THE EMERGENCE OF RANGE LIMITS IN ADVECTIVE ENVIRONMENTS

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Abstract. In this paper, we study the asymptotic profile of the steady state of a reaction-diffusion-advection model in ecology proposed in [13, 17]. The model describes the population dynamics of a single species experiencing a uni-directional flow. We 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 is sometimes subject to the effect of migration from upstream source patches.

1. Introduction

Most species have spatially limited distributions [1]. Ecologists have identified a few basic aspects of dispersal and birth-death dynamics that can explain several mechanisms underlying range limits [7]. For example, local biotic and abiotic conditions determine the basic rate of increase of a population. The species is expected to be present where its rate of increase is positive (its "niche") and absent where this rate is negative. A range limit then indicates a sign change of this rate of increase. Dispersal can enlarge a species' range and maintain a population in regions where the intrinsic growth rate is negative (source-sink dynamics). In streams and rivers, water flow can induce a strong directional bias in dispersal. What then is the effect of this biased dispersal on the emergence of range limits?

Abiotic conditions can change considerably along the course of a river or stream. Temperature and nutrient loading tend to increase downstream whereas shading decreases [18]. But conditions need not change monotonically. Local habitat attributes are also affected by substrate, confluences, dams, or point source disturbances such as waste-water treatment plants. Accordingly, algal community composition varies considerably between upstream and downstream [16, 21] and with it the food chain that it can support. These assemblages are formed by the combined effects of local growth conditions (source and sinks) and of passive transport in the water column. Because of the strong bias of transport, one could expect a species to be absent from the upstream end of its niche or source region and persist in sink habitats further downstream. Can one quantify this effect of hydrology on the actual range of a species?

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The dynamics of a spatially distributed species, moving passively in a stream or river, have been modeled with a reaction-advection-diffusion equation to explore population persistence and the so-called "drift paradox" [13, 17]. In the simplest case, the equation for the density $u(x,t)$ of a population at time t and location x is given by

$$u_t = Du_{xx} - qu_x + u(r - \kappa u), \tag{1}$$

where $D > 0$ is the diffusion coefficient, $q > 0$ is the flow speed in the direction of increasing x, r is the population growth rate at low density, and κ denotes the strength of intra-specific competition. (Subscripts denote partial derivatives.) Lutscher and coauthors studied this model (and a two-species extension) with linearly increasing growth function $r = r(x)$ (i.e. the habitat quality of downstream location is better than the upstream location) and observed the emergence of upstream range limits [11]. Specifically, when the stream was long, the steady state population showed a sharp transition layer from low to high density, much steeper than the local growth conditions would predict. Numerically, the authors found that a species initially occupying a downstream region may propagate upstream in a wave-like fashion with decreasing speed. This upstream invasion wave comes to a halt at some location $\hat{x}$, even though local growth conditions are favorable upstream of that location, i.e. $r(x) > 0$ for $x < \hat{x}$.

Traveling waves are well studied for the Fisher model, given by equation (1) with $q = 0$ and constant r. They arise at a minimal speed $c^* = 2\sqrt{rD}$, the asymptotic spreading speed [20]. In an environment with unidirectional flow of speed $q > 0$, there are two spreading speeds, one in the direction of the flow (downstream), given by $c^* + q$, and one against the flow (upstream), given by $c^* - q$ [13]. When the flow speed is lower than c^*, then the upstream spreading speed is positive and the population can spread against the flow. When the flow speed is higher than c^*, then the upstream speed is negative and the population retreats downstream.

When growth conditions vary spatially, $r = r(x)$ is a non-constant function. It is then tempting to define the "local upstream spreading speed" as $2\sqrt{r(x)D} - q$ [7]. A range limit then emerges where the local upstream spreading speed is zero. For a monotone growth function $r(x)$, there is a unique location x^* defined by $r(x^*) = \frac{q^2}{4D}$. Numerical simulations for model (1) indicated that, indeed, $\hat{x} = x^*$ [11].

To see why the steady state density $\tilde{u}$ can be very small even though the local growth rate $r(x)$ is positive, we introduce the transformation $u(x,t) = w(x,t)e^{qx/(2D)}$. Then w satisfies the equation

$$w_t = Dw_{xx} + w\left(r(x) - \frac{q^2}{4D} - we^{qx/(2D)}\right), \tag{2}$$

with local intrinsic growth rate $r(x) - \frac{q^2}{4D}$. Hence, the stream flow can be viewed as decreasing the local growth rate. Specifically, regions with $r(x) > \frac{q^2}{4D}$ are population dynamic sources whereas regions with $r(x) < \frac{q^2}{4D}$ are sinks.

The first purpose of this paper is to prove the existence of a steady state profile with the steep transition layer as observed in numerical simulations [11] when the growth function is monotone increasing and the stream segment is long. In the second part of the paper, we consider the case that the adjusted growth function $r(x) - \frac{q^2}{4D}$ changes sign more than once. In this case, we could expect multiple transition layers of $\tilde{u}$ occurring at locations x_i^* with $r(x_i^*) - \frac{q^2}{4D} = 0$. We show that there is at most one transition layer per source patch, i.e. an interval where $r > 0$. More specifically, when there is only one source patch and the population persists, then there is only one transition layer, even if the adjusted growth rate is negative somewhere. If there are two or more disjoint source patches, then a second transition layer maybe located further upstream than would be predicted by the locations x_i^*. This phenomenon arises when emigrants from high-density regions upstream contribute to local population growth at the next downstream source patch. We give a precise characterization of the location of a second transition layer.

We introduce the model with boundary conditions and scalings in detail in Section 2. We state all the main results in Section 3, and present numerical illustrations in Section 4. Auxiliary lemmas are given in Section 5. Proofs of the main theorems are presented in Section 6. Finally, an extension of our results concerning a boundary transition layer is discussed in Section 7.

2. Model description

We denote the density of the species at time t and location x in the bounded interval $[0, L]$ with $u(x, t)$, where L is the length of the river. We denote the diffusion constant by $D > 0$ and the flow speed by $q > 0$ so that advection points to increasing x-values. We supplement the equation in model (1) with generalized Danckwerts boundary condition at the upstream ($x = 0$) and downstream ($x = L$) end. The model then reads

$$\text{(3)} \qquad \begin{cases} u_t = Du_{xx} - qu_x + u(r(x) - \kappa u) \quad \text{for } 0 < x < L, \quad t > 0, \\ Du_x(0) - qu(0) = qb_u u(0), \quad Du_x(L) - qu(L) = -qb_d u(L) \quad \text{for } t > 0. \end{cases}$$

The (dimensionless) parameters b_u and b_d determine the magnitude of population loss at the upstream and downstream boundaries, respectively. No-flux condition at the downstream boundary corresponds to $b_d = 0$, whereas hostile condition results as $b_d \to \infty$. An important intermediate case is $b_d = 1$, when net-movement across the boundary results only from diffusion. For a more detailed discussion and derivation from a random walk model, we refer to [8, 10]. The function $r(x)$ stands for the quality of the habitat; the population can grow where $r > 0$ and will decline where $r < 0$.

Based on the numerical results in [11], we consider the case where the river is very long compared to the scales of advective and diffusive movement. We introduce non-dimensional variables $\hat{t} = t/\tau$, $\hat{x} = x/L$ and $\hat{u} = \kappa u$, and a small parameter $\epsilon = q\tau/L$. Since we will study the steady-sate problem, we may choose the time scale $\tau = 1$. With this scaling, the model becomes

$$\text{(4)} \qquad \begin{cases} \hat{u}_{\hat{t}} = \epsilon^2 \hat{D}\hat{u}_{\hat{x}\hat{x}} - \epsilon\hat{u}_{\hat{x}} + \hat{u}(\hat{r} - \hat{u}) \quad \text{for } 0 < \hat{x} < 1, \quad \hat{t} > 0, \\ \epsilon\hat{D}\hat{u}_{\hat{x}}(0, \hat{t}) - \hat{u}(0, \hat{t}) = b_u\hat{u}(0, \hat{t}), \quad \epsilon D\hat{u}_{\hat{x}}(1, \hat{t}) - \hat{u}(1, \hat{t}) = -b_d\hat{u}(1, \hat{t}), \quad \text{for } \hat{t} > 0, \end{cases}$$

where $\hat{D} = D/q^2$ is the rescaled diffusion coefficient and $\hat{r}(\hat{x}) = r(x)$ denotes the rescaled growth profile on $[0, 1]$. After dropping "ˆ" for ease of notation, we finally obtain our dimensionless model system as

$$\text{(5)} \qquad \begin{cases} u_t = \epsilon^2 Du_{xx} - \epsilon u_x + u(r - u) \quad \text{for } 0 < x < 1, \quad t > 0, \\ \epsilon Du_x(0, t) - u(0, t) = b_u u(0, t), \quad \epsilon Du_x(1, t) - u(1, t) = -b_d u(1, t), \quad \text{for } t > 0. \end{cases}$$

The dynamics of this model are completely determined by the linear stability of the trivial solution since the system is monotone [4]. If the zero solution is locally asymptotically stable, then it is globally stable. If it is unstable, then there is a unique positive steady state, which is globally stable among non-negative, non-trivial solutions. The non-trivial steady-state solution $\tilde{u}(x)$ of (5) satisfies the equation

$$\text{(6)} \qquad \begin{cases} \epsilon^2 D\tilde{u}_{xx} - \epsilon\tilde{u}_x + \tilde{u}(r - \tilde{u}) = 0 \quad \text{for } 0 < x < 1, \\ \epsilon D\tilde{u}_x(0) - \tilde{u}(0) = b_u\tilde{u}(0), \quad \epsilon D\tilde{u}_x(1) - \tilde{u}(1) = -b_d\tilde{u}(1). \end{cases}$$

In this paper, we study existence conditions for $\tilde{u}$ and its spatial profile.

3. Main Results

In this section, we explain and interpret our main results about the existence and spatial profile of the positive solution $\tilde{u}(x)$ of (6). We formulate all of our results in terms of the local upstream spreading speed, which, in the parametrization of (5) is given by

$$c(x) = \begin{cases} \epsilon(2\sqrt{r(x)D} - 1) & \text{when } r(x) \geq 0, \\ -\epsilon & \text{when } r(x) < 0. \end{cases}$$

Note that when $r < 0$, then c is simply the transformed flow speed $-\epsilon$.

