semi-stable positive steady state solution so the population always persists if the initial population is large enough. Under zero Dirichlet (hostile) 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.

3.3.1 Comparison with logistic models

If $g(x,u)$ satisfies (g1)-(g3) and (g4a) (logistic growth), then the persistence or extinction of population in (1.4) is completely determined by the stability of the extinction state as shown in Proposition 3.2. 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 (3.6) 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" $\bar{g}(x,u)$ and the "lower growth function" $\underline{g}(x,u)$ as follows

$$\overline{g}(x,u)=\begin{cases} g(x,s(x)), & 0<u<s(x), \\ g(x,u), & u>s(x), \end{cases} \tag{3.8}$$

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

$$\underline{g}(x,u)=\begin{cases} g(x,0), & 0<u<\xi(x), \\ g(x,u), & u>\xi(x), \end{cases} \tag{3.9}$$

where, for $x\in\Omega$, $\xi(x)>s(x)$ satisfies $g(x,\xi(x))=g(x,0)$ (see Fig.3.1). 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 (1.4) 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 3.2).

Theorem 3.5. *Suppose that $g(x,u)$ satisfies (g1)-(g3) and (g4b), and $\overline{g}(x,u)$ and $\underline{g}(x,u)$ are defined as in* (3.8) *and* (3.9). *Let $u(x,t)$ be the solution of* (1.4), *and let $\underline{u}_m(x)$ and $\overline{u}_m(x)$ be the maximal nonnegative steady state solution of* (1.4) *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*

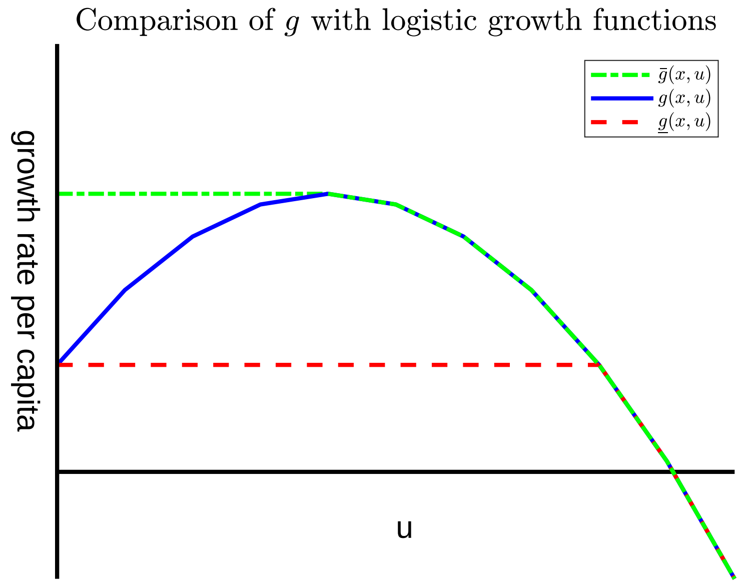

Figure 3.1: The graphs of $g(x,u)$, $\bar{g}(x,u)$ and $\underline{g}(x,u)$ for fixed $x \in \Omega$.

(a) if $0 \leq q < \underline{q}_1$, (1.4) *has at least one positive steady state solution, and*

$$\overline{u}_m(x) \geq \limsup_{t\to\infty} u(x,t) \geq \liminf_{t\to\infty} u(x,t) \geq \underline{u}_m(x) > 0; \tag{3.10}$$

(b) if $q > \overline{q}_1$, (1.4) *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* $q \geq 0$, (1.4) *has a positive steady state solution and* (3.10) *holds.*

Proof. First we consider the open environment case ($b_d > 0$ and $b_u \geq 0$). From Proposition 3.2 part 3(a), for (1.4) 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 (1.4) 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 (1.4) with growth rates $\overline{g}(x,u)$ and $\underline{g}(x,u)$ and same initial condition as in (1.4). From Proposition 3.2, if $0 \leq q < \underline{q}_1$, we obtain (3.10) 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, (1.4) has at leats one positive steady state solution, as $u(x,t)$ converges to a nonnegative steady state from Theorem 3.1, and the steady state is positive from (3.10). 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. □

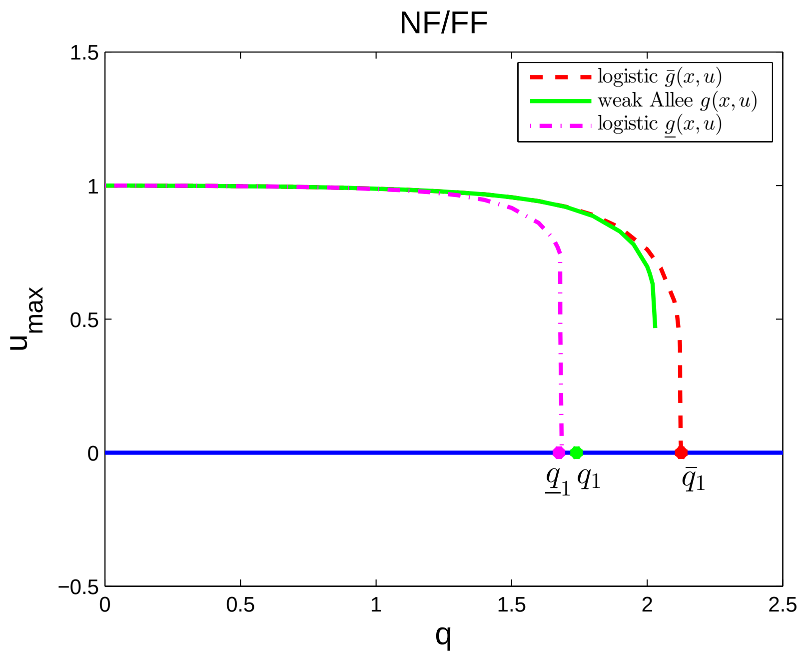

Figure 3.2: Comparison of maximal steady state solutions of (1.4) with growth rates $\overline{g}(x,u)$, $g(x,u) = (1-u)(u+h)$ and $\underline{g}(x,u)$. Here the horizontal axis is the advection rate q, and the vertical axis is the maximum value of the maximal steady state solutions; the parameters used are $d = 4$, $h = 0.3$, $L = 10$, $b_u = 0$ and $b_d = 1$.

Theorem 3.5 shows that the stream population model (1.4) 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 (1.4) in that case. In Fig. 3.2, solutions of (1.4) 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

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

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. Fig. 3.3 shows a comparison of profiles of maximal steady state solutions of three growth rates $\overline{g}(x,u)$, $g(x,u)$ and $\underline{g}(x,u)$.

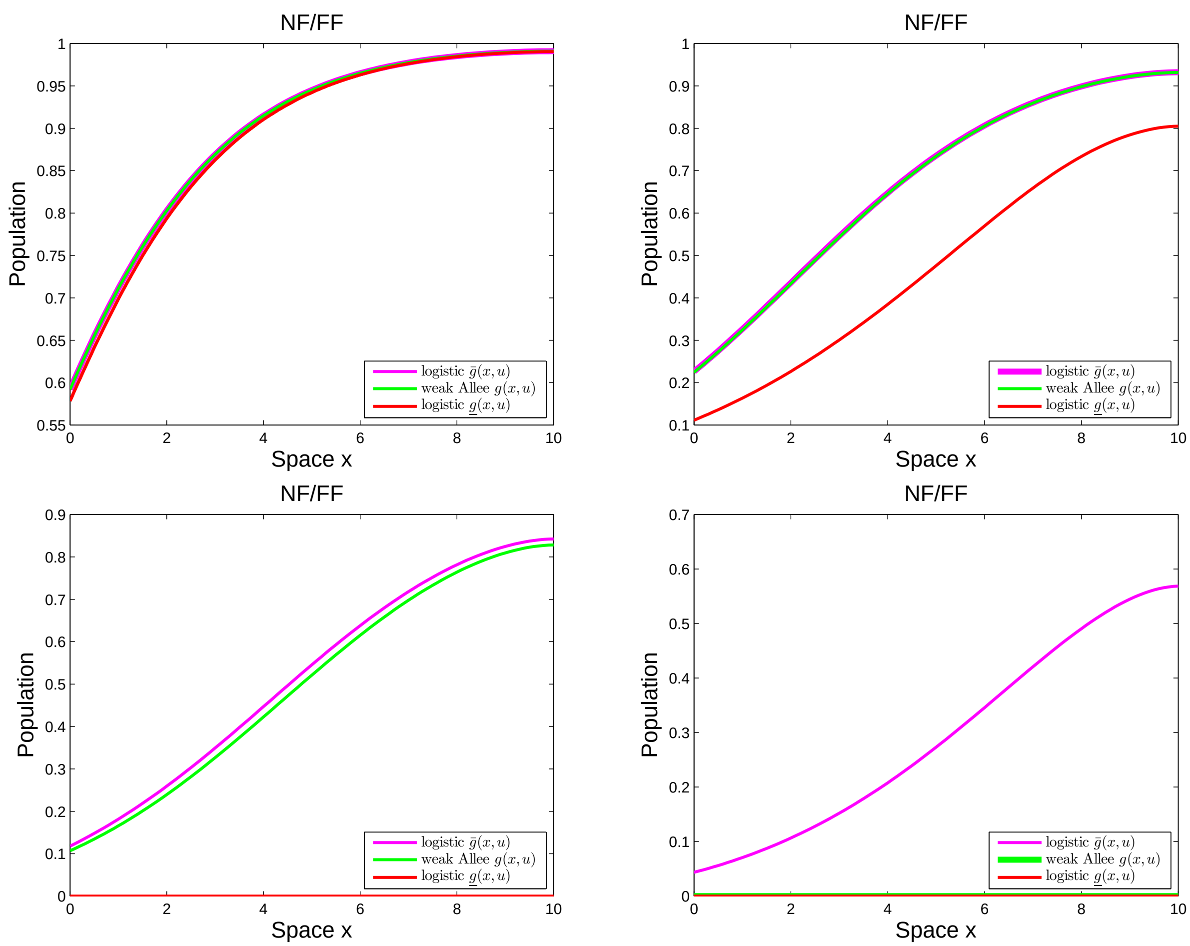

Figure 3.3: Comparison of the maximal steady state solutions to (1.4) of different growth rates. Here $g(x,u) = (r-u)(u+h)$, $r = 1$, $d = 4$, $h = 0.3$, $L = 10$, $b_u = 0$ and $b_d = 1$. Upper left: $q = 0.9$; Upper right: $q = 1.65$; Lower left: $q = 1.9$; Lower right: $q = 2.1$.

3.3.2 Bifurcation: open environment

In this subsection, we consider the structure of the set of positive steady state solutions of (1.4) using the advection rate q as a bifurcation parameter. The steady state equation of system (1.4) is

$$\begin{cases} du_{xx}(x) - qu_x(x) + u(x)g(x,u(x)) = 0, & 0 < x < L, \\ du_x(0) - qu(0) = b_u qu(0), \\ du_x(L) - qu(L) = -b_d qu(L). \end{cases} \tag{3.11}$$

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

$$G(q,u) := \begin{pmatrix} du_{xx} - qu_x + ug(x,u) \\ du_x(0) - (1+b_u)qu(0) \\ du_x(L) - (1-b_d)qu(L) \end{pmatrix}. \tag{3.12}$$

We denote the set of non-negative 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 non-trivial solutions of (1.4) from the zero steady state at some bifurcation point $q = q_1$ which is identified in Proposition 3.2 part 3(a).

Theorem 3.6. *Suppose that $g(x,u)$ satisfies (g1)-(g3) and (g4a) or (g4b), g is twice differentiable in u, $b_u \geq 0$, $b_d \geq \dfrac{1}{2}$, 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* (3.2) *$\lambda_1(q) = 0$. Then*

1. *$q = q_1$ is a bifurcation point for* (3.11) *and there is a connected component Γ_+^1 of the set Γ_+ of positive solutions to* (3.11) *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 (3.2) *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* $\text{Span}\{\phi\}$*;*

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 $s \in (0, \delta)$.*

Proof. We apply a local bifurcation theorem [19, Theorem 1.7] and a global version in [90]. The nonlinear map G defined in (3.12) is differentiable and twice differentiable in u, and $G(q, 0) = 0$ for all $q \geq 0$. At the bifurcation point $(q, u) = (q_1, 0)$,

$$G_u(q_1, 0)[\phi] := \begin{pmatrix} d\phi_{xx} - q_1\phi_x + g(x, 0)\phi \\ d\phi_x(0) - (1 + b_u)q_1\phi(0) \\ d\phi_x(L) - (1 - b_d)q_1\phi(L) \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \\ 0 \end{pmatrix}, \tag{3.13}$$

from Proposition 3.2, $G_u(q_1, 0)$ has a one-dimensional kernel spanned by ϕ as $\lambda_1(q_1) = 0$ is the principal eigenvalue of (3.2), and the codimension of the range of $G_u(q_1, 0)$ is also one from [90]. 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

$$G_u(q_1, 0)[\varphi] := \begin{pmatrix} d\varphi_{xx} - q_1\varphi_x + g(x, 0)\varphi \\ d\varphi_x(0) - (1 + b_u)q_1\varphi(0) \\ d\varphi_x(L) - (1 - b_d)q_1\varphi(L) \end{pmatrix} = \begin{pmatrix} h(x) \\ a \\ b \end{pmatrix}, \tag{3.14}$$

where $(h(x), a, b) \in Y \times \mathbb{R}^2$. Notice that the first equation in (3.13) can be written as

$$d(e^{-\alpha_1 x}\phi_x)_x + g(x, 0)e^{-\alpha_1 x}\phi = 0, \tag{3.15}$$

where $\alpha_1 = \dfrac{q_1}{d}$. Similarly, from (3.14), we have

$$d(e^{-\alpha_1 x}\varphi_x)_x + g(x,0)e^{-\alpha_1 x}\varphi = e^{-\alpha_1 x}h(x). \tag{3.16}$$

Then multiplying (3.15) by φ and (3.16) by ϕ, subtracting each other and integrating from 0 to L, we have

$$-e^{-\alpha_1 L}b\phi(L) + a\phi(0) = -\int_0^L e^{-\alpha_1 x}\phi(x)h(x)dx. \tag{3.17}$$

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

$$l(h(x),a,b) = \int_0^L e^{-\alpha_1 x}\phi(x)h(x)dx + a\phi(0) - e^{-\alpha_1 L}b\phi(L). \tag{3.18}$$

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

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

$$G_{qu}(q_1,0)[\phi] := \begin{pmatrix} -\phi_x \\ -(1+b_u)\phi(0) \\ -(1-b_d)\phi(L) \end{pmatrix}. \tag{3.19}$$

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

$$
\begin{aligned}
l(G_{qu}(q_1,0)[\phi]) =& -\int_0^L e^{-\alpha_1 x}\phi(x)\phi_x(x)dx - (1+b_u)\phi^2(0) + e^{-\alpha_1 L}(1-b_d)\phi^2(L) \\
=& -\frac{1}{2}e^{-\alpha_1 x}\phi^2(x)|_0^L - \int_0^L \frac{\alpha_1}{2}e^{-\alpha_1 x}\phi^2(x)dx - (1+b_u)\phi^2(0) \\
& + e^{-\alpha_1 L}(1-b_d)\phi^2(L) \\
=& -\int_0^L \frac{\alpha_1}{2}e^{-\alpha_1 x}\phi^2(x)dx - (\frac{1}{2}+b_u)\phi^2(0) + e^{-\alpha_1 L}(\frac{1}{2}-b_d)\phi^2(L) \\
<& 0,
\end{aligned}
\tag{3.20}
$$

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

Now from [19, Theorem 1.7], the set of positive solutions of (3.11) 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 Span$\{\phi\}$. Since

$$
G_{uu}(q_1,0)[\varphi_1,\varphi_2] := \begin{pmatrix} 2g_u(x,0)\varphi_1\varphi_2 \\ 0 \\ 0 \end{pmatrix}, \tag{3.21}
$$

where $\varphi_1, \varphi_2 \in X_3$, we also obtain that (see [88])

$$
\begin{aligned}
q'(0) =& -\frac{\langle l, G_{uu}(q_1,0)[\phi,\phi]\rangle}{2\langle l, G_{qu}(q_1,0)[\phi]\rangle} \\
=& \frac{2\int_0^L e^{-\alpha_1 x}g_u(x,0)\phi^3(x)dx}{\alpha_1\int_0^L e^{-\alpha_1 x}\phi^2(x)dx + (2b_u+1)\phi^2(0) + (2b_d-1)e^{-\alpha_1 x}\phi^2(L)}.
\end{aligned}
\tag{3.22}
$$

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 [90, 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 [90, Theorem 4.3, 4.4] can all be verified using standard ways, see [90, 106]. 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 3.5 because 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 non-principal eigenvalue of (3.2) 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 3.1, 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 3.5, we know that there exist a $\overline{q}_1 > 0$ such that positive solutions of system (3.11) only exist when $q < \overline{q}_1$. Therefore $(-\infty, \overline{q}_1) \supset \mathrm{Proj}_q \Gamma_+^1 \supset (-\infty, q_1) \supset [0, q_1)$. □

Remark 3.7. *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 3.5 part 2). Then, no bifurcation occurs from the branch of the trivial steady state solution.*

2. Theorem 3.6 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 $b_d > 0$ ([62, Theorem 2.1]). The bifurcation structure of positive solutions of (3.11) *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 (3.11) can be obtained.

Theorem 3.8. *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 3.6,*

1. *For each $0 \leq q < q_1$, there exists a unique positive solution $u_q(x)$ of (3.11) 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 (1.4) 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 [9, 59]), and the rest parts follow from similar results about logistic type growth functions (see [9]). Figure 3.4 left panel shows a bifurcation diagram in this case.

