ABSTRACT. We study a diffusion-reaction-advection equation describing population dynamics of aquatic organisms subject to a constant downstream drift in a bounded or semi-infinite domain. We analyze the nontrivial steady state solutions satisfying reflecting upstream and outflow downstream boundary conditions (Danckwerts’ boundary conditions). We determine the behavior of the domain size as a function of the upstream/downstream density, show stability of the steady state, and investigate how certain qualitative aspects of the steady-state solution depend on advection speed.

1 Introduction Streams, rivers and coastlines with longshore currents are aquatic ecosystems characterized by unidirectional water movement. As a result, many organisms that inhabit these systems are carried downstream by the bias in movement. Examples include plankton, algae, stream insects, or larvae of benthic organisms such as sea urchins. Despite this bias, populations resist washout and manage to persist over many generations in such advective environments. This biological phenomenon has been recognized and studied for more than half of a century, and is known as the “drift paradox” (see [15, 16]). The most commonly cited resolution for the paradox is that many stream insects have winged adult stages, during which individuals can travel upstream [22].

A different mechanism for persistence that does not require a winged adult stage was given by Speirs and Gurney [21]. Using a linear model, these authors showed that a sufficient amount of (unbiased) random movement can balance the biased movement and lead to population persistence. A similar (nonlinear) model with biased and unbiased movement arises in models for microbes in the gut [2] and in the study of phytoplankton blooms [8, 19]. Gravity causes phytoplankton to sink (biased) whereas diffusion in the water column gives rise to unbiased
movement. Huisman et al. obtained a variety of numerical results for such a model [8], several analytical results were recently given for a similar model by Kolokol’nikov et al. [9]. The model by Speirs and Gurney was recently extended to study more realistic situations by including a benthic compartment [14, 17], spatial heterogeneity [11] or a competing species [12].

Most of the results pertaining to streams and rivers cited above are based either on linear analysis [17, 21] or on numerical simulation [12]. The topic of this paper is to analytically study the underlying nonlinear equation, its nontrivial steady state and its dependence on parameters. More specifically, we study the (nondimensional) reaction-advection-diffusion equation

\[
\frac{\partial u}{\partial t} = \frac{\partial^2 u}{\partial x^2} - q \frac{\partial u}{\partial x} + u(1 - u),
\]

where \( u(t, x) \) is the population density at location \( x \) at time \( t \), and \( q \) is the advection speed. We consider this equation together with reflecting boundary conditions upstream, i.e., \( \frac{\partial u}{\partial x} = qu \) at \( x = 0 \), and “outflow” boundary conditions downstream, i.e., \( \frac{\partial u}{\partial x} = 0 \). A derivation of these boundary conditions from random walks together with a biological interpretation was given in [11].

Equation (1.1) is a generalization of the well-known and well-studied Fisher equation

\[
\frac{\partial u}{\partial t} = \frac{\partial^2 u}{\partial x^2} + u(1 - u),
\]

that describes unbiased random movement [6]. One typically considers this equation on a bounded domain \([0, L]\) with “hostile” boundary conditions \( u = 0 \) at \( x = 0 \) and \( x = L \). The steady-state solutions of (1.2) satisfy a two-dimensional system of ODEs that happens to be Hamiltonian (see, e.g., [10]). Using the explicitly available Hamiltonian function, one can show under what conditions nontrivial steady states exist, give explicit formulas for the domain length \( L \) and establish the bifurcation structure [10].

Unfortunately, the system with advection (1.1) is not Hamiltonian, and none of the analysis mentioned above carries over to the general case. The goal of this paper is to establish existence, uniqueness, stability and qualitative dependence on parameters of the nontrivial steady state of (1.1), using phase-plane methods for the steady-state equations (3.4). Some of our analysis is similar in spirit to the recent work by
Kolokol’nikov et al. [9], who studied a similar equation, but with zero-flux second boundary condition and a different nonlinear reaction term.

This paper is organized as follows. In Section 2, we briefly discuss the linear model and deduce the formula for the “critical domain size” $L^c$ (the minimal length of the interval for which the trivial steady state is unstable) in our context, i.e., with boundary conditions different from the ones used by Speirs and Gurney [21]. In Section 3, we introduce the nonlinear model and make some preliminary observations regarding existence and nonexistence of steady-state solutions. In Section 4, we analyze the behavior of the domain size $L = L_\mu$ or $L = L^c$ as a function of downstream density $\mu = u(L)$ or upstream density $\nu = u(0)$ respectively. We show that $L^c$ ($L_\mu$) is a strictly increasing function of $\nu$ (of $\mu$). Furthermore, $L_\mu$ approaches the critical domain size $L^c$ from the linear model as $\mu \to 0$ and goes to infinity as $\mu$ approaches the carrying capacity (scaled to one). In Section 5, we show existence and uniqueness of a nontrivial steady-state solution for $L > L^c$ for the case of finite and infinite ($L = \infty$) domains. We also show that the positive steady state solution is stable in case of finite domains. The remaining sections are devoted to the qualitative behavior of the positive steady state solution. In Sections 6 and 7, we show that the density at the steady state decreases pointwise for increasing advection $q$ for finite and infinite domains respectively. In Section 8, we investigate the conditions under which the steady-state profile has an inflection point and derive an approximate expression for the distance of the inflection point to the upstream boundary. In Section 9, we summarize our results, give their biological interpretation and present some real life examples.

One final comment is on order before we embark on the analysis. Some of the results presented here could be obtained by PDE methods, e.g., monotone iteration, maybe even in a more elegant way. The challenge that we set ourselves here was to remain within the theory of ODEs and phase-plane analysis and see how many of the results for the Hamiltonian system ($q = 0$) can still be obtained without the Hamiltonian structure available.

2 Model and its linearization

Let $u(t, x)$ be the population density at distance $x$ from the upstream boundary at time $t$. We consider the single population model in an advective environment, described by the reaction-diffusion-advection equation:

$$
\frac{\partial u}{\partial t} = D \frac{\partial^2 u}{\partial x^2} + Q \frac{\partial u}{\partial x} + ru \left( 1 - \frac{u}{K} \right).
$$

(2.1)
The first term on the right in (2.1) corresponds to diffusive movement of individuals (due to self-propelling and/or water turbulence) with diffusion coefficient $D$. The second term represents movement of the organisms that is caused by drift ($Q$ is the effective speed of the current). The third term reflects the assumption that the population grows logistically, with intrinsic growth rate $r$ and environmental carrying capacity $K$. We assume that all parameters are positive. We consider some biological examples in the last section of this paper.

In addition, we consider so-called “Danckwert’s boundary conditions”

\[
\begin{align*}
Q u(t, 0) - D \frac{\partial u}{\partial x}(t, 0) &= 0, \\
\frac{\partial u}{\partial x}(t, L) &= 0.
\end{align*}
\]

These boundary conditions are well-established in the context of so-called Plug Flow Tubular Reactors; see [1, p. 569] and models for nutrient transport in the gut [2]. They have also been derived from an individual random walk in [11].

The reflecting upstream boundary condition tells us that the individuals cannot cross the upstream boundary ($x = 0$) and move beyond the top of the stream. The downstream condition indicates that net out-flux from the domain is due to advection only and not to diffusion. This can be seen in a variety of ways. For example, if one considers the flux $J$ of individuals, as a combination of advective and diffusive fluxes,

\[
J = J_{\text{diff}} + J_{\text{adv}} = -D \frac{\partial u}{\partial x} + Qu,
\]

then this flux reduces to the advective flux at the boundary. The random-walk interpretation in [11] gives the same. Alternatively, if one considers the movement equation only, i.e., (2.1) with $r = 0$, and integrates over the domain, then one obtains

\[
\frac{d}{dt} \int_0^L u(t, x) \, dx = -Qu(L).
\]

Hence, the change is due to individuals leaving the domain by advection. Biologically, this situation may most closely describe a river flowing into nonadvective freshwater habitat, such as a lake. Flow takes individuals
into the lake, but since conditions in the lake are not hostile, individuals can also diffuse back and forth so that the net diffusive flux is zero.

