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INTEGRO-DIFFERENTIAL EQUATIONS FOR THE SELF-ORGANISATION OF LIVER ZONES BY COMPETITIVE EXCLUSION OF CELL-TYPES

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Abstract

A model is developed for the self-organisation of zones of enzymatic activity along a liver capillary (hepatic sinusoid) lined with cells of two types, which contain different enzymes and compete for sites on the wall of the sinusoid. An effectively non-local interaction between the cells arises from local consumption of oxygen from blood flowing through the sinusoid, which gives rise to gradients of oxygen concentration in turn influencing rates of division and of death of the two cell-types. The process is modelled by a pair of coupled non-linear integro-differential equations for the cell-densities as functions of time and position along the sinusoid. Existence of a unique, bounded, non-negative solution of the equations is proved, for prescribed initial values. The equations admit infinitely many stationary solutions, but it is shown that all except one are unstable, for any given set of the model parameters. The remaining solution is shown to be asymptotically stable against a large class of perturbations. For certain ranges of the model parameters, the asymptotically stable stationary solution has a zonal structure, with cells of one type located entirely upstream of cells of the other type, and with jump discontinuities in the cell densities at a certain distance along the sinusoid. Such sinusoidal zones can account for zones of enzymatic activity observed in the intact liver. Exceptional cases are found for singular choices of model parameters, such that stationary cell-densities cannot be asymptotically stable individually, but together form an asymptotically stable set. Certain mathematical questions are left open, notably the behaviour of large deviations from stationary solutions, and the global stability of such solutions. Possible generalisations of the model are described.

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1. Introduction

The liver performs its metabolic functions with the aid of various enzymes fixed inside liver cells (hepatocytes). These immobile cells line the many capillaries (hepatic sinusoids) through which the total hepatic blood flow is manifolded, whereby exchange of substances between blood and the cells is facilitated. The interplay of the unidirectional blood flow with local metabolism generates concentration gradients of blood-borne substances (such as oxygen) between the inlet and the outlet of the liver.

Several metabolic functions of the liver have been found to be organised in spatial zones arranged in relation to the direction of hepatic blood flow [7], in such a way that some enzymes act almost wholly upstream of others [1]. We shall attribute such distributions of enzyme activities to distributions of cell-types. For the simplest case of two enzymes, let there be two corresponding cell-types, each containing only one of the enzymes; separate metabolic zones occur when all cells of the one type are located upstream of all cells of the other type. We shall suppose, furthermore, that each cell-type reproduces itself by division. (A possible alternative proposal, which we shall not consider here, is that there is only one cell-type produced by division, but these cells are subsequently differentiated with regard to their enzymatic activity in response to the variation along the blood flow of the concentration of oxygen or some other controlling substance [1].)

It has been shown recently that, for several kinds of enzyme kinetics, the observed zonal structures would result from the implementation of a certain physiologically desirable optimisation principle [2, 6, 8]. In the present work we consider a mechanism by which that optimisation principle could be implemented in the development of any one liver. If the optimisation principle is the "architect's plan", the mechanism of implementing it is the necessary "builder's craft". Whereas these metaphors were used by Schrödinger [12, p. 21] in foreshadowing molecular biology, the implementation proposed here in terms of competitive exclusion of the two cell-types in space and time is an example of self-organization of gross cellular patterns. Pattern formation at such a macroscopic level has been much discussed, independently of molecular biology, since the work of Wolpert [14]. In the present case the requisite communication between cells [14] is provided naturally by hepatic blood flow. The unidirectionality of that flow is a major influence on the mathematical structure of the model, which appears to be capable of describing the formation of zones having one type of cell located entirely upstream of the other, with a jump discontinuity in the densities of the two types occurring at a certain distance along a capillary.

The model will be formulated in detail in the next section, with mathematical analysis following in subsequent sections. A reader who is not interested in the biological context may jump at this point directly to (2.22) and the ensuing statement of the mathematical problems to be discussed. Although the model is simple and natural physiologically, we have not been able to answer all questions of interest: some unsolved mathematical problems will also be described in what follows.

2. Mathematical formulation of the model

As the many capillaries comprising the liver are similar and act essentially in parallel, we shall model a representative capillary lined with cells of two kinds. We put the x-axis along the blood flow, with inlet at $x = 0$ and outlet at $x = L$. We define the density of cells of the first kind, $\rho_1(t, x)$, as a continuous representation of the number of cells of the first kind per unit length of capillary at time t at the position x. The density $\rho_2(t, x)$ of cells of the second kind is defined analogously. The total cell density $\rho_1 + \rho_2$ cannot exceed some fixed maximum density σ of cell sites, as division of the cells is limited by the familiar phenomenon of contact inhibition.

The local rate of change $\partial\rho_1/\partial t$ of the density of cells of the first kind is assumed to consist of a growth-rate term proportional to ρ_1 (self-generation) and to the density of sites available, $\sigma - \rho_1 - \rho_2$; and of a death-rate term proportional to ρ_1, with a coefficient $\beta_1(c) > 0$ dependent on the local concentration c of a controlling blood-borne substance. In what follows we shall, for definiteness, take oxygen as that substance. Then

$$\partial\rho_1/\partial t = k_1\rho_1(\sigma - \rho_1 - \rho_2) - \beta_1(c)\rho_1 \tag{2.1}$$

with a constant coefficient $k_1 > 0$. A similar equation for ρ_2 is obtained from (2.1) by interchanging the suffices 1, 2.

Let f be the steady rate of blood flow through the capillary, and $A(x)$ be the cross-sectional area of the capillary at position x. If oxygen is transported in the x-direction predominantly by convection with the blood, and used up by the two cell-types at the rates $\kappa_1\rho_1$ and $\kappa_2\rho_2$ (with positive constants κ_1, κ_2), then

$$A\,\partial c/\partial t + f\,\partial c/\partial x = -\kappa_1\rho_1 - \kappa_2\rho_2. \tag{2.2}$$

After a disturbance, a steady concentration profile of oxygen is established along the capillary on the time-scale of the convective transit time of blood through the liver, which is of the order of 10 seconds. Even the fastest liver growth (following partial hepatectomy) occurs on the time-scale of 10 hours. Hence the changes in $c(t, x)$ caused by changes in ρ_1, ρ_2 are quasi-steady. We therefore drop the term $A\,\partial c/\partial t$ and integrate (2.2):

$$c(t, x) = c_0 - \frac{1}{f}\int_0^x \left(\kappa_1\rho_1(t, \xi) + \kappa_2\rho_2(t, \xi)\right) d\xi, \tag{2.3}$$

where c_0 is the steady oxygen concentration (tension) in the blood entering the liver.

We assume that as oxygen concentration falls, the death-rate of cells increases ($d\beta_1/dc \leqslant 0, d\beta_2/dc \leqslant 0$), though not necessarily equally for both cell-types. Without speculating about the detailed functional forms of $\beta_1(c)$, $\beta_2(c)$, it will suffice for our purpose to expand about $c = c_0$, keeping to the linear terms: we take

$$\beta_1(c) \approx \mu_1 + \nu_1(c_0 - c),$$
$$\mu_1 = \beta_1(c_0) \geqslant 0, \qquad \nu_1 = -\left.\frac{d\beta_1}{dc}\right|_{c_0} \geqslant 0 \tag{2.4}$$

and similarly for $\beta_2(c)$.

Introducing (2.3) and (2.4) in (2.1) for each cell-type, we arrive at the pair of equations

$$\begin{aligned} \frac{\partial \rho_1}{\partial t} &= \rho_1\left[k_1(\sigma - \rho_1 - \rho_2) - \mu_1 - \frac{\nu_1}{f}\int_0^x (\kappa_1\rho_1 + \kappa_2\rho_2)\, d\xi\right], \\ \frac{\partial \rho_2}{\partial t} &= \rho_2\left[k_2(\sigma - \rho_1 - \rho_2) - \mu_2 - \frac{\nu_2}{f}\int_0^x (\kappa_1\rho_1 + \kappa_2\rho_2)\, d\xi\right]. \end{aligned} \tag{2.5}$$

We note at once that unless the first cell-type is inevitably to die out, its greatest possible specific growth-rate $k_1\sigma$ must exceed its least possible specific death-rate μ_1. If on the contrary $k_1\sigma \leqslant \mu_1$, one can see from the first equation of (2.5) that there exist no stationary non-negative solutions (ρ_1, ρ_2) of these equations which do not have $\rho_1 = 0$ almost everywhere. Similar remarks apply for the second cell-type, and accordingly we assume from the outset that

$$k_1\sigma > \mu_1, \qquad k_2\sigma > \mu_2. \tag{2.6}$$

For $\nu_1 = \nu_2 = 0$, (2.5) reduce to Volterra's classical equations for competitive exclusion in time only [13]. Space dependence enters our model because death-rates at each position x depend on the cumulative oxygen consumption by all cells located upstream of x. Viewed in terms of ρ_1 and ρ_2 alone, (2.5) involve a seemingly non-local interaction between cells, mediated in reality by oxygen consumption and blood flow. It is this oriented cell-cell interaction that leads to our generalisation of Volterra's equations into space taking the form of coupled integro-differential equations. In contrast, the many ecological and biological generalisations have more often taken the form of coupled partial differential equations. This is true in particular of models which, unlike ours, allow for the migration (diffusion) of competing species. For an introduction to the extensive literature on these models and on pattern formation in biological systems generally, we refer the reader to recent reviews and conference proceedings [10].

To obtain some preliminary heuristic ideas about the formation of zones in our model, we suppose that (2.5) admits solutions which at all finite times are everywhere positive and satisfy $(\rho_1 + \rho_2) < \sigma$. For such solutions we combine equations (2.5) in the form

$$\frac{\partial}{\partial t}\left[\ln\left(\rho_1^{k_2}/\rho_2^{k_1}\right)\right] = A - \frac{B}{f}\int_0^x (\kappa_1\rho_1 + \kappa_2\rho_2)\,d\xi, \tag{2.7}$$

where

$$A = \mu_2 k_1 - \mu_1 k_2, \qquad B = \nu_1 k_2 - \nu_2 k_1 \tag{2.8}$$

and consider the competitive exclusion process at each value of x, in terms of the underlying mechanism. Suppose that

$$\mu_2/k_2 > \mu_1/k_1, \qquad \nu_2/k_2 < \nu_1/k_1, \tag{2.9}$$

so that the constants A and B are positive. Since the integral in (2.7) is bounded above by $(\kappa_1 + \kappa_2)\sigma x$, the right-hand side of (2.7) is positive at all times for sufficiently small x. Volterra's argument [13] then applies: as $t \to \infty$, $\rho_1^{k_2}/\rho_2^{k_1} \to \infty$, and with ρ_1 bounded above by σ, ρ_2 must tend to zero. It is then plausible that, for these values of x, ρ_1 will approach a stationary form determined from the first of equations (2.5) with $\rho_2 = 0$, *viz.*

$$k_1(\sigma - \rho_1) - \mu_1 - \frac{\nu_1}{f}\int_0^x \kappa_1\rho_1\,d\xi = 0, \tag{2.10}$$

yielding

$$\rho_1 = \rho_1^*(x) = (C_1/k_1)\exp(-\nu_1\kappa_1 x/fk_1), \tag{2.11}$$

where we set

$$C_i = k_i\sigma - \mu_i, \qquad i = 1, 2. \tag{2.12}$$

Now we note that, with ρ_2 set equal to zero and ρ_1 equal to ρ_1^*, the right-hand side of (2.7) decreases with increasing x and reaches zero at a value $x = x^*$ determined by

$$\exp\left(\nu_1\kappa_1 x^*/fk_1\right) = BC_1/k_1(\nu_1 C_2 - \nu_2 C_1), \tag{2.13}$$

provided

$$\nu_1 C_2 > \nu_2 C_1. \tag{2.14}$$

The point $x = x^*$ determined by (2.13) lies in the interval $(0, L)$ of interest, provided that

$$\exp(\nu_1\kappa_1 L/fk_1) > BC_1/k_1(\nu_1 C_2 - \nu_2 C_1). \tag{2.15}$$

Under these conditions, it is then reasonable to suppose that, for $x > x^*$, the right-hand side of (2.7) will in fact be negative for sufficiently large values of t. Volterra's argument then indicates that we can expect to find $\rho_1 \to 0$ as $t \to \infty$

for $x > x^*$. Furthermore, we may also expect that, for $x > x^*$, ρ_2 will approach a stationary form determined, from the second equation of (2.5), by

$$k_2(\sigma - \rho_2) - \mu_2 - \frac{\nu_2}{f}\left[\int_0^{x^*} \kappa_1 \rho_1^* \, d\xi + \int_{x^*}^{x} \kappa_2 \rho_2 \, d\xi\right] = 0, \tag{2.16}$$

yielding

$$\rho_2 = \rho_2^*(x) = D \exp\left[-\nu_2 \kappa_2 (x - x^*)/f k_2\right], \qquad x > x^*, \tag{2.17}$$

with

$$D = (\nu_1 C_2 - \nu_2 C_1)/B. \tag{2.18}$$

By such plausible reasoning we are led to conjecture that, when the inequalities (2.9), (2.14) and (2.15) hold, and provided the initial values of ρ_1 and ρ_2 are everywhere positive and satisfy $(\rho_1 + \rho_2) < \sigma$, the solution (ρ_1, ρ_2) of (2.5) will remain everywhere positive and bounded as time evolves and will, as $t \to \infty$, approach the stationary form

$$\begin{aligned} \rho_1 &= \rho_1^*(x),\ \rho_2 = 0, \quad 0 \leqslant x < x^*, \\ \rho_1 &= 0,\ \rho_2 = \rho_2^*(x), \quad x^* < x \leqslant L. \end{aligned} \tag{2.19}$$

If this be so, then the model successfully defines a mechanism for the formation of sharply defined zones in any one capillary (hepatic sinusoid)—in this case, what we could call a 1-2 zone, with cells of type 1 located upstream of cells of type 2. Note that in (2.19), ρ_1 and ρ_2 have jump discontinuities at $x = x^*$. (Interchanging the roles of type 1 and type 2 cells in the above argument would of course lead to the description of a 2-1 zone.) A set of capillaries in parallel, with a distribution of flow rates [3], could by this mechanism generate macroscopically diffuse zones in the liver as a whole.

If the conjecture is correct, the above reasoning suggests also that the approach of a positive solution (ρ_1, ρ_2) of (2.5) to the stationary form (2.19) may proceed at a greater rate for $x < x^*$ than for $x > x^*$, as a consequence of the oriented cell-cell interaction.