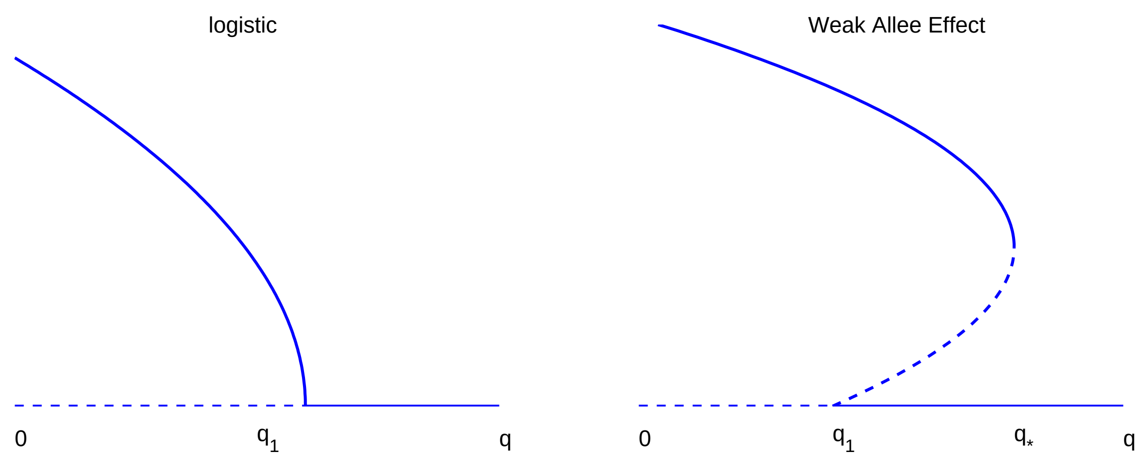

Figure 3.4: Illustrative bifurcation diagrams of nonnegative solutions to (3.11). Left: $g(x,u)$ follows logistic type growth; Right: $g(x,u)$ follows weak Allee effect type growth. Here the horizontal axis is q, and the vertical axis is $||u||_\infty$.

Theorem 3.9. *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 3.6,*

1. *There exists $q_* > q_1 > 0$ such that (3.11) when $q \leq q_*$, (3.11) has a maximal solution $u_m(q,x)$ such that for any positive solution $u(q,x)$ of (3.11), $u_m(q,x) \geq u(q,x)$ for $x \in [0,L]$;*

2. *(3.11) has at least two positive solutions when $q \in (q_1, q_*)$.*

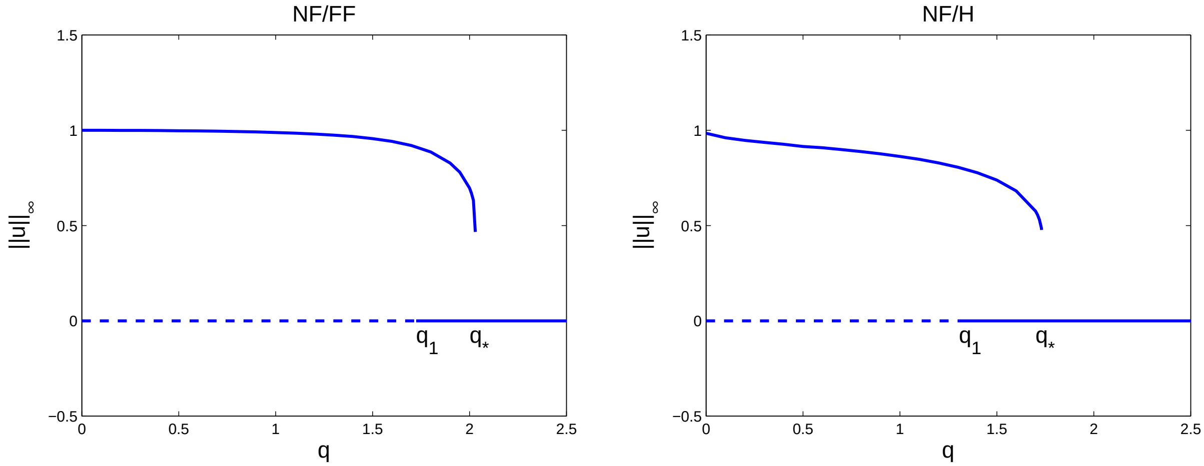

Figure 3.5: Numerical bifurcation diagrams of nonnegative solutions to (3.11) when $g(x, u) = u(1-u)(u+h)$, and only the trivial solutions and maximal solutions are plotted. Left: the NF/FF boundary condition; Right: the NF/H boundary condition. Here $d = 4$, $h = 0.3$ and $L = 10$. Here the horizontal axis is q, and the vertical axis is $||u||_\infty$.

Proof. From Theorem 3.5, we know that there exists a $\overline{q}_1 > 0$, such that (3.11) 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 (3.11), we obtain the following boundary value problem for v:

$$\begin{cases} dv_{xx} + qv_x + vg(x, e^{\alpha x} v) = 0, & 0 < x < L, \\ -dv_x(0) + b_u qv(0) = 0, \\ dv_x(L) + b_d qv(L) = 0. \end{cases} \tag{3.23}$$

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

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

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

$$\begin{cases} d\overline{v}'' + q\overline{v}' + vg(x, e^{\alpha x}\overline{v}) \leq 0, & 0 < x < L, \\ -d\overline{v}'(0) + b_u q\overline{v}(0) \geq 0, \\ d\overline{v}'(L) + b_d q\overline{v}(L) \geq 0, \end{cases} \tag{3.24}$$

which shows that $\overline{v}(x)$ is an upper solution of (3.23) for any $q \geq 0$. For a given $0 \leq q \leq q_*$, if there exists a positive solution $v(x)$ of (3.23), then it satisfies $v(x) \leq \overline{v}(x)$ from Theorem 3.1 part 2. We can set the lower solution of (3.23) to be $\underline{v}(x) = v(x)$. Then there exists a maximal solution $v_m(x)$ of (3.23) satisfying $\underline{v}(x) \leq v_m(x)$. Since $v_m(x)$ is obtained through iteration from $\overline{v}(x)$ and any positive solution v of (3.23) satisfies $v(x) \leq \overline{v}(x)$, then $v_m(x)$ is the maximal solution of (3.23). Hence the maximal solution $v_m(x)$ always exists as long as a positive solution $v(x)$ of (3.23) exists. From Theorem 3.6, under the conditions (g1)-(g3) and (g4b), (3.23) 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 which emerges from the bifurcation point $q = q_1$. Define $q_* = \sup\{q > 0 : \text{there exists a positive solution } (q, u) \in \Gamma_+^1 \text{ of (3.11)}\}$. Then q_* is well-defined and $q_1 < q_* \leq \overline{q}_1$. Because of the continuity of Γ_+^1 and Theorem 3.6, (3.23) (or (3.11)) has a positive solution (q, v) (or (q, u)) for all $q \in [0, q_*)$. Then from above argument, (3.23) has a maximal solution $v_m(q, x)$ for $q \in [0, q_*)$, and consequently (3.11) has a maximal solution $u_m(q, x)$ for $q \in [0, q_*)$.

From Theorem 3.1, the solutions $\{u_m(q, x) : 0 \leq q < q_*\}$ are uniformly bounded, and thus they are also bounded in X_3 from elliptic estimates. By taking a subsequence, we may assume that $u_m(q_*, x) = \lim_{q \to (q^*)^-} u_m(q, x) \geq 0$ exists, and it is a solution of (3.11). 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 (3.11) from the trivial branch Γ_0, but $q = q_1$ is the only bifurcation point where positive solutions of (3.11) can bifurcate from Γ_0. So this is impossible as $q_* > q_1$. Therefore $u_m(q_*, x) > 0$ so (3.11) has a maximal solution $u_m(q, x)$ for $q \in [0, q_*]$. Finally the existence of two positive solutions of (3.11) when $q \in (q_1, q_*)$ follows from the same argument of [89, Theorem 3] but using the energy functional

$$E(u) = \int_0^L e^{-\alpha x} \left[\frac{d}{2}(u')^2 - F(x, u) \right] dx + \frac{q}{2}(1 + b_u)u^2(0) - \frac{q}{2}(1 - b_d)e^{-\alpha L}u^2(L), \tag{3.25}$$

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

Fig 3.4 and Fig. 3.5 show the numerical bifurcation diagrams of maximal solutions for (3.11) under the NF/F 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/F 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 3.9 but a similar proof also holds in that case (see the next subsection).

3.3.3 Hostile boundary conditions

In the boundary condition of (1.4), 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 (1.4) can still be described by Theorem 3.1 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 (3.11) with respect to q follows Fig. 3.5 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 (1.4) with hostile boundary condition becomes

$$\begin{cases} du_{xx}(x) - qu_x(x) + u(x)g(x, u(x)) = 0, & 0 < x < L, \\ u(0) = u(L) = 0. \end{cases} \tag{3.26}$$

Theorem 3.10. *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 3.3.*

1. *If $0 < d < d_1$, there is a connected component Γ_+^1 of the set of positive solutions to* (3.26) *in the space $\mathbb{R}^+ \times X_5$ which connects $(q, u) = (0, u_m)$ and $(q, u) = (q_1, 0)$, where $q_1 > 0$ is the bifurcation point for* (3.26) *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* (3.26) *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 Fig. 3.6 and 3.7 Left)*

2. *If* $d_1 < d < d_*$*, there is a connected component* Γ^1_+ *of the set of positive solutions to* (3.26) *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* (3.26) *when* $q = 0$*, and* u_2 *is another positive solution of* (3.26) *when* $q = 0$*; there exists* $q_* > 0$ *such that* (3.26) *has at least two positive solutions on* Γ^1_+ *for any* $0 \leq q < q_*$*, and one of these two solutions is the maximal solution* $u_m(q, x)$*. (see Fig. 3.6 and 3.7 Right)*

Proof. For the case that $0 < d < d_1$, when $q = 0$, the trivial solution $u = 0$ of (3.26) is unstable and according to Theorem 3.3, (3.4) has a maximal solution u_m. Then we can follow the same proof of Theorems 3.6 and 3.9 to prove that there is a unique bifurcation point $q_1 > 0$ for (3.26) 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 3.6 and 3.9.

For the case that $d_1 < d < d_*$, when $q = 0$, the trivial solution $u = 0$ of (3.26) is stable. From Theorem 3.3, (3.4) 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 (3.26) in $\mathbb{R}^+ \times X_3$ containing $(0, u_m)$. Then from [111, 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 $u_2 \neq u_m$, or (iii) $\Gamma^1_+ \cap \partial(\mathbb{R}^+ \times X_5) \neq \emptyset$ 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 3.5, Γ^1_+ is bounded hence (i) is also not possible. Therefore, Γ^1_+ contains another $(0, u_2) \in \{0\} \times X_5$ with $u_2 \neq u_m$. Other parts can also be obtained using the same proof as the ones of Theorems 3.6 and 3.9. □

Fig. 3.6 and Fig. 3.7 show the numerical bifurcation diagrams of maximal steady state solutions for (3.26) in the cases of $0 < d < d_1$ and $d_1 < d < d_*$.

Remark 3.11. *1. The results in Theorem 3.10 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 Fig. 3.6 and 3.7. As shown in Theorem 3.9, the*

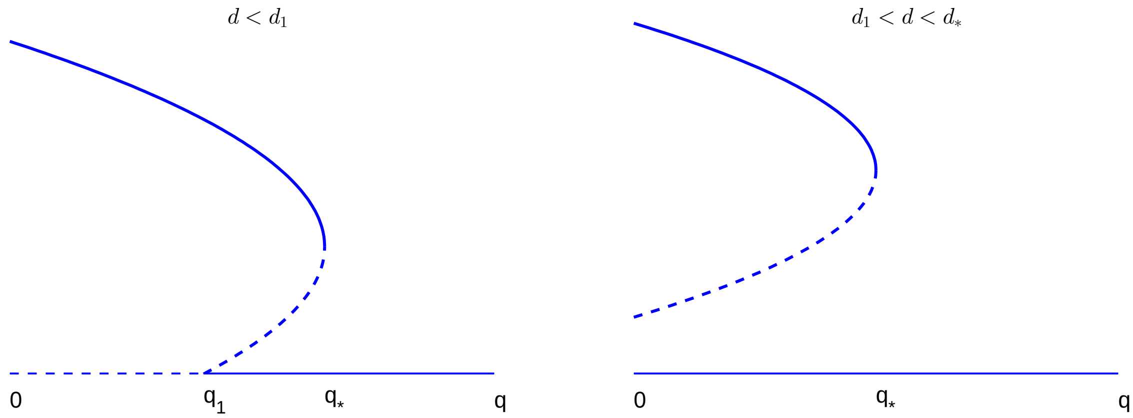

Figure 3.6: Illustrative bifurcation diagrams of nonnegative solutions to (3.26). Left: $0 < d < d_1$; Right: $d_1 < d < d_*$. Here the horizontal axis is q, and the vertical axis is $||u||_\infty$.

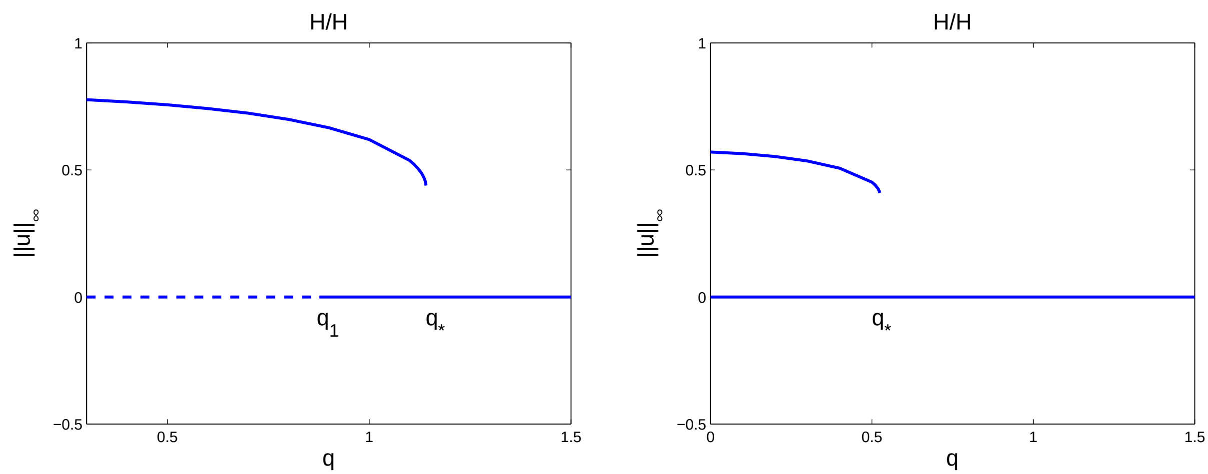

Figure 3.7: Numerical bifurcation diagrams of nonnegative solutions to (3.26) when $g(x,u) = u(1-u)(u+h)$, and only the trivial solutions and maximal solutions are plotted. Here $h = 0.3$, $L = 10$, the horizontal axis is q, and the vertical axis is $||u||_\infty$. Left: $d = 3$; Right: $d = 4$.

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 3.3), (3.26) has no positive solutions when $q = 0$ from Theorem 3.3. But it is not known whether (3.26) 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 3.9 or 3.10 is the largest advection rate for the existence of positive steady states of (1.4) 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 Fig. 3.5 and 3.7 show that the set of positive solutions of* (3.11) *or* (3.26) *is connected.*

Finally we compare the effect of different boundary conditions on the dynamics of (1.4). 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 3.9 and 3.10 identify two critical advection rates q_1 and q_* which separate the ranges of advection rates of these three dynamical regimes: when $0 \leq q \leq q_1$, 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 which 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 Fig. 3.8, we compare bifurcation points q_1, q_* and maximal solutions $u_m(q, x)$ of (1.4) for $0 \leq q \leq q_*$ 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 $q \geq 0$ and there are no bifurcation points. One can observe from Fig. 3.8 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.

In Fig. 3.9, the parameter regions for the three dynamical behavior (monostable, bistable and extinction) are plotted in the (d, q)-plane. For the boundary conditions that has 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

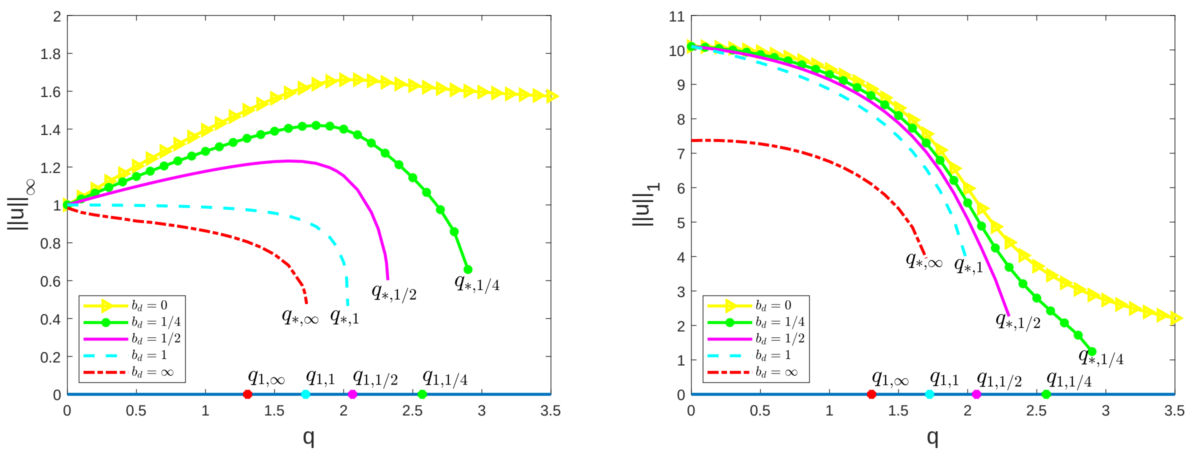

Figure 3.8: Comparison of bifurcation points q_1, q_* and maximal steady state solutions of (1.4) under different boundary conditions. Here $g(x,u) = (r-u)(u+h)$, $r = 1$, $h = 0.3$, $b_u = 0$ (NF boundary condition on the upstream end), $d = 4$, $L = 10$, and the horizontal axis is q. Left: comparison of $||u||_\infty$; Right: comparison of $||u||_1$.

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 3.9, but the behavior is similar to the one for $b_d > 0.5$. For the boundary conditions that has NF on the upstream end and $b_d = 2$, the bifurcation curves $q_1(d)$ and $q_*(d)$ are not monotone increasing but has 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 3.3. The vanishing of the bifurcation point $q_1(d)$ and $q_*(d)$ under hostile boundary condition is shown in Theorem 3.10. When $0 < d < d_1$, the dynamics changes as "monostable-bistable-extinction" as q increases across q_1 and q_* (see Fig. 3.6 left), and when $d_1 < d < d_*$, it changes to "bistable-extinction" (see Fig. 3.6 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 Fig. 3.9 lower panel).

Note that for the logistic growth case, it is known that the dynamics changes in the sequence "extinction-monostable-extinction" [59, 93], and it was concluded that intermediate diffusion coefficient is favourable for the persistence. Here we get similar conclusion for weak Allee effect type growth rate, but there are bistable regime between the transition from extinction to persistence.