Speirs and Gurney [21] studied the reaction-diffusion-advection equation with a linear growth term:

$$\frac{\partial u}{\partial t} = D \frac{\partial^2 u}{\partial x^2} - Q \frac{\partial u}{\partial x} + ru.$$  

Instead of the “outflow” boundary condition $\frac{\partial u}{\partial x}(t,L) = 0$, the authors considered “hostile” downstream boundary condition $u(t,L) = 0$, i.e., organisms are being removed from the system as soon as they reach the left border of domain.

In our case, we get the Speirs-Gurney equation (with outflow downstream boundary condition) if we linearize (2.1) at zero:

$$\begin{cases}
\frac{\partial u}{\partial t} = D \frac{\partial^2 u}{\partial x^2} - Q \frac{\partial u}{\partial x} + ru, \\
Qu(t,0) - D \frac{\partial u}{\partial x}(t,0) = 0, \\
\frac{\partial u}{\partial x}(t,L) = 0.
\end{cases}$$  

\textbf{Proposition 2.1.} The general solution of (2.3) is given by

$$u(t,x) = \sum_{k=1}^{\infty} e^{\lambda_k t} \left( A_k e^{\frac{\lambda_k}{2D} x} \cos \frac{\sqrt{4D(r - \lambda_k) - Q^2}}{2D} x \\
+ B_k e^{\frac{\lambda_k}{2D} x} \sin \frac{\sqrt{4D(r - \lambda_k) - Q^2}}{2D} x \right),$$

where $\lambda_k$ are eigenvalues of the operator

$$D \frac{\partial^2 f}{\partial x^2} - Q \frac{\partial f}{\partial x} + rf$$

with boundary conditions

$$Qf(0) - Df'(0) = 0, \quad f'(L) = 0.$$  

\textbf{Proof.} Standard separation of variables technique. \qed
Classical Sturm-Liouville theory states that the eigenvalues $\lambda_k$ above form an infinite decreasing sequence $\lambda_1 > \lambda_2 > \ldots$ [4]. If $\lambda_k$ are all negative, then the population goes extinct in the long term. On the other hand, if for some $k$ we have $\lambda_k > 0$, the population exhibits unbounded growth. Setting $\lambda_1 = 0$ and applying boundary conditions to the general solution of (2.3) gives us the threshold value for the domain size, referred to as critical domain size $L^c$:

$$L^c(Q) = \begin{cases} \arctan \left( \frac{Q \sqrt{4rD - Q^2}}{2rD - Q^2} \right), & 0 < Q \leq \sqrt{2rD}, \\ \pi + \arctan \left( \frac{Q \sqrt{4rD - Q^2}}{2rD - Q^2} \right), & \sqrt{2rD} < Q < 2\sqrt{rD}, \end{cases}$$

where

$$\theta = \frac{\sqrt{4rD - Q^2}}{2D}.$$

Note that for $Q = \sqrt{2rD}$, both formulas give us $L^c(\sqrt{2rD}) = \pi/2\theta$, and thus $L^c$ depends continuously on $Q$.

Remark 2.2. When advection reaches its critical value $Q_c = 2\sqrt{rD}$, the critical domain size becomes infinite and the entire population is washed downstream, i.e. persistence is not possible. For $Q < Q_c$ and $L < L^c$, the population goes extinct as well. For $Q < Q_c$ and $L > L^c$, the population in the linearized model experiences unlimited growth.

3 Nonlinear system, steady state solutions, and connection with the Fisher equation

We now consider the nonlinear model. We will make our first observations regarding the existence and nonexistence of a nontrivial steady-state solution as we vary the advection speed. We start by nondimensionalizing (2.1) and (2.2). We rescale the population density by the carrying capacity, time and space by characteristic time and length:

$$\tilde{u} = \frac{u}{K}, \quad \tilde{t} = rt, \quad \tilde{x} = \sqrt{\frac{r}{D}} x, \quad q = \frac{Q}{\sqrt{rD}}.$$
We omit the tildes for convenience, so that (2.1, 2.2) become

\[
\frac{\partial u}{\partial t} = \frac{\partial^2 u}{\partial x^2} - q \frac{\partial u}{\partial x} + u(1 - u),
\]

\[
qu(t, 0) - \frac{\partial u(t, 0)}{\partial x} = 0, \quad \frac{\partial u(t, L)}{\partial x} = 0.
\]

We investigate the properties of nonzero steady state solutions of (3.1), i.e., solutions that do not depend on time. Such a steady state solution satisfies

\[
u'' - qu' + u(1 - u) = 0
\]

with boundary conditions

\[
\begin{cases}
u' = qu, & x = 0, \\
u' = 0, & x = L.
\end{cases}
\]

Equation (3.2) is equivalent to the following system of two differential equations:

\[
\begin{cases}
u' = v, \\
v' = qv - u(1 - u),
\end{cases}
\]

with boundary conditions

\[
\begin{cases}v = qu, & x = 0, \\
v = 0, & x = L.
\end{cases}
\]

Hence, we are looking for orbits of (3.4) connecting the straight lines \(v = qu\) and \(v = 0\). Let us refer to such solutions as “connecting orbits.”

Next, we use the classical result of Fisher [6] and point out the similarity of equation (3.1) with the Fisher equation written in travelling wave coordinates.

**Remark 3.1.** (a) For Fisher’s equation (1.2) on the real line, there exists a special solution in form of a monotone, positive travelling wave \(u(t, x) = \phi(x + ct)\) (moving from the right to the left) iff \(c \geq 2 \sqrt{Dr}\)
In travelling wave coordinates, Fisher’s equation takes the form

\[ c\phi' = \phi'' + \phi(1 - \phi) \]  

with boundary conditions \( \phi(\infty) = 1 \) and \( \phi(-\infty) = 0 \). More specifically, a travelling wave solution of Fisher’s equation corresponds to a (unique) heteroclinic connection, located in the first quadrant of the \( uv \)-plane and connecting two fixed points: \((0, 0)\) and \((1, 0)\) of (3.4) obtained from (3.2).

Since equation (3.2) is the same as (3.6), with \( c = q \), we can use Fisher’s results in our setting. Note that one can consider a solution of the form \( u(t, x) = \phi(x - ct) \) with the boundary conditions \( \phi(-\infty) = 1 \) and \( \phi(\infty) = 0 \) (travelling wave moving from the left to the right). However the corresponding heteroclinic orbit is located in the fourth quadrant, and this is not applicable in our discussions.

(b) Note that, if \( q \geq 2 \) the fixed point \((0, 0)\) of the system (3.4) is an unstable node and we have “node-saddle” heteroclinic connection, the “traveling wave.” For \( q < 2 \), point \((0, 0)\) is an unstable spiral and we observe “focus-saddle” heteroclinic connection from \((0, 0)\) to \((1, 0)\), approaching the fixed point \((1, 0)\) from the first quadrant. There is no nonnegative travelling wave in this case.

First we show that when the advection speed is greater than the threshold value \( q^* = 2 \) (\( Q^* = 2\sqrt{D\tau} \) in the dimensional case), then the population will not be able to persist.

**Lemma 3.2.** There are no nontrivial solutions of (3.4, 3.5) for \( q \geq q^* \).

**Proof.** By Remark 3.1(a), we have a heteroclinic connection

\[ u = u_1(x), \quad v = v_1(x), \]

between the origin and the fixed point \((1, 0)\), located entirely in the first quadrant, approaching \((0, 0)\) and \((1, 0)\) as \( x \to -\infty \) and \( x \to \infty \), respectively.

Note that the slope of the vector field defined by (3.4) at any point in the \( uv \)-plane is given by

\[ \frac{v'}{u'} = \frac{qv - u(1 - u)}{v} = q - \frac{u(1 - u)}{v} < q. \]

Thus for any \( 0 < u < 1 \) and \( v > 0 \), the slope of any solution of (3.4) (including the heteroclinic orbit) is less than \( q \). Therefore, for \( u > 0 \), the line \( v = qu \) will always stay above the curve \( u = u_1(x), v = v_1(x) \).
Suppose there exists a solution of (3.4) that starts at \( v = qu \) for \( x = 0 \) and reaches \( v = 0 \) when \( x = L \) for some \( L > 0 \). In this case the solution (connecting orbit) must intersect \( v = 0 \) when \( u \in [0, 1] \). Indeed, if \( u > 1 \), then the slope of the vector field on \( \{ v = 0 \} \) is positive, and we will not be able to reach \( v = 0 \). Thus, since the connecting orbit reaches the segment \([0, 1]\) of \( \{ v = 0 \} \), it must intersect the heteroclinic orbit or pass through the fixed point. Neither one can happen, because two solution curves cannot intersect (by uniqueness), and the fixed point \((1,0)\) cannot be reached for a finite \( L \).