3.1. **Persistence Results.** It is well-known that the persistence of the single species governed by diffusive-logistic equation (5) is characterized by the principal eigenvalue λ_1 of

$$\begin{cases} \epsilon^2 D\phi_{xx} - \epsilon\phi_x + r\phi + \lambda_1\phi = 0 \quad \text{for } 0 < x < 1, \\ \epsilon D\phi_x(0) - \phi(0) = b_u\phi(0), \quad \epsilon D\phi_x(1) - \phi(1) = -b_d\phi(1). \end{cases}$$

Namely, if $\lambda_1 < 0$ then there exists a unique positive steady state of (5) which is also globally asymptotically stable among all non-negative, non-trivial solutions; and if $\lambda_1 \geq 0$, then the zero solution is globally asymptotically stable. See, e.g. [4, P. 150] and also [3, 6, 12, 15]. The principal eigenvalue λ_1 is in general a nonlinear function of coefficients $\epsilon, D, r(x), b_u, b_d$.

We state below two practical persistence/extinction results that are uniform for all (small) values of ϵ which are relevant to our investigation.

Theorem 3.1. *If $\max_{[0,1]} c > 0$, i.e. $\max_{[0,1]} r > \frac{1}{4D}$, then there exists $\epsilon_0 > 0$ such that for all $\epsilon \in (0, \epsilon_0)$ (and all $b_u, b_d \geq 0$), equation (6) has a unique positive solution $\tilde{u}$ that is the globally asymptotically stable steady state for equation (5), among all non-negative and not identically zero initial data.*

Theorem 3.2. *If $\max_{[0,1]} c \leq 0$, i.e. $\max_{[0,1]} r \leq \frac{1}{4D}$, and if $b_d \geq \frac{1}{2}$, then for all $\epsilon > 0$, equation (6) has no positive solution, and the zero solution of equation (5) is globally asymptotically stable among all non-negative and not identically zero initial data.*

Theorem 3.1 states that when the upstream spreading speed is positive somewhere, then a locally introduced population can spread in both directions and persist in the habitat. This result holds only when the habitat is sufficiently long so that potential boundary loss does not impact population survival. Specifically, we are not considering a minimal domain-size problem here.

As a complement to Theorem 3.1, Theorem 3.2 shows that the population cannot persist in any upstream portion of the river if its upstream invasion speed is non-positive. This result arises only when there is some population loss at the downstream end of the habitat. For example, if both boundary conditions are no-flux conditions (i.e. $b_u = b_d = 0$), then the population will persist as long as some appropriate average of the growth rate is positive, i.e. $\int_0^1 r(x)\exp(x/(\epsilon D))dx > 0$.

We refer the interested reader to previous work on population persistence [8, 17, 19]. We note that if no-flux boundary conditions are imposed at both ends (i.e. $b_u = b_d = 0$), and if $r(x) > 0$, then the population always persists, regardless of ϵ, D. In particular, the condition that $b_d \geq \frac{1}{2}$ is indispensable. A recent detailed study of the influence of upstream and downstream loss rates is given in [9].

In the rest of this section, we will focus on the Danckwerts boundary condition, which corresponds to no-flux upstream conditions ($b_u = 0$) and Neumann downstream conditions

($b_d = 1$). We note also that Neumann conditions only describe a no-flux scenario when there is no advection ($q = 0$).

3.2. **Single Internal Transition Layer.** We define the upstream invasion limit as the furthest upstream location where the upstream invasion speed is positive, i.e.

$$z_1 = \inf\{x \in (0,1) : c(x) > 0\} = \inf\{x \in (0,1) : r(x) > 1/4D\}. \tag{7}$$

We note that when $\max_{[0,1]} c > 0$, i.e. $\max_{[0,1]} r > \frac{1}{4D}$, then z_1 is well defined and $z_1 \in [0,1]$. In addition, z_1 is uniquely defined even when $r(x)$ is constant in some intervals.

The following result shows that, in the case of $z_1 > 0$, how the range of species can be characterized by the upstream invasion limit:

Theorem 3.3. *Suppose that* $\max_{[0,1]} c > 0$, $z_1 \in (0,1)$ *and that* $r(x) > 0$ *for* $x > z_1$. *Then, as* $\epsilon \to 0$,

$$\tilde{u} \to r(x)\mathbb{1}_{[z_1,1]} \qquad \textit{locally uniformly in } [0,1] \setminus \{z_1\},$$

where $\mathbb{1}_{[z_1,1]}$ *denotes the characteristic function of the interval* $[z_1, 1]$.

The statement of Theorem 3.3 is illustrated in Figure 1. See also Figure 2 for a numerical example. When the upstream invasion limit z_1 is below the upstream end of the habitat, then, in a long river, the population will approach a spatial profile with a single internal transition layer from near zero density upstream of z_1 to carrying capacity downstream of z_1.

3.3. **Multiple Internal Transition Layers.** Theorem 3.3 requires $r > 0$ downstream of $z_1 = \inf\{x \in [0,1] : r(x) > 1/(4D)\}$. When $r < 0$ for some intermediate region downstream of z_1 and $r(1) > 1/(4D)$, then there will be a second internal transition layer. The main question is the location of this second layer. To this end, we study a representative situation.

Suppose that there exists a partition $0 < x_1 < x_2 < x_3 < 1$, such that

$$r(x) < 0 \quad \text{in } [0, x_1) \cup (x_2, x_3) \quad \text{and} \quad r(x) > 0 \quad \text{in } (x_1, x_2) \cup (x_3, 1]. \tag{8}$$

Naively, we would expect another internal transition layer located at the second invasion limit z_2, given by

$$z_2 := \inf\{x \in (x_3, 1) : r(x) > 1/4D\}. \tag{9}$$

Our next theorem shows that while this situation can occur, more subtle effects may arise. In fact, the second transition layer may be located upstream of z_2; see Figure 3.

Specifically, we require the maximum upstream invasion speed to be positive in both patches $[x_1, x_2]$ and $[x_3, 1]$, i.e.

$$\max_{[x_1,x_2]} c(x) > 0 \quad \text{and} \quad \max_{[x_3,1]} c(x) > 0,$$

or equivalently,

$$\max_{[x_1,x_2]} r(x) > \tfrac{1}{4D} \quad \text{and} \quad \max_{[x_3,1]} r(x) > \tfrac{1}{4D}. \tag{10}$$

When $c(x) < 0$ (i.e. $r(x) < 1/(4D)$), we can define the quantities

$$\alpha^{\pm}(x) := \tfrac{1 \pm \sqrt{1 - 4Dr(x)}}{2D}. \tag{11}$$

Note that α^+ is always positive whereas α^- has the same sign as $r(x)$.

It turns out that the sign of $\int_{x_2}^{z_2} \alpha^-(t)\, dt$ plays a critical role in determining the location of the second internal transition layer.

Theorem 3.4. *Suppose* $r(x)$ *satisfies conditions* (8) *and* (10).

(a) *Assume that* $\int_{x_2}^{z_2} \alpha^-(t)\,dt \le 0$. *Then as* $\epsilon \to 0$,

$$\tilde{u} \to r(x)\left[\mathbb{1}_{[z_1,x_2]} + \mathbb{1}_{[z_2,1]}\right] \qquad \text{locally uniformly in } [0,1] \setminus \{z_1, z_2\},$$

where z_1 *and* z_2 *are defined in* (7) *and* (9), *respectively.*

(b) *Assume that* $\int_{x_2}^{z_2} \alpha^-(t)\,dt > 0$. *Then as* $\epsilon \to 0$,

$$\tilde{u} \to r(x)\left[\mathbb{1}_{[z_1,x_2]} + \mathbb{1}_{[\tilde{z}_2,1]}\right] \qquad \text{locally uniformly in } [0,1] \setminus \{z_1, \tilde{z}_2\},$$

where $\tilde{z}_2 \in (x_3, z_2)$ *is uniquely determined by the relation* $\displaystyle\int_{x_2}^{\tilde{z}_2} \alpha^-(t)\,dt = 0.$

The statement of this theorem is illustrated in Figures 1 and 3. The first transition layer is located at the upstream invasion limit z_1 as before. Downstream of the region where $r < 0$, there is a second point, z_2, where the upstream invasion speed is zero. If we only consider the region downstream of $r < 0$, then we would expect a transition layer at z_2 based on the same reasoning as the layer at z_1. This reasoning is correct when the region $r < 0$ is large. However, if this region is small, then there will be immigration of individuals from the upstream patch $[z_1, x_2]$ to the downstream patch. This influx of individuals allows the population to establish further upstream of z_2, more specifically, at $\tilde{z}_2$.

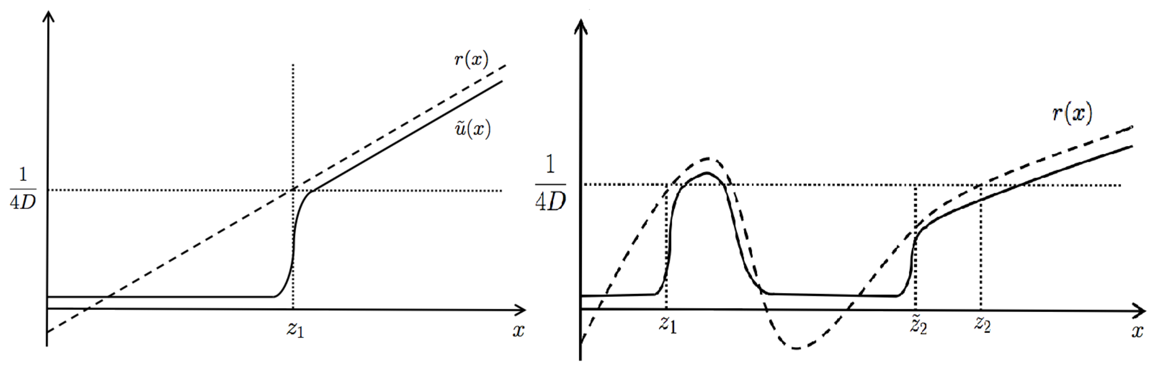

FIGURE 1. Left panel: Illustration of Theorem 3.3. Right panel: Illustration of Theorem 3.4.

4. Numerical Results

In this section, we present some numerical results that complement and illustrate our analytical results from the previous section. We begin with the shape and location of a single transition layer in the case of a monotone, increasing resource function as in Theorem 3.3.

