The Global Structure of a Spatial Model of Infectious Disease

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In this paper we study an SI model of infectious diseases which takes into account spatial inhomogeneities, resulting in a system of reaction-convection-diffusion equations on a bounded domain. The convection process is included to account for social interaction, as modelled by the location of a focal point or *den* where the population will tend to aggregate.

We show that a vertical bifurcation of steady-state solutions occurs in this model when birth rate is taken as the bifurcation parameter, from which emanates a global secondary branch which then bifurcates at infinity. We subsequently use singular perturbation techniques to give a description of the limiting spatial structure along this branch in large and small parameter limits. Finally, the results are illustrated numerically on some biologically relevant cases.

Keywords: SI epidemic model, global bifurcation, spatial structure

1. Introduction

Understanding animal movement is an important factor in understanding their social behaviour which is particularly relevant in the context of epidemiology and disease management (Rogers *et al.* 1998). The difficulty in observing infected individuals and the consequent lack of empirical data has led to the development of models in which the behaviour of healthy individuals is used to study disease dynamics (White *et al.* 1995b). Nevertheless, there have been attempts to observe and quantify the behaviour of infected animals (Cheeseman and Mallison 1981, Kaplan 1977, Bacon 1985, Artois & Aubert 1985) and there has emerged evidence from such studies that infected individuals may display significantly different behaviour from that of healthy individuals (Jeltsch *et al.* 1997 and White *et al.* 1995a). These studies have also found a high variation of behaviour among infected individuals themselves, ranging from the so-called *dumb* (or *paralysis*) forms of disease for which individuals have very restrictive movement, to the *furious* forms whereby individuals move in a random fashion, possibly covering great distances.

In this paper we consider disease dynamics in a single social group of animals. The members of that social group are divided into two classes: *susceptibles* S and *infecteds* I. Infecteds have the disease and can transmit it and we assume that once infected, individuals do not recover. When modelling social structure we take White *et al.* (1995a) as a basis and assume that animal movement comprises of two components: (convective) movement towards the den to feed the offspring, for instance, and (diffusive) dispersal in order to find food and protect the group.

Let $\Omega = (0,1) \subset \mathbb{R}$ and for each $T > 0$ we define $D_T = (0,T] \times \Omega$. The result to follow can all be extended to cover the case $\Omega \subset \mathbb{R}^d$, modulo suitable regularity requirements, but to maintain clarity of the presentation we restrict to a one-dimensional spatial domain.

We now take a well-known ODE model and include inhomogeneous diffusive and convective terms to represent the presence of a *focal point*, providing the following parabolic problem:

$$\begin{array}{rcll} S_t & = & (D_1(x)S_x + C_1(x)S)_x + (a-b)S + aI - \lambda SI, & (t,x) \in D_T, \\ I_t & = & (D_2(x)I_x + C_2(x)I)_x - cI + \lambda SI, & (t,x) \in D_T, \end{array} \tag{1.1}$$

subject to the no-flux boundary conditions

$$0 = D_1(x)S_x + C_1(x) = D_2(x)I_x + C_2(x)I, \qquad (t,x) \in (0,T] \times \partial\Omega. \tag{1.2}$$

We assume throughout that positive and continuous initial data $S(x,0) = S_0(x)$ and $I(x,0) = I_0(x)$ are given.

Movement towards the den is modelled by convection towards a single point in the domain, $x_D \in \Omega$. Various forms for this movement have been discussed in Okubo (1980) but here, with generality in mind, the convection coefficients $C_i(x)$ are assumed to be continuously differentiable functions satisfying

$$C_i(0) < 0 \text{ and } C_i(1) > 0, \qquad (i = 1,2).$$

This condition is required in order to obtain maximum and comparison principles for the system (1.1-1.2). The diffusion coefficients, $D_i(x)$, are continuously differentiable and strictly positive on $\overline{\Omega}$. The parameter λ represents the contact rate between susceptible and infected individuals and c represents the per-capita, disease-induced death rate. Also, a represents the per-capita birth rate of both susceptible and infected individuals and b represents the per-capita natural death rate of the susceptible individuals. We assume no vertical transmission, that is infected individuals give birth to susceptible individuals; this has been observed in badgers infected with tuberculosis (Bentil & Murray 1993, Anderson & May 1985) and foxes infected with rabies (Bacon 1985). Note that all of the above reaction parameters are positive constants.

This model is presented in ODE form in Anderson and May (1981, p.462), where the parameters have a slightly different meaning to those presented here. The reaction terms in (1.1) form part of an ODE model of social interaction which is discussed in Beardmore & White (2001).