3.4 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 [9, 53, 59, 70]. 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 chapter, 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 is 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 favourable for population persistence even when the growth rate has a weak Allee effect. This extends the previous explanation of the "drift paradox" in [64, 78, 93] to the weak Allee effect growth case but with an additional possibility of bistable dynamics in two windows of diffusion coefficients.

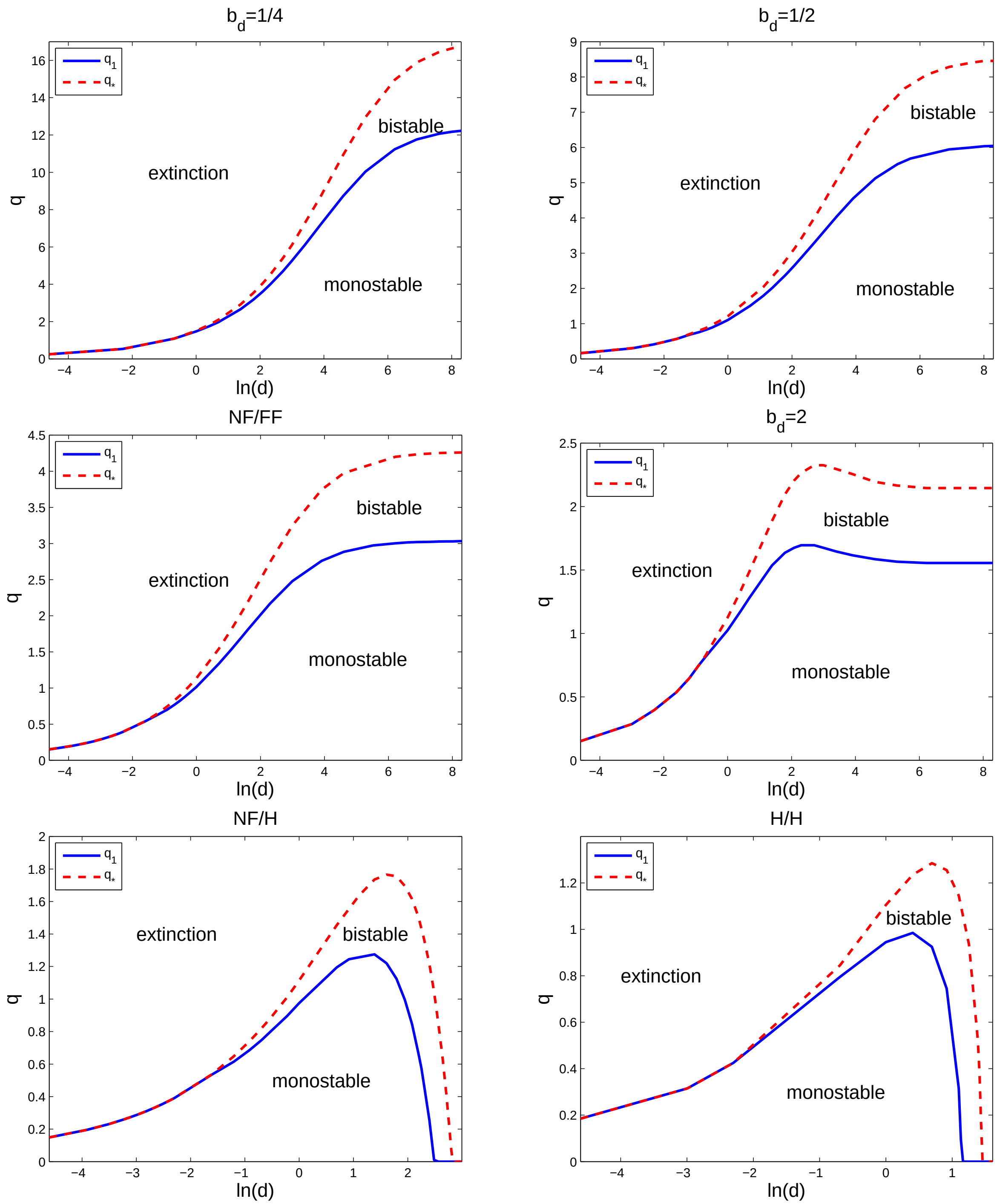

Figure 3.9: Population dynamical behavior of (1.4) for varying advection rate q and diffusion coefficient d. Here $g(x,u) = (r-u)(u+h)$, $r = 1$, $h = 0.3$, $d = 4$, and $L = 10$. In each graph, the horizontal axis is d in log scale, and the vertical axis is q. In all except lower right, $b_u = 0$ (NF). 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).

Chapter 4

Benthic-drift model with strong Allee effect

4.1 Introduction

In this chapter, we investigate how interactions between the benthic zone and the drift zone affect the population dynamics of a benthic-drift model, when the species follows a strong Allee effect population growth in the benthic zone. Our main findings on the dynamics of benthic-drift model with strong Allee effect type growth in the benthic population are

1. If the benthic population release rate is large, then for all the boundary conditions, extinction will always occur regardless of the initial conditions, the diffusive and advective movement and the transfer rate from the drift zone to the benthic zone;

2. If the benthic population release rate is small (but not zero), then for all the boundary conditions, the population persists for large initial conditions and becomes extinct for small initial conditions. Such a bistability in the system exists also independent of the diffusive and advective movement and the transfer rate from the drift zone to the benthic zone;

3. If the benthic population release rate is in the intermediate range, the persistence or

extinction depends on the diffusive and advective movement. It is shown that for the closed environment, the population can persist under small advection rate and large initial condition.

These results are rigorously proved by using the theory of dynamical systems, partial differential equations, upper-lower solution methods, and numerical simulations are also included to verify or demonstrate theoretical results. Compared with the single compartment reaction-diffusion-advection equation with a strong Allee effect growth rate [108], in which the advection rate q plays an important role in the persistence/extinction dynamics, the benthic-drift model dynamics with strong Allee effect relies more critically on the strength of interacting between zones.

The dynamic behavior of the single compartment reaction-diffusion-advection equation modeling a stream population with a strong Allee effect growth rate was investigated in [108]. 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. Corresponding dynamic behavior for weak Allee effect growth rate has been considered in [107].

The benthic-drift model has the feature of a coupled partial differential equation (PDE) for the drift population and an "ordinary differential equation" (ODE) for the benthic population. Note that the benthic population equation is not really an ODE but an ODE at each point of the spatial domain, or a reaction-diffusion equation with zero diffusion coefficient. Such degeneracy causes a noncompactness of the solution orbits in the function space, which brings an extra difficulty in analyzing the dynamics. Such PDE-ODE coupled systems have been also studied in the case of population that has a quiescent phase [109], or some species are immobile [68, 101].

In Section 1.1.3, the benthic-drift model of stream population is established, and all model parameters and growth rate conditions are set up in a general setting. Some preliminary results are stated and proved in Section 4.2: the basic dynamics, global attractor, and linear stability problem. The main results on the population persistence and extinction are proved in Section 4.3, and some numerical simulations are shown in Section 4.4 to provide some more quantitative information of the dynamics. A few concluding remarks are in Section 4.5.

4.2 Basic properties of solutions

This section is devoted to establishing some basic properties of (1.13). Throughout the paper, we assume that the functions $A_b(x)$ and $A_d(x)$ and parameters satisfy the following conditions:

(A1) $A_b(x), A_d(x) \in C[0, L]$, $A_b(x) > 0$ and $A_d(x) > 0$ on $x \in [0, L]$.

(A2) $d > 0$, $q \geq 0$, $\mu > 0$, $\sigma > 0$, $m_1 \geq 0$ and $m_2 \geq 0$.

The boundary conditions for the drift population in (1.13) is given in a flux form following [59, 108] (see also [37] for slightly different setting). Here the parameters $b_u \geq 0$ and $b_d \geq 0$ determine the magnitude of population loss at the upstream end $x = 0$ and the downstream end $x = L$, respectively. At the boundary ends $x = 0$ and $x = L$, if $b_u = 0$ and $b_d = 0$, that is the no-flux (NF) boundary condition $du_x(x, t) - qu(x, t) = 0$, for instance, can be effectively used to study the sinking, self-shading phytoplankton model (see, e.g., [34, 38]); $b_d = 1$ gives the free-flow (FF) boundary condition $u_x(x, t) = 0$, referred as the Danckwerts condition, can be applied to the situation like stream to lake (see [98]); and when b_d becomes sufficiently large, i.e. $b_d \to \infty$, we have the hostile (H) boundary condition $u(x, t) = 0$, which can be used in the scenario of stream to ocean (see [93]).

For later applications, we also define

$$
\begin{aligned}
g_{max} &= \max_{x\in[0,L]} g(x,s(x)) = \max_{x\in[0,L]} \max_{v\geq 0} g(x,v),\\
g_{min} &= \min_{x\in[0,L]} g(x,s(x)) = \min_{x\in[0,L]} \max_{v\geq 0} g(x,v).
\end{aligned}
\tag{4.1}
$$

The growth rate of the population is $f(x,v) = vg(x,v)$, and we also define

$$
\overline{f_v} = \max_{x\in[0,L]} \max_{v\geq 0} f_v(x,v). \tag{4.2}
$$

One can observe that $g_{max} \leq \overline{f_v}$ as $\max_{v\geq 0} f_v(x,v) = \max_{v\geq 0}(g + vg_v) \geq g(x,s(x)) + s(x)g_v(x,s(x)) = g(x,s(x)) = \max_{v\geq 0} g(x,v)$ for $x \in [0,L]$.

In the following we will study the dynamics of system (1.13) under the conditions (A1)-(A2), (g1)-(g3) and (g4c) (strong Allee effect growth). In particular, we are interested in the existence, multiplictity and stability of non-negative steady state solutions $(u(x), v(x))$ which satisfy the following steady state system:

$$
\begin{cases}
du_{xx} - qu_x + \dfrac{A_b(x)}{A_d(x)}\mu v - \sigma u - m_1 u = 0, & 0 < x < L,\\
vg(x,v) - m_2 v - \mu v + \dfrac{A_d(x)}{A_b(x)}\sigma u = 0, & 0 \leq x \leq L,\\
du_x(0) - qu(0) = b_u q u(0), & \\
du_x(L) - qu(L) = -b_d q u(L). &
\end{cases}
\tag{4.3}
$$

4.2.1 The well-posedness

We first study the well-posedness of the initial-boundary-value problem (1.13). Using the transform $u = e^{\alpha x} w, v = e^{\alpha x} z$ on the system (1.13), where $\alpha = \dfrac{q}{d}$, we obtain the following system of new variables (w, z):

$$\begin{cases} w_t = dw_{xx} + qw_x + \dfrac{A_b(x)}{A_d(x)}\mu z - \sigma w - m_1 w, & 0 < x < L,\ t > 0, \\ z_t = zg(x, e^{\alpha x} z) - m_2 z - \mu z + \dfrac{A_d(x)}{A_b(x)}\sigma w, & 0 \le x \le L,\ t > 0, \\ -dw_x(0,t) + b_u q w(0,t) = 0, & t > 0, \\ dw_x(L,t) + b_d q w(L,t) = 0, & t > 0, \\ w(x,0) = e^{-\alpha x} u_0(x) := w_0(x) \ge 0, & x \in (0, L), \\ z(x,0) = e^{-\alpha x} v_0(x) := z_0(x) \ge 0, & x \in (0, L), \end{cases} \tag{4.4}$$

The boundary conditions of system (4.4) are either no-flux ($b_u = b_d = 0$), hostile ($b_u, b_d \to \infty$) or Robin ($b_u, b_d > 0$) types. With $b_u \ge 0$ and $b_d \ge 0$, we have the following settings following similar ones in [36, 37]. Let $X = C([0, L], \mathbb{R})$ be the Banach space with the usual supremum norm $\|u\|_\infty = \max\limits_{x \in [0,L]} |u(x)|$ for $u \in X$. Then the set of non-negative functions forms a solid cone X_+ in the Banach space X. Suppose that $T_1(t)$ is the C_0 semi-group associated with the following linear initial value problem

$$\begin{cases} w_t = dw_{xx} + qw_x - m_1 w, & 0 < x < L,\ t > 0, \\ -dw_x(0,t) + b_u q w(0,t) = 0, & t > 0, \\ dw_x(L,t) + b_d q w(L,t) = 0, & t > 0, \\ w(x,0) = w_0(x) \ge 0, & x \in (0, L). \end{cases} \tag{4.5}$$

From [91, Chapter 7], it follows that the solution of (4.5) is given by $w(x,t) = T_1(t) w_0$ and $T_1(t) : X \to X$ is compact, strongly positive and analytic for any $t > 0$. We also define

$$(T_2(t)\varphi)(x) = e^{-m_2 t}\varphi,$$

for any $\varphi \in X$, $t \geq 0$. Then $T(t) := (T_1(t), T_2(t)) : X \times X \to X \times X$, $t \geq 0$, defines a C_0 semigroup. Define the nonlinear operator $B = (B_1, B_2) : X_+ \times X_+ \to X \times X$ by

$$\begin{aligned} B_1(\phi)(x) &= \frac{A_b(x)\mu}{A_d(x)}\phi_2 - \sigma\phi_1, \\ B_2(\phi)(x) &= \phi_2 g(x, e^{\alpha x}\phi_2) + \frac{A_d(x)\sigma}{A_b(x)}\phi_1 - \mu\phi_2, \end{aligned} \tag{4.6}$$

for $x \in [0, L]$ and $\phi = (\phi_1, \phi_2) \in X_+ \times X_+$. Then system (4.4) can be rewritten as the following integral equation

$$U(t) = T(t)\phi + \int_0^t T(t-s)B(U(s))ds, \tag{4.7}$$

where $U(t) = (w(t), z(t))$ and $\phi = (\phi_1, \phi_2) \in X_+ \times X_+$. By [69, Theorem 1 and Remark 1.1], it follows that for any $(w_0, z_0) \in X_+ \times X_+$, system (4.4) has a unique non-negative mild solution $(w(x, t; w_0, z_0), z(x, t; w_0, z_0))$ with initial condition (w_0, z_0). Moreover, $(w(x, t; w_0, z_0), z(x, t; w_0, z_0))$ is a classical solution of system (4.4) for $t > 0$. Then, we can have the local existence and positivity of solutions of system (4.4) and (1.13).

Lemma 4.1. *Suppose that $A_b(x)$ and $A_d(x)$ and parameters satisfy (A1)-(A2), $g(x, u)$ satisfies (g1)-(g2), then system* (1.13) *has a unique solution for any initial value in $X_+ \times X_+$ and the solutions to* (1.13) *remain non-negative on their interval of existence.*

Next we discuss the global existence of the solutions of system (1.13). To achieve that, we start with the boundedness of the steady state solutions of system (1.13).

Proposition 4.2. *Suppose that $g(x, u)$ satisfies (g1)-(g2) and $r(x)$ is defined in (g2). Let $(u(x), v(x))$ be a positive steady state solution of system* (1.13)*, then for $x \in [0, L]$,*

$$u(x) \leq e^{\alpha x} M \overline{\theta}_1, \quad v(x) \leq e^{\alpha x} M \max\{1, \overline{\theta}_1 \overline{\theta}_2\}, \tag{4.8}$$

where

$$M = \max_{y \in [0, L]} r(y), \quad \alpha = \frac{q}{d}, \tag{4.9}$$

and

$$\bar{\theta}_1 = \max_{y\in[0,L]} \frac{A_b(y)}{A_d(y)} \frac{\mu}{\sigma + m_1}, \quad \bar{\theta}_2 = \max_{y\in[0,L]} \frac{A_d(y)}{A_b(y)} \frac{\sigma}{\mu + m_2}. \tag{4.10}$$

Proof. Using the transform $u = e^{\alpha x}w$ and $v = e^{\alpha x}z$ on system (4.3), we obtain the following system

$$\begin{cases} dw_{xx} + qw_x + \dfrac{A_b(x)}{A_d(x)}\mu z - \sigma w - m_1 w = 0, & 0 < x < L, \\ zg(x, e^{\alpha x}z) - m_2 z - \mu z + \dfrac{A_d(x)}{A_b(x)}\sigma w = 0, & 0 \le x \le L, \\ -dw_x(0) + b_u q w(0) = 0, \\ dw_x(L) + b_d q w(L) = 0. \end{cases} \tag{4.11}$$

Multiplying the second equation of (4.11) by $\dfrac{A_b(x)}{A_d(x)}$ and adding to the first equation of (4.11), we have

$$dw_{xx} + qw_x - m_1 w + \frac{A_b(x)}{A_d(x)} zg(x, e^{\alpha x}z) - \frac{A_b(x)}{A_d(x)} m_2 z = 0. \tag{4.12}$$

Let $w(x_0) = \max_{x\in[0,L]} w(x)$ for $x_0 \in [0, L]$. If $x_0 \in (0, L)$, then $w_{xx}(x_0) \le 0$ and $w_x(x_0) = 0$. Consequently, from (4.12)

$$\frac{A_b(x_0)}{A_d(x_0)} z(x_0) g(x, e^{\alpha x} z(x_0)) > 0. \tag{4.13}$$

Now from (g2) and $z(x_0) > 0$, $e^{\alpha x_0} z(x_0) < r(x_0)$, which implies that $z(x_0) < M_0$, where $M_0 = \max_{y\in[0,L]} e^{-\alpha y} r(y) \le M$. Using the first equation of system (4.11), and the fact that $w_{xx}(x_0) \le 0$, $w_x(x_0) = 0$, we have that for $x \in [0, L]$,

$$\max_{y\in[0,L]} \frac{A_b(y)}{A_d(y)} \mu M \ge \frac{A_b(x_0)}{A_d(x_0)} \mu z(x_0) > (\sigma + m_1) w(x_0) \ge (\sigma + m_1) w(x),$$

which implies the estimate for $u(x)$ in (4.8).

Now for the bound of $z(x)$, if $e^{\alpha x} z(x) \le M$, then we can obtain $z(x) \le Me^{-\alpha x} \le M$; or if $e^{\alpha x} z(x) > M$, from which we have $g(x, e^{\alpha x} z(x)) \le 0$. Then from the second equation of system (4.11), we know that

$$(\mu + m_2)z(x) \le [\mu + m_2 - g(x, e^{\alpha x} z(x))]z(x) = \frac{A_d(x)}{A_b(x)} \sigma w(x),$$

which implies that $z(x) \le \overline{\theta}_1 \overline{\theta}_2 M$ where $\overline{\theta}_1, \overline{\theta}_2$ are defined in (4.10). Combining the two cases, we obtain the estimate for $u(x)$ in (4.8). □

Now we have the following result on the global dynamics of (1.13).