The requirement that the initial values of ρ_1 and ρ_2 be everywhere positive seems essential for the conjecture to hold. In fact the form of (2.5) suggests that, whatever the values of the parameters μ_i, ν_i, k_i, κ_i, $i = 1, 2$, a class of initial conditions having an arbitrary interdigitating piecewise structure, with regions on which $\rho_1 = 0$, $\rho_2 \geqslant 0$ alternating with regions on which $\rho_1 \geqslant 0$, $\rho_2 = 0$, would lead to solutions preserving such a structure as they evolve, possibly towards stationary forms. For if there are initially no cells of one type in some region, there is no mechanism in the model by which they can subsequently appear there. The validity of the main conjecture would however imply that, at least in the case that the parameters satisfy (2.9), (2.14), and (2.15), stationary solutions of that type are unstable against arbitrary small positive perturbations.

Equations (2.5) have the advantage of explicit symmetry between the suffixes 1, 2, but they contain more parameters than necessary for mathematical analysis. We note firstly that the case $\nu_1 = \nu_2 = 0$ is uninteresting from our point of view because, as already discussed above, equations (2.5) degenerate into those for competitive exclusion in time only—whichever cell-type excludes the other as $t \to \infty$ at one value of x does so at all values of x. We therefore assume that at least one of ν_1, ν_2—say ν_1 for definiteness—is positive, and now define new variables

$$t' = C_1 t, \qquad x' = \frac{\nu_1 \kappa_1}{f k_1} x, \qquad v_i(t', x') = \frac{k_1}{C_1} \rho_i(t, x), \tag{2.20}$$

and new parameters

$$\theta = \frac{\kappa_2}{\kappa_1}, \qquad \gamma = \frac{k_2}{k_1}, \qquad \lambda = \frac{k_1 C_2}{k_2 C_1}, \qquad \eta = \frac{\nu_2 k_1}{\nu_1 k_2}. \tag{2.21}$$

Then (2.5) become, on dropping at once the primes from the new independent variables,

$$\begin{aligned} \frac{\partial v_1}{\partial t}(t,x) &= v_1(t,x)\left[1 - v_1(t,x) - v_2(t,x) - \int_0^x [v_1(t,\xi) + \theta v_2(t,\xi)]\, d\xi\right] \\ \frac{\partial v_2}{\partial t}(t,x) &= \gamma v_2(t,x)\left[\lambda - v_1(t,x) - v_2(t,x) - \eta\int_0^x [v_1(t,\xi) + \theta v_2(t,\xi)]\, d\xi\right] \end{aligned} \tag{2.22}$$

with constant parameters

$$\theta > 0, \quad \gamma > 0, \quad \lambda > 0 \quad \text{and} \quad \eta \geqslant 0. \tag{2.23}$$

The spatial interval of interest is now $[0, \Lambda]$, where $\Lambda = \nu_1 \kappa_1 L / f k_1$. Had we interchanged the roles of type 1 and 2 cells in defining new variables $\bar{t}, \bar{x}, \bar{v}_i$ and new parameters $\bar{\theta}, \bar{\gamma}, \bar{\lambda}, \bar{\eta}$ by analogy with (2.20), (2.21), we would have obtained instead of (2.22), the equation

$$\begin{aligned} \frac{\partial \bar{v}_1}{\partial \bar{t}} &= \bar{\gamma}\bar{v}_1\left[\bar{\lambda} - \bar{v}_1 - \bar{v}_2 - \bar{\eta}\int_0^{\bar{x}} \left(\bar{v}_2 + \bar{\theta}\bar{v}_1\right) d\bar{\xi}\right], \\ \frac{\partial \bar{v}_2}{\partial \bar{t}} &= \bar{v}_2\left[1 - \bar{v}_1 - \bar{v}_2 - \int_0^{\bar{x}} \left(\bar{v}_2 + \bar{\theta}\bar{v}_1\right) d\bar{\xi}\right], \end{aligned} \tag{2.22'}$$

with $\bar{\theta} = 1/\theta$, $\bar{\gamma} = 1/\gamma$, $\bar{\eta} = 1/\eta$, $\bar{\lambda} = 1/\lambda$. Evidently there is no loss of generality in concentrating on (2.22). The inequalities (2.9), (2.14) and (2.15) which, according to our conjecture, are sufficient to lead to the formation of a 1-2 zone (given everywhere positive initial data), become

$$\eta < \lambda < 1, \quad \ln\left(\frac{1-\eta}{\lambda - \eta}\right) < \Lambda, \tag{2.24}$$

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and the "zonal" stationary form (2.19) becomes

$$\begin{aligned} &v_1 = \exp(-x), \quad v_2 = 0, && 0 \leqslant x < x^* \\ &v_1 = 0, \quad v_2 = \left(\frac{\lambda - \eta}{1 - \eta}\right)\exp[-\eta\theta(x - x^*)], && x^* < x \leqslant \Lambda \end{aligned} \tag{2.25}$$

where now

$$x^* = \ln\left(\frac{1 - \eta}{\lambda - \eta}\right). \tag{2.26}$$

Our conjecture is that any solution (v_1, v_2) of (2.22)–(2.24) which is bounded and positive on $[0, \Lambda]$ at $t = 0$, will remain so for $t > 0$ and will tend, as $t \to \infty$, to the form (2.25).

In what follows we shall not address directly the latter part of this conjecture. We shall prove firstly, in Section 3, the existence and uniqueness of a solution of (2.22), (2.23) satisfying initial conditions of the form

$$v_i(0, x) = v_i^0(x) \geqslant 0, \qquad i = 1, 2, \tag{2.27}$$

where the v_i^0 are given bounded and (Lebesgue) measurable functions on $[0, \Lambda]$, and show that for this solution, v_1 and v_2 are bounded and satisfy

$$v_i(t, x) \geqslant 0, \qquad i = 1, 2 \tag{2.28}$$

on $[0, \Lambda]$ for all $t > 0$; furthermore, if the inequalities in (2.27) are made strict, then those in (2.28) become strict. (This does not of course preclude the possibility that v_1 or v_2 could go to zero as $t \to \infty$.)

We go on to characterise, in Proposition 4.1, infinitely many stationary solutions of (2.22). Then we show in Theorem 4.1 that, for any given set of values of the parameters (2.23) (excepting the case $\lambda = \eta = 1$ which we treat separately in Section 6), all non-negative stationary solutions except one, to within sets of measure zero, are unstable against small perturbations. In Section 5 we show that, for each parameter set, this remaining one solution is asymptotically stable against a particular class of perturbations. When the parameters satisfy (2.24) this solution has the zonal form (2.25) (Theorem 5.1 and Corollary). While this lends credibility to our conjecture, a complete proof remains to be found. Of the other results, Proposition 4.1 and Theorem 4.1 relate to our earlier speculations on the variety of possible stationary solutions and their stability; and Theorem 5.1, which gives our best estimates of the behaviour in time of v_1 and v_2 following a small perturbation to the zonal stationary solution (2.25), relates to our remark concerning the approach to equilibrium on either side of the singular point $x = x^*$.

As mentioned, the case $\lambda = \eta = 1$ is treated separately in Section 6. In terms of the original variables, this corresponds to a situation where the parameters in (2.5) satisfy

$$k_2 = \gamma k_1, \qquad \mu_2 = \gamma\mu_1, \qquad \nu_2 = \gamma\nu_1 \tag{2.29}$$

for some positive constant γ. Then the specific growth rate of ρ_2 is at all times and at each value of x, a multiple by γ of the specific growth rate for ρ_1, so that wherever well-defined, the ratio of ρ_1^γ to ρ_2 (or $\rho_2^{1/\gamma}$ to ρ_1) is constant in time at each value of x. Our main result in this case is that non-negative stationary solutions are not individually asymptotically stable, but rather there is an asymptotically stable set of such solutions. In order to understand this at least partially, one need only consider any perturbation of a stationary solution which changes the ratio of ρ_1^γ to ρ_2 (or $\rho_2^{1/\gamma}$ to ρ_1) at some value of x. If the resultant solution of (2.5) approaches a stationary solution as time increases, it can only be one with the new ratio holding at that value of x.

In closing this section we remark that in what follows we sometimes denote $(v_1(t,x), v_2(t,x))$ by $\mathbf{v}(t,x)$; $(v_1^0(x), v_2^0(x))$ by $\mathbf{v}^0(x)$, etc. More generally, if $\mathbf{u} = (u_1, u_2)$, we write $\mathbf{u} \geqslant 0$ to mean $u_1 \geqslant 0$ and $u_2 \geqslant 0$; and we define

$$|\mathbf{u}| = |u_1| + |u_2|. \tag{2.30}$$

Finally, if u_1 and u_2 are bounded and measurable real-valued functions on $[0, \Lambda]$, we write

$$\|\mathbf{u}\| = \sup_{x\in[0,\Lambda]} \left(|u_1(x)| + |u_2(x)|\right) = \sup_{x\in[0,\Lambda]} |\mathbf{u}(x)|, \tag{2.31}$$

and we denote by $\mathbf{X}$ the Banach space of such pairs, with this norm.

3. Existence and uniqueness

By a solution of (2.22) we mean a pair of functions $(t,x) \to (v_1(t,x), v_2(t,x))$ defined for all $t \in I$, $x \in [0, \Lambda]$ (where I is an interval of the form $[0,\infty)$, $[0, t_0)$ or $[0, t_0]$ for some $t_0 < \infty$), and satisfying there the following conditions: they must be continuously differentiable in t for each fixed x and measurable in x for each fixed t; they must be such that $\int_0^x v_i(t,\xi)\,d\xi$, $i = 1, 2$, is finite and continuous in t for each fixed x; and they must satisfy (2.22) for each (t,x).

We shall show first that any solution of (2.22), (2.27) is bounded on $I \times [0, \Lambda]$; in fact that, if $C \geqslant \max(1, \lambda)$ is constant, and

$$\sup_{x\in[0,\Lambda]} \left(v_1^0(x) + v_2^0(x)\right) \leqslant C \tag{3.1}$$

then

$$\mathbf{v}(t,x) \geqslant 0, \tag{3.2a}$$

$$v_1(t,x) + v_2(t,x) \leqslant C. \tag{3.2b}$$

Since (2.22) implies

$$\partial v_i(t,x)/\partial t = v_i(t,x) f_i(t,x) \tag{3.3}$$

for some function f_i which is continuous in t, we have

$$v_i(t,x) = v_i^0(x)\exp\left[\int_0^t f_i(\tau,x)\,d\tau\right] \geqslant 0. \tag{3.4}$$

Furthermore, if $v_i^0(x) > 0$, we see that $v_i(t,x) > 0$. Suppose now that $v_1(t_1,x_1) + v_2(t_1,x_1) > C$ for some t_1 and x_1. Since $v_1(0,x_1) + v_2(0,x_1) \leqslant C$, there exists a $t_2 \in [0,t_1)$ such that $v_1(t_2,x_1) + v_2(t_2,x_1) = C$ and $v_1(t,x_1) + v_2(t,x_1) > C$ on $(t_2,t_1]$. But then (2.22) implies $\partial v_i(t,x_1)/\partial t \leqslant 0$ for $t \in [t_2,t_1]$, which gives a contradiction. Thus inequality (3.2b) must also hold.

Turning now to the questions of existence and uniqueness, we introduce the Banach space $\mathbf{X}$ with norm as in (2.31), and also the mapping F: $\mathbf{X} \to \mathbf{X}$ defined by

$$F(\mathbf{u}) = \bar{\mathbf{u}} \tag{3.5}$$

where

$$\begin{aligned}\bar{u}_1(x) &= u_1(x)\left[1 - u_1(x) - u_2(x) - \int_0^x [u_1(\xi) + \theta u_2(\xi)]\,d\xi\right],\\ \bar{u}_2(x) &= \gamma u_2(x)\left[\lambda - u_1(x) - u_2(x) - \eta\int_0^x [u_1(\xi) + \theta u_2(\xi)]\,d\xi\right].\end{aligned} \tag{3.6}$$

We want to show first that (2.22), (2.27) is equivalent to the initial value problem

$$\frac{d\mathbf{u}}{dt} = F(\mathbf{u}), \tag{3.7}$$

$$\mathbf{u}(0) = \left(v_1^0, v_2^0\right) \geqslant 0. \tag{3.8}$$

By a solution of (3.7) and (3.8) we mean a strongly continuous and differentiable function $\mathbf{u}$: $I \to \mathbf{X}$ for some interval I as above, such that (3.8) is satisfied and (3.7) holds for all $t \in I$. If $\mathbf{u}$ is such a solution, then defining $\mathbf{v}(t,x) = \mathbf{u}(t)(x)$ we obtain a solution of (2.22), (2.27) on $I \times [0,\Lambda]$, because the strong continuity and differentiability of $\mathbf{u}$ implies, for each x, continuity and differentiability of $\mathbf{v}(\cdot,x)$ and continuity of $\int_0^x \mathbf{v}(\cdot,\xi)\,d\xi$. On the other hand, if $\mathbf{v}$ is a solution of (2.22), (2.27) then, because of the boundedness of the v_i, the function $\mathbf{u}$: $I \to \mathbf{X}$ defined by $\mathbf{u}(t)(x) = \mathbf{v}(t,x)$ is strongly differentiable and satisfies (3.8) and (3.7) on I.

We can now prove

THEOREM 3.1. *The problem* (2.22), (2.27) *has a unique solution, which exists for all* $t \geqslant 0$.

PROOF. It is sufficient to prove that there exists a unique solution of (3.7), (3.8) for all $t \geqslant 0$. Let $C \geqslant \max(1,\lambda)$ be such that (3.1) holds, so that $\|\mathbf{u}(0)\| \leqslant C$. From the definition of F we see that there exist constants M and K such that $\|F(\mathbf{u})\| \leqslant M$ and $\|F(\mathbf{u}) - F(\mathbf{v})\| \leqslant K\|\mathbf{u} - \mathbf{v}\|$, whenever $\|\mathbf{u} - \mathbf{u}(0)\| \leqslant 1$ and $\|\mathbf{v} - \mathbf{u}(0)\| \leqslant 1$; and that these constants can be taken to be independent of $\mathbf{u}(0)$

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provided $\|\mathbf{u}(0)\| \leqslant C$. It then follows [9, Theorem 5.1.1] that (3.7) and (3.8) have a unique solution for $0 \leqslant t \leqslant \alpha$ where $\alpha = 1/M$. From what was shown above, in particular (3.2b), we know that $\|\mathbf{u}(\alpha)\| \leqslant C$. We can then consider (3.7) with initial value $\mathbf{u}(\alpha)$ at $t = \alpha$, and repeat the argument to obtain a unique solution for $\alpha \leqslant t \leqslant 2\alpha$; altogether we then have a unique solution of (3.7), (3.8) on $[0, 2\alpha]$. Continuing in this way we obtain a unique solution on $[0, \infty)$, thus completing the proof.

We remark in passing that it follows from the foregoing properties of the solution of (2.22), (2.27), that the functions v_1 and v_2 are measurable in (t, x). This justifies our applications of Fubini's theorem in the sequel.