From here on, we assume that \( 0 \leq q < q^* = 2 \). We show that when advection is less than critical, there are nontrivial steady states for some domain size \( L \).

**Lemma 3.3.** For any \( 0 \leq q < q^* \), there exists \( L > 0 \) for which (3.4, 3.5) has a nontrivial solution.

**Proof.** The linearization of system (3.4) at \((0,0)\) is given by

\[
\begin{align*}
\frac{du}{dx} &= v, \\
\frac{dv}{dx} &= qv - u.
\end{align*}
\]

The Jacobian of this system has the two complex roots \( \lambda_{1,2} = \frac{q \pm \sqrt{q^2 - 4}}{2} \). Therefore the origin of the linear system is an unstable focus. By Grobman-Hartman Theorem (see [18]), the origin for the nonlinear system is an unstable focus as well. Thus, there exist solutions for appropriately chosen \( L \). Namely, in a small neighborhood of the origin, the trajectories of system (3.4) spiral away from the origin and cross both lines corresponding to the boundary conditions. Consequently, there exist solutions of the nonlinear system (3.4) that start on the line \( \{ v = qu \} \) and end on the line \( \{ v = 0 \} \) (second boundary condition).

4 More on steady state: domain size as the function of upstream/downstream density

In this section, we analyze the relationship between the domain size \( L \) and the upstream/downstream density in the case of a positive steady state of our model. Essentially, we show that higher density corresponds to larger domains.

Let \((u_1(x), v_1(x))\) be a solution of

\[
\begin{align*}
\frac{du}{dx} &= v, \\
\frac{dv}{dx} &= qv - u(1-u),
\end{align*}
\]

From here on, we assume that \( 0 \leq q < q^* = 2 \). We show that when advection is less than critical, there are nontrivial steady states for some domain size \( L \).

**Lemma 3.3.** For any \( 0 \leq q < q^* \), there exists \( L > 0 \) for which (3.4, 3.5) has a nontrivial solution.

**Proof.** The linearization of system (3.4) at \((0,0)\) is given by

\[
\begin{align*}
\frac{du}{dx} &= v, \\
\frac{dv}{dx} &= qv - u.
\end{align*}
\]

The Jacobian of this system has the two complex roots \( \lambda_{1,2} = \frac{q \pm \sqrt{q^2 - 4}}{2} \). Therefore the origin of the linear system is an unstable focus. By Grobman-Hartman Theorem (see [18]), the origin for the nonlinear system is an unstable focus as well. Thus, there exist solutions for appropriately chosen \( L \). Namely, in a small neighborhood of the origin, the trajectories of system (3.4) spiral away from the origin and cross both lines corresponding to the boundary conditions. Consequently, there exist solutions of the nonlinear system (3.4) that start on the line \( \{ v = qu \} \) and end on the line \( \{ v = 0 \} \) (second boundary condition).

4 More on steady state: domain size as the function of upstream/downstream density

In this section, we analyze the relationship between the domain size \( L \) and the upstream/downstream density in the case of a positive steady state of our model. Essentially, we show that higher density corresponds to larger domains.

Let \((u_1(x), v_1(x))\) be a solution of

\[
\begin{align*}
\frac{du}{dx} &= v, \\
\frac{dv}{dx} &= qv - u(1-u),
\end{align*}
\]
satisfying \((u_1(-\infty), v_1(-\infty)) = (0, 0)\) and \((u_1(\infty), v_1(\infty)) = (1, 0)\). Such a solution exists (and its orbit is unique) by Remark 3.1(b). Since such a curve (the heteroclinic connection) will necessarily intersect the line \(v = qu\), we may assume that \(v_1(0) = qu_1(0)\), and \(u_1(x), v_1(x) > 0\) for \(x > 0\) (i.e., the “last” intersection of heteroclinic connection with \(\{v = qu\}\) happens when \(x = 0\)). Then such a solution is unique.

Let \(\nu_{\max} = u_1(0)\). For any \(0 < \nu < \nu_{\max}\) let \((u_\nu(x), v_\nu(x))\) be the (unique) solution of (4.1) satisfying \((u_\nu(0), v_\nu(0)) = (\nu, q\nu)\). (see Figure 4.1 for illustration).

Considering the region bounded by the line \(v = qu\), the positive \(u\)-axis, and the heteroclinic connection, we see that the curve \((u_\nu(x), v_\nu(x))\) will eventually cross the \(u\)-axis between \(u = 0\) and \(u = 1\). For any \(0 < \nu < \nu_{\max}\), let \(L^\nu > 0\) be such that \(v_\nu(L^\nu) = 0\). Let \(\mu_\nu = u_\nu(L^\nu)\). Then \(0 < \mu_\nu < 1\) (again, see Figure 4.1). Note that \((u_\nu(x), v_\nu(x))\) is a continuous function of \(x\) and \(\nu\) (e.g., see [18, p. 78]), and hence both \(L^\nu\) (as the solution of \(v_\nu(x) = 0\)) and \(\mu_\nu = u_\nu(L^\nu)\) are continuous functions of \(\nu \in (0, \nu_{\max})\).

\[\text{FIGURE 4.1: Connecting orbit for a finite domain and heteroclinic orbit in the } uv\text{-plane.}\]

In this and later sections of the paper, some proofs are more conveniently formulated using upstream density \(\nu\) whereas others become easier using downstream density \(\mu\). The following lemma connects the two parameters.
Lemma 4.1. The mapping $\nu \mapsto \mu_\nu$ is a continuous strictly increasing function from $(0, \nu_{\text{max}})$ onto $(0, 1)$. In particular, $\lim_{\nu \to 0} \mu_\nu = 0$ and $\lim_{\nu \to \nu_{\text{max}}} \mu_\nu = 1$.

Proof. Continuity is observed above, and the fact that $\mu_\nu$ is strictly increasing with respect to $\nu$ follows from the observation that solution curves of (4.1) do not intersect. Note for any $0 < \mu < 1$ there exists a solution curve of (4.1) passing through $(\mu, 0)$. It will necessarily pass through a point $(\nu, q\nu)$ for some $0 < \nu < \nu_{\text{max}}$. Hence, $\mu = \mu_\nu$, and the mapping $\nu \mapsto \mu_\nu$ is onto. $\square$

For $0 < \mu < 1$ let $L_\mu = L_\nu$ where $\mu = \mu_\nu$. So, $L_\mu$ is a continuous function of $\mu \in (0, 1)$. Now, we look at the behavior of $L_\mu$ as $\mu \to 0$. Our goal is to prove that $\lim_{\mu \to 0} L_\mu = L^c$, where $L^c$ is the critical domain size for the linear system, given by (2.4).

It is slightly more convenient to consider the change of variables $x \mapsto -L + x$, i.e., we consider the boundary conditions $v(0) = 0, v(-L_\mu) = q\nu(-L_\mu)$. The solution of the nonlinear system (3.4) is given by the variation of constants formula as

$$
\begin{bmatrix}
u(x) \\
u(x)
\end{bmatrix} = e^{Ax} \begin{bmatrix}
u(0) \\
u(0)
\end{bmatrix} + \int_0^x e^{A(x-s)} \begin{bmatrix}0 \\
u^2(s)
\end{bmatrix} ds, \quad A = \begin{bmatrix}0 & 1 \\
-1 & q
\end{bmatrix}.
$$

We denote by $[\hat{u}, \hat{v}]^T$ the solution of the linearized system (3.7) with $\hat{u} = 1, \hat{v} = 0$. Then $\hat{v}(-L^c) = q\nu(-L^c)$. The solution with $\hat{u} = \mu, \hat{v} = 0$ is given by $\mu[\hat{u}, \hat{v}]^T$.