We choose the simple linear function $r(x) = x$ to represent how habitat quality is increasing downstream, and we fix a diffusion coefficient of $D = 1/2$. The condition $r(z_1) = 1/(4D)$ gives a theoretical upstream invasion limit of $z_1 = 1/2$. We illustrate the statement of Theorem 3.3 in Figure 2. We plot the resource function, $r(x)$, and the steady state solution, $\tilde{u}(x)$, for the three different values of ϵ. As ϵ decreases, the steady state profile becomes steeper and the transition layer "moves closer" to the theoretical value z_1. We evaluated the latter distance by numerically calculating the value y_1 such that $\tilde{u}(y_1) = r(z_1)/2 = 1/2$. The results are summarized in Table 1.

ϵ	0.02	0.01	0.005
$y_1 - z_1$	0.139	0.0775	0.022

TABLE 1. Distance between the transition layer and the upstream invasion limit for linearly increasing $r(x)$. We conjecture that $y_1 - z_1$ is of the order of ϵ, i.e. the actual location of the transition layer lies in an ϵ-neighborhood of z_1.

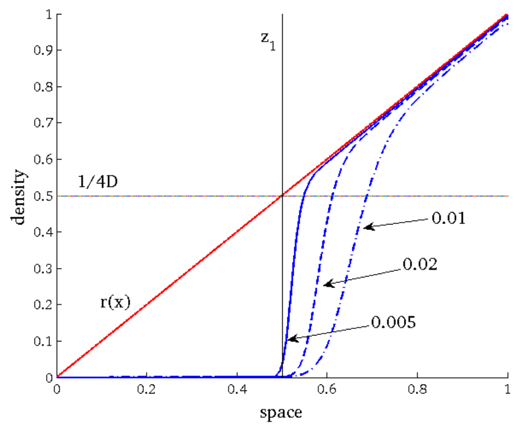

FIGURE 2. Monotone increasing resource function $r(x)$ and steady-state profile $\tilde{u}(x)$ for three values of $\epsilon = 0.02$ (dash-dot), $\epsilon = 0.01$ (dashed), and $\epsilon = 0.005$ (solid).

To illustrate the case of multiple transition layers, we choose a resource function that has a (negative) local minimum at the upstream end and a (positive) local maximum at the downstream end, as well as a (positive) local maximum and (negative) minimum in the interior of the domain. We choose the function

$$\sin\left(3\pi x - \frac{\pi}{2}\right) + 0.8,$$

whose positive part is plotted as $r(x)$ in Figure 3. We denote by K the interval where r is negative in between the two maxima. We then introduce a parameter $\nu > 0$ to modify the above function on K and thereby change the value of the integral of α^-, see (11) and Theorem 3.4.

Specifically, we set

$$r(x) = \sin\left(3\pi x - \frac{\pi}{2}\right) + 0.8 - \nu \mathbb{1}_K,$$

and we fix parameters $\epsilon = 0.005$ and $D = 1/6$. By increasing ν we can decrease the value of $r(x)$ on K and thereby decrease the value of the integral $\int_{x_2}^{z_2} \alpha^-(x)dx$. Accordingly, we find that the second (downstream) transition layer is upstream of the expected limit z_2 when ν is small but moves downstream to z_2 as ν increases, see Figure 3.

The two invasion limits are given by $z_1 = \frac{1}{6} + \frac{1}{3\pi}\sin^{-1}(0.7) \approx 0.249$ and $z_2 = \frac{5}{6} + \frac{1}{3\pi}\sin^{-1}(0.7) \approx 0.916$ as defined in (7) and (9). Furthermore, the left endpoint of K is

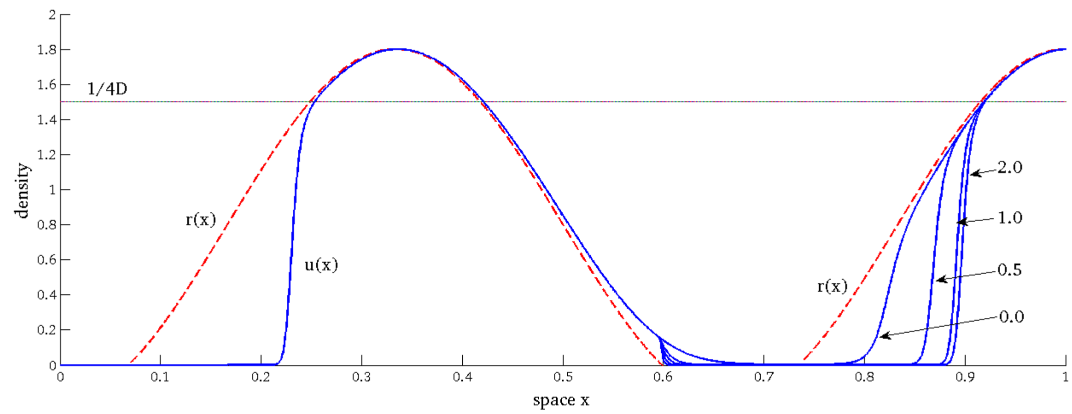

FIGURE 3. An oscillating resource function, $r(x)$, (dashed) and the steady-state profile $\tilde{u}(x)$ for various values of $\nu = 0, 0.5, 1, 2$. Increasing ν changes $r(x)$ in the region where $r < 0$ between the two maxima. Fixed parameters are $\epsilon = 0.005$ and $D = 1/6$.

$x_2 = \frac{1}{2} + \frac{1}{3\pi}\sin^{-1}(0.8) \approx 0.598$. The values of the integral

$$\int_{x_2}^{z_2} \alpha^-(x)dx = \int_{x_2}^{z_2} \frac{1-\sqrt{1-4Dr(x)}}{2D} dx.$$

are listed in Table 2.

ν	0	0.5	1	2	5
$\int_{x_2}^{z_2} \alpha^-(x)dx$	0.1613	0.1003	0.046	-0.0488	-0.2726
$y_1 - z_1$	-0.017	-0.017	-0.017	-0.017	-0.017
$y_2 - z_2$	-0.076	-0.044	-0.0225	-0.0175	-0.0175

TABLE 2. Summary values for the first and second transition layer for different values of ν

We note that the integral $\int_{x_2}^{z_2} \alpha^-(x)dx$ is positive for $c = 0, 0.5, 1$, whereas it is negative for $c = 2, 5$. While the location of the first transition layer (as determined by the distance $y_1 - z_1$) is independent of ν, the second transition layer (as determined by the distance $y_2 - z_2$) moves downstream as ν increases. The locations y_i are calculated as $\tilde{u}(y_i) = 1/2$ and $\tilde{u}'(y_i) > 0$.

5. PRELIMINARIES

We introduce the notion of weak upper (lower) solution, which will play an instrumental role for the rest in the paper. We refer to [5, Ch. 4] for the following definitions and results.

Definition 5.1. *We say that $w \in H^1([0,1])$ is a weak upper (resp. lower) solution to (6) if*

$$\int_0^1 \left[-\left(\epsilon^2 D w_x - \epsilon w\right)\eta_x + w(r-w)\eta\right] dx - \epsilon\left(b_u w(0) + b_d w(1)\right) \le 0 \quad (resp. \ \ge 0)$$

for any $\eta \in C^\infty([0,1])$ such that $\eta \ge 0$ in $[0,1]$.

If $b_u = b_d = \infty$, then we say that $w \in H^1([0,1])$ is a weak upper (resp. lower) solution to (6) if $w(0), w(1) \geq 0$ (resp. ≤ 0), and that

$$\int_0^1 \left[-\left(\epsilon^2 D w_x - \epsilon w\right)\eta_x + w(r-w)\eta \right] dx \leq 0 \quad (resp. \;\geq 0)$$

for any non-negative test functions $\eta \in C_0^\infty([0,1])$.

The next observation will be used frequently in this paper to construct weak upper and lower solutions.

Lemma 5.2. *When $0 \leq b_u, b_d < +\infty$, a function w is a weak upper (resp. lower) solution to (6) if*

(i) *$w \in C([0,1])$;*

and there exists a partition $0 = x_0 < x_1 < x_2 < \cdots < x_{k-1} < x_k = 1$ such that for all $i = 0, \ldots, k-1$,

(ii) *$w = \min_{1 \leq j \leq j_i}\{w_{i,j}\}$, where $w_{i,j} \in C^2([x_i, x_{i+1}])$ and satisfies*

$$Lw_{i,j} := \epsilon^2 D(w_{i,j})_{xx} - \epsilon(w_{i,j})_x + w_{i,j}(r - w_{i,j}) \leq 0 \quad (\text{resp. } \geq 0) \quad \text{ in } (x_i, x_{i+1});$$

(iii) *for all $i = 1, \ldots, k-1$, $w_x(x_i-) \geq w_x(x_i+)$ (resp. $\leq$),*

and at the boundary points $x = 0, 1$,

(iv) $\epsilon D w_x(0) - w(0) \leq b_u w(0)$ (resp. $\geq$) *and* $\epsilon D w_x(1) - w(1) \geq -b_d w(1)$ (resp. $\leq$).

Proof. The lemma can be verified in a straightforward manner, via integration by parts. We skip the details here. □

Theorem 5.3 ([14]). *If $\overline{w}$ and $\underline{w}$ are respectively weak upper and lower solutions of (6), and $\underline{w} \leq \overline{w}$, then (6) has at least one solution u such that $\underline{w} \leq u \leq \overline{w}$. In particular, if $\underline{w} \geq 0, \not\equiv 0$, then u is a positive solution of (6).*

We refer to [5, Theorem 4.15] for the proof of Theorem 5.3.

Theorem 5.4. *Let D, r_0 be given positive numbers.*

(a) *If $4Dr_0 \leq 1$, then there exists a unique positive solution w_{D,r_0} to*

$$\begin{cases} Dw_{yy} - w_y + (r_0 - w)w = 0 & \text{in } (-\infty, +\infty), \\ w(-\infty) = 0, \quad w(0) = r_0/2, \quad w(+\infty) = r_0. \end{cases}$$

Moreover, $w_y > 0$, $w_y/w \nearrow \alpha^-$ as $y \to -\infty$, where $\alpha^- = \frac{1-\sqrt{1-4Dr_0}}{2D}$. And if $4Dr_0 < 1$, then $w(y) \sim \exp(\alpha^- y)$ as $y \to -\infty$.

(b) *If $4Dr_0 > 1$, then there exists a unique positive solution w_{D,r_0} to*

$$\begin{cases} Dw_{yy} - w_y + (r_0 - w)w = 0 & \text{in } (0, +\infty), \\ w(0) = 0, \quad w(+\infty) = r_0. \end{cases}$$

Moreover, $w_y > 0$.