Throughout the paper we shall use the *eigenfunctions*

$$\phi_i(x) = \exp\left(-\int_0^x \frac{C_i(\xi)}{D_i(\xi)} d\xi\right), \qquad (i = 1,2),$$

and these functions satisfy

$$D_i(x)\frac{d\phi_i(x)}{dx} + C_i(x)\phi_i(x) \equiv 0, \qquad x \in \overline{\Omega}.$$

Due to the assumption that the convection functions have zeros, it is typical that each ϕ_i is a unimodal function, or multi-modal if more zeros of C_i are assumed.

Seeking steady state solutions of (1.1-1.2), we are required to solve the boundary-value problem

$$\begin{aligned} -\mathrm{L}_1 S := -(D_1(x)S_x + C_1(x)S)_x &= (a-b)S - \lambda SI + aI, \quad x \in \Omega, \\ -\mathrm{L}_2 I := -(D_2(x)I_x + C_2(x)I)_x &= \lambda SI - cI, \qquad\qquad\quad x \in \Omega, \end{aligned} \tag{1.3}$$

subject to

$$D_1(x)S_x + C_1(x)S = D_2(x)I_x + C_2(x)I = 0, \qquad x \in \partial\Omega. \tag{1.4}$$

When $a = b$, we see that (1.3) has a *vertical branch* of solutions of the form

$$(S, I) = (k\phi_1(x), 0), \tag{1.5}$$

where k is an arbitrary, non-negative constant. Note that this vertical branch bifurcates from the trivial solution branch of (1.3). Taking the birth rate, a, to be the bifurcation parameter, we seek non-negative solutions of (1.3) for $a > 0$ and we are led to consider the following three cases:

$$\text{I. } 0 < a < b < c, \quad \text{II. } 0 < b < c < a, \quad \text{III. } 0 < b < a < c.$$

As a preliminary step, let us consider the ODE

$$\begin{aligned} \dot{S} &= (a-b)S + aI - \lambda SI, \\ \dot{I} &= -cI + \lambda SI. \end{aligned} \tag{1.6}$$

This corresponds to the spatially homogeneous solutions of (1.1-1.2) in the case of zero convection. One can readily show that the dynamics of (1.6) are as described in Figure 1. In case III the steady-state of (1.6) when $a > b$ is given by

$$(S, I) = \frac{c}{\lambda}\left(1, \frac{a-b}{c-a}\right),$$

and we shall demonstrate that a similar form holds for the steady-states of (1.1-1.2). We note that this branch of steady-states bifurcates as a secondary branch from a *vertical* set of solutions which exists when $a = b$.

(a) *Case I*

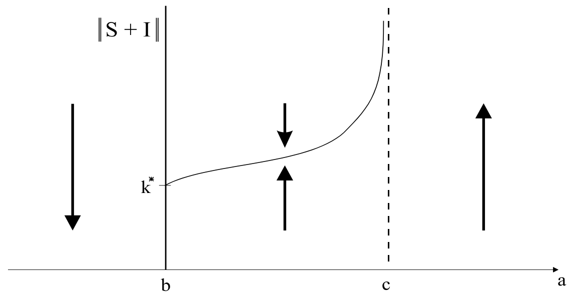
Here we assume that the birth rate parameter is smaller than the natural death rate, which in turn is less than the disease induced mortality rate. In anticipation of Proposition (1.1), we suppose that (1.1-1.2) admits solutions with positive $(S_0, I_0) \in C^0(\overline{\Omega}) \times C^0(\overline{\Omega})$. Let us define the total biomass function, V:

$$V(S, I) := \int_\Omega (S + I)dx.$$

Using (1.1-1.2) we find

$$\frac{dV}{dt} = (a-b)\int_\Omega S dx + (a-c)\int_\Omega I dx \le \max(a-b, a-c)V,$$

Figure 1. Three cases: I (left), II (right) and III (middle).



since $a < b < c$. If $\delta = \max(a-b, a-c)$, it follows that $V(S(t), I(t)) \le e^{\delta t} V(S_0, I_0)$, so that $\|S\|_{L^1} + \|I\|_{L^1} \to 0$ as $t \to \infty$.

This shows that when the birth rate of the total population is smaller than both the natural and disease induced death rates, the population will become extinct.