Theorem 4.3. *Suppose that $g(x, u)$ satisfies (g1)-(g2), then* (1.13) *has a unique positive solution $(u(x,t), v(x,t))$ defined on $t \in [0, \infty)$, and the solutions of* (1.13) *generates a dynamical system in X_1, where*

$$\begin{aligned} X_1 = \{(\phi, \psi) \in W^{2,2}(0, L) \times C(0, L) :\ & \phi(x) \ge 0, \psi(x) \ge 0, \\ d\phi'(0) - q\phi(0) = b_u q\phi(0),\ \ & d\phi'(L) - q\phi(L) = -b_d q\phi(L)\}. \end{aligned} \tag{4.14}$$

Furthermore, (1.13) *is a point dissipative system.*

Proof. We consider the equivalent system (4.4) of (1.13). Assume that $(u(x,t), v(x,t))$ is a solution of system (1.13), then $(w(x,t), z(x,t))$ is a solution of system (4.4). We choose

$$M_1 = \max\left\{ M \max\{1, \overline{\theta}_1, \overline{\theta}_1\overline{\theta}_2\}, \max_{y\in[0,L]} e^{-\alpha y} u_0(y), \max_{y\in[0,L]} e^{-\alpha y} v_0(y) \right\}, \tag{4.15}$$

where $\overline{\theta}_1, \overline{\theta}_2$ are defined in (4.10). Then (M_1, M_1) is an upper solution of (4.4) and $(0, 0)$ is a lower solution of (4.4). According to [80, Theorem 4.1], we obtain that

$$0 \le w(x,t) \le w_1(x,t), \qquad 0 \le z(x,t) \le z_1(x,t),$$

where $(w_1(x,t), z_1(x,t))$ is the solution of (4.4) with initial condition $w_1(x, 0) = M_1$ and $z_1(x, 0) = M_1$. Moreover the solution $(w_1(x,t), z_1(x,t))$ is non-increasing in t and $\lim_{t\to+\infty}(w_1(x,t), z_1(x,t)) = (w_{max}(x), z_{max}(x))$ which is maximum steady state of (4.4) not larger than (M_1, M_1). From Proposition 4.2, we obtain that $(u(x,t), v(x,t))$ exists globally for $t \in (0, \infty)$, stays positive and

$$\limsup_{t\to\infty} u(x,t) \le e^{\alpha x} M\overline{\theta}_1, \quad \limsup_{t\to\infty} v(x,t) \le e^{\alpha x} M \max\{1, \overline{\theta}_1\overline{\theta}_2\}. \tag{4.16}$$

□

4.2.2 Global attractor

From Proposition 4.3, it follows that solutions of system (1.13) are uniformly bounded. Thus, we can define a solution semiflow of (1.13) on $X_+ \times X_+$ by

$$\Sigma(t)\phi = \begin{pmatrix} u(t,\cdot,\phi_1(x)) \\ v(t,\cdot,\phi_2(x)) \end{pmatrix} \qquad \forall \phi = (\phi_1,\phi_2) \in X_+ \times X_+, \ \ t \ge 0. \tag{4.17}$$

$\Sigma(t)\phi$ is the solution of (1.13) with initial condition (ϕ_1, ϕ_2) and $\Sigma(t)$ is a positive semigroup for all $t \ge 0$. Notice that $\Sigma(t)$ is not compact since the second equation in (1.13) has no diffusion term. Due to the lack of compactness, we need to impose the following condition

$$\overline{f_v} < m_2 + \mu, \tag{4.18}$$

where $\overline{f_v}$ is defined in (4.2), and recall that $f(x,v) = vg(x,v)$. Recall that the Kuratowski measure of noncompactness (see [105, Chapter 1]), which is defined by the formula

$$\alpha(K) := \inf\{r : K \ \text{ has a finite cover of diameter} < r\}, \tag{4.19}$$

on any bounded set $K \subset X_+$. And the diameter of the set is defined by the relation $\mathrm{diam}K = \sup\{dist(x,y) : x,y \in K\}$. We set $\alpha(K) = \infty$ whenever K is bounded. From the definition of α-contracting, we know that $\alpha(K) \le \mathrm{diam}K$, $\alpha(K) = 0$ if and only if the closure $\overline{K}$ of K is compact and the set K is bounded if and only if $\alpha(K) < \infty$.

Lemma 4.4. *Suppose that $g(x,u)$ satisfies (g1)-(g2) and* (4.18)*, then $\Sigma(t)$ is α-contracting* *in the sense that*

$$\lim_{t\to\infty} \alpha(\Sigma(t)K) = 0, \tag{4.20}$$

for any bounded set $K \subset X_+$.

Proof. The right hand side of the v-equation in (1.13) is represented by

$$H(u,v) = vg(x,v) - m_2 v - \mu v + \frac{A_d(x)}{A_b(x)}\sigma u. \tag{4.21}$$

Then from (4.18), there exists a real number $r > 0$ satisfies

$$\frac{\partial H(u,v)}{\partial v} = f_v(x,v) - m_2 - \mu < -r < 0. \tag{4.22}$$

With this inequality, the rest of the proof is similar to the one in Lemmas 3.2 and 4.1 in [35]. □

Now we are ready to show that solutions of system (1.13) converge to a compact attractor on $X_+ \times X_+$ when $t \to \infty$ under the condition (4.18).

Theorem 4.5. *Suppose that $g(x,u)$ satisfies (g1)-(g2), then $\Sigma(t)$ admits a global attractor on $X_+ \times X_+$ provided that* (4.18) *holds.*

Proof. From Lemma 4.4 and Theorem 4.3, it follows that $\Sigma(t)$ is α-contracting on X_+ and system (1.13) is point dissipative. By Proposition 4.2, we also know that the positive orbits of bounded subsets of X_+ for $\Sigma(t)$ are uniformly bounded. Then according to [67, Theorem 2.6], $\Sigma(t)$ has a global attractor that attracts every bounded set in X_+. □

From the discussion above, we can obtain the convergence of the solutions to equilibria of system (1.13) by constructing a Lyapunov function.

Theorem 4.6. *Suppose that $g(x,u)$ satisfies (g1)-(g2) and* (4.18)*, then for any $(u_0, v_0) \in X_1$ and $u_0 \not\equiv 0$, $v_0 \not\equiv 0$, the ω-limit set $\omega((u_0,v_0)) \subset S$, where S is the set of non-negative steady state solutions of* (1.13).

Proof. We prove that the solution $(u(x,t), v(x,t))$ is always convergent. For that purpose, we define a function

$$\begin{aligned}E(u,v) =& \int_0^L e^{-\alpha x}\left[\frac{d}{2}(u_x)^2 - \frac{A_b(x)}{A_d(x)}\mu uv + \frac{\sigma+m_1}{2}u^2\right]dx \\ &- \frac{\mu}{\sigma}\int_0^L e^{-\alpha x}\frac{A_b^2(x)}{A_d^2(x)}\left[F(x,v) - \frac{\mu+m_2}{2}v^2\right]dx + \frac{q}{2}(1+b_u)u^2(0,t) \\ &- \frac{q}{2}(1-b_d)e^{-\alpha L}u^2(L,t),\end{aligned} \tag{4.23}$$

for $(u,v)\in X_1$, where $F(x,v) = \displaystyle\int_0^v f(x,s)ds$. Assume that $(u(x,t), v(x,t))$ is a solution of system (1.13), we have

$$\begin{aligned}\frac{d}{dt}E(u(\cdot,t),v(\cdot,t)) =& \int_0^L e^{-\alpha x}(du_xu_{xt} - \frac{A_b(x)}{A_d(x)}\mu(u_tv+uv_t) + (\sigma+m_1)uu_t)dx \\ &- \frac{\mu}{\sigma}\int_0^L e^{-\alpha x}\frac{A_b^2(x)}{A_d^2(x)}(fv_t - (\mu+m_2)vv_t)dx \\ &+ q(1+b_u)u(0,t)u_t(0,t) - q(1-b_d)e^{-\alpha L}u(L,t)u_t(L,t) \\ =&[de^{-\alpha x}u_xu_t]\,|_0^L + q(1+b_u)u(0,t)u_t(0,t) \\ &- q(1-b_d)e^{-\alpha L}u(L,t)u_t(L,t) - \int_0^L (de^{-\alpha x}u_x)_xu_tdx \\ &- \int_0^L e^{-\alpha x}(\frac{A_b(x)}{A_d(x)}\mu(u_tv+uv_t) - (\sigma+m_1)uu_tdx \\ &- \frac{\mu}{\sigma}\int_0^L e^{-\alpha x}\frac{A_b^2(x)}{A_d^2(x)}(fv_t - (\mu+m_2)vv_t)dx \\ =&-\int_0^L e^{-\alpha x}u_t(du_{xx} - qu_x + \frac{A_b(x)}{A_d(x)}\mu v - \sigma u - m_1u)dx \\ &- \int_0^L e^{-\alpha x}v_t\frac{\mu A_b^2(x)}{\sigma A_d^2(x)}(f + \frac{A_d(x)}{A_b(x)}\sigma u - \mu v - m_2v)dx \\ =&-\int_0^L e^{-\alpha x}(u_t)^2dx - \frac{\mu}{\sigma}\int_0^L e^{-\alpha x}\frac{A_b^2(x)}{A_d^2(x)}(v_t)^2dx \\ \le&0.\end{aligned}$$

According to (g2), we have $F(x,v)\le F(x,r(x))$ and $r(x)\le M$. Hence when $t>T$ for some

$T > 0$ large, from (4.16),

$$
\begin{aligned}
&E(u(\cdot,t),v(\cdot,t)) \\
\geq& -\mu\int_0^L e^{-\alpha x}\frac{A_b(x)}{A_d(x)}uvdx - \frac{\mu}{\sigma}\int_0^L e^{-\alpha x}\frac{A_b^2(x)}{A_d^2(x)}F(x,r(x))dx - \frac{q}{2}e^{-\alpha L}u^2(L,t) \\
\geq& -\max_{y\in[0,L]}\frac{\mu A_b(x)}{A_d(x)}e^{2\alpha L}M^2L\overline{\theta}_1\max\{1,\overline{\theta}_1\overline{\theta}_2\} - \max_{y\in[0,L]}\frac{\mu A_b^2(x)}{\sigma A_d^2(x)}M_2L - \frac{qM^2\overline{\theta}_1^2}{2}e^{\alpha L},
\end{aligned}
$$

where $M_2 = \max_{y\in[0,L]} F(y,r(y))$. Therefore $E(u(\cdot,t),v(\cdot,t))$ is bounded from below. Notice $\frac{d}{dt}E(u,v) = 0$ holds if and only if $u_t = 0$ and $v_t = 0$, which also means that (u,v) is a steady state solution of system (1.13). From Lemma 4.4, the solutions of orbits or (1.13) are pre-compact, then from the LaSalle's Invariance Principle [33, Theorem 4.3.4], we have that for any initial condition $u_0(x) \geq 0$ and $v_0(x) \geq 0$, the ω-limit set of (u_0,v_0) is contained in the largest invariant subset of S. If every element in S is isolated, then the ω-limit set is a single steady state. □

4.2.3 Eigenvalue problem

We consider the eigenvalue problem of system (1.13). Suppose that (u^*,v^*) is a non-negative steady state solution of system (1.13). Substituting $u = e^{\lambda t}\phi_1$ and $v = e^{\lambda t}\phi_2$, where $\phi = (\phi_1,\phi_2) \in X_1$, into system (1.13), we get the following associated eigenvalue problem:

$$
\begin{cases}
\lambda\phi_1 = d(\phi_1)_{xx} - q(\phi_1)_x + \dfrac{A_b(x)}{A_d(x)}\mu\phi_2 - \sigma\phi_1 - m_1\phi_1, & 0 < x < L, \\
\lambda\phi_2 = f_v(x,v^*)\phi_2 - m_2\phi_2 - \mu\phi_2 + \dfrac{A_d(x)}{A_b(x)}\sigma\phi_1, & 0 \leq x \leq L, \\
d(\phi_1)_x(0) - q\phi_1(0) = b_u q\phi_1(0), \\
d(\phi_1)_x(L) - q\phi_1(L) = -b_d q\phi_1(L),
\end{cases}
\tag{4.24}
$$

where $f_v(x,v^*) = g(x,v^*) + v^* g_v(x,v^*)$. Let $Y = C([0,L]) \times C([0,L])$ and denote the linearized operator $\mathcal{L} : X_1 \to Y$ of system (4.3) by

$$\mathcal{L} = \begin{pmatrix} d\dfrac{\partial^2}{\partial x^2} - q\dfrac{\partial}{\partial x} \\ 0 \end{pmatrix} + \begin{pmatrix} -\sigma - m_1 & \dfrac{A_b(x)\mu}{A_d(x)} \\ \dfrac{A_d(x)\sigma}{A_b(x)} & f_v(x,v^*) - \mu - m_2 \end{pmatrix}. \tag{4.25}$$

The following proposition provides the information of the spectral set $\sigma(\mathcal{L})$ of the linearized operator $\mathcal{L}$, especially the principal eigenvalue of (4.24).

Proposition 4.7. *Suppose that $g(x,u)$ satisfies (g1)-(g3), $d > 0$ and $q, b_u, b_d \geq 0$. Let $(u^*(x), v^*(x))$ be a non-negative steady state solution. Then*

1. *The eigenvalue problem* (4.24) *has a simple principal eigenvalue $\lambda_1 = \lambda(q)$ with a positive eigenfunction. Moreover, the principal eigenvalue λ_1 has the variational characterization*

$$-\lambda_1 = \inf_{\psi \in X_2, \psi \neq 0} \frac{E_1(\psi_1,\psi_2)}{\kappa(\psi_1,\psi_2)}, \tag{4.26}$$

where

$$\begin{aligned} E_1(\psi_1,\psi_2) &= \int_0^L e^{\alpha x}\left[d(\psi_1)_x^2 - 2\frac{A_b(x)}{A_d(x)}\mu\psi_1\psi_2 + (\sigma+m_1)\psi_1^2\right]dx \\ -\frac{\mu}{\sigma}&\int_0^L e^{\alpha x}\frac{A_b^2(x)}{A_d^2(x)}(f_v(x,v^*) - \mu - m_2)\psi_2^2 dx + qb_u\psi_1^2(0) + qb_d e^{\alpha L}\psi_1^2(L), \end{aligned} \tag{4.27}$$

and

$$\kappa(\psi_1,\psi_2) = \int_0^L e^{\alpha x}\left(\psi_1^2 + \frac{A_b^2(x)\mu}{A_d^2(x)\sigma}\psi_2^2\right)dx, \tag{4.28}$$

$\alpha = q/d$ and $X_2 = H^1(0,L) \times C(0,L)$.

2. *The spectral set $\sigma(\mathcal{L})$ of the linearized operator $\mathcal{L}$ consists of isolated eigenvalues and the set $[\min_{x\in[0,L]} f_v(x,v^*(x)) - m_2 - \mu, \max_{x\in[0,L]} f_v(x,v^*(x)) - m_2 - \mu]$. In particular, if $(u^*(x), v^*(x))$ is a non-negative steady state solution of* (1.13)*, and there exists $x_0 \in \overline{\Omega}$ such that $f_v(x_0, v(x_0)) > m_2 + \mu$, then $(u^*(x), v^*(x))$ is unstable.*

3. If $\max_{x\in[0,L]} f_v(x, v^*(x)) < m_2 + \dfrac{\mu m_1}{m_1+\sigma}$, *then* $(u^*(x), v^*(x))$ *is locally asymptotically stable. In particular, when* g *also satisfies (g4c), the zero steady state solution is always locally asymptotically stable.*

Proof. 1. The existence of the simple eigenvalue λ_1 with positive eigenfunction follows from [105, Lemma 4.1] (see also [37, Theorem 3]). Using the transform $\phi = e^{\alpha x}\psi$, system (4.24) becomes

$$\begin{cases} \lambda\psi_1 = d(\psi_1)_{xx} + q(\psi_1)_x + \dfrac{A_b(x)}{A_d(x)}\mu\psi_2 - \sigma\psi_1 - m_1\psi_1, & 0 < x < L, \\ \lambda\psi_2 = f_v(x, v^*)\psi_2 - m_2\psi_2 - \mu\psi_2 + \dfrac{A_d(x)}{A_b(x)}\sigma\psi_1, & 0 \le x \le L, \\ -d(\psi_1)_x(0) + b_u q\psi_1(0) = 0, \\ d(\psi_1)_x(L) + b_d q\psi_1(L) = 0. \end{cases} \tag{4.29}$$

A direct calculation shows that the variational minimizer defined in (4.26) satisfies (4.29).