4. Stationary solutions: instability

By a stationary solution of (2.22) we mean a pair $\mathbf{v}$ of measurable, bounded functions on $[0, \Lambda]$, satisfying on that interval

$$\begin{aligned} v_1(x)\left[1 - v_1(x) - v_2(x) - \int_0^x [v_1(\xi) + \theta v_2(\xi)]\, d\xi\right] &= 0, \\ v_2(x)\left[\lambda - v_1(x) - v_2(x) - \eta\int_0^x [v_1(\xi) + \theta v_2(\xi)]\, d\xi\right] &= 0. \end{aligned} \tag{4.1}$$

Let $\mathbf{v}^s$ be a such a solution. Since we are interested in non-negative solutions of (2.22), we suppose that $\mathbf{v}^s \geqslant 0$ on $[0, \Lambda]$. In this Section we shall assume also that λ and η are not both equal to 1; the special case $\lambda = \eta = 1$ will be treated in Section 6.

Given that $\mathbf{v}^s$ satisfies (4.1), it is easily seen that each $x \in [0,\Lambda]$ must belong to one of the following sets:

$$E_0 = \{x\colon \mathbf{v}^s(x) = 0\}, \tag{4.2a}$$

$$E_1 = \left\{x\colon v_1^s(x) > 0,\ v_2^s(x) = 0,\ 1 - v_1^s(x) - \int_0^x [v_1^s(\xi) + \theta v_2^s(\xi)]\, d\xi = 0\right\}, \tag{4.2b}$$

$$E_2 = \left\{x\colon v_1^s(x) = 0,\ v_2^s(x) > 0,\ \lambda - v_2^s(x) - \eta\int_0^x [v_1^s(\xi) + \theta v_2^s(\xi)]\, d\xi = 0\right\}, \tag{4.2c}$$

$$\begin{aligned} E_3 = \Big\{x\colon & 1 - v_1^s(x) - v_2^s(x) - \int_0^x [v_1^s(\xi) + \theta v_2^s(\xi)]\, d\xi = 0, \\ & \lambda - v_1^s(x) - v_2^s(x) - \eta\int_0^x [v_1^s(\xi) + \theta v_2^s(\xi)]\, d\xi = 0\Big\}. \end{aligned} \tag{4.2d}$$

It is obvious that E_0, E_1 and E_2 are disjoint. Consider E_3, and suppose it is non-empty. If $\eta = 1$, it then follows from (4.2d) that $\lambda = 1$; hence $\eta \neq 1$. On E_3 we have, again from (4.2d),

$$v_1^s(x) + v_2^s(x) = \frac{\lambda - \eta}{1 - \eta}, \tag{4.3a}$$

$$\int_0^x \left[v_1^s(\xi) + \theta v_2^s(\xi)\right] d\xi = \frac{1 - \lambda}{1 - \eta}. \tag{4.3b}$$

If E_3 has positive measure, it follows from (4.3b) that $v_1^s + \theta v_2^s = 0$ almost everywhere on E_3 and hence, because $\mathbf{v}^s \geqslant 0$, that $\mathbf{v}^s = 0$ a.e. on E_3. Then (4.3a) implies $\lambda = \eta$, and consequently, that $\mathbf{v}^s = 0$ everywhere on E_3. Thus $E_3 \subseteq E_0$. Furthermore, if $x_1 < x_2$ are two points in E_3, it follows from (4.3b), with $\lambda = \eta$, that $\int_0^x (v_1^s + \theta v_2^s)\, d\xi = 1$ on $[x_1, x_2]$, since the integrand is non-negative. It then follows that no point from $[x_1, x_2]$ can belong to $E_1 \cup E_2$, and consequently that $[x_1, x_2] \subseteq E_3 \subseteq E_0$. Thus E_3 must in fact be an interval, on which $\mathbf{v}^s$ is everywhere zero.

If $m(E_3) = 0$, it still follows from (4.3b) that if $x_1 < x_2$ are two points in E_3, then $\mathbf{v}^s = 0$ a.e. on $[x_1, x_2]$. Since we are not interested in distinguishing solutions which differ only on sets of measure zero, we can in this case redefine $\mathbf{v}^s$ to be zero on E_3. We thereby obtain another stationary solution which is unchanged outside the old E_3, and for which the new E_3 is contained in the new E_0.

In this way we see that there is no essential loss of generality in assuming that, for any given non-negative stationary solution of (2.22), every $x \in [0, \Lambda]$ belongs to one of the corresponding disjoint sets E_0, E_1, E_2.

The following proposition characterises infinitely many stationary (though not necessarily non-negative) solutions of (2.22).

PROPOSITION 4.1. *Let A_1 and A_2 be arbitrary measurable, disjoint subsets of* $[0, \Lambda]$. *Then there exists a unique solution* $\mathbf{v}$ *of* (4.1) *such that*

$$v_2(x) = 0, \qquad 1 - v_1(x) - \int_0^x \left[v_1(\xi) + \theta v_2(\xi)\right] d\xi = 0 \quad \text{on } A_1, \tag{4.4a}$$

$$v_1(x) = 0, \qquad \lambda - v_2(x) - \eta \int_0^x \left[v_1(\xi) + \theta v_2(\xi)\right] d\xi = 0 \quad \text{on } A_2, \tag{4.4b}$$

$$\mathbf{v}(x) = 0 \quad \text{on } [0, \Lambda] \backslash (A_1 \cup A_2). \tag{4.4c}$$

All non-negative stationary solutions of (2.22) *are obtained in this way* (*possibly after redefinition on sets of measure zero*).

PROOF. We shall show that there exist uniquely determined measurable and bounded functions v_1 and v_2 such that

$$\begin{aligned} v_1(x) &= \chi_{A_1}(x)\left[1 - \int_0^x [v_1(\xi) + \theta v_2(\xi)]\,d\xi\right], \\ v_2(x) &= \chi_{A_2}(x)\left[\lambda - \eta \int_0^x [v_1(\xi) + \theta v_2(\xi)]\,d\xi\right] \end{aligned} \tag{4.5}$$

hold for all $x \in [0, \Lambda]$, where χ_A denotes the characteristic function of the set A.

Let $\mathbf{X}_K$ be the Banach space of all pairs $\mathbf{v} = (v_1, v_2)$ of measurable, bounded functions on $[0, \Lambda]$ with norm

$$\|\mathbf{v}\|_K = \sup_{x \in [0,\Lambda]} e^{-2Kx}\big(|v_1(x)| + |v_2(x)|\big) \tag{4.6}$$

where

$$K = (1 + \eta)\max(1, \theta). \tag{4.7}$$

Introduce the mapping $T\colon \mathbf{X}_K \to \mathbf{X}_K$ defined by

$$\begin{aligned} T(\mathbf{v}) &= \bar{\mathbf{v}}, \\ \bar{v}_1(x) &= \chi_{A_1}(x)\left[1 - \int_0^x [v_1(\xi) + \theta v_2(\xi)]\,d\xi\right], \\ \bar{v}_2(x) &= \chi_{A_2}(x)\left[\lambda - \eta \int_0^x [v_1(\xi) + \theta v_2(\xi)]\,d\xi\right]. \end{aligned} \tag{4.8}$$

For any $\mathbf{u}, \mathbf{v} \in \mathbf{X}_K$ we have

$$\begin{aligned} \|T(\mathbf{u}) - T(\mathbf{v})\|_K &= \sup_{x \in [0,\Lambda]} e^{-2Kx}\left[\chi_{A_1}(x)\left|\int_0^x (u_1 - v_1)\,d\xi + \theta \int_0^x (u_2 - v_2)\,d\xi\right|\right. \\ &\qquad \left. + \chi_{A_2}(x)\left|\eta \int_0^x (u_1 - v_1)\,d\xi + \eta\theta \int_0^x (u_2 - v_2)\,d\xi\right|\right] \\ &\leqslant \sup_{x \in [0,\Lambda]} e^{-2Kx}\left[(1+\eta)\int_0^x |u_1 - v_1|\,d\xi + \theta(1+\eta)\int_0^x |u_2 - v_2|\,d\xi\right] \\ &\leqslant \sup_{x \in [0,\Lambda]} e^{-2Kx} K \int_0^x e^{2K\xi}\|\mathbf{u} - \mathbf{v}\|_K\,d\xi \\ &< \tfrac{1}{2}\|\mathbf{u} - \mathbf{v}\|_K. \end{aligned} \tag{4.9}$$

Thus T is a contraction, implying that the equation $T(\mathbf{v}) = \mathbf{v}$ has a unique solution in $\mathbf{X}_K$ [11, Chapter 4, Theorem 1.1]. Therefore (4.5), and hence (4.4), has a unique solution.

This solution is not necessarily non-negative, but when it is, we can construct as above the sets E_0, E_1, E_2 and E_3, and we see at once that $E_1 \subseteq A_1$, $E_2 \subseteq A_2$. Note however that different pairs A_1, A_2 could lead to the same solution and, in the non-negative case, to the same E_1, E_2. On the other hand, in order to prove the last part of the proposition it suffices to set $A_1 = E_1$, $A_2 = E_2$ to show that any given non-negative solution, redefined if necessary so that $E_3 \subseteq E_0$, is obtained as the unique solution of (4.4) for some A_1, A_2.

Now, consider again the non-negative stationary solution $\mathbf{v}^s$. Let $\mathbf{v}$ be the solution of (2.22) and (2.27), and define, for all $x \in [0, \Lambda]$,

$$\mathbf{w}(t,x) = \mathbf{v}(t,x) - \mathbf{v}^s(x), \qquad \mathbf{w}^0(x) = \mathbf{v}^0(x) - \mathbf{v}^s(x). \tag{4.10}$$

Note that

$$\left(\mathbf{w}^0(x) + \mathbf{v}^s(x)\right) \geqslant 0 \tag{4.11}$$

for all $x \in [0, \Lambda]$. Then w_1 and w_2 satisfy

$$\begin{aligned} \frac{\partial w_1}{\partial t} &= (w_1 + v_1^s)\Big[1 - w_1 - w_2 - \int_0^x (w_1 + \theta w_2)\, d\xi \\ &\qquad\qquad - v_1^s - v_2^s - \int_0^x (v_1^s + \theta v_2^s)\, d\xi\Big], \\ \frac{\partial w_2}{\partial t} &= \gamma(w_2 + v_2^s)\Big[\lambda - w_1 - w_2 - \eta\int_0^x (w_1 + \theta w_2)\, d\xi \\ &\qquad\qquad - v_1^s - v_2^s - \eta\int_0^x (v_1^s + \theta v_2^s)\, d\xi\Big]. \end{aligned} \tag{4.12}$$

Define

$$\psi(x) = \int_0^x [v_1^s + \theta v_2^s]\, d\xi, \qquad \mu(x) = \lambda - 1 + (1 - \eta)\psi(x). \tag{4.13}$$

Then we have, from (4.12) and the definitions (4.2), that

$$\text{on } E_1\colon \quad \partial w_2/\partial t = \gamma\mu(x)w_2 + f_2(t,x) \tag{4.14}$$

$$\text{on } E_2\colon \quad \partial w_1/\partial t = -\mu(x)w_1 + g_1(t,x) \tag{4.15}$$

$$\text{on } E_0\colon \quad \begin{cases} \partial w_1/\partial t = (1 - \psi(x))w_1 + g_1(t,x), \\ \partial w_2/\partial t = \gamma(\lambda - \eta\psi(x))w_2 + f_2(t,x) \end{cases} \tag{4.16}$$

where

$$\begin{aligned} f_2 &= -\gamma w_2\Big[w_1 + w_2 + \eta\int_0^x (w_1 + \theta w_2)\, d\xi\Big], \\ g_1 &= -w_1\Big[w_1 + w_2 + \int_0^x (w_1 + \theta w_2)\, d\xi\Big]. \end{aligned} \tag{4.17}$$

We want to investigate the stability of stationary non-negative solutions with respect to certain perturbations $\mathbf{w}^0$. Many different definitions of stability can be considered, depending on which class of perturbations we want to allow. For instance, it may be desirable to allow only perturbations that vanish where $\mu = 0$, or that go to zero at a specified rate as x approaches a point where $\mu = 0$. (See Section 5.) The following definition covers many such possibilities:

DEFINITION 4.1. Let ϕ be a class of pairs of measurable functions $\boldsymbol{\varphi} = (\varphi_1, \varphi_2)$ on $[0, \Lambda]$ such that

(a) $0 \leqslant \varphi_i(x) \leqslant B$, for all $x \in [0, \Lambda]$, $\boldsymbol{\varphi} \in \phi$, $i = 1, 2$, for some positive constant B.

(b) $\{x: \varphi_1(x) = 0\} = \{x: \varphi_2(x) = 0\} = N_{\boldsymbol{\varphi}}$, say.

(c) for every $\alpha > 0$ there exists a $\boldsymbol{\varphi} \in \phi$ such that $m(N_{\boldsymbol{\varphi}}) < \alpha$.

A stationary solution $\mathbf{v}^s \geqslant 0$ is said to be *ϕ-stable* if, for every $\boldsymbol{\varphi} \in \phi$ and $\varepsilon > 0$, there exists a $\delta > 0$ such that if (4.11) and $|w_i^0(x)| \leqslant \varphi_i(x)\delta$ hold for all $x \in [0, \Lambda]$, $i = 1, 2$, then $|w_i(t, x)| < \varepsilon$ for all $x \in [0, \Lambda] \setminus N_{\boldsymbol{\varphi}}$, $t \geqslant 0$, $i = 1, 2$. Such a solution is said to be *asymptotically ϕ-stable* if, in addition, for every $\boldsymbol{\varphi} \in \phi$ there exists a $\delta' > 0$ such that if (4.11) and $|w_i^0(x)| \leqslant \varphi_i(x)\delta'$ hold for all $x \in [0, \Lambda]$, $i = 1, 2$, then $w_i(t, x) \to 0$ as $t \to \infty$ for all $x \in [0, \Lambda] \setminus N_{\boldsymbol{\varphi}}$, $i = 1, 2$. We can proceed for the remainder of this section without specifying ϕ completely.