The proof of Theorem 5.4 is based on standard phase plane analysis. We refer to [22] for the proof of (a), and [2] for the proof of (b).

6. Proofs

6.1. **Proof of Persistence Results.** The following results hold true for diffusive logistic equations of indefinite weight, see [4, P. 150] and also [3, 6, 12, 15].

Lemma 6.1. (a) *If* (5) *has a positive steady state* $\tilde{u}$*, then it is globally asymptotically stable among all non-negative, non-trivial solutions.*
(b) *If* (5) *has no positive steady state, then the trivial solution is globally asymptotically stable among all non-negative solutions.*

Proof of Theorem 3.2. By Lemma 6.1, it suffices to show that (6) has no positive solution. Suppose to the contrary that (6) has a positive solution $\tilde{u}$.

By the assumption $r \leq 1/(4D)$, $b_u \geq 0$ and $b_d \geq 1/2$, it is easy to see that for any positive constant $M > 0$, $\overline{w} := Me^{x/(2\epsilon D)} \in C^\infty([0,1])$ is an upper solution of (6), i.e. $\overline{w}$ satisfies

$$\begin{cases} \epsilon^2 D\overline{w}_{xx} - \epsilon\overline{w}_x + (r - \overline{w})\overline{w} < 0 & \text{in } [0,1], \\ -\epsilon D\overline{w}_x(0) + \overline{w}(0) \geq -b_u\overline{w}(0), & \epsilon D\overline{w}_x(1) - \overline{w}(1) \geq -b_d\overline{w}(1). \end{cases} \tag{12}$$

Next, let $M_0 = \inf\{M > 0 : \tilde{u}(x) \leq Me^{x/(2\epsilon D)} \text{ for all } x \in [0,1]\}$, and define $z := M_0 e^{x/2\epsilon D} - \tilde{u}$. Then it can be verified that z satisfies

$$\begin{cases} \epsilon^2 Dz_{xx} - \epsilon z_x + (r - \tilde{u} - M_0 e^{x/(2\epsilon D)})z < 0 & \text{in } [0,1], \\ -\epsilon Dz_x(0) + z(0) \geq -b_u z(0), \quad \text{and} & \epsilon Dz_x(1) - z(1) \geq -b_d z(1). \end{cases} \tag{13}$$

Moreover, by the definition of M_0,

$$z \geq 0 \quad \text{in } [0,1], \qquad \text{and} \qquad z(x_0) = 0 \quad \text{for some } x_0 \in [0,1]. \tag{14}$$

We consider the following cases separately: (i) $b_u = b_d = +\infty$, (ii) $b_u < +\infty = b_d$, (iii) $b_d < +\infty = b_u$, (iv) $b_u, b_d < +\infty$.

Case (i): Then $z(0)$ and $z(1)$ are positive and $x_0 \in (0,1)$, but then by (14), we deduce that $z(x_0) = z_x(x_0) = 0$ and $z_{xx}(x_0) \geq 0$, which contradicts (13).

Case (ii): Then $z(1) > 0$. By the arguments in Case (i), the minimum value cannot be attained in $(0,1)$, hence we deduce that $x_0 = 0$, i.e. $z(0) = 0$. Then (14) implies that $z_x(0) \geq 0$. But then the boundary condition in (13) implies that $z_x(0) \leq (1 + b_u)z(0) = 0$. Hence $z_x(0) = 0$. By (13), we deduce that $z_{xx}(0) < 0$, and hence $z(x) < 0$ for all $0 < x \ll 1$. This is a contradiction to the non-negativity of z.

Cases (iii) and (iv) can be handled similarly.

Therefore, (6) has no positive solution. We thus conclude by Lemma 6.1 that the zero solution is globally asymptotically stable among all non-negative initial data. □

Proof of Theorem 3.1. By Lemma 6.1, it is enough to show that (6) has a positive solution. In view of Theorem 5.3, and the fact that $\bar{u} = Me^{x/(\epsilon D)}$ is an upper solution for all large $M > 0$, it suffices to construct a non-trivial, non-negative weak lower solution. (See, e.g. [4, Theorem 1.24].) Since $\max_{[0,1]} r > \frac{1}{4D}$, there exist positive constants r_0 and δ, and $x_0 \in (0, 1 - 3\delta)$ such that $r_0 > \frac{1}{4D}$, and $r(x) > r_0$ in $[x_0, x_0 + \delta] \subset [0,1]$.

Define

$$w(x) := \rho\left(\frac{x - x_0}{\epsilon}\right),$$

where

$$\rho(s) = \begin{cases} \exp\left(\frac{s}{2D}\right)\sin\left(\frac{\sqrt{4r_0 D - 1}}{2D}s\right) & \text{for } 0 < s < \frac{2\pi D}{\sqrt{4r_0 D - 1}}, \\ 0 & \text{otherwise.} \end{cases}$$

Then, since ρ satisfies $D\rho_{ss} - \rho_s + r_0\rho = 0$, one can easily verify that ηw is a weak upper solution of (6), provided $\left[x_0, x_0 + \epsilon\frac{2\pi D}{\sqrt{4r_0D-1}}\right] \subset [x_0, x_0+\delta]$, i.e. $\epsilon < \delta/\frac{2\pi D}{\sqrt{4r_0D-1}}$ and η is a sufficiently small positive constant. □

6.2. **Proof of Theorem** 3.3.

Lemma 6.2. *Suppose $r(0) < \frac{1}{4D} < \max_{[0,1]} r$, then for all δ small, there is a weak upper solution $\bar{u}_1$ such that*

(i) $\bar{u}_1 \le \max\{r(x), 0\} + \delta$,
(ii) $\bar{u}_1 = \delta$ *and* $(\bar{u}_1)_x = 0$ *in* $\{x \in [z_1, 1] : r(x) \le 0\}$,
(iii) $\bar{u}_1 \le \delta$ *in* $[0, z_1 - \delta]$, *where* $z_1 = \inf\{x \in [0,1] : r(x) \ge 1/(4D)\}$.

Here and throughout this article we denote $z_1 = \inf\{x \in [0,1] : r(x) > 1/(4D)\}$.

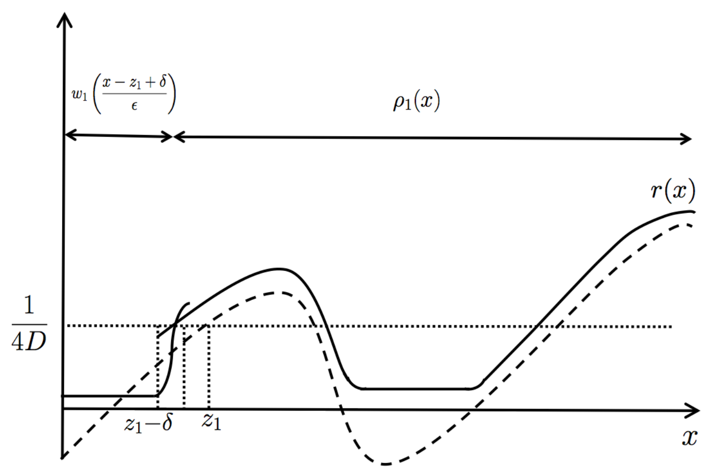

FIGURE 4. Lemma 6.2: Construction of weak upper solution $\overline{u}_1$.

Proof of Lemma 6.2. Fix $\delta > 0$. Define

$$w_1(x) = r(z_1 - \delta)\exp\left(\frac{x - z_1 + \delta}{2\epsilon D}\right).$$

Then take any smooth function ρ_1 such that $(\rho_1)_x(1) = 0$, and

$$\max\{r(x), 0\} < \rho_1 \le \max\{r(x), 0\} + \delta \quad \text{in } [0,1], \tag{15}$$

$\rho_{1,x}(1) = 0$ and

$$\rho_1 \equiv \delta \quad \text{and} \quad \rho_{1,x} \equiv 0 \quad \text{when } r(x) \le 0. \tag{16}$$

Then define

$$\overline{u}_1 := \begin{cases} w_1(x) & \text{in } [0, z_1 - \delta), \\ \min\{w_1(x), \rho_1\} & \text{in } [z_1 - \delta, z_1 - \delta/2], \\ \rho_1 & \text{in } (z_1 - \delta/2, 1]. \end{cases}$$

We claim that $\overline{u}_1$ is a weak upper solution of (6). Firstly, we verify the continuity of $\overline{u}_1$, which follows from the fact that at $x = z_1 - \delta$, by definition of w_1,

$$w_1(z_1 - \delta) = r(z_1 - \delta) < \rho_1(z_1 - \delta),$$

which implies that, in a neighborhood of $x = z_1 - \delta$, $\overline{u}_1 \equiv w_1$ is smooth. On the other hand, at $x = z_1 - \delta/2$, one can deduce by (15) that for all ϵ small,

$$w_1(z_1 - \delta/2) = r(z_1 - \delta)\exp\left(\frac{\delta}{2\epsilon D}\right) > \max\{r(z_1 - \delta/2), 0\} + \delta > \rho_1(z_1 - \delta/2).$$

This implies that, in a neighborhood of $x = z_1 - \delta/2$, $\overline{u}_1 \equiv \rho_1$ is smooth. Hence $\overline{u}_1$ is continuous.