2. To consider the spectral set of $\mathcal{L}$, we analyze the following resolvent equation for $\lambda \in \mathbb{C}$ and $(p_1, p_2) \in Y$,

$$\begin{cases} d\phi_1'' - q\phi_1' - (\sigma + m_1 + \lambda)\phi_1 + \dfrac{A_b(x)\mu}{A_d(x)}\phi_2 = p_1, & 0 < x < L, \\ \dfrac{A_d(x)\sigma}{A_b(x)}\phi_1 + (f_v(x, v^*) - m_2 - \mu - \lambda)\phi_2 = p_2, & 0 \le x \le L, \\ d\phi_1(0) - q\phi_1(0) = b_u q\phi_1(0), \\ d\phi_1(L) - q\phi_1(L) = -b_d q\phi_1(L). \end{cases} \tag{4.30}$$

Let $\underline{A} = \min_{x\in[0,L]} f_v(x, v^*(x))$ and $\overline{A} = \max_{x\in[0,L]} f_v(x, v^*(x))$. If $\lambda \notin [\underline{A} - m_2 - \mu, \overline{A} - m_2 - \mu]$, then from the second equation in (4.30), we have

$$\phi_2 = \frac{p_2 A_b(x) - A_d(x)\sigma\phi_1}{A_b(x)(f_v(x, v^*) - m_2 - \mu - \lambda)}, \tag{4.31}$$

and hence the first equation of (4.30) becomes

$$\begin{aligned}&d\phi_1'' - q\phi_1' - (\sigma + m_1 + \lambda)\phi_1 - \frac{\sigma\mu}{f_v(x, v^*) - m_2 - \mu - \lambda}\phi_1 \\ =&p_1 - \frac{\mu A_b(x)p_2}{A_d(x)(f_v(x, v^*) - m_2 - \mu - \lambda)}.\end{aligned} \tag{4.32}$$

It is well-known that the eigenvalue problem

$$\begin{cases} d\phi''(x) - q\phi'(x) = l\phi(x), & 0 < x < L, \\ d\phi'(0) - q\phi(0) = b_u q\phi(0), & \\ d\phi'(L) - q\phi(L) = -b_d q\phi(L), & \end{cases} \tag{4.33}$$

has a sequence of eigenvalues $l = l_1 > l_2 > \cdots > l_n \to -\infty$. Therefore from the Fredholm alternative, (4.32) has a unique solution if and only if

$$\sigma + m_1 + \lambda + \frac{\sigma\mu}{f_v(x, v^*) - m_2 - \mu - \lambda} \notin \{l_i\}_{i=1}^{\infty}. \tag{4.34}$$

Moreover, if (4.34) holds, (4.31) determines ϕ_2 uniquely and $\mathcal{L} - \lambda I$ has a bounded inverse. On the other hand, if (4.34) is not satisfied, which means λ satisfies the characteristic equation

$$\lambda^2 - (f_v(x, v^*) - m_2 - \mu - \sigma - m_1 + l_i)\lambda - (\sigma + m_1 - l_i)(f_v(x, v^*) - m_2 - \mu) - \sigma\mu = 0, \tag{4.35}$$

for some $i \geq 1$. This equation has two roots $\lambda_{1,j}$ and $\lambda_{2,j}$:

$$\begin{aligned}\lambda_{1,j} &= \frac{1}{2}(f_v - m_2 - \mu - \sigma - m_1 + l_i - \sqrt{(f_v(x, v^*) - m_2 - \mu + \sigma + m_1 - l_i)^2 + 4\sigma\mu}), \\ \lambda_{2,j} &= \frac{1}{2}(f_v - m_2 - \mu - \sigma - m_1 + l_i + \sqrt{(f_v(x, v^*) - m_2 - \mu + \sigma + m_1 - l_i)^2 + 4\sigma\mu}),\end{aligned}$$

and $\lambda_{1,j}$ and $\lambda_{2,j}$ are also the eigenvalues of $\mathcal{L}$. This determines all eigenvalues of $\mathcal{L}$. By following the same proof as [68, Theorem 4.5], we can show that each point in $[\underline{A} - m_2 - \mu, \overline{A} - m_2 - \mu]$ is in the continuous spectrum of $\mathcal{L}$. If $(u^*(x), v^*(x))$ is a non-negative steady state solution of (1.13), and there exists $x_0 \in \overline{\Omega}$ such that $f_v(x_0, v(x_0)) > m_2 + \mu$, then $[\underline{A} - m_2 - \mu, \overline{A} - m_2 - \mu] \cap (0, \infty) \neq \emptyset$, so $(u^*(x), v^*(x))$ must be unstable.

3. Since $f_v(x, v^*(x)) < \mu + m_2 - \dfrac{\mu\sigma}{m_1 + \sigma}$, then

$$
\begin{aligned}
&E_1(\psi_1, \psi_2)\\
=&\int_0^L e^{\alpha x}[d(\psi_1)_x^2(x) - 2\frac{A_b(x)}{A_d(x)}\mu\psi_1\psi_2 + (\sigma + m_1)\psi_1^2]dx\\
&-\frac{\mu}{\sigma}\int_0^L e^{\alpha x}\frac{A_b^2(x)}{A_d^2(x)}(f_v(x, v^*) - \mu - m_2)\psi_2^2 dx + qb_u\psi_1^2(0) + qb_d e^{\alpha L}\psi_1^2(L)\\
>&\int_0^L e^{\alpha x}[-2\frac{A_b(x)}{A_d(x)}\mu\psi_1\psi_2 + (\sigma + m_1)\psi_1^2 + \frac{A_b^2(x)\mu}{A_d^2(x)\sigma}(\mu + m_2 - f_v(x, v^*))\psi_2^2]dx\\
=&\int_0^L e^{\alpha x}(\frac{A_b(x)\mu}{A_d(x)\sqrt{\sigma + m_1}}\psi_2 - \sqrt{\sigma + m_1}\psi_1)^2 dx\\
&+\int_0^L e^{\alpha x}\frac{A_b^2(x)\mu[(m_1 + \sigma)(\mu + m_2) - \mu\sigma - (m_1 + \sigma)f_v]}{A_d^2(x)\sigma(\sigma + m_1)}\psi_2^2 dx > 0.
\end{aligned}
$$

Then from (4.26) and $\kappa(\psi_1, \psi_2) > 0$, the principal eigenvalue $\lambda_1 < 0$. On the other hand, since $\max_{x \in [0,L]} f_v(x, v^*(x)) - m_2 - \mu < 0$, then all continuous spectrum point is also negtive. Hence the non-negative steady state solution $(u^*(x), v^*(x))$ is locally asymptotically stable. Since $f_v(x, 0) = g(x, 0) < 0$, we have $\max_{x \in [0,L]} g(x, 0) < \mu + m_2 - \dfrac{\mu\sigma}{m_1 + \sigma}$, therefore the extinct state $(0, 0)$ is always locally asymptotically stable. □

4.3 Persistence/Extinction dynamics

In this section, we consider the dynamical behavior of system (1.13) with the strong Allee effect growth rate in the bethic population. Assume that $(u(x), v(x))$ is a positive solution of system (4.3), then from the second equation of system (4.3), we have

$$
u(x) = \frac{A_b(x)v(x)}{A_d(x)\sigma}(\mu + m_2 - g(x, v(x))), \tag{4.36}
$$

which implies that $g(x, v(x)) < m_2 + \mu$ for every $x \in [0, L]$. This implies that the transfer rate μ from benthos to drift zone needs to be large to ensure the existence of positive steady state solutions. Notice that we consider the following three possible scenarios: (see Fig. 4.1)

$$(H1) \qquad \mu > (g_{max} - m_2)\frac{\sigma + m_1}{m_1} := \mu_1,$$

$$(H2) \qquad \mu_3 := g_{min} - m_2 < \mu < (g_{min} - m_2)\frac{\sigma + m_1}{m_1} := \mu_2,$$

$$(H3) \qquad \mu < g_{min} - m_2 := \mu_3.$$

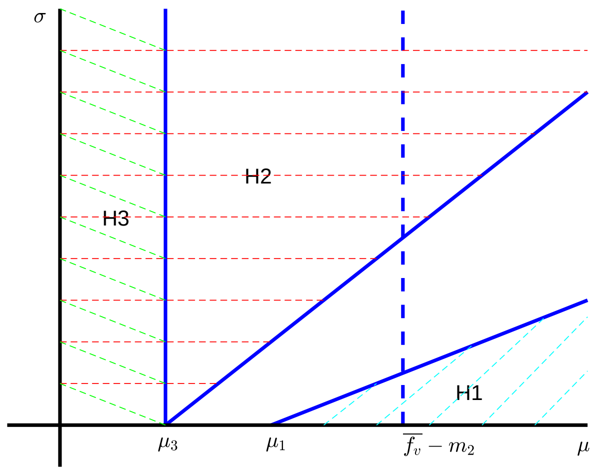

Figure 4.1: Parameter regions on $\mu - \sigma$ plane satisfying (H1), (H2) or (H3).

In the following, we will discuss the dynamical behavior of system (1.13) under $(H1)$, $(H2)$ or $(H3)$, respectively. When $(H1)$ is satisfied, we show in subsection 4.3.1 that system (1.13) has no positive steady state solutions, which indicates a global extinction of the population for all initial conditions. And in subsection 4.3.2, under the condition $(H3)$, we prove the existence of multiple positive steady state solutions for any diffusion coefficient d and advection rate q, and the persistence of population for all large initial conditions. Finally under the condition $(H2)$, which is in between $(H1)$ and $(H3)$, we show the existence of multiple positive steady state solutions in closed environment when the advection rate q is small. This indicates that the extinction/persistence of benthic-drift population in the intermediate parameter range $(H2)$ is more complicated, and it depends on the movement parameters q, d and also boundary conditions. Note that when $g(x, v) \equiv g(v)$ (spatially homogeneous), the conditions $(H1)$, $(H2)$ and $(H3)$ completely partitions the positive parameter quadrant $\{(\mu,\sigma) : \mu,\sigma > 0\}$, but there is a gap between $(H1)$ and $(H2)$ when $g(x,v)$ is spatially heterogeneous.

4.3.1 Extinction

First we prove the following nonexistence results of steady state solution $(u(x), v(x))$ to (1.13).

Theorem 4.8. *Suppose $g(x,u)$ satisfies (g1)-(g3) and (g4c), $d > 0$ and $q, b_u, b_d \geq 0$.*

1. *If $(H1)$ is satisfied, then the system (1.13) has no positive steady state solutions.*

2. *The system (1.13) has no positive steady state solutions satisfying $v(x) < h(x)$ for all $x \in [0,L]$, where $h(x)$ is defined in (g4c).*

Proof. 1. Suppose that $(u(x), v(x))$ is a positive solution of (4.3). Substituting (4.36) into the first equation of (4.3), we obtain

$$\begin{cases} du_{xx} - qu_x + \dfrac{A_b(x)}{A_d(x)} v \left[\mu - \dfrac{\sigma + m_1}{\sigma}(m_2 + \mu - g(x,v))\right] = 0, \quad 0 < x < L, \\ du_x(0) - qu(0) = b_u qu(0), \\ du_x(L) - qu(L) = -b_d qu(L). \end{cases} \tag{4.37}$$

Integrating (4.37), we get

$$-b_d qu(L) - b_u qu(0) + \int_0^L \frac{A_b(x)}{A_d(x)} v(x) \left[\mu - \frac{\sigma + m_1}{\sigma}(\mu + m_2 - g(x, v(x)))\right] dx = 0. \tag{4.38}$$

Note that $(H1)$ implies that the function

$$\tilde{v}(x) = \mu - \frac{\sigma + m_1}{\sigma}(\mu + m_2 - g(x, v(x))) \tag{4.39}$$

is strictly negative. Since $v(x) > 0$ and $b_u, b_d \geq 0$, we reach a contradiction with (4.38). Hence there is no positive steady state solutions of (1.13) when $(H1)$ is satisfied.

2. Suppose that $(u(x), v(x))$ is a positive solution of (4.3). If $0 < v(x) < h(x)$, then $g(x, v(x)) < 0$ for all $x \in [0, L]$ and consequently $\tilde{v}(x) < \mu - \dfrac{\sigma + m_1}{\sigma}(\mu + m_2) < 0$. This again leads to a contradiction. Therefore, there is no positive solution $(u(x), v(x))$ of (4.3) satisfying $v(x) < h(x)$ for all $x \in [0, L]$. □

A direct corollary of Theorem 4.8 and Theorem 4.6 is the global extinction of population when the transfer rate μ of the benthic population to the drift population is too large.

Corollary 4.9. *Suppose $g(x, u)$ satisfies (g1)-(g3) and (g4c), $d > 0$ and $q, b_u, b_d \geq 0$. If*

$$\mu > \max\left\{(g_{max} - m_2)\frac{\sigma + m_1}{m_1}, \overline{f_v} - m_2\right\}, \tag{4.40}$$

then for any initial condition $(u_0(x), v_0(x)) \geq 0$, the solution $(u(x,t), v(x,t)$ of (1.13) *satisfies $\lim_{t\to+\infty} u(x,t) = 0$ and $\lim_{t\to+\infty} v(x,t) = 0$.*

Proof. The condition (4.40) implies both $(H1)$ and (3.10). Then from Theorem 4.6, the solution converges to a nonnegative steady state as $t \to \infty$, and from Theorem 4.8, the trivial steady state is the only nonnegative steady state. Therefore $\lim_{t\to+\infty} u(x,t) = 0$ and $\lim_{t\to+\infty} v(x,t) = 0$. □

The global extinction shown in Corollary 4.9 indicates that when the the transfer rate μ of the benthic population to the drift population is too high, the benthic population becomes too low and the Allee effect drives it to extinction when the benthic population is below the threshold level. We conjecture that the global extinction described in Corollary 4.9 holds when $(H1)$ is satisfied, and the condition (3.10) is not necessary. But it is not known whether the solution flow has sufficient compactness without (3.10).

From part 5 of Proposition 4.7, we know that the zero steady state solution is locally asymptotically stable. In the following proposition, we describe the basin of attraction of the zero steady state solution of system (1.13) for different boundary conditions.

Proposition 4.10. *Suppose $g(x,u)$ satisfies (g1)-(g3) and (g4c), $d>0$ and $q,b_u,b_d\geq 0$. Assume that the cross-section $A_b(x)$ and $A_d(x)$ are homogeneous. Let $(u(x,t),v(x,t))$ be the solution of* (1.13) *with initial condition $(u_0(x),v_0(x))$. Then*

1. *When $b_u\geq 0$ and $b_d\geq 0$, if $0<u_0(x)<\theta_1 e^{\alpha x}\min\limits_{y\in[0,L]}e^{-\alpha y}h(y)$ and $0<v_0(x)<e^{\alpha x}\min\limits_{y\in[0,L]}e^{-\alpha y}h(y)$, then $\lim\limits_{t\to+\infty}u(x,t)=0$ and $\lim\limits_{t\to+\infty}v(x,t)=0$;*

2. *When $b_u\geq 0$ and $b_d\geq 1$, if $0<u_0(x)<\theta_1\min\limits_{y\in[0,L]}h(y)$ and $0<v_0(x)<\min\limits_{y\in[0,L]}h(y)$, then $\lim\limits_{t\to+\infty}u(x,t)=0$ and $\lim\limits_{t\to+\infty}v(x,t)=0$.*

Proof. 1. When $b_u\geq 0$ and $b_d\geq 0$, we set $\overline{w}_1=\theta_1\min\limits_{y\in[0,L]}e^{-\alpha y}h(y)$ and $\overline{z}_1=\min\limits_{y\in[0,L]}e^{-\alpha y}h(y)$. Then we have

$$d(\overline{w}_1)_{xx}+q(\overline{w}_1)_x+\frac{A_b}{A_d}\mu\overline{z}_1-\sigma\overline{w}_1-m_1\overline{w}_1=0,$$

and

$$\begin{aligned}&\overline{z}_1 g(x,e^{\alpha x}\overline{z}_1)-m_2\overline{z}_1-\mu\overline{z}_1+\frac{A_d\sigma}{A_b}\overline{w}_1\\ \leq&\overline{z}_1 g(x,e^{\alpha x}\overline{z}_1)-(m_2+\mu-\frac{\sigma\mu}{\sigma+m_1})\overline{z}_1\leq\min_{y\in[0,L]}e^{-\alpha y}h(y)g(x,e^{\alpha x}\min_{y\in[0,L]}e^{-\alpha y}h(y))\\ \leq&\min_{y\in[0,L]}e^{-\alpha y}h(y)g(x,e^{\alpha x}e^{-\alpha x}h(x))=\min_{y\in[0,L]}e^{-\alpha y}h(y)g(x,h(x))=0,\end{aligned}$$

and the boundary conditions $-d(\overline{w}_1)_x(0)+b_uq\overline{w}_1(0)\geq 0$, $d(\overline{w}_1)_x(L)+b_dq\overline{w}_1(L)\geq 0$. Thus, $(\overline{w}_1,\overline{z}_1)$ is an upper solution of system (4.11). Let $(\underline{w}_1,\underline{z}_1)=(0,0)$ to be the lower solution of system (4.11). Now assume that $0<w_0(x)<\theta_1\min\limits_{y\in[0,L]}e^{-\alpha y}h(y)$ and $0\leq z_0(x)\leq\min\limits_{y\in[0,L]}e^{-\alpha y}h(y)$, and let $(w(x,t),v(x,t))$ be the solution of (4.4). Then there exist solutions $(\overline{W}_1(x,t),\overline{Z}_1(x,t))$ and $(\underline{W}_1(x,t),\underline{Z}_1(x,t))$ of system (4.4),

$$\underline{W}_1(x,t)\leq w(x,t)\leq\overline{W}_1(x,t),\ \ \underline{Z}_1(x,t)\leq z(x,t)\leq\overline{Z}_1(x,t),\tag{4.41}$$

where $(\overline{W}_1(x,t),\overline{Z}_1(x,t))$ and $(\underline{W}_1(x,t),\underline{Z}_1(x,t))$ are the solutions of system (4.4) with the initial condition $(\overline{W}_1(x,0),\overline{Z}_1(x,0))=(\overline{w}_1,\overline{z}_1)$ and $(\underline{W}_1(x,0),\underline{Z}_1(x,0))=(\underline{w}_1,\underline{z}_1)$. Moreover,

$$\lim_{t\to+\infty}(\overline{W}_1(x,t),\overline{Z}_1(x,t)) = (w_{max}(x), z_{max}(x)),$$
$$\lim_{t\to+\infty}(\underline{W}_1(x,t),\underline{Z}_1(x,t)) = (w_{min}(x), z_{min}(x)), \tag{4.42}$$

where $(w_{max}(x), z_{max}(x))$, $(w_{min}(x), z_{min}(x))$ are the maximal and minimal solution of (4.11) between $(0,0)$ and $(\overline{w}_1, \overline{z}_1)$. From Proposition 4.8, there is no positive solution $(u(x), v(x))$ satisfying $v(x) < h(x)$ for all $x \in [0, L]$, hence $z_{min}(x) = z_{max}(x) = 0$. And consequently $w_{min}(x) = w_{max}(x) = 0$. This implies that $\lim_{t\to+\infty} u(x,t) = 0$ and $\lim_{t\to+\infty} v(x,t) = 0$;.

2. When $b_u \geq 0$ and $b_d \geq 1$, we apply the upper and lower solution method directly to (1.13), and we choose $(\overline{u}_1(x), \overline{v}_1(x)) = (\theta_1 \min_{y\in[0,L]} h(y), \min_{y\in[0,L]} h(y))$ to be the upper solution and $(\underline{u}_1(x), \underline{v}_1(x)) = (0,0)$ be the lower solution. We can follow the same argument in the above paragraph to reach the conclusion. □

4.3.2 Persistence

In this section, we provide some criteria for the population persistence of system (1.13) with the strong Allee effect growth rate in the benthic population. We first show some properties of the set of positive steady state solutions of (4.3) if there exists any.