LEMMA 4.1. *Suppose $\mathbf{v}^s \geqslant 0$ is ϕ-stable for some ϕ. Then the sets $E_1 \cap \{x: \mu(x) > 0\}$ $(= \tilde{E}_1$, say$)$, $E_2 \cap \{x: \mu(x) < 0\}$ and $E_0 \cap \{x: \psi(x) < 1$ or $\eta\psi(x) < \lambda\}$ all have measure zero.*

PROOF. Suppose $m(\tilde{E}_1) > 0$. Then we can find a compact set $K \subset \tilde{E}_1$ with $m(K) > 0$. Since μ is continuous there is a $\mu_0 > 0$ such that $\mu(x) \geqslant \mu_0$ for all $x \in K$. By the results of Section 3, there exists a positive constant c_1 such that, for all perturbations satisfying (4.11) and having $|w_i^0(x)| \leqslant B$ for all $x \in [0, \Lambda]$, $i = 1, 2$, (B as in Definition 4.1), we have $|w_i(t, x)| \leqslant c_1$ for all $x \in [0, \Lambda]$, $t \geqslant 0$, $i = 1, 2$. Now, by (c) in Definition 4.1, there is a $\boldsymbol{\varphi} \in \phi$ such that

$$m(N_{\boldsymbol{\varphi}}) < \min(m(K), \mu_0/4\eta c_1(1 + \theta)). \tag{4.18}$$

For this $\boldsymbol{\varphi}$ we have $K \setminus N_{\boldsymbol{\varphi}} \neq \varnothing$, so we can choose an $x_1 \in K \setminus N_{\boldsymbol{\varphi}}$. Let χ be the characteristic function of $[0, \Lambda] \setminus N_{\boldsymbol{\varphi}}$. We note that there is an $\varepsilon > 0$ such that

$$\left| w_1(x_1) + w_2(x_1) + \eta \int_0^{x_1} \chi(x)[w_1(x) + \theta w_2(x)]\, dx \right| \leqslant \frac{1}{4}\mu(x_1) \tag{4.19}$$

for all measurable functions w_1 and w_2 having $|w_i(x)| < \varepsilon$ for all $x \in [0, \Lambda] \setminus N_{\boldsymbol{\varphi}}$, $i = 1, 2$. We now use this $\boldsymbol{\varphi}$ and this ε in Definition 4.1 and find a corresponding $\delta \leqslant 1$. Suppose (4.11) holds and $|w_i^0(x)| \leqslant \varphi_i(x)\delta$ for all $x \in [0, \Lambda]$, $i = 1, 2$. Then $|w_i(t, x)| < \varepsilon$ for all $x \in [0, \Lambda] \setminus N_{\boldsymbol{\varphi}}$, $t \geqslant 0$, $i = 1, 2$, and $|w_i(t, x)| < c_1$ for all $x \in N_{\boldsymbol{\varphi}}$, $t \geqslant 0$, $i = 1, 2$. It then follows from (4.17), (4.18) and (4.19) that

$$|f_2(t, x_1)| \leqslant \tfrac{1}{2}\gamma\mu(x_1)|w_2(t, x_1)|, \qquad t \geqslant 0. \tag{4.20}$$

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Since $\varphi_2(x_1) \neq 0$, we can choose $w_2^0(x_1) > 0$. Then (4.14) implies with (4.17) that $w_2(t, x_1) > 0$ for all t, and from (4.14) and (4.20) we get

$$\partial w_2/\partial t \geqslant \gamma\mu(x_1)w_2 - |f_2| \geqslant \tfrac{1}{2}\gamma\mu(x_1)w_2, \tag{4.21}$$

so that

$$w_2(t, x_1) \geqslant w_2^0(x_1)\exp\left[\tfrac{1}{2}\gamma\mu(x_1)t\right], \tag{4.22}$$

which is a contradiction. Therefore $m(\tilde{E}_1) = 0$. The other assertions are proved in similar fashion.

COROLLARY. *If there is a* $\varphi_0 \in \phi$ *such that* $m(N_{\varphi_0}) = 0$, *then the sets mentioned in Lemma* 4.1 *are subsets of* N_{φ_0}.

PROOF. If $\tilde{E}_1 \setminus N_{\varphi_0} \neq \varnothing$, choose any $x_1 \in \tilde{E}_1 \setminus N_{\varphi_0}$. Then a contradiction is obtained as in the proof of the lemma.

THEOREM 4.1. *Of all stationary non-negative solutions of* (4.1), *only the following are possibly* ϕ*-stable*:
When $\eta < \lambda < 1$:

$$\begin{aligned} v_1^s &= e^{-x}, \quad v_2^s = 0 \qquad a.e.\ on\ [0, x^*) \\ v_1^s &= 0, \quad v_2^s = \frac{\lambda - \eta}{1 - \eta}\exp[-\eta\theta(x - x^*)] \qquad a.e.\ on\ (x^*, \Lambda] \end{aligned} \tag{4.23}$$

if $x^* = \ln[(1 - \eta)/(\lambda - \eta)] < \Lambda$;

$$v_1^s = e^{-x}, \quad v_2^s = 0 \qquad a.e.\ on\ [0, \Lambda] \tag{4.24}$$

if $x^* \geqslant \Lambda$.
When $\lambda < 1$ *and* $\eta \geqslant \lambda$:

$$v_1^s = e^{-x}, \quad v_2^s = 0 \qquad a.e.\ on\ [0, \Lambda]. \tag{4.25}$$

When $\lambda = 1$ *and* $\eta < 1$;

$$v_1^s = 0, \quad v_2^s = e^{-\eta\theta x} \qquad a.e.\ on\ [0, \Lambda]. \tag{4.26}$$

When $\lambda = 1$ *and* $\eta > 1$:

$$v_1^s = e^{-x}, \quad v_2^s = 0 \qquad a.e.\ on\ [0, \Lambda]. \tag{4.27}$$

When $\lambda > 1$ *and* $\eta \leqslant \lambda$:

$$v_1^s = 0, \quad v_2^s = \lambda e^{-\eta\theta x} \qquad a.e.\ on\ [0, \Lambda]. \tag{4.28}$$

When $\eta > \lambda > 1$:

$$\begin{aligned} v_1^s &= 0, \quad v_2^s = \lambda e^{-\eta\theta x} && a.e.\ on\ [0, x^*) \\ v_1^s &= \frac{\eta - \lambda}{\eta - 1} e^{-(x-x^*)}, \quad v_2^s = 0 && a.e.\ on\ (x^*, \Lambda] \end{aligned} \tag{4.29}$$

if $x^* = (1/\eta\theta)\ln[\lambda(\eta - 1)/(\eta - \lambda)] < \Lambda$;

$$v_1^s = 0, \quad v_2^s = \lambda e^{-\eta\theta x} \qquad a.e.\ on\ [0, \Lambda] \tag{4.30}$$

if $x^* \geqslant \Lambda$.
To this list should be added the stationary solutions when $\lambda = \eta = 1$, *investigated in Section* 6.

PROOF. Let $\mathbf{v}^s \geqslant 0$ be a ϕ-stable, stationary solution. Suppose that $\lambda < 1$. Since $\mu(0) = \lambda - 1 < 0$, either $\mu(x) < 0$ for all $x \in [0, \Lambda]$ or there is an $x^* \in [0, \Lambda]$ such that $\mu(x^*) = 0$ and $\mu(x) < 0$ for $x \in [0, x^*)$. Assume the latter case, which is possible only if $\eta < 1$. Then either $\psi(x) < 1$ on $[0, x^*]$ or there is an $a \in [0, x^*]$ such that $\psi(a) = 1$ and $\psi(x) < 1$ on $[0, a)$. In the second case it follows from Lemma 4.1 (and the fact that $E_3 \setminus E_0$ is a null-set) that almost all points of $[0, a)$ belong to E_1. Therefore $v_1^s = e^{-x}$, $v_2^s = 0$ a.e. on $[0, a]$, so that $\psi(a) = \int_0^a e^{-x}\,dx = 1 - e^{-a} < 1$, which is a contradiction. Thus $\psi(x) < 1$ on $[0, x^*]$, almost all points of $[0, x^*)$ belong to E_1, and $v_1^s = e^{-x}$, $v_2^s = 0$ a.e. on $[0, x^*)$. From $\mu(x^*) = 0$ we get $(1 - \lambda)/(1 - \eta) = 1 - e^{-x^*} < 1$, so that $\eta < \lambda$. Thus we see that if $\lambda < 1$ and $\eta \geqslant \lambda$, or if $\lambda < 1$, $\eta < \lambda$ and $x^* = \ln[(1 - \eta)/(\lambda - \eta)] \geqslant \Lambda$, we get $v_1^s = e^{-x}$, $v_2^s = 0$ a.e. on $[0, \Lambda]$.

Assume now that $\eta < \lambda < 1$ and $x^* < \Lambda$. Then $v_1^s = e^{-x}$, $v_2^s = 0$ a.e. on $[0, x^*)$. Since μ is non-decreasing, there is a maximal interval $[x^*, b]$ where $\mu = 0$. If $x^* < b$, then $\mu(x) = 0$, $\psi(x) = \int_0^x (v_1^s + \theta v_2^s)\,d\xi = (1 - \lambda)/(1 - \eta) < 1$ on $[x^*, b]$. Then $v_1^s = v_2^s = 0$ a.e. on $[x^*, b]$, so that almost all points of $[x^*, b]$ belong to E_0, in contradiction of Lemma 4.1. Therefore $b = x^*$, and $\mu > 0$ on $(x^*, \Lambda]$. Now $\psi(x^*) = (1 - \lambda)/(1 - \eta) < 1 < \lambda/\eta$. Either $\psi(x) < \lambda/\eta$ for all $x \in [x^*, \Lambda]$ or there is a $c \in (x^*, \Lambda]$ such that $\psi(c) = \lambda/\eta$ and $\psi(x) < \lambda/\eta$ for $x \in [x^*, c)$. Assume the latter is true. According to Lemma 4.1 almost all points of (x^*, c) belong to E_2. Since $v_1^s(x) = 0$ and $v_2^s(x)$ satisfies

$$v_2^s(x) = \lambda - \eta\psi(x^*) - \eta\theta \int_{x^*}^{x} v_2^s\,d\xi \tag{4.31}$$

for almost all $x \in (x^*, c)$, we find that

$$v_2^s(x) = [\lambda - \eta\psi(x^*)]\,e^{-\eta\theta(x - x^*)} \tag{4.32}$$

a.e. on (x^*, c). It follows that

$$\psi(c) = \psi(x^*) + \theta \int_{x^*}^{c} v_2^s \, dx = \psi(x^*) + \frac{1}{\eta}[\lambda - \eta\psi(x^*)][1 - e^{-\eta\theta(x - x^*)}]$$
$$< \psi(x^*) + \frac{1}{\eta}[\lambda - \eta\psi(x^*)] = \frac{\lambda}{\eta}. \tag{4.33}$$

This contradiction shows that $\psi(x) < \lambda/\eta$ for all $x \in [x^*, \Lambda]$, so that almost all points of $(x^*, \Lambda]$ belong to E_2, and

$$v_1^s = 0, \qquad v_2^s = [(\lambda - \eta)/(1 - \eta)] \exp[-\eta\theta(x - x^*)]$$

a.e. on $(x^*, \Lambda]$.

Let us next consider the case $\lambda = 1$, $\eta < 1$. We have $\mu(x) = (1 - \eta)\psi(x) \geqslant 0$. If $\psi(x_1) = 0$ for some $x_1 > 0$, then $v_1^s = v_2^s = 0$ a.e. on $(0, x_1)$, which is impossible by Lemma 4.1. Therefore $\psi(x) > 0$ and $\mu(x) > 0$ for $x > 0$. Just as in the previous case, we can now show that almost all points of $[0, \Lambda]$ belong to E_2, and that $v_1^s = 0$, $v_2^s = e^{-\eta\theta x}$ a.e. on $[0, \Lambda]$.

The remaining cases can be treated similarly, or by noting that a change of variables like that leading to (2.22′) transforms these cases to ones already treated.

Corollary. *If there is a $\varphi_0 \in \phi$ such that $m(N_{\varphi_0}) = 0$, then v_1^s and v_2^s are of the stated forms for all x except for a subset of N_{φ_0} and except that it can only be said of the point $x = x^*$ in* (4.23) *or* (4.29), *and of the point $x = 0$ in* (4.26) *or* (4.27), *that it belongs to* $([0, \Lambda] \setminus E_0) \cup N_{\varphi_0}$.

Proof. Consider the proof of the theorem. In the case $\eta < \lambda < \Lambda$, $x^* \leqslant \Lambda$, we obtain

$$[0, x^*) \subset E_1 \cup (E_3 \setminus E_0) \cup N_{\varphi_0} \tag{4.34}$$

by the Corollary to Lemma 4.1. However, $[0, x^*] \cap E_3$ can consist of at most one point (otherwise v_1^s and v_2^s would both vanish almost everywhere on an interval in $[0, x^*]$, giving a contradiction to (4.34)) and at that point we have $\psi = (1 - \lambda)/(1 - \eta)$. But since $\psi(x^*) = (1 - \lambda)/(1 - \eta)$, this point can only be x^*. Thus $[0, x^*) \subset E_1 \cup N_{\varphi_0}$ and $x^* \in ([0, \Lambda] \setminus E_0) \cup N_{\varphi_0}$. The other cases are treated similarly.

5. Stationary solutions: stability

In the previous section we saw that most stationary non-negative solutions are unstable. We now wish to examine the possibly stable solutions described in Theorem 4.1. The most interesting cases are those where two zones occur.

Consider in particular the case

$$0 \leqslant \eta < \lambda < 1, \qquad \ln\frac{1-\eta}{\lambda-\eta} < \Lambda \tag{5.1}$$

and the stationary solution

$$\begin{aligned} v_1^s(x) &= \exp(-x) \quad \text{for } 0 \leqslant x < x^* \\ &= 0 \quad \text{for } x^* < x \leqslant \Lambda \\ v_2^s(x) &= 0 \quad \text{for } 0 \leqslant x < x^* \\ &= \exp(-x^*)\exp[-\eta\theta(x-x^*)] \quad \text{for } x^* < x \leqslant \Lambda, \end{aligned} \tag{5.2}$$

where

$$x^* = \ln\left(\frac{1-\eta}{\lambda-\eta}\right). \tag{5.3}$$

Defining $\mathbf{w}$ as in (4.10), we proceed to estimate its time-dependence for suitably small initial perturbations $\mathbf{w}^0$ satisfying (4.11). It is necessary to consider first the inverval $0 \leqslant x < x^*$ and then $x^* < x \leqslant \Lambda$; we shall not consider the behaviour of $\mathbf{w}$ at the exceptional point $x = x^*$.