Secondly, we check that $\overline{u}_1$ satisfies the required differential inequality,

$$L[\overline{u}_1] := \epsilon^2 D(\overline{u}_1)_{xx} - \epsilon(\overline{u}_1)_x + \overline{u}_1(r - \overline{u}_1) \le 0,$$

whenever it is smooth. This follows from the fact that in $[0, z_1 - \delta/2]$, $r(x) \le 1/(4D)$ and

$$L[w_1] = w_1\left(\frac{1}{4D} - \frac{1}{2D} + r - w_1\right) < 0.$$

And that in $[z_1 - \delta/2, 1]$, for all ϵ sufficiently small,

$$L[\rho_1] \le \epsilon(1 + \epsilon D)\|\rho_1\|_{C^2} - \left(\inf_{[z_1-\delta/2,1]} \rho_1\right)\left(\inf_{[z_1-\delta/2,1]} (\rho_1 - r)\right) < 0.$$

Finally, we check the boundary conditions.

$$[-\epsilon D(\overline{u}_1)_x + \overline{u}_1]_{x=0} = [-\epsilon D(w_1)_x + w_1]_{x=0} = w_1\left[-\epsilon D\frac{1}{2\epsilon D} + 1\right] > 0,$$

and $(\overline{u}_1)_x(1) = (\rho_1)_x(1) = 0$ by definition of ρ_1. This completes the proof. □

Lemma 6.3. *Suppose* $\max_{[0,1]} r > \frac{1}{4D}$*, and there exists* $x_1 \in (0, 1)$ *such that*

$$r \le 0 \quad \text{in } [0, x_1], \qquad \text{and} \qquad r > 0 \quad \text{in } (x_1, 1].$$

Then for each $\delta_0 > 0$*, for* ϵ *sufficiently small, there is weak lower solution* $\underline{u}_1$ *such that*

$$\underline{u}_1 = \begin{cases} 0 & \text{in } [0, z_1], \\ r(x) - \delta_0 \le \underline{u}_1 \le r(x) & \text{in } [z_1 + \delta_0, 1]. \end{cases}$$

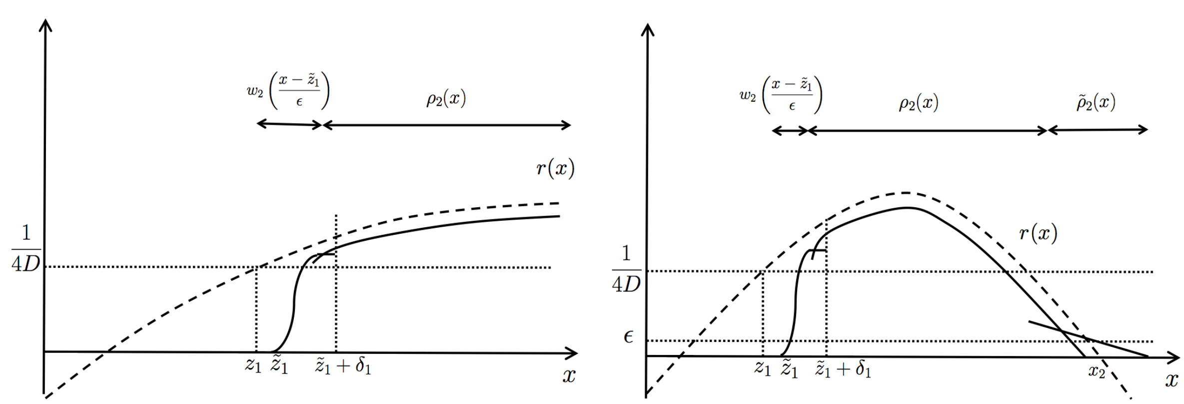

FIGURE 5. Left panel: Lemma 6.3: Construction of weak lower solution $\underline{u}_1$. Right Panel: Lemma 6.4: Construction of weak lower solution $\underline{u}_1$.

Lemma 6.4. *Suppose* $0 < x_1 < x_2 < 1$ *satisfies*

$$r(x_1) = r(x_2) = 0 \quad \text{and} \quad r > 0 \quad \text{in } (x_1, x_2).$$

Assume $\frac{1}{4D} \in (0, \max_{[x_1,x_2]} r)$. *Then for each* $\delta_0 > 0$, *if* ϵ *is sufficiently small, there is a weak lower solution* $\underline{u}_1$ *such that*

$$\underline{u}_1 = \begin{cases} 0 & \text{in } [0, z_1], \\ r(x) - \delta_0 \le \underline{u}_1 \le r(x) & \text{in } [z_1 + \delta_0, x_2 - 3\delta_0), \\ \epsilon & \text{at } x = x_2, \\ 0 & \text{in } [x_2 + 2\delta_0, 1], \end{cases}$$

where $z_1 = \inf\{x \in (x_1, x_2) : r(x) > 1/(4D)\}$.

Note that Theorem 3.3 follows directly from Lemmas 6.2 and 6.3. We will prove Lemma 6.3, and indicate the modifications to get Lemma 6.4. The latter result plays an important role in the construction of the second transition layer.

Proof of Lemma 6.3. Let $\delta_0 > 0$ be given. By definition of $z_1 = \inf\{x \in [0,1] : r(x) > 1/(4D)\}$, we may choose $\tilde{z}_1 \in (z_1, z_1 + \delta_0/2)$, such that $r(\tilde{z}_1) > 1/(4D)$. Given any $0 < \delta < \min\{\delta_0/2, r(\tilde{z}_1) - 1/(4D)\}$, there exists $\delta_1 = \delta_1(\delta) \in (0, \delta_0/2)$ such that

$$|r(x) - r(y)| < \frac{\delta}{2} \quad \text{for any } x, y \in [0,1] \text{ such that } |x - y| < \delta_1. \tag{17}$$

Next, let w_2 be the unique positive solution to

$$\begin{cases} Dw_{yy} - w_y + (r(\tilde{z}_1) - \delta/2 - w)w = 0 & \text{in } (0, +\infty), \\ w(0) = 0, \quad w(+\infty) = r(\tilde{z}_1) - \delta/2, \end{cases}$$

which exists since $4D(r(\tilde{z}_1) - \delta/2) > 1$ (Theorem 5.4). Next, choose $\rho_2 \in C^\infty([\tilde{z}_1 + \delta_1/2, 1])$ such that

$$\begin{cases} r(x) - \delta < \rho_2(x) < r(x) \quad \text{in } [\tilde{z}_1 + \delta_1/2, 1], \quad (\rho_2)_x(1) = 0, \\ \rho_2(\tilde{z}_1 + \delta_1/2) < r(\tilde{z}_1) - \delta/2, \quad \rho_2(\tilde{z}_1 + \delta_1) > r(\tilde{z}_1) - \delta/2, \end{cases} \tag{18}$$

which is possible, as $r(\tilde{z}_1 + \delta_1/2) - \delta < r(\tilde{z}_1) - \delta/2 < r(\tilde{z}_1 + \delta_1)$ by (17). Finally, we define

$$\underline{u}_1 := \begin{cases} 0 & \text{in } [0, \tilde{z}_1), \\ w_2\left(\frac{x - \tilde{z}_1}{\epsilon}\right) & \text{in } [\tilde{z}_1, \tilde{z}_1 + \delta_1/2), \\ \max\left\{w_2\left(\frac{x - \tilde{z}_1}{\epsilon}\right), \rho_2(x)\right\} & \text{in } [\tilde{z}_1 + \delta_1/2, \tilde{z}_1 + \delta_1), \\ \rho_2(x) & \text{in } [\tilde{z}_1 + \delta_1, 1]. \end{cases}$$

It remains to check, for ϵ sufficiently small, that $\underline{u}_1$ is a weak lower solution of (6). Firstly, we check that $\underline{u}_1$ is continuous at $x = \tilde{z}_1, \tilde{z}_1 + \delta_1/2, \tilde{z}_1 + \delta_1$. This follows from

$$\underline{u}_1(\tilde{z}_1+) = w_2(0) = 0 = \underline{u}_1(\tilde{z}_1-)$$

and that when $x = \tilde{z}_1 + \delta_1/2$, (and ϵ small), by (18),

$$w_2\left(\frac{x - \tilde{z}_1}{\epsilon}\right)\Bigg|_{x = \tilde{z}_1 + \delta_1/2} \approx r(\tilde{z}_1) - \delta/2 > \rho_2(\tilde{z}_1 + \delta_1/2)$$

which implies that $\underline{u}_1 \equiv w_2$ is smooth in a neighborhood of $\tilde{z}_1 + \delta_1/2$; and that when $x = \tilde{z}_1 + \delta_1$, by (18),

$$w_2\left(\frac{x - \tilde{z}_1}{\epsilon}\right)\Bigg|_{x = \tilde{z}_1 + \delta_1} \approx r(\tilde{z}_1) - \delta/2 < \rho_2(\tilde{z}_1 + \delta_1)$$

which implies that, in a neighborhood of $\tilde{z}_1 + \delta_1$, $\underline{u}_1 \equiv \rho_2$ is smooth.

Secondly, we check that at $x = \tilde{z}_1, \tilde{z}_1 + \delta_1/2, \tilde{z}_1 + \delta_1$, $(\underline{u}_1)_x$ satisfies $(\underline{u}_1)_x(x-) \leq (\underline{u}_1)_x(x+)$. This is clearly satisfied when $\tilde{x} = \tilde{z}_1$, and also at $x = \tilde{z}_1 + \delta_1/2, \tilde{z}_1 + \delta_1$ since $\underline{u}_1$ is smooth near those points.

Finally, we check that $\underline{u}_1$ satisfies the required differential inequality $L[\underline{u}_1] \geq 0$ whenever it is smooth. Now, in $(\tilde{z}_1, \tilde{z}_1 + \delta_1)$, $r(x) > r(\tilde{z}_1) - \delta/2$ (from (17)) and

$$L\left[w_2\left(\frac{x - \tilde{z}_1}{\epsilon}\right)\right] \geq Dw_{2,yy} - w_{2,y} + w_2(r(\tilde{z}_1) - \delta/2 - w_2) = 0,$$

whereas in $[\tilde{z}_1 + \delta_1/2, 1]$,

$$L[\rho_2] \geq -\epsilon(1 + D)\|\rho_2\|_{C^2} + \left(\inf_{[\tilde{z}_1+\delta_1/2,1]} \rho_2\right)\left(\inf_{[\tilde{z}_1+\delta_1/2,1]} (r - \rho_2)\right) > 0$$

for all ϵ sufficiently small. This completes the proof of Lemma 6.3. □

Next, we indicate the modifications to show Lemma 6.4.