If $u(0) = \mu$, then $u(x) < \mu$ for all $x < 0$. Hence, we can bound the distance between the solution of the nonlinear problem and the linear problem, starting at $(\mu, 0)$ for $x = -L_\mu$ from above by

$$
\|u(x) - \mu \hat{u}(x), v(x) - \mu \hat{v}(x)\| \leq \mu^2 \left\| \int_0^x e^{A(x-s)} ds \right\|.
$$

Therefore, there is a constant $C > 0$, for which

$$
|\mu \hat{v}(-L_\mu) - q\mu \hat{u}(-L_\mu)| \leq \mu^2 C.
$$

Since the solution of the linear problem satisfies the condition $\hat{v}(-L^c) = q\hat{u}(-L^c)$, we have proved the following theorem.

Theorem 4.2. $L_\mu \to L^c$ as $\mu \to 0$ (equivalently, $L_\nu \to L^c$ as $\nu \to 0$).
Remark 4.3. Figure 4.2 shows the graph of $L^\nu$ vs. $\nu$ for $q = 1$, obtained numerically. Note that by (2.4) for $q = 1$, $L^\nu(1) = \frac{2\nu}{3\sqrt{\nu}} \approx 1.2$, which agrees with the graph. Note also that $L^\nu$ appears to increase with $\nu$, and goes to infinity as $\nu$ approaches a threshold value $\nu_{\text{max}} \approx 0.212$.

Next, we give an analytical proof that $L^\nu$ is an increasing function of $\nu$ (as suggested by the numerics), following the idea of the proof of Lemma 2.1 in [3].

**Proposition 4.4.** If $\nu_1 < \nu_2 < \nu_{\text{max}}$, then $L^{\nu_1} < L^{\nu_2}$.

**Proof.** Let $u(x)$ be the steady state solution of (1.1). Then

$$-(e^{-q^2 x_{\nu_2}})_{x x} u_{\nu_2} = -e^{-q^2} (-qu_{x} + u_{xx}) = e^{-q^2} u(1 - u).$$

Thus the following equalities take place:

$$-(e^{-q^2 u_{\nu_2}^\nu_1})_{x x} u^\nu_2 = e^{-q^2} u^\nu_1 (1 - u^\nu_1) u^\nu_2,$$

$$-(e^{-q^2 u_{\nu_2}^\nu_1})_{x x} u^\nu_1 = e^{-q^2} u^\nu_2 (1 - u^\nu_2) u^\nu_1.$$ 

Taking difference between the above expressions and then integrating it between 0 and any $\alpha \in (0, \min(L^{\nu_1}, L^{\nu_2})]$ we obtain
\[
e^{-q x} \left[u_{x}^{2}(x)u^{2_{1}}(x) - u_{x}^{2_{1}}(x)u^{2_{2}}(x)\right] \bigg|_{0}^{\alpha} \\
= \int_{0}^{\alpha} e^{-q x} u^{2_{1}}(x)u^{2_{2}}(x)(u^{2_{2}}(x) - u^{2_{1}}(x)) \, dx.
\]

Using the boundary conditions at \( x = 0 \) we get

\begin{equation}
(4.2) \quad e^{-q x} \left[u_{x}^{2_{1}}(\alpha)u^{2_{1}}(\alpha) - u_{x}^{2_{1}}(\alpha)u^{2_{2}}(\alpha)\right] \\
= \int_{0}^{\alpha} e^{-q x} u^{2_{1}}(x)u^{2_{2}}(x)(u^{2_{2}}(x) - u^{2_{1}}(x)) \, dx.
\end{equation}

Next we want to show that for all \( x \in [0, \min(L^{v_{1}}, L^{v_{2}})] \) \( u^{v_{1}}(x) < u^{v_{2}}(x) \). Note that since \( u^{v_{1}}(0) = \nu_{1} < \nu_{2} = u^{v_{2}}(0) \) this is true for \( x = 0 \).

Suppose the statement is not true, then there exists \( 0 < \beta \leq \min(L^{v_{1}}, L^{v_{2}}) \) such that \( u^{v_{1}}(x) < u^{v_{2}}(x) \) for \( x \in [0, \beta) \), but \( u^{v_{1}}(\beta) = u^{v_{2}}(\beta) \). Then taking \( \alpha = \beta \) in (4.2) and using

\[
u^{v_{1}}(\beta) = u^{v_{2}}(\beta),
\]

we get

\begin{equation}
(4.3) \quad e^{-q \beta} u^{v_{1}}(\beta) \left[u_{x}^{v_{2}}(\beta) - u_{x}^{v_{1}}(\beta)\right] \\
= \int_{0}^{\beta} e^{-q x} u^{2_{1}}(x)u^{2_{2}}(x)(u^{2_{2}}(x) - u^{2_{1}}(x)) \, dx.
\end{equation}

Note that the right hand side of (4.3) is positive, and therefore \( u_{x}^{v_{2}}(\beta) > u_{x}^{v_{1}}(\beta) \). On the other hand, for \( z(x) = u^{v_{2}}(x) - u^{v_{1}}(x) \) we have \( z(x) > 0 \) for \( x \in [0, \beta) \) and \( z(\beta) = 0 \), which implies \( z'(\beta) = u_{x}^{v_{2}}(\beta) - u_{x}^{v_{1}}(\beta) \leq 0 \), a contradiction. Thus we have proved that for any \( x \in [0, \min(L^{v_{1}}, L^{v_{2}})] \) \( u^{v_{1}}(x) < u^{v_{2}}(x) \).

Now, suppose \( L^{v_{2}} \leq L^{v_{1}} \), so \( \min(L^{v_{1}}, L^{v_{2}}) = L^{v_{2}} \). Then taking (4.2) with \( \alpha = L^{v_{2}} \) and using the boundary condition \( u_{x}^{v_{1}}(L^{v_{2}}) = 0 \), we get

\[
e^{-q L^{v_{2}}} \left[-u_{x}^{v_{2}}(L^{v_{2}})u^{v_{2}}(L^{v_{2}})\right] \\
= \int_{0}^{L^{v_{2}}} e^{-q x} u^{2_{1}}(x)u^{2_{2}}(x)(u^{2_{2}}(x) - u^{2_{1}}(x)) \, dx > 0.
\]

In the above equality, the right hand side is positive since \( u^{v_{2}}(x) > u^{v_{1}}(x) \) on \([0, L^{v_{2}}] \), while the left hand side is negative, a contradiction. Thus \( L^{v_{1}} < L^{v_{2}} \).
Finally, we look at the behavior of $L'$ as $\nu \to \nu_{\text{max}}$, or, equivalently, the behavior of $L_\mu$ as $\mu \to 1$. In the following theorem we confirm the numerical observations made in Remark 4.3.

**Theorem 4.5.** $L_\mu \to \infty$ as $\mu \to 1$ (equivalently, $L' \to \infty$ as $\nu \to \nu_{\text{max}}$).

**Proof.** We use the standard result on continuous dependence on initial data to prove this theorem; see, e.g., [18, Theorem 1, Section 2.3]. Pick any $0 < X < \infty$ and $\epsilon > 0$. Since $(1, 0)$ is a steady state, we can pick $\delta > 0$ small enough so that the solution with initial data $(\mu, 0)$ and $|\mu - 1| < \delta$ remains within $\epsilon$ of $(1, 0)$ up to "time" $X$. Hence, as $\mu \to 1$, it will take the solution arbitrarily long to leave an $\epsilon$-neighborhood of $(1, 0)$. In particular, $L_\mu \to \infty$.

5 Existence, uniqueness and stability of the steady state

We use the results about $L'$ to show existence and uniqueness of the solution of (3.4, 3.5) for any $L > L^c$.

**Theorem 5.1.** For any $L > L^c$ (3.4, 3.5) has a unique positive solution. Equivalently, for any $L > L^c$ (3.1) has a unique positive steady state.

**Proof. Case 1:** finite domain.

We know that $L'$ (as a function of $\nu$) is continuous and increasing on $(0, \nu_{\text{max}})$. It has finite limit $L'$ at 0 and goes to infinity as $\nu \to \nu_{\text{max}}$. Clearly, for any $L > L^c$, there is exactly one $\nu \in (0, \nu_{\text{max}})$ such that $L' = L$. By the definition of $L'$, this means that there exists $(u(x), v(x))$ satisfying (3.4, 3.5), such that $(u(0), v(0)) = (\nu, q\nu)$. Since $\nu \neq 0$, this solution is positive. Moreover, such a solution is unique (as a solution of an initial value problem).