Suppose then that $0 \leqslant x < x^*$. From (4.12) we get

$$\begin{aligned} \frac{\partial w_1}{\partial t} &= -v_1^s(x)\left[w_1 + w_2 + \int_0^x (w_1 + \theta w_2)\,d\xi\right] + f_1, \\ \frac{\partial w_2}{\partial t} &= -\nu(x) w_2 + f_2, \end{aligned} \tag{5.4}$$

where

$$\begin{aligned} f_1 &= -w_1\left[w_1 + w_2 + \int_0^x (w_1 + \theta w_2)\,d\xi\right], \\ f_2 &= -\gamma w_2\left[w_1 + w_2 + \eta\int_0^x (w_1 + \theta w_2)\,d\xi\right], \end{aligned} \tag{5.5}$$

$$\nu(x) = \gamma[(1-\eta)e^{-x} + \eta - \lambda] = -\gamma\mu(x). \tag{5.6}$$

We see that ν is positive and decreasing on $[0, x^*)$ and that $\nu(x^*) = 0$. From (5.4) we obtain

$$w_2(t,x) = w_2^0(x)e^{-\nu(x)t} + \int_0^t e^{-\nu(x)(t-\tau)} f_2(\tau, x)\,d\tau \tag{5.7}$$

and

$$\frac{\partial w_1}{\partial t} = -v_1^s\left[w_1 + \int_0^x w_1\,d\xi\right] + F, \tag{5.8}$$

where

$$F(t,x) = -v_1^s(x)\left[w_2(t,x) + \theta\int_0^x w_2(t,\xi)\,d\xi\right] + f_1(t,x). \tag{5.9}$$

If F is considered known, (5.8) can be solved. This is a consequence of the following lemma, which for later applications covers a slightly more general situation:

LEMMA 5.1. *Assume that the real-valued function w is defined for $t \geqslant 0$, $x_0 \leqslant x \leqslant x_1$, bounded, continuously differentiable in t and measurable in x, and that it satisfies*

$$\begin{aligned} \frac{\partial w}{\partial t}(t,x) &= -\alpha(x)\left[w(t,x) + \int_{x_0}^{x} g(\xi)w(t,\xi)\,d\xi\right] + G(t,x), \\ w(0,x) &= w^0(x) \end{aligned} \tag{5.10}$$

where α, g, G and w^0 are bounded; α, g and w^0 are measurable; G is continuous in t and measurable in x; and $\alpha(x) \geqslant \alpha_0 > 0$ for all $x \in [x_0, x_1]$. Then the Laplace transform $\tilde{w}$ of w with respect to t is given by

$$\begin{aligned} \tilde{w}(s,x) &= \frac{1}{s+\alpha(x)}\left[w^0(x) + \tilde{G}(s,x)\right] \\ &\quad - \frac{\alpha(x)}{s+\alpha(x)}\int_{x_0}^{x} \frac{g(\xi)}{s+\alpha(\xi)} \exp\left[-\int_{\xi}^{x} \frac{g(y)\alpha(y)}{s+\alpha(y)}\,dy\right]\left[w^0(\xi) + \tilde{G}(s,\xi)\right] d\xi \end{aligned} \tag{5.11}$$

where $\tilde{G}$ is the Laplace transform of G.

PROOF. By Laplace-transforming (5.10) we get

$$s\tilde{w} - w^0 = -\alpha\left[\tilde{w} + \int_{x_0}^{x} g\tilde{w}\,d\xi\right] + \tilde{G}. \tag{5.12}$$

Let $p(s,x) = \tilde{w}(s,x)/\alpha(x)$ and $H(s,x) = [w^0(x) + \tilde{G}(s,x)]/\alpha(x)$. Then

$$(s+\alpha)p + \int_{x_0}^{x} g\alpha p\,d\xi = H. \tag{5.13}$$

Let us for a moment assume that α and H are continuously differentiable with respect to x. Then we get from (5.13)

$$(s+\alpha)\frac{\partial p}{\partial x} + (\alpha' + g\alpha)p = \frac{\partial H}{\partial x}, \qquad p(s,x_0) = \frac{H(s,x_0)}{s+\alpha(x_0)}. \tag{5.14}$$

Equations (5.14) are easily solved to give

$$\begin{aligned} p(s,x) &= \frac{1}{s+\alpha(x)}H(s,x) \\ &\quad - \frac{1}{s+\alpha(x)}\int_{x_0}^{x} \frac{H(s,\xi)g(\xi)\alpha(\xi)}{s+\alpha(\xi)} \exp\left[-\int_{\xi}^{x} \frac{g(y)\alpha(y)}{s+\alpha(y)}\,dy\right] d\xi. \end{aligned} \tag{5.15}$$

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But it is now easily seen that (5.15) gives the solution of (5.13) without any extra assumptions on α and H. Then (5.11) follows.

We now apply this result to (5.8). In this case $g = 1$ and $\alpha = v_1^s$, so that $\alpha' = -\alpha$. Thus

$$\exp\left[-\int_\xi^x \frac{g(y)\alpha(y)}{s+\alpha(y)}\,dy\right] = \frac{s+\alpha(x)}{s+\alpha(\xi)}, \tag{5.16}$$

and (5.11) becomes

$$\tilde{w}_1(s,x) = \frac{1}{s+v_1^s(x)}\left[w_1^0 + \tilde{F}(s,x)\right] - v_1^s(x)\int_0^x \frac{\left[w_1^0(\xi) + \tilde{F}(s,\xi)\right]}{\left[s+v_1^s(\xi)\right]^2}\,d\xi \tag{5.17}$$

so that

$$\begin{aligned} w_1(t,x) = {}& w_1^0(x)\exp(-v_1^s(x)t) - tv_1^s(x)\int_0^x w_1^0(\xi)\exp(-v_1^s(\xi)t)\,d\xi \\ & + \int_0^t F(\tau,x)\exp\left[-v_1^s(x)(t-\tau)\right]d\tau \\ & - v_1^s(x)\int_0^t (t-\tau)\left[\int_0^x F(\tau,\xi)\exp\left[-v_1^s(\xi)(t-\tau)\right]d\xi\right]d\tau. \end{aligned} \tag{5.18}$$

Now choose a number $a < x^*$ so close to x^* that $\nu(a) < \exp(-x^*)$, and then choose ω such that

$$\nu(a) < \omega < \exp(-x^*). \tag{5.19}$$

Then for all $x \in [0, x^*)$,

$$\begin{aligned} &\exp(-v_1^s(x)t) \leqslant e^{-\omega t}, \\ &t\exp(-v_1^s(x)t) \leqslant t\exp\left[-(e^{-x^*} - \omega)t\right]e^{-\omega t} \leqslant c_0 e^{-\omega t} \end{aligned} \tag{5.20}$$

for some positive constant c_0. Let

$$\begin{aligned} W_i(t,x) &= \sup_{\xi\in[0,x]} |w_i(t,\xi)|, \qquad i = 1,2 \\ W(t,x) &= \max_{i=1,2} W_i(t,x). \end{aligned} \tag{5.21}$$

It follows from the fact that the w_i are continuous in t, uniformly with respect to x, which in turn follows from the results obtained for the v_i in Section 3, that W_i and W are continuous in t. We consider perturbations $\mathbf{w}^0$ satisfying (4.11) and

$$|w_1^0(x)| \leqslant \delta, \qquad |w_2^0(x)| \leqslant \nu(x)^p\delta \tag{5.22}$$

for all $x \in [0, x^*)$, where $p > 1$, and $\delta > 0$ is a number to be chosen later.

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It follows from (5.5) that

$$|f_i| \leqslant c_1 |w_i| W, \qquad i = 1, 2, \tag{5.23}$$

for some constant c_1. Then (5.7) gives

$$e^{\nu(x)t}|w_2(t,x)| \leqslant \nu(x)^p \delta + c_1 \int_0^t e^{\nu(x)\tau}|w_2(\tau,x)| W(\tau,x)\, d\tau, \tag{5.24}$$

and Gronwall's inequality [11, Chapter 6, Proposition 1.4] then gives

$$|w_2(t,x)| \leqslant \nu(x)^p e^{-\nu(x)t} \exp\left[c_1 \int_0^t W(\tau,x)\, d\tau\right] \delta. \tag{5.25}$$

From (5.9), (5.18) and (5.23) we get

$$|F| \leqslant |w_2| + \theta \int_0^x |w_2|\, d\xi + c_1 |w_1| W \leqslant c_2 W_2 + c_1 |w_1| W, \tag{5.26}$$

$$\int_0^x |F|\, d\xi \leqslant c_3 W_2 + c_4 W_1 W,$$

$$\begin{aligned} |w_1(t,x)| \leqslant{}& |w_1^0(x)| e^{-\omega t} + c_0 e^{-\omega t} \int_0^x |w_1^0(\xi)|\, d\xi \\ &+ \int_0^t e^{-\omega(t-\tau)} \left[c_2 W_2(\tau,x) + c_1 |w_1(\tau,x)| W(\tau,x)\right] d\tau \\ &+ c_0 \int_0^t e^{-\omega(t-\tau)} \left[c_3 W_2(\tau,x) + c_4 W_1(\tau,x) W(\tau,x)\right] d\tau \\ \leqslant{}& c_5 \delta e^{-\omega t} + c_6 \int_0^t e^{-\omega(t-\tau)} W_2(\tau,x)\, d\tau \\ &+ c_7 \int_0^t e^{-\omega(t-\tau)} W_1(\tau,x) W(\tau,x)\, d\tau. \end{aligned} \tag{5.27}$$

Since the right-hand side is non-decreasing in x we get

$$e^{\omega t} W_1(t,x) \leqslant c_5 \delta + c_6 \int_0^t e^{\omega t} W_2(\tau,x)\, d\tau + c_7 \int_0^t e^{\omega t} W_1(\tau,x) W(\tau,x)\, d\tau, \tag{5.28}$$

and then from Gronwall's inequality,

$$W_1(t,x) \leqslant \left[c_5 \delta e^{-\omega t} + c_6 \int_0^t e^{-\omega(t-\tau)} W_2(\tau,x)\, d\tau\right] \exp\left[c_7 \int_0^t W(\tau,x)\, d\tau\right]. \tag{5.29}$$

For small t we have $\int_0^t W(\tau,x)\, d\tau \leqslant 1$ for all $x \in [0, x^*)$. As long as this is so we have from (5.25) and (5.29)

$$\begin{aligned} &|w_2(t,x)| \leqslant e^{c_1} \nu(x)^p e^{-\nu(x)t} \delta, \\ &|w_1(t,x)| \leqslant W_1(t,x) \leqslant c_8 e^{-\omega t} \delta + c_9 \int_0^t e^{-\omega(t-\tau)} W_2(\tau,x)\, d\tau. \end{aligned} \tag{5.30}$$

The function $\nu \to \nu^p e^{-\nu t}$ attains its maximum value $(p/te)^p$ at $\nu = p/t$. Since ν decreases to zero on $[0, x^*)$, it follows that

$$\max_{\xi \in [0, x^*)} \nu(\xi)^p e^{-\nu(\xi)t} = \begin{cases} (p/te)^p, & t \geqslant p/\nu(0) \\ \nu(0)^p e^{-\nu(0)t}, & 0 \leqslant t < p/\nu(0) \end{cases}$$
$$\leqslant c_{10}/(t^p + 1), \qquad t \geqslant 0. \tag{5.31}$$

Then, from (5.30) and (5.21)

$$|w_2(t,x)| \leqslant W_2(t,x) \leqslant c_{11}\delta/(t^p + 1) \tag{5.32}$$

and

$$\int_0^t e^{-\omega(t-\tau)} W_2(\tau, x)\, d\tau \leqslant c_{11}\delta \left\{ \int_0^{\frac{1}{2}t} \frac{e^{-\omega(t-\tau)}}{\tau^p + 1}\, d\tau + \int_{\frac{1}{2}t}^t \frac{e^{-\omega(t-\tau)}}{\tau^p + 1}\, d\tau \right\}$$
$$\leqslant c_{11}\delta \left\{ \frac{1}{2} t e^{-\frac{1}{2}\omega t} + \frac{1}{\left(\frac{1}{2}t\right)^p + 1} \frac{1}{\omega} \right\}$$
$$\leqslant \frac{c_{12}\delta}{t^p + 1}, \tag{5.33}$$

$$|w_1(t,x)| \leqslant W_1(t,x) \leqslant c_8 \delta e^{-\omega t} + \frac{c_9 c_{12}\delta}{t^p + 1} \leqslant \frac{c_{13}\delta}{t^p + 1}. \tag{5.34}$$

Therefore,

$$\int_0^t W(\tau, x)\, d\tau \leqslant c_{14}\delta \tag{5.35}$$

for all $x \in [0, x^*)$ and all t in question. Now c_{14} is a constant determined by given quantities, and in particular, it is independent of δ. Let us assume that δ from the outset was chosen so that $\delta < 1/c_{14}$. Let

$$h(t) = \sup_{x \in [0, x^*)} \int_0^t W(\tau, x)\, d\tau. \tag{5.36}$$

If $h(t) \geqslant 1$ for some t, there is a t_1 such that $h(t_1) = 1$ and $h(t) < 1$ for $t \in [0, t_1)$, since h is continuous. But on $[0, t_1]$ the above estimates are valid, and in particular we would get $h(t_1) \leqslant c_{14}\delta < 1$, which is a contradiction. Thus $h(t) < 1$ for all t, and (5.30), (5.32) and (5.34) are valid for all $t \geqslant 0$ and $x \in [0, x^*)$.

It follows from above that

$$\int_0^{x^*} W_2(t,x)\, dx \leqslant \frac{c_{11} x^* \delta}{t^p + 1}, \tag{5.37}$$

but this estimate can be improved. There are positive constants m_1 and m_2 such that

$$m_1(x^* - x) \leqslant \nu(x) \leqslant m_2(x^* - x) \tag{5.38}$$

for $x \in [0, x^*]$. Thus, from (5.30),

$$\begin{aligned} W_2(t,x) &\leqslant e^{c_1}\delta \max_{\xi\in[0,x]} \nu(\xi)^p e^{-\nu(\xi)t} \\ &\leqslant e^{c_1}\delta m_2^p \max_{\xi\in[0,x]} (x^* - \xi)^p e^{-m_1(x^*-\xi)t}. \end{aligned} \tag{5.39}$$

Suppose $t > p/m_1x^*$. Then

$$\max_{\xi\in[0,x]} (x^* - \xi)^p e^{-m_1(x^*-\xi)t} = \begin{cases} (x^* - x)^p e^{-m_1(x^*-x)t}, & x \leqslant x^* - \dfrac{p}{m_1 t} \\ (p/m_1te)^p, & x > x^* - \dfrac{p}{m_1 t}, \end{cases} \tag{5.40}$$

and so

$$\begin{aligned} \int_0^{x^*} \max_{\xi\in[0,x]} (x^* - \xi)^p e^{-m_1(x^*-\xi)t}\, dx &= \int_0^{x^*-p/m_1t} (x^* - x)^p e^{-m_1(x^*-x)t}\, dx \\ &\quad + \int_{x^*-p/m_1t}^{x^*} (p/m_1te)^p\, dx \\ &= \int_{p/m_1t}^{x^*} x^p e^{-m_1xt}\, dx + e^{-p}\left(\frac{p}{m_1t}\right)^{p+1}, \end{aligned} \tag{5.41}$$

where

$$\int_{p/m_1t}^{x^*} x^p e^{-m_1xt}\, dx = \frac{1}{(m_1t)^{p+1}} \int_p^{m_1x^*t} y^p e^{-y}\, dy < \frac{1}{(m_1t)^{p+1}} \int_p^{\infty} y^p e^{-y}\, dy. \tag{5.42}$$

Thus

$$\int_0^{x^*} W_2(t,x)\, dx \leqslant \frac{c_{15}\delta}{t^{p+1}+1}, \qquad t \geqslant 0 \tag{5.43}$$

and it follows that

$$\int_0^{x^*} |w_i(t,x)|\, dx \leqslant \frac{c_{16}\delta}{t^{p+1}+1}, \qquad i = 1, 2,\ t \geqslant 0. \tag{5.44}$$