Proof of Lemma 6.4. We first modify ρ_2 to satisfy, in addition to (18),

$$\rho_2 = \begin{cases} \frac{1}{2\delta}\left(\inf_{[x_2-2\delta,x_2-\delta]} r\right)(x_2 - \delta - x) & \text{in } [x_2 - 2\delta, x_2 - \delta], \\ 0 & \text{in } (x_2 - \delta, 1], \end{cases} \tag{19}$$

and let

$$\tilde{\rho}_2 = \epsilon\left[2\frac{x - x_2}{(x_2 - 2\delta) - x_2} + \frac{x - (x_2 - 2\delta)}{x_2 - (x_2 - 2\delta)}\right] = \epsilon\frac{x_2 + 2\delta - x}{2\delta}. \tag{20}$$

Then it can be easily seen that, for $\epsilon > 0$ sufficiently small,

$$\underline{u}_1 := \begin{cases} 0 & \text{in } [0, \tilde{z}_1) \cup [x_2 + 2\delta, 1], \\ w_2\left(\frac{x-\tilde{z}_1}{\epsilon}\right) & \text{in } [\tilde{z}_1, \tilde{z}_1 + \delta_1/2), \\ \max\{w_2\left(\frac{x-\tilde{z}_1}{\epsilon}\right), \rho_2(x)\} & \text{in } [\tilde{z}_1 + \delta_1/2, \tilde{z}_1 + \delta_1), \\ \rho_2(x) & \text{in } [\tilde{z}_1 + \delta_1, x_2 - 2\delta), \\ \max\{\rho_2(x), \tilde{\rho}_2(x)\} & \text{in } [x_2 - 2\delta, x_2 - \delta), \\ \tilde{\rho}_2(x) & \text{in } [x_2 - \delta, x_2 + 2\delta) \end{cases}$$

is a weak lower solution. The boundary inequalities are satisfied, as $\underline{u}_1 \equiv 0$ near to the boundary points. The continuity of $\underline{u}_1$ follows from previous arguments, and the fact that

$$\begin{cases} \rho_2(x_2 - 2\delta) = \frac{1}{2}\inf_{[x_2-2\delta,x_2-\delta]} r > 2\epsilon = \tilde{\rho}_2(x_2 - 2\delta), \\ \rho_2(x_2 - \delta) = 0 < \tilde{\rho}_2(x_2 - \delta), \end{cases}$$

so that $\underline{u}_1$ is smooth near $x = \tilde{z}_1 + \delta_1/2, \tilde{z}_1 + \delta_1, x_2 - 2\delta, x_2 - \delta$. It remains to check the differential inequalities for ρ_2 and $\tilde{\rho}_2$. The differential inequality $L[\rho_2] \geq 0$ in $[\tilde{z}_1 + \delta_1/2, x_2 - 2\delta]$ can be verified as in proof of Lemma 6.3. In $[x_2 - 2\delta, x_2 - \delta]$, ρ_2 is linear and satisfies $\rho_2(r - \rho_2) \geq 0$, so $L[\rho_2] \geq -\epsilon\left(\frac{-1}{2\delta}\inf_{[x_2-2\delta,x_2-\delta]} r\right) > 0$. Also, in $[x_2 - 2\delta, x_2 + 2\delta]$, $0 \leq \tilde{\rho}_2 \leq 2\epsilon$ and

$$L[\tilde{\rho}_2] \geq -\epsilon\tilde{\rho}_{2,x} - (\tilde{\rho}_2)^2 \geq -\epsilon\left(-\frac{\epsilon}{2\delta}\right) - (2\epsilon)^2 > 0$$

independent of all small ϵ, since δ is a small and fixed constant. □

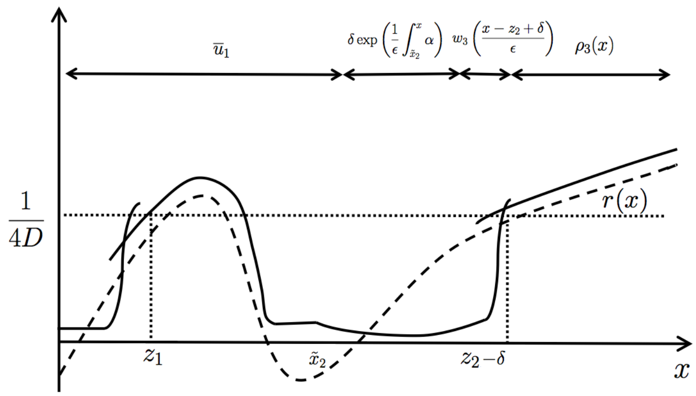

FIGURE 6. Construction of upper solution $\overline{u}$ in the proof of Theorem 3.4(a).

6.3. Proof of Theorem 3.4(a).

Proof of Theorem 3.4(a). Let α^- be given by (11) for $x \in (x_2, z_2)$. By choosing δ smaller, we may assume without loss that $r(x) > \delta$ for all $x \in [z_2 - 2\delta, z_2]$.

Claim 6.5. *There exists a smooth function α such that*

(i) $\alpha^- < \alpha < \alpha^+$ *in* $[x_2, z_2)$,

(ii) *there exists* $\tilde{x}_2 \in (x_2, x_3)$ *such that* $\alpha(\tilde{x}_2) < 0$ *and* $\int_{\tilde{x}_2}^{z_2-\delta} \alpha = 0$, *and α change sign exactly once, from negative to positive, in* $[\tilde{x}_2, z_2 - \delta]$,

(iii) $\alpha(z_2 - \delta) > \alpha^-(z_2) = \frac{1}{2D}$.

To see the claim, observe that $\alpha^- < 0$ in (x_2, x_3) and $\alpha^- > 0$ in (x_3, z_2). Therefore for $\delta > 0$ small

$$\int_{x_2}^{z_2-\delta} \alpha^- < \int_{x_2}^{z_2} \alpha^- \leq 0.$$

Therefore, we may choose a function α satisfying (i) and (iii) such that $\int_{x_2}^{z_2-\delta} \alpha < 0$ and that it changes sign exactly twice, i.e.

$$\alpha > 0 \quad \text{in } [x_2, x') \cup (x'', z_2 - \delta], \qquad \text{and} \qquad \alpha < 0 \quad \text{in } (x', x'') \tag{21}$$

for some $x', x'' \in (x_2, x_3)$ such that $x_2 < x' < x'' < x_3 < z_2$. Finally, (21) implies (ii) with some $\tilde{x}_2 \in (x', x'')$. We then define

$$\overline{u} := \begin{cases} \overline{u}_1 & \text{in } [0, \tilde{x}_2), \\ \delta \exp\left(\frac{1}{\epsilon}\int_{\tilde{x}_2}^{x} \alpha\right) & \text{in } (\tilde{x}_2, z_2 - \delta), \\ \min\{w_3(x), \rho_3\} & \text{in } [z_2 - \delta, z_2 - \delta/2), \\ \rho_3 & \text{in } [z_2 - \delta/2, 1], \end{cases}$$

where $\bar{u}_1$ is given by Lemma 6.2, so that

$$\bar{u}_1(\tilde{x}_2) = \delta \quad \text{and} \quad (\bar{u}_1)_x(\tilde{x}_2) = 0. \tag{22}$$

We also choose the smooth function ρ_3 such that $r < \rho_3 < r + \delta$ in $[z_2 - \delta, 1]$, $\rho_3(z_2 - \delta/2) < r(z_2) = \frac{1}{4D}$ and $\rho_{3,x}(1) = 0$. And that w_3 is given by

$$w_3(x) = \delta \exp\left(\frac{x - z_2 + \delta}{2\epsilon D}\right).$$

Now, we proceed to show that $\overline{u}$ is a weak upper solution of (6). First, we check the continuity. The continuity at $x = \tilde{x}_2$ follows since

$$\bar{u}_1(\tilde{x}_2) = \delta = \delta \exp\left(\frac{1}{\epsilon}\int_{\tilde{x}_2}^{x} \alpha\right)\Big|_{x=\tilde{x}_2}$$

by Lemma 6.2(ii). At $x = z_2 - \delta$, by Claim 6.5(ii), $\overline{u}((z_2-\delta)-) = \delta\exp\left(\frac{1}{\epsilon}\int_{\tilde{x}_2}^{z_2-\delta}\alpha\right) = \delta$, while $w_3\,(z_2-\delta) = \delta < r(z_2-\delta) < \rho(z_2-\delta)$, which implies that $\overline{u}((z_2-\delta)+) = \delta$ as well. At $x = z_2 - \delta/2$,

$$w_3(z_2-\delta/2) = \delta\exp\left(\frac{\delta}{4\epsilon D}\right) > \rho(z_2-\delta/2),$$

for all ϵ small. Hence $\bar{u} \equiv \rho_3$ near $z_2 - \delta/2$.

Next, we check that discontinuities of $\overline{u}_x$ at $x = \tilde{x}_2, z_2-\delta, z_2-\delta/2$ are consistent with the definition of weak upper solutions. At $\tilde{x}_2$, $\overline{u}_x(\tilde{x}_2-) = 0 > \frac{\delta}{\epsilon}\alpha(\tilde{x}_2) = \overline{u}_x(\tilde{x}_2+)$, by (22) and Claim 6.5(ii). At $x = z_2 - \delta$,

$$\overline{u}_x((z_2-\delta)-) = \frac{\delta}{\epsilon}\alpha(z_2-\delta) > \frac{\delta}{\epsilon}\frac{1}{2D} = (w_3)_x(z_2-\delta) = \bar{u}_x((z_2-\delta)+),$$

by Claim 6.5(iii). Hence $\overline{u}_x((z_2-\delta)-) > \overline{u}_x((z_2-\delta)-)$. Also, $\bar{u} \equiv \rho_3$ is smooth near $z_2 - \delta/2$.

Next, we check the differential inequality. By Lemma 6.2, $L[\bar{u}_1] \le 0$. Let $\tilde{w} = \delta\exp\left(\frac{1}{\epsilon}\int_{\tilde{x}_2}^{x}\alpha\right)$, then, for $x \in [\tilde{x}_2, z_2-\delta]$,

$$\begin{aligned} L[\tilde{w}] &\le \epsilon^2 D\tilde{w}_{xx} - \epsilon\tilde{w}_x + r\tilde{w} \\ &= \tilde{w}\left[D\alpha^2 + \epsilon D\alpha_x - \alpha + r\right] \\ &\le \tilde{w}\left[\sup_{[\tilde{x}_2, z_2-\delta]}(D\alpha^2 - \alpha - r\alpha) + D\epsilon\|\alpha\|_{C^1}\right] < 0 \end{aligned}$$

for all ϵ sufficiently small, where the last inequality holds since $\alpha^- < \alpha < \alpha^+$ on a compact interval $[\tilde{x}_2, z_2-\delta]$, whence $\sup_{[\tilde{x}_2,z_2-\delta]}(D\alpha^2 - \alpha - r) < 0$. Also, in $[z_2-\delta_1, z_2-\delta_1/2]$, $r(x) \le 1/(4D)$ and

$$L\,[w_3] = w_3\left(\frac{1}{4D} - \frac{1}{2D} + r - w_3\right) \le 0.$$

Also, $L[\rho_3] \le 0$ for all ϵ sufficiently small as before.

Finally, the boundary conditions are satisfied since $\overline{u} \equiv \overline{u}_1$ in a neighborhood of 0, and $\overline{u}_x(1) = \rho_{3,x}(1) = 0$. Hence $\bar{u}$ is a weak upper solution.