Proposition 4.11. *Suppose $g(x, u)$ satisfies (g1)-(g3), $d > 0$, $q, b_u, b_d \geq 0$, and the cross-section $A_b(x)$ and $A_d(x)$ are homogeneous. If there exists a positive steady state solution of* (1.13)*, then there exists a maximal steady state solution $(u_{max}(x), v_{max}(x))$ such that for any positive steady state $(u(x), v(x))$ of system* (1.13), *$(u_{max}(x), v_{max}(x)) \geq (u(x), v(x))$.*

Proof. We consider the equivalent steady state equation (4.11). Set

$$\overline{w}_2 = \theta_1 \max_{y\in[0,L]} e^{-\alpha y} r(y), \quad \overline{z}_2 = \max_{y\in[0,L]} e^{-\alpha y} r(y).$$

From (g3), we have $g_v(x, v) \leq 0$ for $v \geq r(x)$. Hence

$$g(x, e^{\alpha x}\overline{z}_2) = g(x, e^{\alpha x} \max_{y\in[0,L]} e^{-\alpha y} r(y)) \leq g(x, e^{\alpha x} e^{-\alpha x} r(x)) = g(x, r(x)) = 0.$$

Substituting $(\overline{w}_2, \overline{z}_2)$ into system (4.11), we have

$$\begin{cases} d(\overline{w}_2)_{xx} + q(\overline{w}_2)_x + \dfrac{A_b}{A_d}\mu\overline{z}_2 - \sigma\overline{w}_2 - m_1\overline{w}_2 = 0, & 0 < x < L, \\ \overline{z}_2 g(x, e^{\alpha x}\overline{z}_2) - m_2\overline{z}_2 - \mu\overline{z}_2 + \dfrac{A_d\sigma}{A_b}\overline{w}_2 \leq 0, & 0 \leq x \leq L, \\ -d\overline{w}_2'(0) + b_u q\overline{w}_2(0) \geq 0, \\ d\overline{w}_2'(L) + b_d q\overline{w}_2(L) \geq 0. \end{cases} \tag{4.43}$$

Thus $(\overline{w}_2, \overline{z}_2)$ is an upper solution of system (4.11). Moreover from Proposition 4.2, any positive steady state solution $(w(x), z(x))$ of (4.11) satisfies $(w(x), z(x)) \leq (\overline{w}_2, \overline{z}_2)$. Since $(u(x), v(x))$ is a positive steady state of (1.13), we can set the lower solution of (4.11) to be $(\underline{w}_2(x), \underline{z}_2(x)) = (e^{-\alpha x}u(x), e^{-\alpha x}v(x))$. Then there exists a maximal solution $(w_{max}(x), z_{max}(x))$ of (4.11) satisfying $(\underline{w}_2(x), \underline{z}_2(x)) \leq (w_{max}(x), z_{max}(x))$. Since $(w_{max}(x), z_{max}(x))$ is obtained through the monotone iteration process (see [4, 79]) from the upper solution $(\overline{w}_2, \overline{z}_2(x))$ and any positive steady state solution $(w(x), z(x))$ of (4.11) satisfies $(w(x), z(x)) \leq (\overline{w}_2, \overline{z}_2(x))$, we conclude that $(w_{max}(x), z_{max}(x))$ is the maximal steady state solution of (4.11). □

Next we show a monotonicity result for the maximal steady state solution.

Proposition 4.12. *Suppose $g(x, u)$ satisfies (g1)-(g3), $g(x, v) \equiv g(v)$, that is g is spatially homogeneous and the cross-section $A_b(x)$ and $A_d(x)$ are also homogeneous. Then if $b_u \geq 0$ and $0 \leq b_d \leq 1$, the maximal steady state solution $(u_{max}(x), v_{max}(x))$ of equation (1.13) is strictly increasing in $[0, L]$.*

Proof. We prove that $(u_{max})_x > 0$ and $(v_{\max})_x > 0$ for $x \in (0, L)$. From [87, Page 992], the maximal solution (u_{max}, v_{max}) is semistable, and the corresponding eigenvalue problem is (4.24). From Proposition 4.7, the eigenvalue problem (4.24) has a principal eigenvalue $\lambda_1 \leq 0$ with positive eigenfunction $\phi = (\phi_1, \phi_2) > 0$.

We first prove that u_{max} and v_{max} always have the same sign for $x \in [0, L]$. Differentiating (4.3) with respect to x, we have

$$d(u_{max})_{xxx} - q(u_{max})_{xx} - (m_1 + \sigma)(u_{max})_x + \frac{A_b\mu}{A_d}(v_{max})_x = 0, \tag{4.44}$$

$$f_v(v_{max})(v_{max})_x - (m_2 + \mu)(v_{max})_x + \frac{A_d\sigma}{A_b}(u_{max})_x = 0, \tag{4.45}$$

where $f(v) = vg(v)$. Multiplying equation (4.45) by ϕ_2 and multiplying the first equation in (4.24) by $(v_{max})_x$, then subtracting, we obtain

$$\frac{A_d\sigma}{A_b}\phi_2(u_{max})_x = \left(\frac{A_d\sigma}{A_b}\phi_1 - \lambda_1\phi_2\right)(v_{max})_x. \tag{4.46}$$

Then u_{max} and v_{max} always have the same sign as $\phi_1 > 0$, $\phi_2 > 0$ and $\lambda_1 \leq 0$.

We prove the proposition by contradiction. Assuming that the maximal solution (u_{max}, v_{max}) is not increasing for all $x \in [0, L]$. From boundary conditions in (1.13) and the condition $b_u \geq 0$, $0 \leq b_d \leq 1$, we have

$$(u_{max})_x(0) = \alpha(b_u + 1)u_{max}(0) > 0,$$
$$(u_{max})_x(L) = \alpha(-b_d + 1)u_{max}(L) \geq 0.$$

Then $(u_{max})_x(x)$ has at least two zero points in $(0, L]$. We choose the two smallest zero points $x_1, x_2 \in (0, L]$ $(x_1 < x_2)$ such that $(u_{max})_x(x_1) = (u_{max})_x(x_2) = 0$, $(u_{max})_x(x) < 0$ on (x_1, x_2). We claim that $(u_{max})_{xx}(x_1) < 0$ and $(u_{max})_{xx}(x_2) > 0$. Since $(u_{max})_x(x) < 0$ on (x_1, x_2), then $(u_{max})_{xx}(x_1) \leq 0$ and $(u_{max})_{xx}(x_2) \geq 0$. If $(u_{max})_{xx}(x_1) = 0$, then from $(u_{max})_x(x_1) = 0$, we conclude that $(u_{max})_x(x) \equiv 0$ near $x = x_1$ from the uniqueness of solution of ordinary differential equation, which contradicts with the assumption that $(u_{max})_x(x) < 0$ on (x_1, x_2). Hence we have $(u_{max})_{xx}(x_1) < 0$, and similarly we can show that $(u_{max})_{xx}(x_2) > 0$. Since u_{max} and v_{max} have the same sign, then we also have $(v_{max})_x(x) < 0$ on (x_1, x_2).

Multiplying equation (4.44) by $e^{-\alpha x}\phi_1$ and multiplying the first equation in (4.24) by

$e^{-\alpha x}(u_{max})_x$, then subtracting, we obtain

$$\begin{aligned} & de^{-\alpha x}(-(u_{max})_x\phi_{1xx} + (u_{max})_{xxx}\phi_1) + qe^{-\alpha x}(-(u_{max})_{xx}\phi_1 + (u_{max})_x\phi_{1x}) \\ & + e^{-\alpha x}\frac{A_b\mu}{A_d}((v_{max})_x\phi_1 - \phi_2(u_{max})_x) = -\lambda_1 e^{-\alpha x}\phi_1(u_{max})_x. \end{aligned} \tag{4.47}$$

Then solving $(u_{max})_x\phi_2 - (v_{max})_x\phi_1$ from (4.46), substituting into (4.47), we have

$$\begin{aligned} & de^{-\alpha x}(-(u_{max})_x\phi_{1xx} + (u_{max})_{xxx}\phi_1) + qe^{-\alpha x}(-(u_{max})_{xx}\phi_1 + (u_{max})_x\phi_{1x}) \\ = & -\lambda_1 e^{-\alpha x}\phi_1(u_{max})_x - \frac{A_b^2\mu}{A_d^2\sigma}\lambda_1 e^{-\alpha x}\phi_2(v_{max})_x. \end{aligned} \tag{4.48}$$

Integrating (4.48) on $[x_1, x_2]$, the right hand side becomes

$$-\lambda_1 \int_{x_1}^{x_2} e^{-\alpha x}\left[\phi_1(u_{max})_x + \frac{A_b^2\mu}{A_d^2\sigma}e^{-\alpha x}\phi_2(v_{max})_x\right] dx < 0, \tag{4.49}$$

as $(u_{max})_x(x) < 0$ and $(v_{max})_x(x) < 0$ on (x_1, x_2), $\phi_1 > 0$, $\phi_2 > 0$ and $\lambda_1 \leq 0$. On the other hand, the left hand side becomes

$$\begin{aligned} & - d\int_{x_1}^{x_2}[(e^{-\alpha x}\phi_{1x})_x(u_{max})_x - (e^{-\alpha x}(u_{max})_{xx})_x\phi_1]dx \\ = & - de^{-\alpha x}(\phi_{1x}(u_{max})_x - \phi_1(u_{max})_{xx})\Big|_{x_1}^{x_2} \\ = & - de^{-\alpha x_1}\phi_1(x_1)(u_{max})_{xx}(x_1) + de^{-\alpha x_2}\phi_1(x_2)(u_{max})_{xx}(x_2) > 0, \end{aligned} \tag{4.50}$$

as $(u_{max})_{xx}(x_1) < 0$ and $(u_{max})_{xx}(x_2) > 0$. So (4.49) and (4.50) are in contradiction. Thus the maximal solution $(u_{max}(x), v_{max}(x))$ of (4.3) is increasing for $x \in [0, L]$. Moreover the strong maximum principle implies that $(u_{,max}(x), v_{max}(x))$ must be strictly increasing. □

Next we assume that the condition $(H3)$ holds, i.e. $g_{min} > m_2 + \mu$. Then for every $x \in [0, L]$, from (g3) and (g4c), there exist $v_1(x)$ and $v_2(x)$ such that $v_1(x) < v_2(x)$ and $g(x, v_i(x)) = m_2 + \mu$, $i = 1, 2$. Moreover there also exist $v_3(x)$ and $v_4(x)$ such that $v_3(x) < v_4(x)$, $g(x, v_i(x)) = m_2 + \dfrac{m_1\mu}{\sigma + m_1}$, $i = 3, 4$. It is clear that $h(x) < v_3(x) < v_1(x) < v_2(x) < v_4(x) < r(x)$. When $(H2)$ is satisfied but $(H3)$ is not, $v_3(x)$ and $v_4(x)$ still exist but not

$v_1(x)$ and $v_2(x)$. When $(H1)$ is satisfied, then all $v_i(x)$ $(i = 1, 2, 3, 4)$ do not exist (see Fig. 4.2).

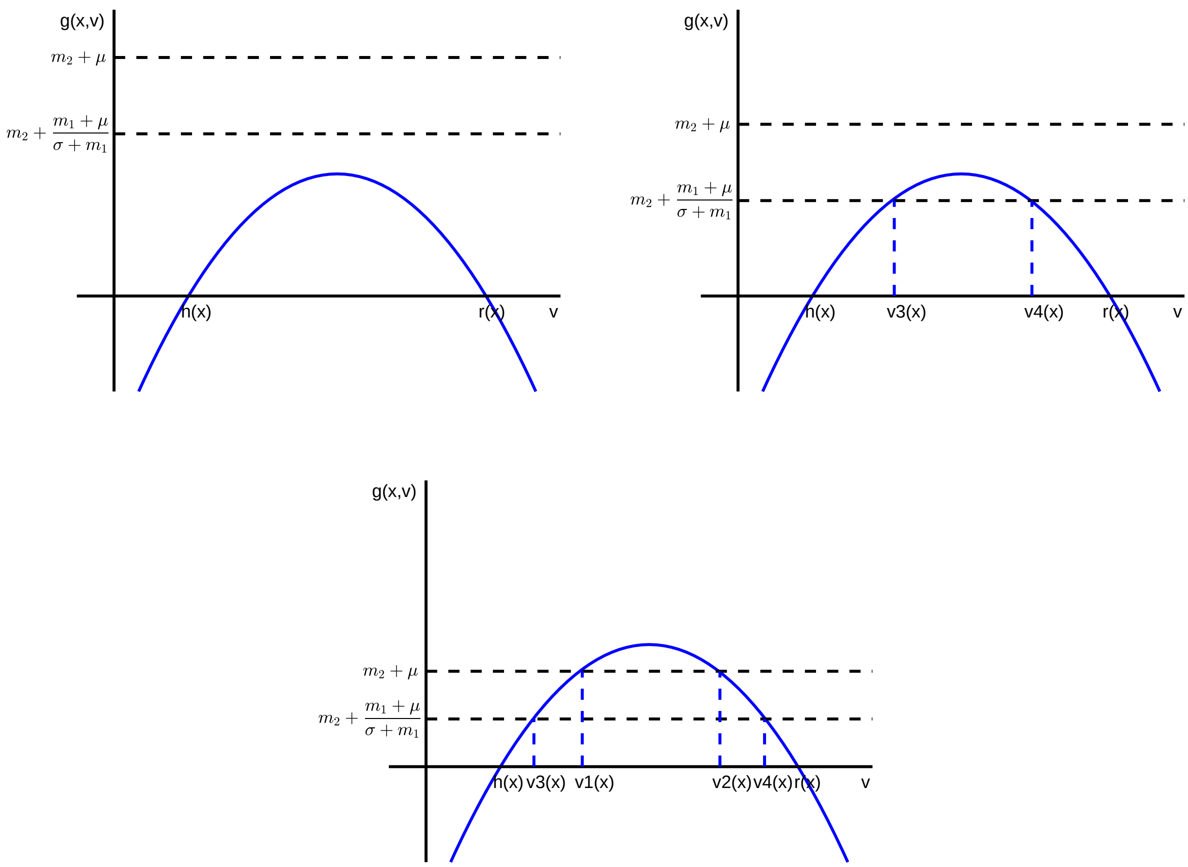

Figure 4.2: Graph of $g(x, v)$ under conditions $(H1)$, $(H2)$ or $(H3)$. Upper left: $(H1)$; Upper right: $(H2)$; Lower: $(H3)$.

We first prove the following lemma which will used to construct a lower solution of the system (4.11).

Lemma 4.13. *Let $p(x) \in C[0, L]$ and $d > 0$, $q \geq 0$. Then the system*

$$\begin{cases} dw_{xx} + qw_x + p(x) - (\sigma + m_1)w = 0, & 0 < x < L, \\ -dw_x(0) + b_u qw(0) = 0, \\ dw_x(L) + b_d qw(L) = 0, \end{cases} \tag{4.51}$$

has a unique positive solution $w_p(x)$.

Proof. Consider the following eigenvalue problem

$$\begin{cases} d\phi_{xx} + q\phi_x - (\sigma + m_1)\phi = \lambda\phi, & 0 < x < L, \\ -d\phi_x(0) + b_u q\phi(0) = 0, \\ d\phi_x(L) + b_d q\phi(L) = 0, \end{cases} \tag{4.52}$$

Then (4.52) has a principal eigenvalue λ_1 satisfying

$$-\lambda_1 = \inf_{\phi \in H^1(0,L), \phi \neq 0} \frac{\int_0^L e^{\alpha x}(d\phi_x^2 + (\sigma + m_1)\phi^2)dx}{\int_0^L e^{\alpha x}\phi^2 dx} \tag{4.53}$$

Then $\lambda_1 < 0$ and the corresponding eigenfunction $\phi_1 > 0$. We use the upper-lower solution method to prove the existence of a positive steady state solution. Let $\overline{W}(x) = \frac{1}{\sigma + m_1} \max_{x \in [0,L]} p(x)$, and $\underline{W}(x) = \varepsilon\phi_1(x)$ where $\varepsilon > 0$ is small so that $\underline{W}(x) < \overline{W}(x)$ and ϕ_1 is the positive eigenfunction corresponding to λ_1 of (4.52). Then it is easy to verify that $\overline{W}(x)$ and $\underline{W}(x)$ is a pair of upper-lower solution. From [80, Theorem 4.1], there exists a solution $w_p(x)$ of system (4.51) satisfying $\underline{W}(x) \le w_p(x) \le \overline{W}(x)$. The uniqueness follows from the maximum principle: if $w_1(x)$ and $w_2(x)$ are two solutions of system (4.51), then $w_1(x) - w_2(x)$ satisfies a boundary value problem of linear ODE, and $w_1(x) - w_2(x) = 0$ is the unique solution. Hence the solution of (4.51) is unique. □

Now we show that under condition $(H3)$, the benthic-drift population system is always persistent for large initial condition for any diffusion coefficient $d > 0$ and advection rate $q \ge 0$, despite of strong Allee growth rate.

Theorem 4.14. *Suppose that $g(x, v)$ satisfies (g1)-(g3) and (g4c), $d > 0$ and $q \ge 0$, $b_u \ge 0$ and $b_d \ge 0$. Assume that $(H3)$ holds. Define*

$$\Sigma_1 = \{(u(x), v(x)) \in X_1 : u(x) \ge e^{\alpha x} w_1(x), v(x) \ge v_1(x)\}, \tag{4.54}$$

where $v_1(x)$ is the smaller root of $g(x, v) = \mu + m_2$ and $w_1(x)$ is the unique positive solution *of the system*

$$\begin{cases} dw_{xx} + qw_x + \dfrac{A_b(x)\mu}{A_d(x)} e^{-\alpha x} v_1(x) - (\sigma + m_1)w = 0, & 0 < x < L, \\ -dw_x(0) + b_u q w(0) = 0, \\ dw_x(L) + b_d q w(L) = 0. \end{cases} \tag{4.55}$$

Then Σ_1 *is a positive invariant set for system* (1.13)*. Moreover, system* (1.13) *has a maximum steady state* $(u_{max}(x), v_{max}(x)) \in \Sigma_1$*, and at least another positive steady state.*

Proof. Assume that $(H3)$ is satisfied, we consider the equivalent system (4.4) of (1.13). From Lemma 4.13, system (4.55) has a unique solution $w_1(x)$. We set $(\underline{w}(x), \underline{z}(x)) = (w_1(x), e^{-\alpha x} v_1(x))$. Then

$$\begin{cases} d\underline{w}_{xx} + q\underline{w}_x + \dfrac{A_b(x)\mu}{A_d(x)} \underline{z}(x) - (\sigma + m_1)\underline{w} = 0, & 0 < x < L, \\ \underline{z} g(x, e^{\alpha x}\underline{z}) - (m_2 + \mu)\underline{z} + \dfrac{A_d(x)\sigma}{A_b(x)} \underline{w} \geq 0, & 0 < x < L, \\ -d\underline{w}_x(0) + b_u q \underline{w}(0) = 0, \\ d\underline{w}_x(L) + b_d q \underline{w}(L) = 0. \end{cases} \tag{4.56}$$

So $(\underline{w}(x), \underline{z}(x))$ is a lower solution of (4.11). On the other hand, from Proposition 4.11, $(\overline{w}(x), \overline{z}(x)) = (\overline{\theta}_1 \max_{x \in [0,L]} e^{-\alpha x} r(x), \max_{x \in [0,L]} e^{-\alpha x} r(x))$ is an upper solution of (4.11). It is easy to check that $\overline{z}(x) = \max_{x \in [0,L]} e^{-\alpha x} r(x)) > e^{-\alpha x} v_1(x) = \underline{z}(x)$ and $\overline{w}(x) = \overline{\theta}_1 \max_{x \in [0,L]} e^{-\alpha x} r(x) > \underline{w}(x)$ from the construction of $\underline{w}(x)$ in Lemma 4.13. So from [80, Theorem 4.1], there exists a positive solution $(w(x), z(x))$ of system (4.11) satisfying $\underline{w}(x) < w(x) < \overline{w}(x)$ and $\underline{z}(x) < z(x) < \overline{z}(x)$. From Proposition 4.11, there exists a maximal solution $(u_{max}(x), v_{max}(x)) \in \Sigma_1$. Since the solution of (4.4) with initial condition $(\underline{w}(x), \underline{z}(x))$ is increasing, then Σ_1 is positively invariant for the dynamics of (1.13). The existence of another positive steady state follows from [4, Theorem 14.2] and the existence of another pair of upper-lower solutions in the proof of Proposition 4.10 part 1. $\square$

In the last we show that the persistence of population in the intermediate μ range (satisfying $(H2)$) may depend on the diffusion coefficient d and advection rate q. The following result on the existence of positive steady state solutions only holds for the closed environment (NF/NF $b_u = b_d = 0$) case.