We now turn to the interval $x^* < x \leqslant \Lambda$. There

$$\begin{aligned}\frac{\partial w_1}{\partial t} &= -\mu(x) w_1 + g_1 \\ \frac{\partial w_2}{\partial t} &= -\gamma v_2^s(x)\left[w_1 + w_2 + \eta \int_{x^*}^{x} (w_1 + \theta w_2)\, d\xi\right] + g_2\end{aligned} \tag{5.45}$$

where

$$g_1 = -w_1\left[w_1 + w_2 + \int_0^x (w_1 + \theta w_2)\, d\xi\right],$$

$$g_2 = -\gamma w_2\left[w_1 + w_2 + \eta\int_0^x (w_1 + \theta w_2)\, d\xi\right] - \gamma\eta v_2^s(x)\int_0^{x^*} (w_1 + \theta w_2)\, d\xi,$$

$$\mu(x) = \frac{\lambda - \eta}{\eta}\left[1 - e^{-\eta\theta(x - x^*)}\right] \quad \text{if } \eta > 0,$$

$$\mu(x) = \theta\lambda(x - x^*) \quad \text{if } \eta = 0. \tag{5.46}$$

We see that $\mu(x)$ is positive and increasing and that $\mu(x^*) = 0$. Then we get from (5.45)

$$w_1(t, x) = e^{-\mu(x)t} w_1^0(x) + \int_0^t e^{-\mu(x)(t-\tau)} g_1(\tau, x)\, d\tau \tag{5.47}$$

and

$$\frac{\partial w_2}{\partial t} = -\gamma v_2^s(x)\left[w_2 + \eta\theta\int_{x^*}^{x} w_2\, d\xi\right] + G(t, x), \tag{5.48}$$

where

$$G(t, x) = -\gamma v_2^s(x)\left[w_1(t, x) + \eta\int_{x^*}^{x} w_1(t, \xi)\, d\xi\right] + g_2(t, x). \tag{5.49}$$

Again we apply Lemma 5.1, this time with $\alpha = \gamma v_2^s$, $g = \eta\theta$ and $\alpha' = -\eta\theta\alpha$, so that

$$\exp\left[-\int_\xi^x \frac{g\alpha}{s + \alpha}\, dy\right] = \frac{s + \alpha(x)}{s + \alpha(\xi)}, \tag{5.50}$$

$$\tilde{w}_2(s, x) = \frac{1}{s + \alpha(x)}\left[w_2^0(x) + \tilde{G}(s, x)\right] - \alpha(x)\int_{x^*}^{x} \eta\theta \frac{\left[w_2^0(\xi) + \tilde{G}(s, \xi)\right]}{\left[s + \alpha(\xi)\right]^2}\, d\xi, \tag{5.51}$$

$$\begin{aligned} w_2(t, x) = {} & w_2^0(x)\exp\left[-\gamma v_2^s(x)t\right] - \eta\theta\gamma v_2^s(x)t\int_{x^*}^{x} \exp\left[-\gamma v_2^s(\xi)t\right] w_2^0(\xi)\, d\xi \\ & + \int_0^t \exp\left[-\gamma v_2^s(x)(t - \tau)\right] G(\tau, x)\, d\tau \\ & - \eta\theta\gamma v_2^s(x)\int_0^t (t - \tau)\left[\int_{x^*}^{x} \exp\left[-\gamma v_2^s(\xi)(t - \tau)\right] G(\tau, \xi)\, d\xi\right] d\tau. \end{aligned} \tag{5.52}$$

Choose ρ such that $0 < \rho < \gamma v_2^s(\Lambda)$. Then

$$\exp\left(-\gamma v_2^s(x)t\right) \leqslant e^{-\rho t}, \qquad t\exp\left(-\gamma v_2^s(x)t\right) \leqslant c_{17}e^{-\rho t}. \tag{5.53}$$

We define

$$W_i(t,x) = |w_i(t,x)| + \int_{x^*}^{x} |w_i(t,\xi)|\,d\xi, \qquad i = 1,2, \tag{5.54}$$

$$W(t,x) = \max_{i=1,2} \sup_{\xi \in (x^*,x]} W_i(t,\xi) \tag{5.55}$$

and assume that, for all $x \in (x^*, \Lambda]$, (4.11) holds and, in addition

$$|w_1^0(x)| \leqslant \mu(x)^p\delta, \quad |w_2^0(x)| \leqslant \delta, \qquad \delta < 1/c_{14}. \tag{5.56}$$

Using (5.44) and (5.46) we get

$$\begin{aligned}|g_1(t,x)| &\leqslant c_{18}|w_1(t,x)|W(t,x) + |w_1(t,x)|\int_0^{x^*} \left[|w_1(t,\xi)| + \theta|w_2(t,\xi)|\right] d\xi \\ &\leqslant |w_1(t,x)|\left[c_{18}W(t,x) + c_{19}\frac{\delta}{t^{p+1}+1}\right],\end{aligned} \tag{5.57}$$

so that

$$e^{\mu(x)t}|w_1(t,x)| \leqslant |w_1^0(x)| + \int_0^t e^{\mu(x)\tau}|w_1(\tau,x)|\left[c_{18}W(\tau,x) + c_{19}\frac{\delta}{\tau^{p+1}+1}\right] d\tau \tag{5.58}$$

and hence

$$\begin{aligned}|w_1(t,x)| &\leqslant \delta\mu(x)^p e^{-\mu(x)t}\exp\left[\int_0^t \left(c_{18}W(\tau,x) + c_{18}\frac{\delta}{\tau^{p+1}+1}\right) d\tau\right] \\ &\leqslant \delta\mu(x)^p e^{-\mu(x)t}\exp\left[c_{18}\int_0^t W(\tau,x)\,d\tau + c_{20}\delta\right].\end{aligned} \tag{5.59}$$

Next we note that

$$\begin{aligned}|G(t,x)| &\leqslant c_{21}W_1(t,x) + |g_2(t,x)| \\ &\leqslant c_{21}W_1(t,x) + |w_2(t,x)|\left[c_{22}W(t,x) + c_{23}\frac{\delta}{t^{p+1}+1}\right] + c_{24}\frac{\delta}{t^{p+1}+1},\end{aligned} \tag{5.60}$$

and

$$\begin{aligned}\int_{x^*}^{x} |G(t,\xi)|\,d\xi &\leqslant c_{25}W_1(t,x) + W_2(t,x)\left[c_{26}W(t,x) + c_{27}\frac{\delta}{t^{p+1}+1}\right] \\ &\quad + c_{28}\frac{\delta}{t^{p+1}+1}\end{aligned} \tag{5.61}$$

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$$
\begin{aligned}
|w_2(t,x)| \leqslant{}& |w_2^0(x)|e^{-\rho t} + c_{17}\eta\theta\gamma e^{-\rho t}\int_{x^*}^{x} |w_2^0(\xi)|\,d\xi \\
&+ \int_0^t e^{-\rho(t-\tau)}|G(\tau,x)|\,d\tau + c_{17}\eta\theta\gamma\int_0^t e^{-\rho(t-\tau)}\left[\int_{x^*}^{x}|G(\tau,\xi)|\,d\xi\right]d\tau \\
\leqslant{}& c_{29}\delta e^{-\rho t} + \int_0^t e^{-\rho(t-\tau)}\left[c_{30}W_1(\tau,x) + c_{31}\frac{\delta}{\tau^{p+1}+1}\right]d\tau \\
&+ \int_0^t e^{-\rho(t-\tau)}W_2(\tau,x)\left[c_{32}W(\tau,x) + c_{33}\frac{\delta}{\tau^{p+1}}\right]d\tau,
\end{aligned} \tag{5.62}
$$

$$
\begin{aligned}
e^{\rho t}W_2(t,x) \leqslant{}& c_{34}\delta + \int_0^t e^{\rho\tau}\left[c_{35}W_1(\tau,x) + c_{36}\frac{\delta}{\tau^{p+1}+1}\right]d\tau \\
&+ \int_0^t e^{\rho\tau}W_2(\tau,x)\left[c_{37}W(\tau,x) + c_{38}\frac{\delta}{\tau^{p+1}+1}\right]d\tau,
\end{aligned} \tag{5.63}
$$

$$
\begin{aligned}
W_2(t,x) \leqslant{}& \left\{c_{34}\delta e^{-\rho t} + \int_0^t e^{-\rho(t-\tau)}\left[c_{35}W_1(\tau,x) + c_{36}\frac{\delta}{\tau^{p+1}+1}\right]d\tau\right\} \\
&\times\exp\left(\int_0^t\left[c_{37}W(\tau,x) + c_{38}\frac{\delta}{\tau^{p+1}+1}\right]d\tau\right).
\end{aligned} \tag{5.64}
$$

As long as

$$
\int_0^t W(\tau,x)\,d\tau \leqslant 1 \tag{5.65}
$$

we have

$$
\begin{aligned}
&|w_1(t,x)| \leqslant c_{39}\delta\mu(x)^p e^{-\mu(x)t} \\
&W_2(t,x) \leqslant c_{40}\left\{c_{34}\delta e^{-\rho t} + \int_0^t e^{-\rho(t-\tau)}\left[c_{35}W_1(\tau,x) + c_{36}\frac{\delta}{\tau^{p+1}+1}\right]d\tau\right\}.
\end{aligned} \tag{5.66}
$$

It then follows by an argument similar to that leading from (5.30) to (5.32), (5.34) and (5.35), that

$$
\begin{aligned}
|w_1(t,x)| &\leqslant W_1(t,x) \leqslant c_{41}\delta/(t^p+1), \\
|w_2(t,x)| &\leqslant W_2(t,x) \leqslant c_{42}\delta/(t^p+1)
\end{aligned} \tag{5.67}
$$

and

$$
\int_0^t W(\tau,x)\,d\tau \leqslant c_{43}\delta. \tag{5.68}
$$

With the same kind of argument as before, it follows that if δ is chosen so small that, in addition to (5.56) we have $\delta < 1/c_{43}$, then (5.66), (5.67) and (5.68) hold for all t and all $x \in (x^*, \Lambda]$.

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Finally, we can estimate $\int_{x^*}^{\Lambda} |w_i(t,x)|\,dx$. There are positive constants n_1 and n_2 such that

$$n_1(x - x^*) \leqslant \mu(x) \leqslant n_2(x - x^*) \tag{5.69}$$

for all $x \in [x^*, \Lambda]$. Then

$$\begin{aligned}\int_{x^*}^{\Lambda} |w_1(t,x)|\,dx &\leqslant c_{39}\delta \int_{x^*}^{\Lambda} \mu(x)^p e^{-\mu(x)t}\,dx \\ &\leqslant c_{39}\delta n_2^p \int_{x^*}^{\Lambda} (x - x^*)^p e^{-n_1(x-x^*)t}\,dx \\ &< c_{39}\delta n_2^p \frac{1}{(n_1 t)^{p+1}} \int_0^{\infty} y^p e^{-y}\,dy.\end{aligned} \tag{5.70}$$

Thus

$$\int_{x^*}^{\Lambda} |w_1(t,x)|\,dx \leqslant c_{44}\frac{\delta}{t^{p+1}+1}, \tag{5.71}$$

$$\int_{x^*}^{\Lambda} W_1(t,x)\,dx \leqslant c_{45}\frac{\delta}{t^{p+1}+1}, \tag{5.72}$$

$$\begin{aligned}\int_{x^*}^{\Lambda} |w_2(t,x)|\,dx &\leqslant c_{46}\delta e^{-\rho t} + \int_0^t e^{-\rho(t-\tau)} c_{47}\frac{\delta}{\tau^{p+1}+1}\,d\tau \\ &\leqslant c_{48}\frac{\delta}{t^{p+1}+1}.\end{aligned} \tag{5.73}$$

Our results can be summarized as follows:

THEOREM 5.1. *Assume the inequalities* (5.1) *hold, and define* $\mathbf{w}$ *as in* (4.10), (4.11), *with* $\mathbf{v}^s$ *as in* (5.2), (5.3). *Then there is a* $\delta_0 \geqslant 0$ *such that if* $0 < \delta < \delta_0$, *and if* (5.22) *and* (5.56) *are satisfied, then for* $i = 1, 2$, *and* $t \geqslant 0$,

$$|w_i(t,x)| \leqslant \frac{a_1\delta}{t^p+1}, \quad 0 \leqslant x \leqslant \Lambda,\ x \neq x^*, \tag{5.74}$$

$$\int_0^{\Lambda} |w_i(t,x)|\,dx \leqslant \frac{a_2\delta}{t^{p+1}+1}; \tag{5.75}$$

and furthermore, for $0 \leqslant x < x^*$,

$$|w_i(t,x)| \leqslant a_3\delta \exp[-\min(\nu(a), \nu(x))t], \tag{5.76}$$

with ν *as in* (5.6), a *as in* (5.19). *The constants* a_1, a_2, *and* a_3 *are independent of* x, t *and* δ.

COROLLARY. *The stationary solution* $\mathbf{v}^s$ *in* (5.2) *is asymptotically* ϕ-*stable with* $\phi = \{(\varphi_1, \varphi_2)\}$ *(a one-point set) where, for any fixed* $p > 1$,

$$\varphi_1(x) = \begin{cases} 1, & 0 \leqslant x < x^* \\ \mu(x)^p, & x^* \leqslant x \leqslant \Lambda, \end{cases} \tag{5.77}$$

$$\varphi_2(x) = \begin{cases} \nu(x)^p, & 0 \leqslant x \leqslant x^* \\ 1, & x^* < x \leqslant \Lambda. \end{cases} \tag{5.78}$$

Note that N_φ *here consists of the single point* x^*.

If instead of (5.1) we have the case $\lambda < 1$, $\eta \geqslant \lambda$, and we take (4.25) to hold everywhere on $[0, \Lambda]$, then the function ν of (5.6) satisfies $\nu(x) \geqslant \nu_0 > 0$ for all x for some constant ν_0. Choose $0 < \beta < \min(\nu_0, e^{-\Lambda})$. Then, using (5.7), (5.18), (5.23) and (5.26) we find that $|w_i(t,x)| \leqslant a_4 e^{-\beta t}\delta$, $t \geqslant 0$, $x \in [0, \Lambda]$, $i = 1, 2$, if $|w_i^0(x)| \leqslant \delta$ and δ is sufficiently small.

In the case where $\lambda = 1$, $\eta > 1$, and $\mathbf{v}^s$ is given by (4.27) for all x, ν is increasing and $\nu(0) = 0$. As above (in the analysis of the first case on $(x^*, \Lambda]$), we find that $|w_i(t,x)| \leqslant a_5\delta/(t^p + 1)$ for $x \in (0, \Lambda]$, and $\int_0^\Lambda |w_i(t,x)|\,dx \leqslant a_6\delta/(t^{p+1} + 1)$ if $|w_1^0(x)| \leqslant \delta$, $|w_2^0(x)| \leqslant \delta\nu(x)^p$ and δ is sufficiently small.