Next, we construct the weak lower solution. To this end, we take the lower solution $\underline{u}_1$ supported within (x_1, x_2) which was constructed in Lemma 6.4, and construct a lower solution $\underline{u}_2$ analogously to Lemma 6.3, supported within $(z_2, 1]$. Finally, define

$$\underline{u} = \begin{cases} \underline{u}_1 & \text{in } [0, x_2), \\ 0 & \text{in } [x_2, z_2+\delta), \\ \underline{u}_2 & \text{in } [z_2+\delta, 1]. \end{cases}$$

Then $\underline{u}$ clearly satisfies (i) - (iv) of Lemma 5.2. Hence $\underline{u}$ qualifies as a weak lower solution. The pair of weak upper and lower solutions given by $\bar{u}$ and $\underline{u}$ proves that (6) has a positive solution $\tilde{u}$ with the asserted profile. By uniqueness of positive solution $\tilde{u}$, Theorem 3.4(a) is proved. □

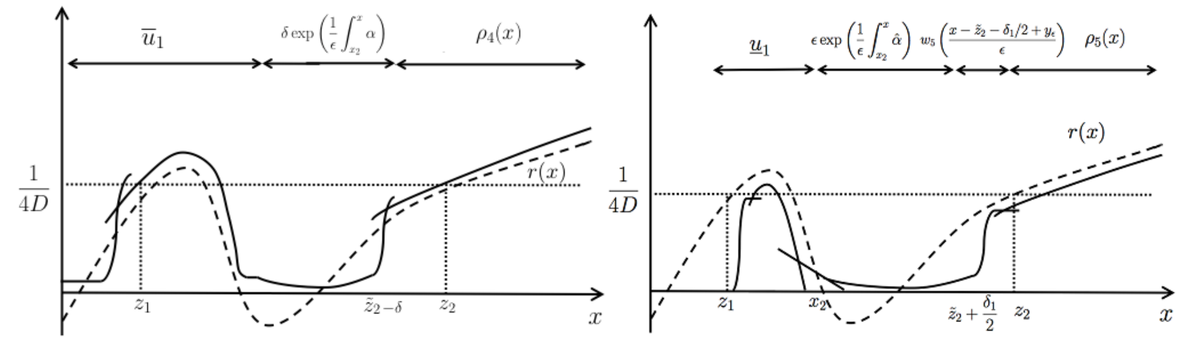

FIGURE 7. Left panel: Construction of upper solution in the proof of Theorem 3.4(b). Right panel: Construction of lower solution in the proof of Theorem 3.4(b).

6.4. **Proof of Theorem 3.4(b).**

Proof of Theorem 3.4(b). Fix $\delta > 0$, and let δ_1 be given by the uniform continuity of r as in (17). Suppose $\int_{x_2}^{z_2} \alpha^- > 0$. By the fact that α^- changes sign exact once from negative to positive in (x_2, z_2), there exists a unique number $\tilde{z}_2 \in (x_3, z_2)$ such that $\int_{x_2}^{\tilde{z}_2} \alpha^- = 0$. Let $\alpha : [x_2 + \delta_1, z_2]$ be a smooth function that changes sign only once from negative to positive,

$$\alpha^- < \alpha < \alpha^+ \quad \text{for } [x_2+\delta_1, \tilde{z}_2 - \delta_1], \int_{x_2+\delta_1}^{\tilde{z}_2-\delta_1} \alpha = 0, \tag{23}$$

and

$$\alpha(x_2+\delta_1) < 0, \quad \alpha(\tilde{z}_2 - \delta_1) > 0. \tag{24}$$

We claim that this is possible for δ_1 small (and still satisfy (17)). To see the claim, let $g(t) = \int_{x_2+t}^{\tilde{z}_2-t} \alpha^-$, then $g(0) = 0$ and

$$g'(0) = -\alpha^-(\tilde{z}_2) - \alpha^-(x_2) = -\alpha^-(\tilde{z}_2) < 0.$$

So $\int_{x_2+\delta_1}^{\tilde{z}_2-\delta_1} \alpha^- < 0$ for all $\delta_1 > 0$ small. And we may choose a function α that approximates α^- such that it changes sign exactly once from negative to positive, and that (23) and (24) hold.

Choose a smooth function ρ_4 defined on $[\tilde{z}_2 - \delta_1, 1]$ such that $r(x) < \rho_4(x) < r(x) + \delta$, $\rho_{4,x}(1) = 0$. We also define

$$\tilde{w} = \delta \exp\left(\frac{1}{\epsilon}\int_{x_2+\delta_1}^{x} \alpha\right),$$

and define our weak upper solution by

$$\overline{u} := \begin{cases} \overline{u}_1 & \text{in } [0, x_2+\delta_1), \\ \min\{\overline{u}_1, \tilde{w}\} & \text{in } [x_2+\delta_1, \tilde{z}_2-\delta_1), \\ \min\{\tilde{w}, \rho_4\} & \text{in } [\tilde{z}_2-\delta_1, \tilde{z}_2-\delta_1/2), \\ \rho_4 & \text{in } [\tilde{z}_2-\delta_1/2, 1], \end{cases}$$

where $\overline{u}_1(x_2+\delta_1) = \delta$ and $(\overline{u}_1)_x(x_2+\delta_1) = 0$. The continuity of $\overline{u}$ at $x = x_2+\delta_1, \tilde{z}_2-\delta_1, \tilde{z}_2-\delta_1/2$ follows from (i) $\overline{u}_1(x_2+\delta_1) = \delta = \tilde{w}(x_2+\delta_1)$; (ii) at $\tilde{z}_2-\delta_1$, $\overline{u}_1(\tilde{z}_2-\delta_1) = \delta = \tilde{w}(\tilde{z}_2-\delta_1)$, and $(\overline{u}_1)_x(\tilde{z}_2-\delta_1) = 0 < \alpha(\tilde{z}_2-\delta_1) = \tilde{w}_x(\tilde{z}_2-\delta_1)$, so $\overline{u} \equiv \tilde{w}$ for $x \nearrow \tilde{z}_2-\delta_1$. Since also $\tilde{w}(\tilde{z}_2-\delta_1) = \delta < r(\tilde{z}_2-\delta_1) < \rho_4(\tilde{z}_2-\delta_1)$, we have $\overline{u} \equiv \tilde{w}$ in a neighborhood of $\tilde{z}_2-\delta_1$; (iii) at

$x = \tilde{z}_2 - \delta_1/2$: $\tilde{w}(\tilde{z}_2 - \delta_1/2) = \delta \exp\left(\frac{1}{\epsilon}\int_{\tilde{z}_2-\delta_1}^{\tilde{z}_2-\delta_1/2} \alpha\right) > \rho_4(\tilde{z}_2 - \delta_1/2)$ for $0 < \epsilon \ll 1$ since $\alpha > 0$ in $(\tilde{z}_2 - \delta_1, \tilde{z}_2 - \delta_1/2)$. So $\bar{u} \equiv \rho_4$ in a neighborhood of $\tilde{z}_2 - \delta_1/2$.

Next, we claim that the discontinuities of $\overline{u}_x$ have the correct signs: At $x = x_2 + \delta_1$, it is a minimum of two smooth functions, so $\bar{u}_x((x_2 + \delta_1)-) \geq \bar{u}_x((x_2 + \delta_1)+)$. In a neighborhood of $x = \tilde{z}_2 - \delta_1$, $\bar{u} \equiv \tilde{w}$ as explained previously, so $\bar{u}$ is smooth near $\tilde{z}_2 - \delta_1$. Also $\bar{u} \equiv \rho_4$ is smooth in a neighborhood of $\tilde{z}_2 - \delta_1/2$.

Next, we check the differential inequalities. We already have $L[\bar{u}_1] \leq 0$ by Lemma 6.2. Also, we may deduce that for $[x_2 + \delta_1, \tilde{z}_2 - \delta_1/2)$,

$$L\left[\tilde{w}\right] \leq \tilde{w}(D\alpha^2 + \epsilon D\alpha_x - \alpha + r - \tilde{w}) \leq \left(\sup_{[x_2+\delta_1,\tilde{z}_2-\delta_1]} (D\alpha^2 - \alpha + r) + \epsilon\|\alpha\|_{C^1}\right) < 0,$$

for all ϵ small, similar as proof of Theorem 3.4(a). Next, $L[\rho_4] \leq 0$ in $[\tilde{z}_2 - \delta_1, 1]$ for all ϵ sufficiently small same as before.

The function $\overline{u}$ satisfies the boundary conditions for upper solution, as $\bar{u}_1$ satisfies the boundary conditions at $x = 0$, $-\epsilon D\overline{u}_{1,x}(0) + \overline{u}_1(0) \geq 0$ and $\rho_{4,x}(1) = 0$ (by definition of ρ_4). This proves that $\bar{u}$ is a weak upper solution. Since α changes sign only once, from negative to positive in $[x_2 + \delta_1, \tilde{z}_2 - \delta_1]$ and that $\int_{x_2+\delta_1}^{\tilde{z}_2-\delta_1} \alpha = 0$, we see that $\tilde{w} \leq \delta$ in $[x_2 + \delta_1, \tilde{z}_2 - \delta_1]$, which proves the desired property for the upper solution $\bar{u}$.

Next, we construct the weak lower solution $\underline{u}$. Given $\delta > 0$, let $\underline{u}_1$ be given by Lemma 6.4. Choose a smooth function $\hat{\alpha} : [x_2, \tilde{z}_2 + \delta_1]$ which satisfies

(25)
$$\int_{x_2}^{\tilde{z}_2+\delta_1/3} \hat{\alpha} = 0, \quad \hat{\alpha} < \alpha^- \text{ in } [x_2, \tilde{z}_2 + \delta_1], \quad \hat{\alpha}(\tilde{z}_2 + \delta_1/3) < \hat{\alpha}_0 := \frac{1 - \sqrt{1 - 4D(r(\tilde{z}_2) - \delta/2)}}{2D},$$

and $\hat{\alpha}$ changes sign only once in $[x_2, \tilde{z}_2 + \delta_1]$, from negative to positive.