Theorem 4.15. *Suppose that $g(x,u)$ satisfies (g1)-(g3) and (g4c), $d > 0$ and $q \geq 0$. Assume that $(H2)$ holds, and the cross-section $A_b(x)$ and $A_d(x)$ are spatially homogeneous. Let $v_3(x)$ and $v_4(x)$ be the roots of $g(x,v) = m_2 + \dfrac{m_1\mu}{\sigma + m_1}$ satisfying $v_3(x) < v_4(x)$, and assume that*

$$\max_{y\in[0,L]} e^{-\alpha y} v_3(y) < \min_{y\in[0,L]} e^{-\alpha y} v_4(y). \tag{4.57}$$

Then when $b_u = 0$ and $b_d = 0$, (1.13) has at least two positive steady state solutions. In particular the condition (4.57) is satisfied if

$$0 < \frac{q}{d} < \frac{1}{L} \ln\left(\frac{\min_{y\in[0,L]} v_4(y)}{\max_{y\in[0,L]} v_3(y)}\right). \tag{4.58}$$

Proof. Using transform $u = e^{\alpha x} w$ and $v = e^{\alpha x} z$, the steady state equation in this case is of the form

$$\begin{cases} dw_{xx} + qw_x + \dfrac{A_b}{A_d}\mu z - \sigma w - m_1 w = 0, & 0 < x < L, \\ zg(x, e^{\alpha x} z) - m_2 z - \mu z + \dfrac{A_d}{A_b}\sigma w = 0, & 0 \leq x \leq L, \\ w_x(0) = 0, \quad w_x(L) = 0. \end{cases} \tag{4.59}$$

From Proposition 4.11, $(\overline{w}_2, \overline{z}_2) = (\theta_1 \max_{y\in[0,L]} e^{-\alpha y} r(y), \max_{y\in[0,L]} e^{-\alpha y} r(y))$ is an upper solution of (4.59). Set

$$\underline{w}_2 = \theta_1 \max_{y\in[0,L]} e^{-\alpha y} v_3(y), \quad \underline{z}_2 = \max_{y\in[0,L]} e^{-\alpha y} v_3(y).$$

Then from (4.57),

$$\begin{aligned} g(x, e^{\alpha x}\underline{z}_2) =& g(x, e^{\alpha x} \max_{y\in[0,L]} e^{-\alpha y} v_3(y)) \\ &\geq g(x, e^{\alpha x} e^{-\alpha x} v_3(x)) = g(x, v_3(x)) = m_2 + \mu - \frac{\mu\sigma}{\sigma + m_1}, \end{aligned}$$

we obtain that

$$\begin{cases} d\underline{w}_2'' + q\underline{w}_2' + \dfrac{A_b}{A_d}\mu\underline{z}_2 - \sigma\underline{w}_2 - m_1\underline{w}_2 = 0, & 0 < x < L, \\ \underline{z}_2 g(x, e^{\alpha x}\underline{z}_2) - m_2\underline{z}_2 - \mu\underline{z}_2 + \dfrac{A_d}{A_b}\sigma\underline{w}_2 \geq 0, & 0 \leq x \leq L, \\ \underline{w}_2'(0) = 0, \quad \underline{w}_2'(L) = 0. \end{cases}$$

So $(\underline{w}_2, \underline{z}_2)$ is a lower solution of (4.59), and we have $\underline{w}_2 < \overline{w}_2$, $\underline{z}_2 < \overline{z}_2$. Therefore (4.59) has at least one positive solution between $(\underline{w}_2, \underline{z}_2)$ and $(\overline{w}_2, \overline{z}_2)$. Moreover $(\underline{w}_1, \underline{z}_1) = (0, 0)$ is a lower solution of (4.59), and from Proposition 4.10, $(\overline{w}_1, \overline{z}_1)$ is an upper solution of (4.59), hence we have two pairs of upper and lower solutions which satisfy

$$(\underline{w}_1, \underline{z}_1) < (\overline{w}_1, \overline{z}_1) < (\underline{w}_2, \underline{z}_2) < (\overline{w}_2, \overline{z}_2).$$

From [4, Theorem 14.2], (4.59) has at least three nonnegative solutions, which implies that there exist at least two positive solutions. The condition (4.58) can be derived from (4.57) since

$$\max_{y \in [0,L]} e^{-\alpha y} v_3(y) \leq \max_{y \in [0,L]} v_3(y), \quad e^{-\alpha L} \min_{y \in [0,L]} v_4(y) \leq \min_{y \in [0,L]} e^{-\alpha y} v_4(y).$$

□

4.4 Numerical simulations

In this section we show some numerical simulation results to demonstrate our theoritical results proved above and also provide some further quantitative information on the dynamical behavior of the system (1.13). In particular we show the effect of the tranfer rate μ and advection q on the maximal steady states. In this section we always assume that

$$\begin{aligned} &f(x, v) = vg(x, v) = v(1 - v)(v - 0.4), \quad d = 0.02, \quad L = 10, \\ &m_1 = m_2 = 0.02, \quad \sigma = 0.2, \quad A_d(x) = A_b(x) = 1. \end{aligned} \tag{4.60}$$

and we consider the special case of (1.13):

$$\begin{cases} u_t = du_{xx} - qu_x + \dfrac{A_b}{A_d}\mu v - m_1 u, & 0 < x < L,\ t > 0, \\ v_t = v(1-v)(v-h) - m_2 v - \mu v + \dfrac{A_d}{A_b}\sigma u, & 0 \le x \le L,\ t > 0, \\ du_x(0,t) - qu(0,t) = 0, & t > 0, \\ du_x(L,t) - qu(L,t) = -b_d q u(L,t), & t > 0, \\ u(x,0) = u_0(x) \ge 0,\ v(x,0) = v_0(x) \ge 0, & x \in (0,L). \end{cases} \tag{4.61}$$

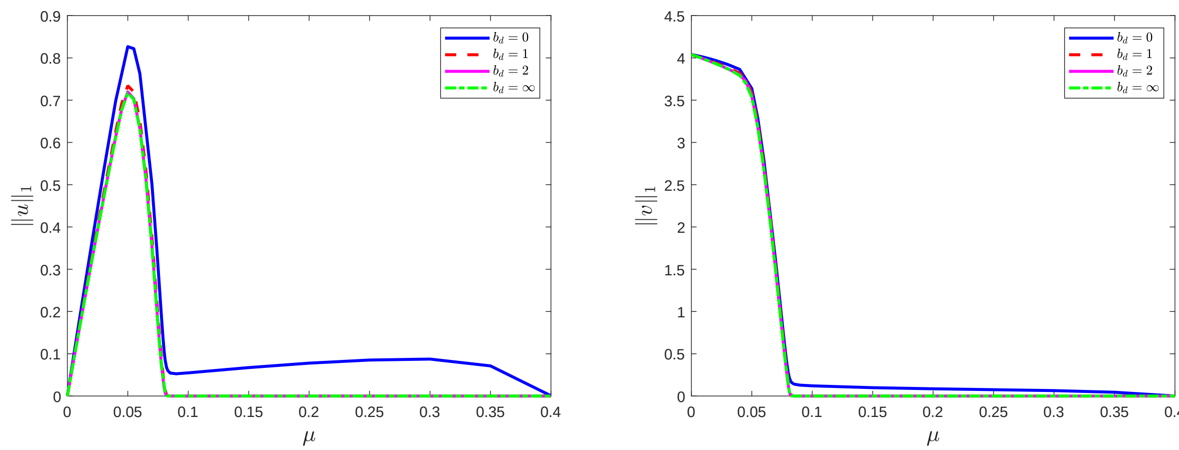

Figure 4.3: The total biomass of the maximal steady state solution of (4.61) with respect to the transfer rate μ under different boundary conditions. The horizontal axis is μ, the vertical axis are $\|u(\cdot,t)\|_1 = \int_0^L u(x,t)dx$ (Left) and $\|v(\cdot,t)\|_1 = \int_0^L v(x,t)dx$ (Right). Here the parameters satisfy (4.60), $q = 0.2$ and the initial condition is $u_0 = 0.2$, $v_0 = 0.2$.

Figure 4.3 shows the variation of total biomass of the maximal steady states for different b_d and varying transfer rate μ from the benthic zone to the drift zone. It can be observed from the right panel that The total biomass of the benthic population is always decreasing with respect to μ since it can be regarded as a loss of the benthic population. When $\mu = 0$, the drift population does not have the source of growing and it cannot live. At the lower μ level, with the increase of transfer rate μ, the drift population becomes larger, but after an optimal intermediate μ value (about $\mu^* \approx 0.05$) , the drift population starts to decline with respect to μ for the drift population. We can calculate the two threshold values $\mu_1 = \mu_2 = 0.77$ and $\mu_3 = 0.07$, defined in the conditions $(H1)$-$(H3)$. One can observe that in $(H3)$ regime

$(0 < \mu < \mu_3)$, the population persists robustly for all boundary conditions (see Theorem 4.14); and in $(H2)$ regime $(\mu_3 < \mu < \mu_2)$, the biomass is nearly zero for open environment and is larger than zero for closed environment (see Theorem 4.15 for a partial justification). Figure 4.3 only shows the biomass up to $\mu = 0.4$, and for $0.4 < \mu < \mu_2$, the biomass for even the NF/NF boundary condition becomes so small which cannot be distinguished from zero. For $\mu > \mu_2$ ($(H1)$ regime), the extinction of population is ensured in Theorem 2.8.

In Figure 4.4, the maximal steady state solutions under three types boundary conditions (NF/H, NF/FF, NF/FF) and for varying transfer rate μ are plotted. For all boundary conditions, the benthic population is decreasing in μ. The drift population is increasing in μ for $0 < \mu < \mu^*$ (μ^* is the peak transfer rate where the drift biomass reachs the maximum), and for $\mu^* < \mu < \mu_3$, the drift population is decreasing in downstream part but increasing in upstream part. Similarly in Figure 4.5, the maximal steady state solutions under three types boundary conditions (NF/H, NF/FF, NF/FF) and for varying advection rate q. One can observe that a larger advection rate leads to a larger benthic population for every point in the river, but for drift population, a larger advection rate decreases the downstream population and increases the upstream population.

Finally Figure 4.6 demonstrates the bistable nature of system (4.61) under NF/FF ($b_u = 0$ and $b_d = 1$) boundary condition and $(H3)$ is satisfied, and Figure 4.7 describes the bistable phenomenon under NF/NF ($b_u = b_d = 0$) boundary condition and $(H2)$ is satisfied. And when the cross-sectional areas of the benthic zone $A_b(x)$ and drift zone $A_b(x)$ are spatially heterogeneous, then the bistable structure is shown in Figure 4.8. The population becomes extinct when starting from small initial population (first panel in Figure 4.6, 4.7 and 4.8); and the population reaches the maximal steady state when starting from relatively large initial population (third panel in Figure 4.6, 4.7 and 4.8). And the second panel in Figure 4.6, 4.7 and 4.8 also shows a “stable” pattern with a transition layer. We conjecture that the transition layer solution is unstable and metastable (with a small positive eigenvalue), so the pattern can be observed for a long time in numerical simulation.

4.5 Conclusion

For a aquatic species that reproduce on the bottom of the river and release their larval stages into the water column, the longitudinal movement occurs only in the drift zone and individuals in the benthic zone in stream channel stays immobile. Through a benthic-drift model, we investigated the population persistence and extinction regarding the strength of interacting between zones. Moreover, this benthic-drift model has the feature of a coupled partial differential equation (PDE) for the drift population and an "ordinary differential equation" (ODE) for the benthic population. This degenerate model causes a lack of the compactness of the solution orbits, which brings extra obstacles in the analysis. To overcome these difficulties, we turn to the Kuratowski measure of noncompactness in order to use the Lyapunov function.

For single compartment reaction-diffusion-advection equation, when the growth rate exhibits logistic type, it is well-known that the dynamics is either the population extinction or convergence to a positive steady state (monostable). If the species follows the strong Allee effect growth, 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 [108].

Unlike the single compartment reaction-diffusion-advection equation with a strong Allee effect growth rate, in which the advection rate q plays a important role in the persistence/extinction dynamics, the benthic-drift model dynamics with strong Allee effect relies more critically on the strength of interacting between zones, especially the transfer rate from the benthic zone to the drift zone μ. In this paper, we show that how the transfer rates between benthic zone to the drift zone influence the population dynamics. We divided the μ (transfer rate from benthic zone to drift zone) and σ (transfer rate from drift zone to benthic zone) phase plane into regions and studied the dynamical behavior on these parameter regions. When we have a relatively large μ (in H1), population extinction will happen independent of the initial conditions, the boundary condition, the diffusive and advective movement and the transfer rate from the drift zone to the benthic zone σ. For small μ (in (H3)), for large initial conditions, population persistence will happen regardless of the boundary condition, the diffusive and advective movement and the transfer rate from the drift zone to the benthic zone σ. Along with the locally stability of the zero steady state solution, bistable dynamical behavior can be confirmed. When the transfer rate μ is in the intermediate range (in (H2)), the persistence or extinction depends on the diffusive and advective movement. And under closed environment, a multiplicity result for the steady state solutions is also obtained for small advection rate.

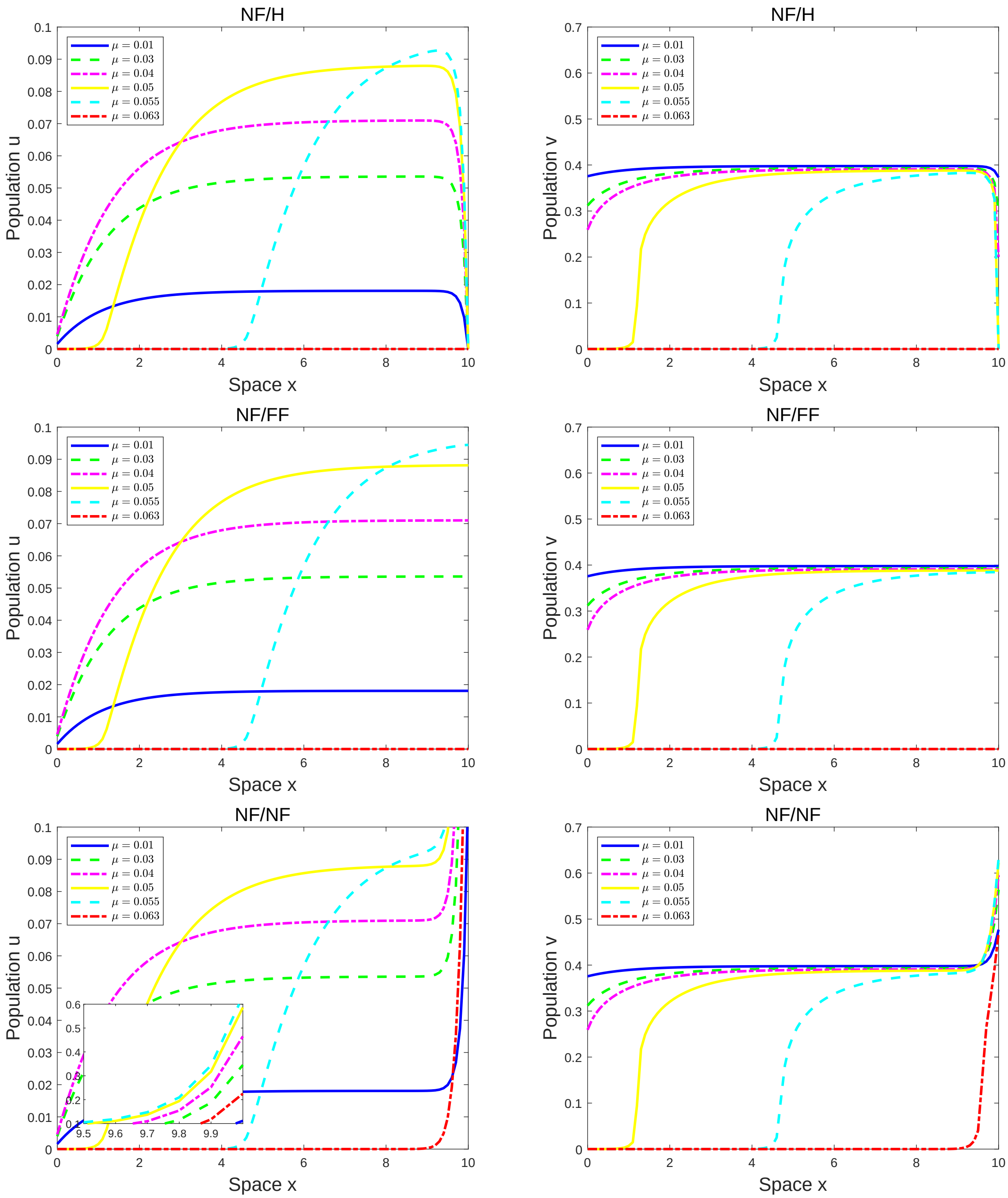

Figure 4.4: The dependence of maximal steady state solution of (4.61) on the varying transfer rate μ under three types boundary conditions. Here the parameters satisfy (4.60), $q = 0.2$, and the initial condition is $u_0 = 0.2$, $v_0 = 0.2$. Left: The drift population; Right: The benthic population.