The remaining cases mentioned in Theorem 4.1 (except $\lambda = \eta = 1$) are treated similarly. In every case the non-negative stationary solution (with (4.23)–(4.30) taken to hold everywhere) is asymptotically ϕ-stable for a suitable choice of ϕ.

REMARK 5.1. If we consider perturbations satisfying (4.11) and $\sup_{x \in [0,\Lambda]} |w_i^0(x)| < \delta$, $i = 1, 2$, which might seem natural, then we can show in the case (5.1)–(5.3) the following: If $0 \leqslant x < x^*$, there exists a $\delta_0(x)$ such that $\sup_{\xi \in [0,\Lambda]} |w_i(t,\xi)| \leqslant b_1\delta \exp[-\min(\nu(a), \nu(x))t]$ if $\delta \leqslant \delta_0(x)$. But this $\delta_0(x)$ tends to zero as $x \to x^*_-$, and therefore we cannot obtain a good estimate for $\int_0^{x^*}(w_1 + \theta w_2)\,d\xi$; consequently we cannot obtain any useful results for $x > x^*$.

REMARK 5.2. The sub-case $\eta = 0$ is an exception in regard to Remark 5.1. Here it is possible to show also that for $x^* < x \leqslant \Lambda$, we have

$$\sup_{\xi \in [x, \Lambda]} |w_i(t,\xi)| \leqslant b_2\delta \exp\left[-\tfrac{1}{2}\min(\rho, \mu(x))t\right],$$

with ρ as in (5.53), μ as in (5.46), provided $\delta \leqslant \delta_1(x)$, where $\delta_1(x) \to 0$ as $x \to x^*_+$.

6. The case $\lambda = \eta = 1$

When $\lambda = \eta = 1$, the system (2.22) becomes

$$\begin{aligned} \frac{\partial v_1}{\partial t} &= v_1\left[1 - v_1 - v_2 - \int_0^x (v_1 + \theta v_2)\,d\xi\right], \\ \frac{\partial v_2}{\partial t} &= \gamma v_2\left[1 - v_1 - v_2 - \int_0^x (v_1 + \theta v_2)\,d\xi\right]. \end{aligned} \tag{6.1}$$

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Let $\mathbf{v}^s \geqslant 0$ be a stationary solution of (6.1). With the notation of Section 4 we have this time that $E_1 \subseteq E_3$ and $E_2 \subseteq E_3$, so we need only consider the sets E_0 and E_3:

$$\mathbf{v}^s(x) = 0 \quad \text{on } E_0 \tag{6.2a}$$

$$1 - v_1^s(x) - v_2^s(x) - \int_0^x [v_1^s(\xi) + \theta v_2^s(\xi)]\, d\xi = 0 \quad \text{on } E_3. \tag{6.2b}$$

From (4.12), (4.13) and (4.16) we get

$$\left.\begin{aligned} \frac{\partial w_1}{\partial t} &= [1 - \psi(x)]w_1 + g_1 \\ \frac{\partial w_2}{\partial t} &= \gamma[1 - \psi(x)]w_2 + f_2 \end{aligned}\right\} \text{on } E_0 \tag{6.3}$$

$$\left.\begin{aligned} \frac{\partial w_1}{\partial t} &= -v_1^s(x)\left[w_1 + w_2 + \int_0^x (w_1 + \theta w_2)\, d\xi\right] + g_1 \\ \frac{\partial w_2}{\partial t} &= -\gamma v_2^s(x)\left[w_1 + w_2 + \int_0^x (w_1 + \theta w_2)\, d\xi\right] + f_2 \end{aligned}\right\} \text{on } E_3 \tag{6.4}$$

where

$$\begin{aligned} g_1 &= -w_1\left[w_1 + w_2 + \int_0^x (w_1 + \theta w_2)\, d\xi\right], \\ f_2 &= -\gamma w_2\left[w_1 + w_2 + \int_0^x (w_1 + \theta w_2)\, d\xi\right] \end{aligned} \tag{6.5}$$

and

$$\psi(x) = \int_0^x [v_1^s(\xi) + \theta v_2^s(\xi)]\, d\xi. \tag{6.6}$$

Suppose that $\mathbf{v}^s$ is ϕ-stable with respect to a certain class ϕ, as in Definition 4.1. Since $\psi(0) = 0$ and ψ is continuous, either $\psi(x) < 1$ for all $x \in [0, \Lambda]$ or there is an $x_0 \in (0, \Lambda]$ such that $\psi(x_0) = 1$ and $\psi(x) < 1$ for $x \in [0, x_0)$. Assume the latter case. From Lemma 4.1, which continues to hold if $\lambda = \eta = 1$, we conclude that $x \in E_3 \setminus E_0$ for almost all $x \in [0, x_0)$. Then on $[0, x_0) \cap (E_3 \setminus E_0)$,

$$v_1^s(x) + v_2^s(x) = \int_x^{x_0} [v_1^s(\xi) + \theta v_2^s(\xi)]\, d\xi, \tag{6.7}$$

so that $(v_1^s + v_2^s)$ is positive and decreasing on that set, and consequently

$$v_1^s(x) + v_2^s(x) \leqslant \max(1, \theta)[v_1^s(x) + v_2^s(x)](x_0 - x) \tag{6.8}$$

there. But this is self-contradictory for small positive $(x_0 - x)$. Therefore $\psi(x) < 1$ for all $x \in [0, \Lambda]$, $m(E_0) = 0$ and $x \in E_3$ for almost all $x \in [0, \Lambda]$.

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In view of this we shall now consider, with no significant loss of generality, only those non-negative stationary solutions $\mathbf{v}^s$ for which $E_3 = [0, \Lambda]$ and $E_0 = \varnothing$. Denoting the set of all such solutions by S, we shall show that S is asymptotically stable. By this we mean the following: For every $\varepsilon > 0$ there exists a $\delta > 0$ such that

$$\inf_{\mathbf{v}^s \in S} \|\mathbf{v}^0 - \mathbf{v}^s\| < \delta \tag{6.9}$$

implies

$$\inf_{\mathbf{v}^s \in S} \|\mathbf{v}(t, \cdot) - \mathbf{v}^s\| < \varepsilon \tag{6.10}$$

for all $t \geqslant 0$; and furthermore there exists a δ' such that

$$\inf_{\mathbf{v}^s \in S} \|\mathbf{v}^0 - \mathbf{v}^s\| < \delta' \tag{6.11}$$

implies

$$\lim_{t \to \infty} \inf_{\mathbf{v}^s \in S} \|\mathbf{v}(t, \cdot) - \mathbf{v}^s\| = 0. \tag{6.12}$$

It will be shown also that the individual solutions in S are ϕ-stable for $\phi = \{(1, 1)\}$, but are not asymptotically ϕ-stable for any ϕ.

Before proceeding to prove these statements, we need the following observations. Let E be an arbitrary measurable subset of $[0, \Lambda]$ and ζ an arbitrary measurable non-negative function defined on E. Denote by $\mathbf{v}^s_{E,\zeta}$ a non-negative solution of

$$\begin{aligned} &1 - v_1^s(x) - v_2^s(x) - \int_0^x \left[v_1^s(\xi) + \theta v_2^s(\xi)\right] d\xi = 0, \qquad x \in [0, \Lambda] \\ &v_2^s(x) = \zeta(x)\left[v_1^s(x)\right]^\gamma, \qquad x \in E \\ &v_1^s(x) = 0, \qquad x \notin E. \end{aligned} \tag{6.13}$$

We shall show below that there exists a unique such solution. It is obvious that, for each E and ζ, $\mathbf{v}^s_{E,\zeta} \in S$, and it is also easily seen that any $\mathbf{v}^s \in S$ can be obtained in this way—given $\mathbf{v}^s$, use the third equation of (6.13) to define a corresponding E, and then the second to define a corresponding ζ. Now consider (6.1) with non-negative initial values $\mathbf{v}^0(x)$ satisfying $(v_1^0 + v_2^0) > 0$ on $[0, \Lambda]$. If $v_i^0(x) = 0$ for some i and x, then $v_i(t, x) = 0$ for all $t \geqslant 0$. Furthermore, if $v_1^0(x) > 0$ for some x, then (6.1) implies $v_1(t, x) > 0$ for $t \geqslant 0$ and $\partial(v_2(t, x)/[v_1(t, x)]^\gamma)/\partial t = 0$. Hence, for such x,

$$\frac{v_2(t, x)}{\left[v_1^0(t, x)\right]^\gamma} = \frac{v_2^0(x)}{\left[v_1^0(x)\right]^\gamma}, \qquad t \geqslant 0. \tag{6.14}$$

Taking

$$E = \{x: v_1^0(x) > 0\}$$

$$\zeta(x) = \frac{v_2^0(x)}{[v_1^0(x)]^\gamma}, \qquad x \in E, \tag{6.15}$$

we call $\mathbf{v}^s_{E,\zeta}$ the stationary solution *associated with* $\mathbf{v}^0$.

The stability results for S and its members, referred to above, can be seen to be consequences of the following two results which we shall now prove:

Result 1. For every $\varepsilon > 0$ there is a $\delta > 0$ such that, for any $\mathbf{v}^s \in S$ and $\mathbf{v}^0 \geqslant 0$ satisfying

$$\|\mathbf{v}^0 - \mathbf{v}^s\| < \delta, \tag{6.16}$$

it follows that, for all $x \in [0, \Lambda]$

$$v_1^0(x) + v_2^0(x) > 0 \tag{6.17}$$

and

$$\|\mathbf{v}^s_{E,\zeta} - \mathbf{v}^s\| < \varepsilon, \tag{6.18}$$

where $\mathbf{v}^s_{E,\zeta}$ is the stationary solution associated with $\mathbf{v}^0$, and is in general distinct from $\mathbf{v}^s$.

Result 2. There exist positive constants δ_0, c and k such that, if $\mathbf{v}^0 \geqslant 0$ satisfies

$$|\mathbf{v}^0(x) - \mathbf{v}^s_{E,\zeta}(x)| < \delta \leqslant \delta_0 \tag{6.19}$$

for all $x \in [0, \Lambda]$, where $\mathbf{v}^s_{E,\zeta}$ is the stationary solution associated with $\mathbf{v}^0$, then

$$|\mathbf{v}(t, x) - \mathbf{v}^s_{E,\zeta}(x)| < c\delta e^{-kt} \tag{6.20}$$

for all $x \in [0, \Lambda]$, $t \geqslant 0$.

Proof 1. For given E and ζ, and $x \in E$, consider the equation

$$u = v_1 + \zeta(x) v_1^\gamma, \qquad v_1 \geqslant 0. \tag{6.21}$$

Since the function $v_1 \to v_1 + \zeta(x) v_1^\gamma$ is strictly increasing on $[0, \infty)$, (6.21) has a unique non-negative solution $v_1 = F(x, u)$ for $u \geqslant 0$. The function $u \to F(x, u)$ is continuous for $u \geqslant 0$. Moreover, it is continuously differentiable for $u > 0$, with

$$\frac{\partial F}{\partial u}(x, u) = 1/\{1 + \gamma\zeta(x)[F(x, u)]^{\gamma - 1}\}. \tag{6.22}$$

The right-hand derivative of F at $u = 0$ exists as well and equals the limit of the right-hand side of (6.22) as $u \to 0_+$. We see also that the function $x \to F(x, u)$ is measurable on E (since $\{\zeta \geqslant 0: \exists v_1$ such that $0 \leqslant v_1 < \alpha,\ v_1 + \zeta v_1^\gamma = u \geqslant 0\}$ is an interval for any $\alpha > 0$). Finally, if $x \notin E$, we define $F(x, u) = 0$ for all $u \geqslant 0$. In this way we have defined a function F on $[0, \Lambda] \times [0, \infty)$, measurable in x and continuously differentiable in u, and such that

$$0 \leqslant F(x,u) \leqslant u, \qquad 0 \leqslant \frac{\partial F}{\partial u}(x,u) \leqslant 1. \tag{6.23}$$

We consider also the function $G(x,u) = u - F(x,u)$ and see that $v_2 = G(x,u)$ is the solution of

$$v_2 + \chi(x) v_2^{1/\gamma} = u \geqslant 0, \qquad v_2 \geqslant 0, \tag{6.24}$$

for $x \in ([0, \Lambda] \setminus E) \cup \{x \in E\colon \zeta(x) > 0\}$, where

$$\chi(x) = \begin{cases} [\zeta(x)]^{-1/\gamma}, & \text{if } x \in E \text{ and } \zeta(x) > 0 \\ 0, & \text{if } x \in [0, \Lambda] \setminus E. \end{cases} \tag{6.25}$$

Now it follows that (6.13) is equivalent to

$$1 - u(x) - \int_0^x [F(\xi, u(\xi)) + \theta G(\xi, u(\xi))]\, d\xi = 0, \tag{6.26}$$

with the connections $v_1^s = F(x, u(x))$, $v_2^s(x) = G(x, u(x))$, or equivalently $u(x) = v_1^s(x) + v_2^s(x)$. But (6.26) is equivalent (in Carathéodory's sense) to the ordinary differential equation

$$\begin{aligned} du/dx &= -F(x,u) - \theta G(x,u), \\ u(0) &= 1 \end{aligned} \tag{6.27}$$

and from the properties of F and G it follows [4, Chapter 2] that there exists a unique absolutely continuous function u satisfying (6.27) almost everywhere, and (6.26) everywhere. We denote this solution of (6.26) by $u^s_{E,\zeta}$ or simply by u^s.

It follows from (6.27) that $du^s/dx \geqslant -\max(1,\theta)u^s$, so that $u^s(x) \geqslant \exp(-\max(1,\theta)x)$ and hence there is a constant $\kappa > 0$ such that

$$v_1^s(x) + v_2^s(x) \geqslant \kappa, \quad x \in [0, \Lambda] \tag{6.28}$$

for every $\mathbf{v}^s \in S$.

From (6.28) it follows that there is a $\delta_1 > 0$ such that any non-negative $\mathbf{v}^0$ with

$$|\mathbf{v}^0(x) - \mathbf{v}^s(x)| < \delta_1 \tag{6.29}$$

for all $x \in [0, \Lambda]$ and some $\mathbf{v}^s \in S$, satisfies $v_1^0(x) + v_2^0(x) \geqslant \frac{1}{2}\kappa$ for all $x \in [0, \Lambda]$.