**Case 2:** infinite domain.

We now turn to the case of infinite domain. Suppose $0 \leq q < 2$. We know that the solution $(u_1(x), v_1(x))$ of (4.1) with $u_1(0) = \nu_{\text{max}}$ satisfies

$$\lim_{x \to \infty} (u_1(x), v_1(x)) = (1, 0).$$

This implies existence of a steady state solution. Uniqueness follows from the fact that there is a unique solution of (4.1) satisfying $(u(0), v(0)) = (\nu_{\text{max}}, q\nu_{\text{max}})$, and if the solution does not pass through this point, it either reaches $u$-axis in finite "time" $L$, or does not approach to it at all.

Hence, we have
Theorem 5.2. For any $0 \leq q < 2$ there exists a unique solution $(u(x), v(x))$ of (4.1) satisfying $v(0) = qu(0)$ and $v(\infty) = 0$.

Our next goal is to prove stability of the positive steady state solution of (3.1) (when it exists). We linearize around the steady state, and make the ansatz $u(t, x) = u(x) + \phi(x)e^{-\lambda t}$. Substituting into (3.1) and keeping the leading order terms, gives the following eigenvalue problem:

$$
\begin{align*}
-\lambda \phi(x) &= \phi''(x) - q\phi'(x) + \phi(x)(1 - 2u(x)), \\
\phi'(0) &= q\phi(0), \\
\phi'(L) &= 0.
\end{align*}
$$

To eliminate the advection term, we consider $\psi(x) = e^{-\frac{q}{2}x}\phi(x)$. Then (5.1) becomes

$$
\begin{align*}
\psi''(x) + \left(1 - \frac{q^2}{4} - 2u(x) + \lambda\right)\psi(x) &= 0, \\
\psi'(0) - \frac{q}{2}\psi(0) &= 0, \\
\psi'(L) + \frac{q}{2}\psi(L) &= 0.
\end{align*}
$$

This problem has the same eigenvalues as (5.1). They form an increasing sequence $\lambda_1 < \lambda_2 < \ldots$ [4]. To prove stability we need to show $\lambda_1 > 0$. Suppose $\psi_1(x)$ is the eigenfunction corresponding to the dominant eigenvalue $\lambda_1$. From classical Sturm-Liouville theory it follows that $\psi_1(x)$ is of one sign in $[0, L]$, so we may assume that $\psi_1(x) > 0$ for any $x \in (0, L)$.

Let $w(x) = e^{-\frac{q}{2}x}u(x)$. Substituting into (3.2) we get

$$
\begin{align*}
w'''(x) + \left(1 - \frac{q^2}{4}\right)w(x) - e^{\frac{q}{2}x}w(x) &= 0, \\
w'(0) - \frac{q}{2}w(0) &= 0, \\
w'(L) + \frac{q}{2}w(L) &= 0.
\end{align*}
$$

Multiplying the equations in (5.3) by $\psi_1(x)$, and in (5.2) by $w(x)$, integrating between 0 and $L$, and taking the difference of the two expressions, we get
\[
\int_0^L \psi''_1(x) w(x) \, dx - \int_0^L w''(x) \psi_1(x) \, dx + \lambda_1 \int_0^L \psi_1(x) w(x) \, dx \\
- 2 \int_0^L u(x) \psi_1(x) w(x) \, dx + \int_0^L e^{\frac{q^2}{2} (w(x))^2} \psi_1(x) \, dx = 0.
\]

Note that
\[
\int_0^L \psi''_1(x) w(x) \, dx - \int_0^L \psi_1(x) w''(x) \, dx \\
= \left( \psi'_1(x) w(x) \right|_0^L - \int_0^L \psi'_1(x) w'(x) \, dx \right) \\
- \left( \psi_1(x) w'(x) \right|_0^L - \int_0^L \psi_1(x) w'(x) \, dx \right) \\
= -\frac{q}{2} \psi_1(L) w(L) - \psi'_1(0) w(0) \\
- \left( -\frac{q}{2} w(L) \psi_1(L) - w'(0) \psi_1(0) \right) = 0.
\]

Also note that \( e^{\frac{q^2}{2} (w(x))^2} = u(x) w(x) \). Thus we have
\[
\lambda_1 \int_0^L \psi_1(x) w(x) \, dx - \int_0^L u(x) w(x) \psi_1(x) \, dx = 0,
\]
or
\[
\lambda_1 = \frac{\int_0^L u(x) w(x) \psi_1(x) \, dx}{\int_0^L \psi_1(x) w(x) \, dx} > 0.
\]

With this result on eigenvalues, we are ready to prove stability of the steady state.

**Theorem 5.3.** The positive steady state solution \( u = u^*(x) \) of (3.1) with \( 0 < L < \infty \) is stable.

**Proof.** The operator \( A = \partial^2 / \partial x^2 \), defines an analytic semigroup on \( L^1(0, L) \) with domain
\[
\mathcal{D} = \{ U \in W^{2,1}(0, L) | U_x(0) - q_1 U(0) = 0, U_x(L) + q_1 U(L) = 0 \},
\]
\((q_1 = q/2)\) whose spectrum equals the point spectrum; see [5, Section 4b), Chap. VI]. The semigroup generated by \( A + (1 - q_1^2 - 2w^*) I \)
is also analytic so that the spectral mapping theorem applies ([5, 3.12, Chap. IV]). By the preceding eigenvalue calculation and Theorem 11.20 in [20], the steady state \( u^* \) is linearly stable, and by Theorem 11.22 in [20] it is stable.

6 Dependence of the steady state on advection speed for infinite domains

In this section, we investigate how changes in advection affect the steady state profile in the case of infinite domain.

Consider the diffusion-advection-reaction equation with logistic growth term, reflecting boundary condition upstream and no-flux condition at \( \infty \).

\[
\begin{align*}
\frac{\partial u}{\partial t} &= \frac{\partial^2 u}{\partial x^2} - q \frac{\partial u}{\partial x} + u(1-u), \\
qu(t,0) &= \frac{\partial u(t,0)}{\partial x} = 0, \\
\lim_{x \to \infty} \frac{\partial u(t,x)}{\partial x} &= 0.
\end{align*}
\]

We are interested in the steady state solutions, i.e., we set \( u_t = 0 \) and \( u = u(x) \). Thus we consider the equation \( u'' - qu' + u(1-u) = 0 \), or written as a first order system

\[
\begin{align*}
u' &= v, \\
v' &= qu - u(1-u).
\end{align*}
\]

The above system has two fixed points: \((0,0)\) and \((1,0)\). It is known (see Remark 3.1b) that for \( q < q^* (= 2) \) the origin is an unstable spiral and \((1,0)\) is a saddle point. The heteroclinic orbit that connects these two fixed points also intersects the line corresponding to boundary condition \( v = qu \), in the first quadrant of the \( uv \)-space. More specifically, there exists an orbit \((u_q, v_q)\) such that

\[
\begin{align*}v_q(0) &= qu_q(0) \\
\lim_{x \to \infty} (u_q(x), v_q(x)) &= (1,0).
\end{align*}
\]

We have changed notations to stress the fact that we study dependence of steady states on advection speeds, assuming that \( \mu = 1 \). Thus we are interested in the behavior of \((u_q(x), v_q(x))\) with respect to the
advection speed $q$. We may view this orbit as the graph of $v = v_q(u)$ (since $u'(x) = v(x) > 0$ in the first quadrant). Note that the curve $v = v_q(u)$ is the stable manifold of the fixed point $(1, 0)$. Therefore, at this point, the curve is tangent to an eigenvector of the Jacobian of (6.2) at $(1, 0)$ corresponding to the negative eigenvalue. Thus we can find the slope of $v = v_q(u)$ at $u = 1$ by analyzing that Jacobian. Namely, we have

$$J(u, v) = \begin{pmatrix} 0 & 1 \\ -1 + 2u & q \end{pmatrix}$$

and

$$J(1, 0) = \begin{pmatrix} 0 & 1 \\ 1 & q \end{pmatrix}.$$

The eigenvalues of $J(1, 0)$ are

$$\lambda_1 = \frac{q - \sqrt{q^2 + 4}}{2} < 0 \quad \text{and} \quad \lambda_2 = \frac{q + \sqrt{q^2 + 4}}{2} > 0.$$

An eigenvector corresponding to $\lambda_1$ is given by $\bar{v}_1 = (1, \frac{q - \sqrt{q^2 + 4}}{2})$. Thus the slope of $v = v_q(u)$ at $(1, 0)$ is $m(q) = \frac{q - \sqrt{q^2 + 4}}{2}$.