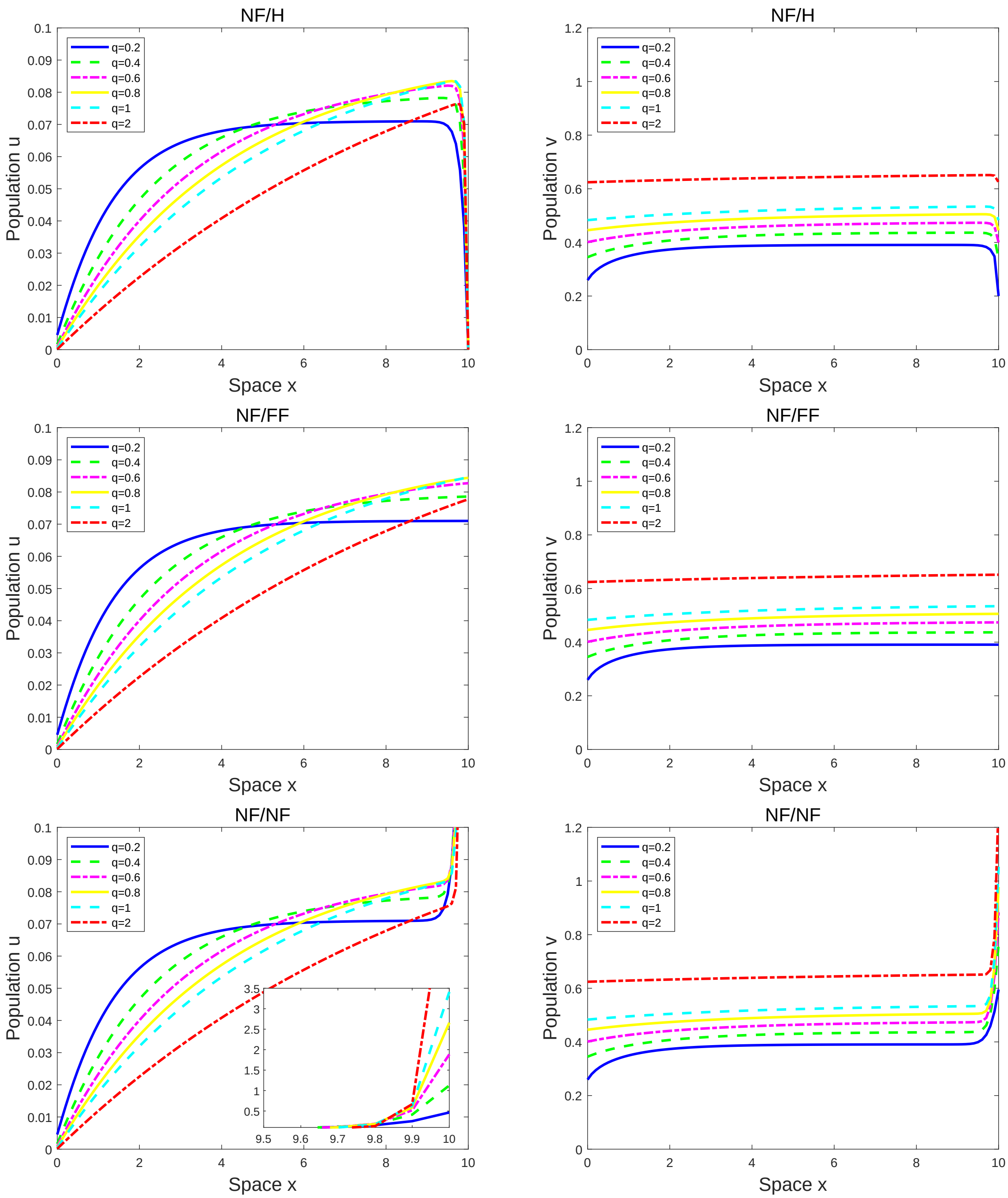

Figure 4.5: The dependence of maximal steady state solution of (4.61) on the varying advection rate q under three types boundary conditions. Here the parameters satisfy (4.60), $\mu = 0.04$, and the initial condition is $u_0 = 0.2$, $v_0 = 0.2$. Left: The drift population; Right: The benthic population.

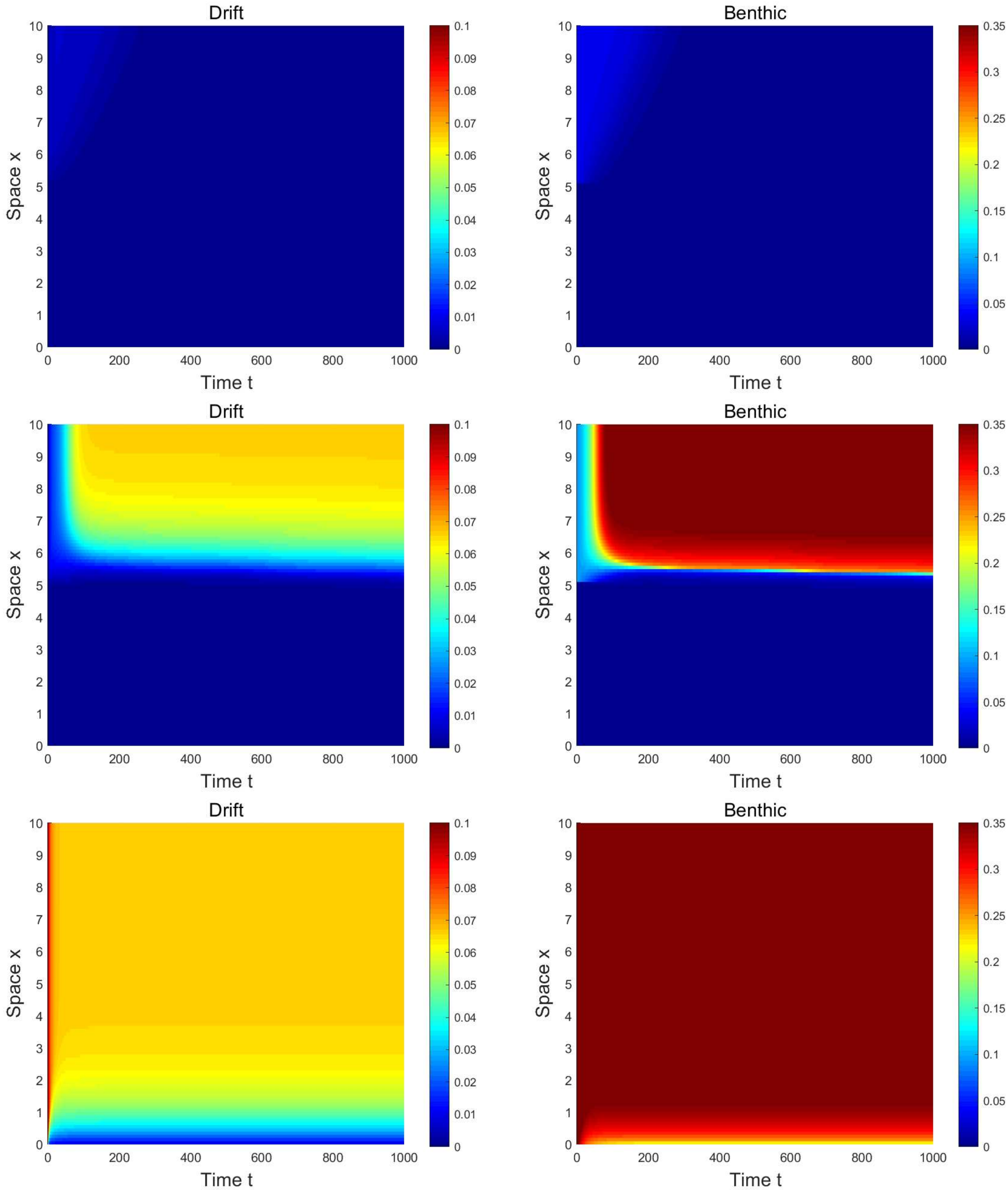

Figure 4.6: Bistable dynamics for different initial conditions. Here the parameters satisfy (4.60), $q = 0.11$, $\mu = 0.04$, $b_u = 0$, $b_d = 1$. The initial conditions from first row to thrid row are $u_0(x) = 0$, $v_0(x) = 0$ for $x \in [0, L/2]$ and $v_0(x) = 0.04$ for $x \in [L/2, L]$; $u_0(x) = 0$, $v_0(x) = 0$ for $x \in [0, L/2]$ and $v_0(x) = 0.1$ for $x \in [L/2, L]$; $u_0(x) = 0.1$, $v_0(x) = 0$ for $x \in [0, L/2]$ and $v_0(x) = 0.1$ for $x \in [L/2, L]$; $u_0(x) = 0.1$, $v_0(x) = 0.4$. Left: the drift population; Right: the benthic population.

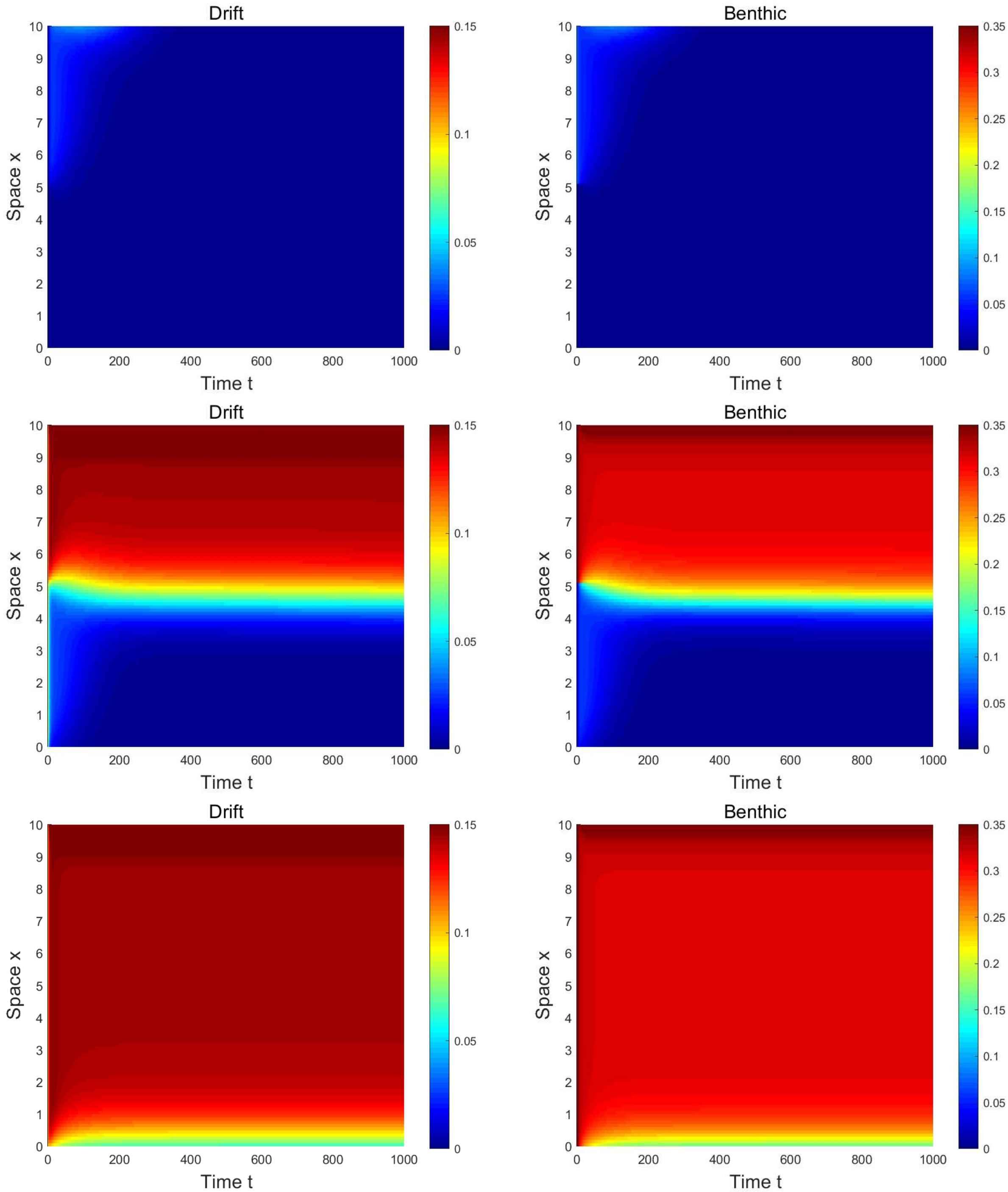

Figure 4.7: Bistable dynamics for different initial conditions. Here the parameters satisfy (4.60), $q = 0.025$, $\mu = 0.1$, $b_u = b_d = 0$. The initial conditions from first row to third row are $u_0(x) = 0$, $v_0(x) = 0$ for $x \in [0, L/2]$ and $v_0(x) = 0.08$ for $x \in [L/2, L]$; $u_0(x) = 0.1$, $v_0(x) = 0$ for $x \in [0, L/2]$ and $v_0(x) = 0.4$ for $x \in [L/2, L]$; $u_0(x) = 0.1$, $v_0(x) = 0.4$. Left: the drift population; Right: the benthic population.

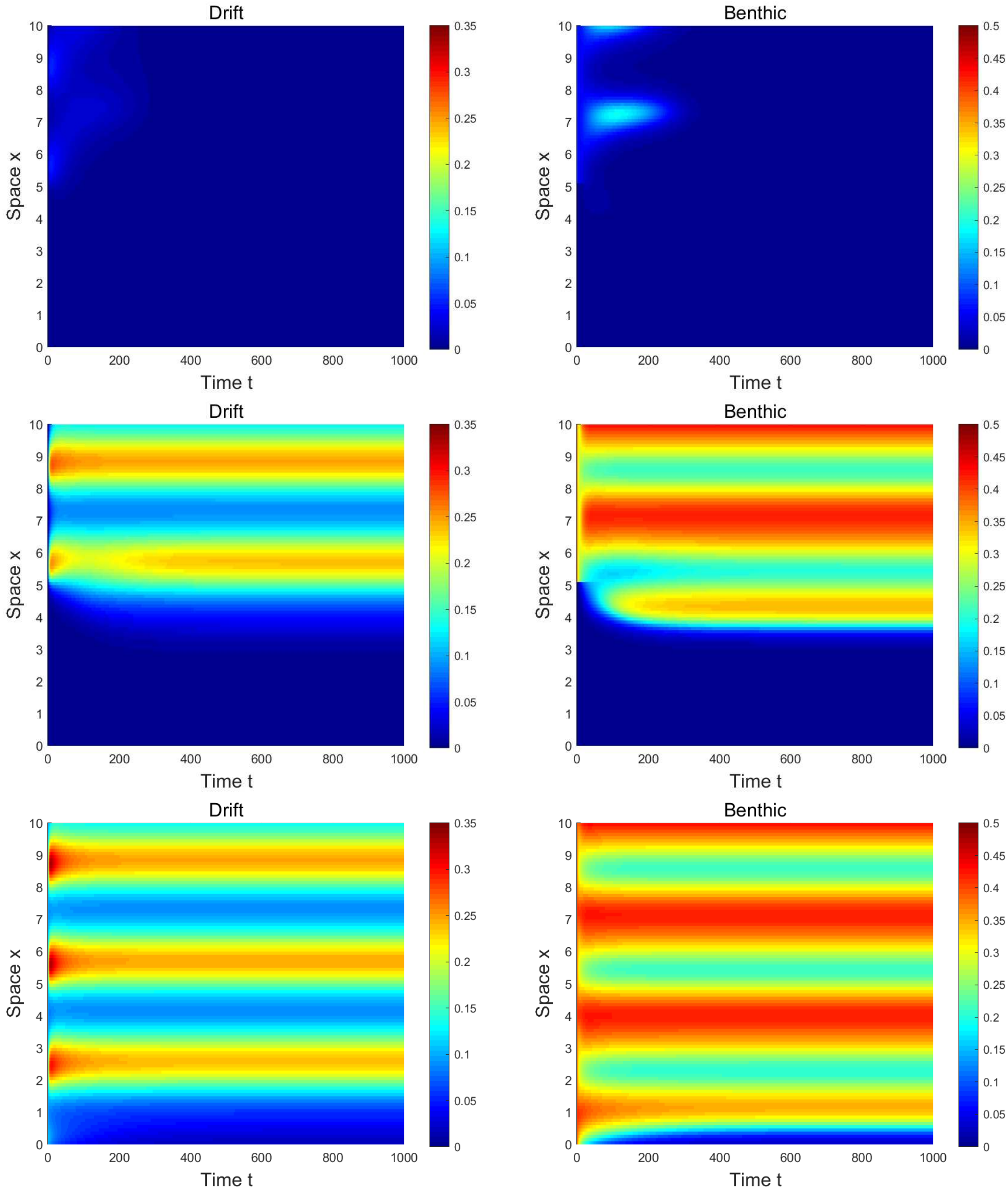

Figure 4.8: Bistable dynamics for different initial conditions. Here the parameters satisfy (4.60) (except $A_b(x)$ and $A_d(x)$), $q = 0.025$, $\mu = 0.1$, $A_d(x) = \sin 2x + 2$, $A_d(x) = \sin(2x - 10) + 2$. The initial conditions from first row to third row are $u_0(x) = 0$, $v_0(x) = 0$ for $x \in [0, L/2]$ and $v_0(x) = 0.1$ for $x \in [L/2, L]$; $u_0(x) = 0.08$, $v_0(x) = 0$ for $x \in [0, L/2]$ and $v_0(x) = 0.4$ for $x \in [L/2, L]$; $u_0(x) = 0.1$, $v_0(x) = 0.4$. Left: the drift population; Right: the benthic population.

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Vita

Yan Wang is an international student from Harbin, China. She completed her B.S and M.S in Applied Mathematics from Harbin Institute of Technology before coming to the U.S. She joined William and Mary to pursue a Ph.D. in Applied Science at in the Fall of 2014 and has been researching on mathematical modeling of stream population with strong Allee effect growth under the guidance of Professor Junping Shi from the Department of Mathematics at William & Mary.