Now consider an arbitrary $\mathbf{v}^s \in S$. According to (6.28), for each $x \in [0, \Lambda]$, either $v_1^s(x) \geqslant \frac{1}{2}\kappa$ or $v_2^s(x) \geqslant \frac{1}{2}\kappa$. As above, set

$$\begin{aligned} E &= \{x\colon v_1^s(x) > 0\} \\ \zeta(x) &= \frac{v_2^s(x)}{[v_1^s(x)]^\gamma}, \qquad v_1^s(x) > 0 \\ \chi(x) &= \frac{v_1^s(x)}{[v_2^s(x)]^{1/\gamma}}, \qquad v_2^s(x) > 0. \end{aligned} \tag{6.30}$$

Supposing $\mathbf{v}^0 \geqslant 0$ satifies (6.29) for all x, define

$$\tilde{E} = \{x: v_1^0(x) > 0\}$$

$$\tilde{\zeta}(x) = \frac{v_2^0(x)}{[v_1^0(x)]^{\gamma}}, \qquad v_1^0(x) > 0 \tag{6.31}$$

$$\tilde{\chi}(x) = \frac{v_1^0(x)}{[v_2^0(x)]^{1/\gamma}}, \qquad v_2^0(x) > 0$$

and let $\tilde{\mathbf{v}}^s$ denote the associated member of S. We also define F, G, u and $\tilde{F}, \tilde{G}, \tilde{u}$, respectively, as above. If $|\mathbf{v}^0(x) - \mathbf{v}^s(x)| < \delta \leqslant \delta_1$ for all x, and δ is small enough, $|\tilde{\zeta}(x) - \zeta(x)|$ can be made arbitrarily small on the set where $v_1^s(x) \geqslant \frac{1}{2}\kappa$, and $|\tilde{\chi}(x) - \chi(x)|$ can be made arbitrarily small on the set where $v_2^s(x) \geqslant \frac{1}{2}\kappa$. Since the solutions of (6.21) and (6.24) depend continuously on $\zeta(x)$ and $\chi(x)$, respectively, we find that $|\tilde{F}(x,u) - F(x,u)| = |\tilde{G}(x,u) - G(x,u)|$ can be made arbitrarily small, uniformly in $x \in [0, \Lambda]$ and $u \in [\kappa, 1]$; and since the solution of (6.27) depends continuously on the right-hand side we can make $|\tilde{u}(x) - u(x)|$ arbitrarily small, uniformly in x. Finally,

$$|\tilde{v}_1^s(x) - v_1^s(x)| \leqslant |\tilde{F}(x, \tilde{u}(x)) - F(x, \tilde{u}(x))| + |F(x, \tilde{u}(x)) - F(x, u(x))| \tag{6.32}$$

can be made small, and similarly for $|\tilde{v}_2^s(x) - v_2^s(x)|$. In all, for any $\varepsilon > 0$ we can find a $\delta \leqslant \delta_1$ such that $|\mathbf{v}^0(x) - \mathbf{v}^s(x)| < \delta$ for all x implies that $|\tilde{\mathbf{v}}^s(x) - \mathbf{v}^s(x)| < \varepsilon$ for all x; δ can be chosen independently of $\mathbf{v}^s$.

PROOF 2. The system (6.1) can be written in the equivalent form

$$\frac{\partial u}{\partial t} = [F(x,u) + \gamma G(x,u)]\left\{1 - u - \int_0^x [F(\xi,u) + \theta G(\xi,u)]\,d\xi\right\} \tag{6.33}$$

with initial condition

$$u(0,x) = u^0(x) = \begin{cases} v_1^0(x) + \zeta(x)[v_1^0(x)]^{\gamma}, & x \in E \\ v_2^0(x), & x \notin E \end{cases} \tag{6.34}$$

where E and ζ are as in (6.15), and with the identifications $v_1(t,x) = F(x, u(t,x)), v_2(t,x) = G(x, u(t,x))$, or $u(t,x) = v_1(t,x) + v_2(t,x)$. We want to show that $u(t,x) \to u^s(x) = u_{E,\zeta}^s(x)$ as $t \to \infty$, uniformly in x, if u^0 is sufficiently close to u^s.

Let

$$w = u - u^s, \qquad w_0 = u^0 - u^s. \tag{6.35}$$

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Then

$$\frac{\partial w}{\partial t}(t,x) = -\alpha(x)\left[w(t,x) + \int_0^x g(\xi)w(t,\xi)\,d\xi\right] + h(t,x), \qquad (6.36)$$

where

$$\begin{aligned} \alpha(x) &= F(x,u^s(x)) + \gamma G(x,u^s(x)), \\ g(x) &= \theta + (1-\theta)\frac{\partial F}{\partial u}(x,u^s(x)) \end{aligned} \qquad (6.37)$$

and h is a function which is continuous in t, measurable in x, and such that

$$|h(t,x)| \leqslant c_1 \sup_{\xi\in[0,\Lambda]} |w(t,\xi)|^2 \qquad (6.38)$$

for a certain constant c_1, independent of E and ζ, provided

$$\sup_{x\in[0,\Lambda]} |w(t,x)| \leqslant \frac{1}{2}\kappa. \qquad (6.39)$$

Since $\alpha(x) \geqslant \alpha_0 > 0$ for a certain constant α_0, also independent of E and ζ, we can apply Lemma 5.1 to obtain

$$\begin{aligned} \tilde{w}(s,x) = {} & \frac{1}{s+\alpha(x)}\left[w^0(x) + \tilde{h}(s,x)\right] \\ & - \frac{\alpha(x)}{s+\alpha(x)}\int_0^x \frac{g(\xi)}{s+\alpha(\xi)}\exp\left[-\int_\xi^x \frac{g(y)\alpha(y)}{s+\alpha(y)}\,dy\right]\left[w^0(\xi) + \tilde{h}(s,\xi)\right]d\xi \end{aligned} \qquad (6.40)$$

for the Laplace transform of w. We can write

$$\exp\left[-\int_\xi^x \frac{g(y)\alpha(y)}{s+\alpha(y)}\,dy\right] = 1 + \frac{\beta(\xi,x)}{s+\alpha_0} + \tilde{q}_0(s,\xi,x) \qquad (6.41)$$

where $|\beta(\xi,x)| \leqslant c_2$, $\tilde{q}_0$ is analytic in s for $\operatorname{Re} s > -\alpha_0$, and $|\tilde{q}_0(s,\xi,x)| \leqslant c_3/|s+\alpha_0|^2$ for $\operatorname{Re} s \geqslant -\frac{1}{2}\alpha_0$. It then follows [5, Theorem 28.2] that $\tilde{q}_0$ is the Laplace transform of

$$q_0(t,\xi,x) = \frac{1}{2\pi i}\int_{-\alpha_0/2-i\infty}^{-\alpha_0/2+i\infty} e^{st}\tilde{q}_0(s,\xi,x)\,ds, \qquad (6.42)$$

with

$$|q_0(t,\xi,x)| \leqslant \frac{1}{2\pi}\int_{-\infty}^{\infty} e^{-\alpha_0 t/2}\frac{c_3}{(\alpha_0/2)^2 + r^2}\,dr = c_4 e^{-\alpha_0 t/2}. \qquad (6.43)$$

Then

$$\exp\left[-\int_\xi^x \frac{g(y)\alpha(y)}{s+\alpha(y)}\,dy\right] = 1 + \tilde{q}(s,\xi,x), \qquad (6.44)$$

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where $\tilde{q}$ is the Laplace transform of

$$q(t,\xi,x) = \beta(\xi,x)e^{-\alpha_0 t} + q_0(t,\xi,x), \tag{6.45}$$

so that

$$|q(t,\xi,x)| \leqslant c_2 e^{-\alpha_0 t} + c_4 e^{-\alpha_0 t/2} \leqslant c_5 e^{-\alpha_0 t/2}. \tag{6.46}$$

Then $\tilde{w}(s,x)$ is the Laplace transform of

$$\begin{aligned} w(t,x) = {} & w^0(x)e^{-\alpha(x)t} + \int_0^t e^{-\alpha(x)(t-\tau)}h(\tau,x)\,d\tau \\ & -\alpha(x)\int_0^x g(\xi)\{e^{-\alpha(x)t}\} * \{e^{-\alpha(\xi)t}\} w^0(\xi)\,d\xi \\ & -\alpha(x)\int_0^x g(\xi)\{e^{-\alpha(x)t}\} * \{e^{-\alpha(\xi)t}\} * \{h(t,\xi)\}\,d\xi \\ & -\alpha(x)\int_0^x g(\xi)\{e^{-\alpha(\xi)t}\} * \{e^{-\alpha(\xi)t}\} * \{q(t,\xi,x)\} w^0(\xi)\,d\xi \\ & -\alpha(x)\int_0^x g(\xi)\{e^{-\alpha(x)t}\} * \{e^{-\alpha(\xi)t}\} * \{q(t,\xi,x)\} * \{h(t,\xi)\}\,d\xi \end{aligned} \tag{6.47}$$

where $*$ denotes convolution in the t-variable:

$$\{f(t)\} * \{g(t)\} = \int_0^t f(t-\tau)g(\tau). \tag{6.48}$$

We have the following estimates:

$$0 < \{e^{-\alpha(x)t}\} * \{e^{-\alpha(\xi)t}\} \leqslant \{e^{-\alpha_0 t}\} * \{e^{-\alpha_0 t}\} = te^{-\alpha_0 t}, \tag{6.49}$$

$$\left|\{e^{-\alpha(x)t}\} * \{e^{-\alpha(\xi)t}\} * \{q(t,\xi,x)\}\right| \leqslant \{te^{-\alpha_0 t}\} * \left\{c_5 e^{-\alpha_0 t/2}\right\} \leqslant c_6 e^{-\alpha_0 t/2} \tag{6.50}$$

so that

$$\begin{aligned} |w(t,x)| < {} & |w^0(x)|e^{-\alpha_0 t} + c_7 e^{-\alpha_0 t/2} \sup_{\xi\in[0,\Lambda]} |w^0(\xi)| \\ & + \int_0^t e^{-\alpha_0(t-\tau)}|h(\tau,x)|\,d\tau \\ & + c_7\int_0^t e^{-\alpha_0(t-\tau)/2} \sup_{\xi\in[0,\Lambda]} |h(\tau,\xi)|\,d\tau. \end{aligned} \tag{6.51}$$

Suppose

$$\sup_{x\in[0,\Lambda]} |w^0(x)| \leqslant \delta < \tfrac{1}{2}\kappa \tag{6.52}$$

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and let

$$W(t) = \sup_{x \in [0,\Lambda]} |w(t,x)|. \tag{6.53}$$

Then, as long as $W(t) \leqslant \frac{1}{2}\kappa$, (6.38) gives

$$|h(t,x)| \leqslant c_1 W(t)^2, \tag{6.54}$$

so we have

$$W(t) \leqslant c_8 \delta e^{-\alpha_0 t/2} + c_9 \int_0^t e^{-\alpha_0 (t-\tau)/2} W(\tau)^2 \, d\tau \tag{6.55}$$

and hence

$$W(t) \leqslant c_8 \delta e^{-\alpha_0 t/2} \exp\left[c_9 \int_0^t W(\tau) \, d\tau \right]. \tag{6.56}$$

As long as $W(t) \leqslant \frac{1}{2}\kappa$ and $\int_0^t W(\tau)\,d\tau \leqslant 1$, we then have

$$W(t) \leqslant c_{10} \exp\left[-\tfrac{1}{2}\alpha_0 t \delta\right], \tag{6.57}$$

and so

$$\int_0^1 W(\tau)\,d\tau < \frac{2}{\alpha_0} c_{10}\delta = c_{11}\delta. \tag{6.58}$$

If δ is chosen so small that $c_{10}\delta < \frac{1}{2}\kappa$ and $c_{11}\delta < 1$, then (6.57) and (6.58) must hold for all $t \geqslant 0$. Therefore there is a δ_0 such that if $0 < \delta < \delta_0$, then

$$|w(t,x)| \leqslant c_{10} \exp\left[-\tfrac{1}{2}\alpha_0 t \delta\right] \tag{6.59}$$

for all $t \geqslant 0$, $x \in [0,\Lambda]$. This proves Result 2, since all the constants are independent of E and ζ.

7. Concluding Remarks

Our interest is mainly in the asymptotically stable stationary solution (2.19) [or (2.25)] which arises when the growth-rate constants characterizing the two cell-types satisfy the inequalities (2.9), (2.14) and (2.15) [or (2.24)] and which has a zonal structure. To be precise, we have shown only that this solution is asymptotically stable against a particular class of perturbations, which are required to be vanishingly small near the singular point $x = x^*$ where the discontinuities ultimately occur in the densities of the two cell types. The question obviously arises as to whether or not one can prove (asymptotic) stability against a wider class of perturbations. It would be interesting in particular to know the behaviour at $x = x^*$ following a perturbation to the densities near and at that point. More generally we have the question as to whether indeed, as conjectured

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in Section 2, this zonal solution is globally asymptotically stable for everywhere positive initial data. These questions remain open.

We have obtained estimates for the rates at which a small perturbation of the allowed type decays away as time t progresses, and found an exponential rate for $x < x^*$ (with a decay constant which goes to zero as $x \to x^*_-$). But for $x > x^*$ our best estimate of the behaviour is of the form t^{-p}, where $p > 1$ is a constant involved in the definition of the class of allowed perturbations as in (5.22). These results do suggest that the rate may indeed be qualitatively different to the left and to the right of $x = x^*$, as speculated in Section 2, but perhaps improved estimates can be found which disprove this.

Turning to possible generalisations, we remark firstly that it seems likely that the model can be applied to a whole class of processes including, for example, the distribution of certain plant species in a river with a limited resource originating upstream. The extension to N competing species is immediate, at least in so far as obtaining the appropriate coupled equations is concerned: we get for $i = 1, 2 \cdots N$, in place of (2.5),

$$\frac{\partial \rho_i}{\partial t}(t,x) = \rho_i(t,x)\left\{k_i\left(\sigma - \sum_{j=1}^{N} \rho_j(t,x)\right) - \mu_i - \frac{\nu_i}{f}\int_0^x \sum_{j=1}^{N} \kappa_j \rho_j(t,\xi)\, d\xi\right\}. \tag{7.1}$$

The analysis of stationary solutions, and in particular the identification of the stable ones amongst them, naturally becomes rather complicated with increasing N, but it is easily seen that multi-zonal solutions can occur. Even in the case $N = 1$, where we have members of a single species competing for a resource flowing from $x = 0$ to $x = L$, the model is not without some interest for applications, though there is of course no question of zones forming in this case.

It is more difficult to envisage a simple generalisation of the model to two or more spatial dimensions, but the radially symmetric case in n-dimensions, with N species competing for a resource flowing radially outwards from a central point, seems straightforward.

Another generalisation which could be considered involves taking a more general form for the $\beta_i(c)$ than the linear approximation (2.4). Under mild conditions on these functions one can still prove existence and uniqueness of bounded non-negative solutions, much as in Section 3, but the analysis of stationary states and their stability is then a more difficult task.

As remarked earlier, the model does not allow for migration of species. This undoubtedly limits the range of applicability. But it also accounts for the degree of mathematical tractability we have found, enabling us to show that the model can account for the appearance of stable spatial patterns within a simple conceptual framework.

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