In the following, let $2 > q_1 > q_2$.

**Lemma 6.1.** $m(q_1) > m(q_2)$.

**Proof.** Note that $m'(q) = \frac{1}{q} \left(1 - \frac{q}{\sqrt{q^2 + 4}}\right) > 0$. Therefore, $m(q)$ is an increasing function of $q$ and $m(q_1) > m(q_2)$.

**Lemma 6.2.** There exists $0 < u^* < 1$ such that $v_{q_1}(u) < v_{q_2}(u)$ for all $u \in (u^*, 1)$.

**Proof.** Let $w(u) = v_{q_1}(u) - v_{q_2}(u)$. The statement now follows from $w(1) = 0$ and $w'(1) = v'_{q_1}(1) - v'_{q_2}(1) = m(q_1) - m(q_2) > 0$.

**Lemma 6.3.** $v_{q_1}(u) < v_{q_2}(u)$ for all $\max(u_{q_1}(0), u_{q_2}(0)) \leq u < 1$ (common domain of $v_{q_1}(u)$ and $v_{q_2}(u)$).

**Proof.** We know that $v_{q_1}(u) < v_{q_2}(u)$ for all $u^* < u < 1$. If this is not true for all

$$\max(u_{q_1}(0), u_{q_2}(0)) \leq u < 1,$$
there exists $0 < \bar{u} < 1$ such that $v_{q_1}(\bar{u}) = v_{q_2}(\bar{u}) = \bar{v}$. Then

$$
(v_{q_2})_u(\bar{u}) = \lim_{u \to \bar{u}^+} \frac{v_{q_2}(u) - v_{q_2}(\bar{u})}{u - \bar{u}} = \lim_{u \to \bar{u}^+} \frac{v_{q_2}(u) - v_{q_1}(\bar{u})}{u - \bar{u}} \geq \lim_{u \to \bar{u}^+} \frac{v_{q_1}(u) - v_{q_1}(\bar{u})}{u - \bar{u}} = (v_{q_1})_u(\bar{u}).
$$

On the other hand,

$$
(v_{q_2})_u(\bar{u}) = q_2 - \frac{\bar{u}(1-\bar{u})}{\bar{v}} < q_1 - \frac{\bar{u}(1-\bar{u})}{\bar{v}} = (v_{q_1})_u(\bar{u}),
$$

a contradiction.

**Lemma 6.4.** $u_{q_1}(0) < u_{q_2}(0)$.

**Proof.** Note that the slope of the line $v = q_2 u$ is $q_2$. The slope of the solution $v = v_{q_2}(u)$ is less than $q_2$:

$$
\frac{dv}{du} = q_2 - \frac{u(1-u)}{v} < q_2.
$$

Therefore, $v_{q_2}(u) < q_2 u$ for any $u \in [\max(u_{q_1}(0), u_{q_2}(0)), 1)$. Thus, by the above lemma, we have

$$
v_{q_1}(u) < v_{q_2}(u) < q_2 u < q_1 u,
$$

so $v_{q_1}(u) < q_1 u$ for all $u \in [\max(u_{q_1}(0), u_{q_2}(0)), 1)$. Since $v_{q_1}(u_{q_1}(0)) = q_1 u_{q_1}(0)$, we conclude that $u_{q_1}(0) < \max(u_{q_1}(0), u_{q_2}(0)) = u_{q_2}(0)$. \qed

We are now ready to prove the main result of this section: the steady-state density decreases pointwise with increasing advection.

**Theorem 6.5.** $u_{q_1}(x) < u_{q_2}(x)$ for any $x \geq 0$.

**Proof.** By the above lemma, this is true for $x = 0$. If this is not true for some $x > 0$, then there exists $\bar{x} > 0$ such that $u_{q_1}(\bar{x}) = u_{q_2}(\bar{x})$. We may assume that $\bar{x}$ is the smallest such. Let $u = u_{q_1}(\bar{x}) = u_{q_2}(\bar{x})$. First, note that by Lemma 6.3,

$$
(u_{q_1})_x(\bar{x}) = v_{q_1}(u_{q_1}(\bar{x})) = v_{q_1}(\bar{u}) < v_{q_2}(\bar{u}) = v_{q_2}(u_{q_2}(\bar{x})) = (u_{q_2})_x(\bar{x}).
$$
On the other hand, by the choice of $\tilde{x}$, for any $0 < x < \tilde{x}$ we have $u_{q_1}(x) < u_{q_2}(x)$, so

$$u_{q_1}(x) - u_{q_1}(\tilde{x}) = u_{q_1}(x) - \tilde{u} < u_{q_2}(x) - \tilde{u} = u_{q_2}(x) - u_{q_2}(\tilde{x}).$$

(6.9)

Since $x - \tilde{x} < 0$, we get

$$\frac{u_{q_1}(x) - u_{q_1}(\tilde{x})}{x - \tilde{x}} > \frac{u_{q_2}(x) - u_{q_2}(\tilde{x})}{x - \tilde{x}}.$$

(6.10)

Taking a limit as $x \to \tilde{x}^-$, we get

$$u_{q_1}(x) \geq u_{q_2}(x).$$

(6.11)

This is a contradiction.

7 Dependence of the steady state on advection speed for finite domains

Now we will consider the case of a domain of finite length and investigate the dependence of the steady state solution of (3.1) on the advection speed. The situation here is somewhat more complicated than in the previous section for an infinite domain, where the “endpoint” ($u(\infty) = 1$) was the same for all possible solutions.

Our goal is to prove

Theorem 7.1. If $0 < q_2 < q_1 < 2$, $u_{q_1}(x)$ and $u_{q_2}(x)$ are the steady state solutions of (3.1) with $q = q_1$ and $q = q_2$ respectively, then

$$u_{q_1}(x) < u_{q_2}(x), \quad x \in [0, L].$$

(7.2)
Note that in the first quadrant \((u, v > 0)\) any trajectory of the system (7.1) can be viewed as a graph of a function \(v = \tilde{v}(u)\) (since \(u' = v \neq 0\)). Moreover, such curves are solution curves of the ODE \(dv/du = q - \frac{u(1-u)}{v}\). In particular, no two such curves intersect.

First, we notice the effect of increasing the advection on the phase portrait of ODE \(dv/du = q - \frac{u(1-u)}{v}\).

Lemma 7.2. Given \(q_1 > q_2\), at any point \((u^*, v^*)\) (in the first quadrant), the slope of the direction field of \(dv/du = q_1 - \frac{u(1-u)}{v^*}\) is greater than that of the equation \(dv/du = q_2 - \frac{u(1-u)}{v^*}\).

Proof. Follows easily from assumption \(q_1 > q_2\).

Lemma 7.3. Suppose \(q_1 > q_2\). Let \(v = \tilde{v}_1(u)\) and \(v = \tilde{v}_2(u)\) be the solutions of

\[
\frac{dv}{du} = q_1 - \frac{u(1-u)}{v}
\]

and

\[
\frac{dv}{du} = q_2 - \frac{u(1-u)}{v},
\]

respectively, both passing through a point \((u^*, v^*)\) with \(u^*, v^* > 0\). Then \(\tilde{v}_1(u) < \tilde{v}_2(u)\) for \(u < u^*\) and \(\tilde{v}_2(u) < \tilde{v}_1(u)\) for \(u > u^*\) (on the common domain of \(\tilde{v}_1\) and \(\tilde{v}_2\); see Figure 7.1).

Proof. Let \(w(u) = \tilde{v}_1(u) - \tilde{v}_2(u)\). Thus \(w(u^*) = \tilde{v}_2(u^*) - \tilde{v}_1(u^*) = 0\) and \(\frac{dw}{du}|_{u=u^*} = \frac{d}{du}(\tilde{v}_1(u) - \tilde{v}_2(u))|_{u=u^*} = \frac{dv}{du}|_{u=u^*} - \frac{dv}{du}|_{u=u^*} = q_1 - q_2 > 0\). This means that \(w(u)\) has at most one zero and we have \(w(u) < 0\) for \(u < u^*\) and \(w(u) > 0\) for \(u > u^*\), as needed.