Next, let w_5 be the unique positive solution to

$$\begin{cases} Dw_{yy} - w_y + w(r(\tilde{z}_2) - \delta/2 - w) = 0 & \text{in } (-\infty, +\infty), \\ w(-\infty) = 0, \quad w(+\infty) = r(\tilde{z}_2) - \delta/2, & w(0) = (r(\tilde{z}_2) - \delta/2)/2. \end{cases}$$

Again, w_5 exists since $4D(r(\tilde{z}_2) + \delta/2) < 1$ for δ small. By Theorem 5.4,

$$w_5(y) \sim O\left(\exp(\hat{\alpha}_0 y)\right) \quad \text{and} \quad \frac{w_{5,y}}{w_5} \nearrow \hat{\alpha}_0, \quad \text{as } y \to -\infty. \tag{26}$$

Since $w_y > 0$ in $(-\infty, \infty)$, let y_ϵ be the unique number such that $w_5(y_\epsilon) = \epsilon$, then (by (26)) $y_\epsilon < 0$ satisfies $|y_\epsilon| \sim O(\log \epsilon)$. In particular, for any fixed constant $K > 0$,

$$\lim_{\epsilon \to 0} w_5\left(y_\epsilon + \frac{K}{\epsilon}\right) = w_5(+\infty) = r(\tilde{z}_2) - \frac{\delta}{2}. \tag{27}$$

Next, choose $\rho_5 \in C^2([\tilde{z}_2, 1])$ such that $r(x) - \delta < \rho_5(x) < r(x)$ in $[\tilde{z}_2, 1]$,

$$\rho_5(\tilde{z}_2 + 2\delta_1/3) < r(\tilde{z}_2) - \delta/2, \quad \rho_5(\tilde{z}_2 + \delta_1) > r(\tilde{z}_2) - \delta/2, \quad (\rho_5)_x(1) = 0. \tag{28}$$

Such a choice of ρ_5 is possible since $r(\tilde{z}_2+2\delta_1/3)-\delta < r(\tilde{z}_2)-\delta/2 < r(\tilde{z}_2+\delta_1)$ by (17). With that, we define

$$\underline{u} := \begin{cases} \underline{u}_1 & \text{in } [0,x_2), \\ \max\left\{\underline{u}_1, \epsilon\exp\left(\frac{1}{\epsilon}\int_{x_2}^x \hat{\alpha}\right)\right\} & \text{in } [x_2, \tilde{z}_2+\delta_1/3), \\ w_5\left(\frac{x-\tilde{z}_2-\delta_1/3}{\epsilon}+y_\epsilon\right) & \text{in } [\tilde{z}_2+\delta_1/3, \tilde{z}_2+2\delta_1/3), \\ \max\left\{w_5\left(\frac{x-\tilde{z}_2-\delta_1/3}{\epsilon}+y_\epsilon\right), \rho_5(x)\right\} & \text{in } [\tilde{z}_2+2\delta_1/3, \tilde{z}_2+\delta_1), \\ \rho_5(x) & \text{in } [\tilde{z}_2+\delta_1, 1]. \end{cases}$$

We verify that $\underline{u}$ is a weak lower solution for (6) in detail. We claim that $\underline{u}$ is continuous at $x = x_2, \tilde{z}_2+\delta_1/3, \tilde{z}_2+2\delta_1/3, \tilde{z}_2+\delta_1$. At $x = x_2$, $\bar{u}_1(x_2) = \epsilon = \epsilon\exp\left(\frac{1}{\epsilon}\int_{x_2}^x \hat{\alpha}\right)\Big|_{x=x_2}$, so $\underline{u}$ is continuous at $x = x_2$. At $\tilde{z}_2+\delta_1/3$, since $\underline{u}_1 = 0$, we have, by (25) and definition of y_ϵ,

$$\underline{u}((\tilde{z}_2+\delta_1/3)-) = \left[\epsilon\exp\left(\frac{1}{\epsilon}\int_{x_2}^x \alpha\right)\right]_{x=\tilde{z}_2+\delta_1/3} = \epsilon = w(y_\epsilon) = \underline{u}((\tilde{z}_2+\delta_1/2)+).$$

At $x = \tilde{z}_2+2\delta_1/3$, by (27) and (28), we have

$$w_5\left(\frac{x-\tilde{z}_2-\delta_1/3}{\epsilon}+y_\epsilon\right) = w_5\left(\frac{\delta_1}{3\epsilon}+y_\epsilon\right) \approx r(\tilde{z}_2)-\delta/2 > \rho_5(\tilde{z}_2-2\delta_1/3).$$

Hence $\underline{u} \equiv w_5$ in a neighborhood of $\tilde{z}_2+2\delta_1/3$. Similarly, at $x = \tilde{z}_2+\delta_1$,

$$w_5\left(\frac{x-\tilde{z}_2-\delta_1/3}{\epsilon}+y_\epsilon\right) = w_5\left(\frac{2\delta_1}{3\epsilon}+y_\epsilon\right) \approx r(\tilde{z}_2)-\delta/2 < \rho_5(\tilde{z}_2-\delta_1).$$

Hence $\underline{u} \equiv \rho_5$ is smooth in a neighborhood of $\tilde{z}_2+\delta_1$. This proves the continuity of the function $\bar{u}$.

Secondly, we verify that at $x = x_2, \tilde{z}_2+\delta_1/3, \tilde{z}_2+2\delta_1/3, \tilde{z}_2+\delta$, we have $\underline{u}_x(x-) \le \underline{u}_x(x+)$. This holds when $x = x_2$, as $\underline{u}$ is a maximum of two functions there. For x less than and close to $\tilde{z}_2+\delta_1/3$, $\underline{u}_1(x) \equiv 0$, so $\underline{u}(x) = \epsilon\exp\left(\frac{1}{\epsilon}\int_{x_2}^x \hat{\alpha}\right)$. Hence $\underline{u}_x((\tilde{z}_2+\delta_1/3)-) = \hat{\alpha}(\tilde{z}_2+\delta_1/3)$. Next, by (26)

$$\underline{u}_x((\tilde{z}_2+\delta_1/3)+) = \frac{1}{\epsilon}w_{5,y}(y_\epsilon) = \frac{w_{5,y}}{w_5}\Big|_{y=y_\epsilon} \approx \frac{w_{5,y}}{w_5}(-\infty) = \hat{\alpha}_0.$$

Hence, $\underline{u}_x((\tilde{z}_2+\delta_1/3)+) \ge \underline{u}_x((\tilde{z}_2+\delta_1/3)-)$ by (25). The remaining possible discontinuities of $\underline{u}_x$ are consistent, as $\underline{u}$ is smooth in some neighborhoods of $x = \tilde{z}_2+2\delta_1/3, \tilde{z}_2+\delta_1$.

Thirdly, we claim that $L[\underline{u}] \ge 0$ whenever it is smooth. This has already been verified for $\underline{u}_1$. Letting $\hat{w} = \epsilon\exp\left(\frac{1}{\epsilon}\int_{\hat{x}_2}^x \hat{\alpha}\right)$, we then proceed to compute in $[x_2, \tilde{z}_2+\delta_1/2]$,

$$L[\hat{w}] = \hat{w}\left[(D\hat{\alpha}^2 - \hat{\alpha} + r) + \epsilon D\hat{\alpha}_x - \hat{w}\right]$$

Since $\inf_{[x_2,\tilde{z}_2+\delta_1/3]}(D\hat{\alpha}^2-\hat{\alpha}+r) > 0$ independent of ϵ, it suffices to show the following claim.

Claim 6.6. $\tilde{w} = \epsilon\exp\left(\frac{1}{\epsilon}\int_{\hat{x}_2}^x \hat{\alpha}\right) \le \epsilon$ *in* $[x_2, \tilde{z}_2+\delta_1/3]$.

To see the claim, first recall that $\hat{\alpha}$, changing sign only once (from negative to positive) in $[x_2, \tilde{z}_2+\delta_1/3]$, and hence $\int_{\hat{x}_x}^x \hat{\alpha}$, which vanishes when $x = x_2$ and $\tilde{z}_2+\delta_1/3$, is always non-positive in $[x_2, \tilde{z}_2+\delta_1/3]$. This proves Claim 6.6.

Hence, $L[\hat{w}] \ge 0$ in $[x_2, \tilde{z}_2+\delta_1/3]$ for ϵ sufficiently small. It follows as before that $L\left[w_5\left(\frac{x-\tilde{z}_2-\delta_1/3+y_\epsilon}{\epsilon}\right)\right] \ge 0$ in $[\tilde{z}_2+\delta_1/3, \tilde{z}_2+\delta_1]$ and $L[\rho_5] \ge 0$ in $[\tilde{z}_2+2\delta_1/3, 1]$.

Finally, we verify that $\underline{u}$ has the correct boundary conditions. Now, we have verified previously that $\underline{u}_1$ has the correct boundary condition at $x = 0$. The other boundary condition at $x = 1$ follows by (28). □

7. Extension

In this work, we focused on internal transition layers. When the upstream invasion limit is at the upstream end, i.e. $z_1 = 0$, then the population is only limited by the boundary condition at the upstream habitat end. We expect there to be a boundary transition layer at the upstream end, in which the population is below the carrying capacity.

Remark 7.1. Suppose that $z_1 = 0$. We can show that as $\epsilon \to 0$, $\tilde{u} \to r_+(x)$ (i.e. the positive part of $r(x)$) locally uniformly in $(0, 1]$ and that $\lim_{\epsilon\to 0} \tilde{u}(0)$ exists.

We illustrate this case in Figure 8. We choose the linearly decreasing resource function $r(x) = 0.8 - x$ and fix $D = 1/4$. As ϵ decreases, the transition layer decreases in width, and the value $\tilde{u}(0)$ converges, as Table 3 indicates.

ϵ	0.02	0.01	0.005
$\tilde{u}(0)$	0.0116	0.014	0.016

Table 3. Linearly decreasing r.

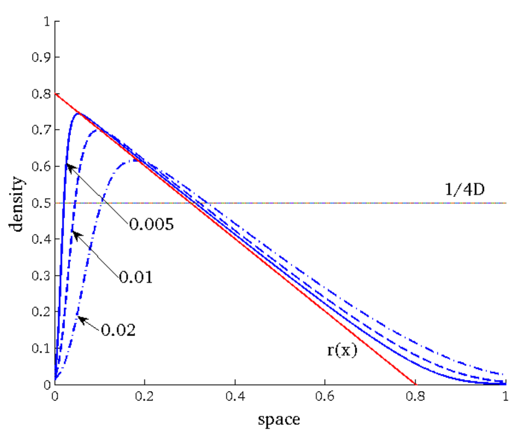

Figure 8. Decreasing resource function $r(x)$ and steady state $\tilde{u}(x)$ for the three values of $\epsilon = 0.020$ (dash-dot), $\epsilon = 0.01$ (dashed), and $\epsilon = 0.005$ (solid).

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