Let \((u_q(x), v_q(x))\) be the solution of (7.1) with \(q = q_1\). Let \(v = \tilde{v}_1(u)\) be the corresponding solution of \(\frac{dv}{du} = q_1 - \frac{u(1-u)}{v}\), defined on the interval \((u_q(0), u_q(L))\). Let \((\tilde{u}(x), \tilde{v}(x))\) be the solution of (6.2) with \(q = q_2\) passing through the point \((u_q(L), 0)\) such that \(\tilde{v}(0) = q_2\tilde{u}(0)\), and let \(v = \tilde{v}(u)\) be the equation of this curve as a solution of \(\frac{dv}{du} = q_2 - \frac{u(1-u)}{v}\), defined on the interval \((\tilde{u}(0), \tilde{u}_q(L)) = (a, b)\).

Lemma 7.4. For any \(a \in (a, b)\), \(\tilde{v}(u) > \tilde{v}_q(u)\).
Proof. Take any $\mu \in (a, b)$. Let $v = \tilde{v}^\mu(u)$ be the solution of $dv/du = q_2 - u(1-u)/v$ passing through the point $(\mu, \tilde{v}_q(\mu))$. By Lemma 7.3, with $(u^*, v^*) = (\mu, \tilde{v}_q(\mu))$, $\tilde{v}^\mu(u) < \tilde{v}_q(u)$ for any $u \in (\mu, c)$, where $c < b$ is the point where the curve $v = \tilde{v}^\mu(u)$ crosses the $u$-axis (see Figure 7.2).

Since $v = \tilde{v}(u)$ and $v = \tilde{v}^\mu(u)$ cannot intersect, we have $\tilde{v}(\mu) > \tilde{v}^\mu(\mu) = \tilde{v}_q(\mu)$, as needed. \hfill \Box

Let $L' > 0$ be such that $\tilde{v}(L') = 0$. Let us prove that in order to reach a certain downstream density (in our case, $b$), a population that is subject to a higher advection needs a larger habitat. In other words,

**Lemma 7.5.** $L > L'$.

**Proof.**

\[
L = \int_{u_{q1}(0)}^{b} \frac{du}{\tilde{v}_q(u)} > \int_{a}^{b} \frac{du}{\tilde{v}_q(u)} > \int_{a}^{b} \frac{du}{\tilde{v}(u)} = L'.
\]
For any $0 < \mu < 1$, let $L_\mu > 0$ be such that for the solution of

\[
\begin{cases}
  u' = v, \\
  v' = q_2 v - u(1 - u), \\
  v(0) = q_2 u(0), \\
  v(L_\mu) = 0.
\end{cases}
\]

(7.5)

We have $u(L_\mu) = \mu$. In other words, $L_\mu$ is the size of the habitat corresponding to the downstream density $\mu$ in the case of the smaller advection $q_2$.

As proved earlier, $L_\mu \to \infty$ as $\mu \to 1$, and as we know, $L_\mu$ is increasing with respect to $\mu$. Thus if $(u_{q_2}(x), v_{q_2}(x))$ is the solution of (6.2) with advection $q = q_2$, then $L > L'$ implies $u_{q_2}(L) > \hat{u}(L') = u_{q_1}(L)$.

We are now ready to prove our theorem.

**Proof of Theorem 7.1.** We consider two cases.

Case 1: $u_{q_1}(L) < u_{q_2}(0)$ (the ranges of $u_{q_1}$ and $u_{q_2}$ do not overlap).

In this case, for any $x \in [0, L]$ we have

\[ u_{q_1}(x) \leq u_{q_1}(L) < u_{q_2}(0) \leq u_{q_2}(x), \]

as needed.
Case 2: $u_{q_2}(L) \geq u_{q_2}(0)$ (there is an overlap, see Figure 7.3).

Note first that since $u_{q_2}(L) > \hat{u}(L')$, the curve $v = \bar{v}_{q_2}(u)$ is located above the curve $v = v(u)$ on the common domain $[u_{q_2}(0), u_{q_1}(L)]$. Thus by Lemma 7.4, for any $u \in [u_{q_2}(0), u_{q_1}(L)]$,

$$\bar{v}_{q_1}(u) < \bar{v}_{q_2}(u).$$

Note that $v_{q_2}(u_{q_2}(0)) = q_2(u_{q_2}(0))$ and

$$d\bar{v}_{q_2} \bigg|_{u=u_{q_2}(0)} = q_2 - \frac{u_{q_2}(0)(1 - u_{q_2}(0))}{\bar{v}_{q_2}(u_{q_2}(0))} < q_2,$$

and therefore, since $v = \bar{v}_{q_2}(u)$ is concave down, we have $\bar{v}_{q_2}(u) < q_2u$ for $u > u_{q_2}(0)$. Now, for $u \in [u_{q_2}(0), u_{q_1}(L)]$ we have $\bar{v}_{q_1}(u) < \bar{v}_{q_2}(u) \leq q_2u < q_1u$.

So, $\bar{v}_{q_1}(u) < q_1u$ for all $u \in [u_{q_2}(0), u_{q_1}(L)]$.

Since $\bar{v}_{q_1}(u_{q_1}(0)) = q_1u_{q_1}(0)$, we conclude that $u_{q_1}(0) \notin [u_{q_2}(0), u_{q_1}(L)]$, i.e., $u_{q_1}(0) < u_{q_2}(0)$.

We want to show that for any $x \in [0, L]$ $u_{q_1}(x) < u_{q_2}(x)$. Suppose this is not the case, and consider the smallest $\bar{x} > 0$ such that $u_{q_1}(\bar{x}) = u_{q_2}(\bar{x})$. Let $\bar{u} = u_{q_1}(\bar{x}) = u_{q_2}(\bar{x})$. Note that $\bar{u} \in [u_{q_2}(0), u_{q_1}(L)]$. 

\*\*\* 

**FIGURE 7.3:** The case of overlapping domains.
Now, we have

\[
\left. \frac{du_{q_1}}{dx} \right|_{x=\bar{x}} = \tilde{v}_{q_1}(u_{q_1}(\bar{x})) = \tilde{v}_{q_1}(\bar{u}) < \tilde{v}_{q_2}(\bar{u})
\]

\[
= \tilde{v}_{q_2}(u_{q_2}(\bar{x})) = \left. \frac{du_{q_2}}{dx} \right|_{x=\bar{x}}.
\]

On the other hand, by the choice of \( \bar{x} \), for any \( 0 < x < \bar{x} \), we have

\[
(7.8) \quad u_{q_1}(x) - u_{q_1}(\bar{x}) = u_{q_1}(x) - \bar{u} < u_{q_2}(x) - \bar{u} = u_{q_2}(x) - u_{q_2}(\bar{x}).
\]

Since \( x - \bar{x} < 0 \), we get

\[
(7.9) \quad \frac{u_{q_1}(x) - u_{q_1}(\bar{x})}{x - \bar{x}} > \frac{u_{q_2}(x) - u_{q_2}(\bar{x})}{x - \bar{x}}.
\]

Taking the limit as \( x \to \bar{x}^- \), we get

\[
(7.10) \quad \left. \frac{du_{q_1}}{dx} \right|_{x=\bar{x}} > \left. \frac{du_{q_2}}{dx} \right|_{x=\bar{x}},
\]

a contradiction. \( \square \)

8 Qualitative aspects of the steady state solution

Although we do not have an explicit formula for the positive steady state solution \( u = u(x) \) of \( (3.1) \), we know (e.g., from the phase plane analysis) that \( u(x) \) is an increasing function on \( [0, L] \), and for \( x \) close to \( L \), it is concave down (since \( u'(L) = 0 \)). A natural question is whether \( u(x) \) is concave down throughout the habitat \( [0, L] \), or \( u(x) \) has an inflection point \( x^* \in [0, L] \).

We start by analyzing the cases of low, intermediate and high advection.

**Lemma 8.1.** The solution \( u = u(x) \) of \( (3.2, 3.3) \) has an inflection point if and only if \( u(0) > 1 - q^2 \).

**Proof.** Let \( (u(x), v(x)) = (u(x), u'(x)) \). Then \( u(x) \) has an inflection point if and only if its orbit in the \( uv \)-plane intersects the \( v \)-nullcline \( v = \frac{1}{q}u(1-u) \), which happens exactly when the point \( (u(0), v(0)) = (u(0), qu(0)) \) lies above the \( v \)-nullcline. This is equivalent to

\[
qu(0) > \frac{1}{q}u(0)(1-u(0)) \]


or

\[ u(0) > 1 - q^2, \]

as needed.

**Proposition 8.2.**

(i) For \( q > 1 \) every solution of (3.2, 3.3) has an inflection point.

(ii) For \( q < 1 / \sqrt{2} \) no solution of (3.2, 3.3) has an inflection point (see Figure 8.1).

**FIGURE 8.1:** No inflection points for \( q < 1 / \sqrt{2} \).

**Proof.** (i) By Lemma 8.1 and the fact that \( u(0) > 0 \) (upstream density is positive).

(ii) If \( u(x) \) has an inflection point, by Lemma 8.1, we have \( u(0) > 1 - q^2 > \frac{1}{2} \). But if an orbit of (3.4) starts at a point located above the v-nullcline and to the right from \( u = 1/2 \), from phase plane analysis we can conclude that it will never cross the \( u \)-axis, hence will not satisfy the second boundary condition. Thus \( u(x) \) has no inflection point.

**Remark 8.3.** If \( \frac{1}{\sqrt{2}} < q < 1 \), then
• if \( \nu_{\text{max}} \leq 1 - q^2 \), then no solution has an inflection point;
• if \( \nu_{\text{max}} > 1 - q^2 \), then by lemma 8.1, the solutions with \( 1 - q^2 < u(0) \leq \nu_{\text{max}} \) have inflection points, and solutions with \( u(0) < 1 - q^2 \) do not have inflection points; in other words, inflection points only occur for large domains (equivalently, for high upstream/downstream densities, see Figure 8.2).

![Graph of population dynamics in rivers](image)

**FIGURE 8.2**: The case of intermediate advection (\( \frac{1}{q^2} < q < 1 \)).

In the case when upstream density is low, we can use linearization around the zero steady state to obtain the distance from the upstream boundary to the inflection point (length of boundary layer). Note that the solution of the linear system will only have an inflection point if \( q > 1 \) (otherwise the \( v \)-nullcline \( v = \frac{1}{q} u \) will be above the first boundary condition \( v = qu \)). The system linearized at the origin takes the form

\[
\begin{align*}
u' &= v, \\
v' &= qv - u.
\end{align*}
\]

The general solution of the above system is given by

\[
u(x) = e^{\frac{4}{q^2} } (\alpha \cos \theta x + \beta \sin \theta x),\]
where
\[ \theta = \frac{\sqrt{1 - q^2}}{2}. \]
Using the first boundary condition we obtain
\[ u(x) = u'(x) = \alpha e^{\frac{q^2}{4\theta}} \left( q \cos \theta x + \left( \frac{q^2}{4\theta} - \theta \right) \sin \theta x \right). \]
Differentiating of the above expression gives
\[
(8.2) \quad u''(x) = \frac{\alpha q}{2} e^{\frac{q^2}{4\theta}} \left( q \cos \theta x + \left( \frac{q^2}{4} - \theta \right) \sin \theta x \right) \\
+ \alpha e^{\frac{q^2}{4\theta}} \left( -q \theta \sin \theta x + \left( \frac{q^2}{4} + \theta \right) \theta \cos \theta x \right).
\]
If \( u(x) \) has an inflection point at \( x = x^* \), then \( u''(x^*) = 0 \). Setting the right hand side of (8.2) equal to zero, we find the expression for \( x^* \):
\[
(8.3) \quad x^* = \begin{cases} \\
\frac{1}{\theta} \arctan \left( \frac{\frac{q^2}{4\theta} - \theta^2}{\frac{q^2}{8\theta}} \right), & 1 < q \leq \sqrt{3}, \\
\frac{1}{\theta} \left( \pi + \arctan \left( \frac{\frac{q^2}{4\theta} - \theta^2}{\frac{q^2}{8\theta}} \right) \right), & \sqrt{3} < q < 2.
\end{cases}
\]
As we can see from Figure 8.3, for small upstream densities, formula (8.3) gives a good approximation of the inflection point of the solution in nonlinear case (found numerically).

9 Conclusions and biological implications In this work, we considered a reaction-advection-diffusion equation with logistic growth term on a bounded domain with Danckwert’s boundary conditions. We proved the existence, uniqueness and stability of a positive steady state for domain lengths above a critical threshold. Below this threshold, the zero steady state is stable. In particular, a transcritical bifurcation occurs at this threshold. The positive steady state solution is an increasing function of the spatial variable. For large enough advection, the solution has an inflection point; we gave an approximate formula for the distance of this inflection point from the upstream boundary. We also showed that the solution is a decreasing function of advection speed.
These results complement and contrast results on reaction-diffusion equations without advection, but with hostile boundary conditions; see, e.g., [10]. Those models also exhibit a transcritical bifurcation at the “critical domain size.” Loss of individuals in that case is entirely due to diffusion, while in our case, it is purely due to advection. Also, the positive steady state in those models have no inflection point.

While this work focuses on mathematical analysis, our model is inspired by the biological question of population dynamics in advective environments, such as streams and rivers. Speirs and Gurney [21] first applied a linear analogue of our model (albeit with slightly different boundary conditions) to study the persistence conditions of plankton and insects in small streams in Southeast England. They demonstrated that, under certain conditions, diffusive movement of individuals can counterbalance the loss of individuals through directed movement with the water and thereby lead to population persistence.

For example, their model explains the absence of plankton organisms in Broadstone Stream (Southeast England), which is relatively short and shallow with significant advection. The authors argue that due to its shallowness and the nature of plankton, the organisms would have
to be present throughout the water column, and would be subjected to average advection, which exceeds the critical value for any realistic growth rate and diffusivity of plankton. On the other hand, stoneflies are actually found in the creek. Their nymphs are primarily benthic organisms, and enter the stream for only 0.01% of time. Therefore, they experience an effective advection speed that is reduced by a factor of $10^{-4}$, well below the critical advection value for this species. Thus, even though the time scale of the growth dynamics is typically much slower than that of the advective movement, the latter is significantly smaller for predominantly benthic species and is actually comparable with the former.

Stoneflies have winged adult stages that can easily move upstream for egg-deposition. It is unclear whether this movement can be accurately captured by the diffusion operator. Potentially more realistic could be a discrete-time model with a dispersal kernel as in [13]. The reaction-advection-diffusion approach does, however, seem appropriate for many benthic species that never emerge from the water, for example, *Dreissena polymorpha* (zebra mussels), meroplanktonic copepod (*Caullana canadensis*), and mysid shrimp (*Neomysis integer*), where a similar reduction of the actual advection speed occurs. Benthic algae can be considered within this framework as well. Some “best guesses” for parameter values were given in [12].

Our model makes some testable hypotheses. Is it true that the abundance of these organisms increases downstream from an insurmountable barrier? And does the location of the inflection point (8.3) predict the spatial scale over which the influence of this upstream barrier is present?

The reduction of population density at the upstream end can also be a mechanism for coexistence of two competing species that would not coexist in the absence of advection. This has been demonstrated numerically in [12]. We are currently working on a more detailed mathematical analysis of the reaction-advection-diffusion model with two competing species. Effects of advection on predator-prey systems have recently been studied by Hilker and Lewis [7]. In the future, we plan to analyze the positive steady state(s) of an extension of our model that include a benthic compartment explicitly; see [17].

**Acknowledgements** We thank an anonymous referee for suggestions to significantly shorten several proofs. OV acknowledges support from MITACS. FL is grateful for an NSERC discovery grant and for an Early Researcher Award from the Ontario Ministry of Research and Innovation.
REFERENCES


Department of Mathematics and Statistics, University of Ottawa,
585 King Edward Avenue, Ottawa, ON K1N 6N5

E-mail address: ovass031@uottawa.ca
E-mail address: flutsche@uottawa.ca