(*b*) *Case II*

In this section we consider (1.1-1.2) when $0 < b < c < a$ and for $x \in \overline{\Omega}$. Since ϕ_i is continuous on the compact set $\overline{\Omega}$, there exist $\phi_{i\,\max}, \phi_{i\,\min} \in \mathbb{R}$ such that

$$0 < \phi_{i\,\min} \le \phi_i(x) \le \phi_{i\,\max}, \qquad x \in \overline{\Omega},$$

and for brevity of the notation, we set

$$r = \frac{\phi_{1\,\min}}{\phi_{1\,\max}} \le 1. \tag{1.7}$$

Proposition 1.1. *Suppose* $0 < b < c < a$ *and* $\frac{c}{a} < r$. *Given continuous initial data* (S_0, I_0) *such that* $S_0 > 0$ *and*

$$I_0 \ge \frac{(a-c)+(a-b)}{\lambda \phi_{2\,\min}} \exp\left(\frac{a}{(a-c)+(a-b)}\right)\phi_2, \tag{1.8}$$

there is a unique solution (S, I) *of (1.1-1.2) with this initial data which also satisfies*

$$\|(S(x,t), I(x,t))\|_{C^0} \to \infty,$$

as $t \to \infty$. *Moreover* S *stays* C^0*-bounded while* $\|I\|_{C^0} \to \infty$ *as* $t \to \infty$.

Proof. Since the disease-dynamics terms in (1.1) do not form a quasi-monotone function, in order to prove the proposition we construct a pair of *generalised* upper and lower solutions of (1.1-1.2) according to Pao (1992, definition 9.1, p.436). Conditions for $(\overline{S}, \overline{I})$ and $(\underline{S}, \underline{I})$ to be a pair of *generalised* upper and lower solutions of (1.1-1.2) as set out in Pao (1992) yield

$$\frac{\partial \overline{S}}{\partial t} - D_1(x)\frac{\partial^2 \overline{S}}{\partial x^2} - (D_1'(x) + C_1(x))\frac{\partial \overline{S}}{\partial x} \ge C_1'(x)\overline{S} + (a-b)\overline{S} - \lambda \overline{S} I + aI, \tag{1.9a}$$

$$\frac{\partial \underline{S}}{\partial t} - D_1\frac{\partial^2 \underline{S}}{\partial x^2} - (D_1'(x) + C_1(x))\frac{\partial \underline{S}}{\partial x} \le C_1'(x)\underline{S} + (a-b)\underline{S} - \lambda \underline{S} I + aI, \tag{1.9b}$$

for all continuous functions I on $\overline{D_T}$ such that $\underline{I} \le I \le \overline{I}$, together with

$$\frac{\partial \overline{I}}{\partial t} - D_2 \frac{\partial^2 \overline{I}}{\partial x^2} - (D_2'(x) + C_2(x)) \frac{\partial \overline{I}}{\partial x} \ \ge \ C_2'(x)\overline{I} + \lambda S \overline{I} - c\overline{I}, \quad (1.10a)$$

$$\frac{\partial \underline{I}}{\partial t} - D_2 \frac{\partial^2 \underline{I}}{\partial x^2} - (D_2'(x) + C_2(x)) \frac{\partial \underline{I}}{\partial x} \ \le \ C_2'(x)\underline{I} + \lambda S \underline{I} - c\underline{I}, \quad (1.10b)$$

for all continuous functions S on $\overline{D_T}$ such that $\underline{S} \le S \le \overline{S}$.

Let β, γ, N_1, N_2 and k be positive constants satisfying $N_1 > N_2$ and

$$N_2 \ \ge \ \frac{(a-c)+(a-b)}{\lambda \phi_{2\,\min}}, \quad (1.11)$$

$$\beta \ \le \ \lambda N_2 \phi_{2\,\min}, \quad (1.12)$$

$$\gamma \ \ge \ a\frac{1}{r} + \frac{\lambda}{k}\phi_{1\,\max} - c, \quad (1.13)$$

$$k \ \le \ \frac{\lambda \phi_{1\,\min}}{a(a-b)}(\lambda N_2 \phi_{2\,\min} - (a-c) - (a-b)). \quad (1.14)$$

Then the pair $(\overline{S}, \overline{I}) := (p_1(t)\phi_1, q_1(t)\phi_2)$ and $(\underline{S}, \underline{I}) := (p_2(t)\phi_1, q_2(t)\phi_2)$, where $g(t) = (ar-c)t + \frac{a}{\beta}e^{-\beta t}$ and

$$\begin{array}{lll} p_1(t) = \frac{a}{\lambda\phi_{1\,\min}} + \frac{1}{k}\exp(-g(t)), & p_2(t) = \frac{a}{\lambda\phi_{1\,\max}}(1-\exp(-\beta t)), \\ q_1(t) = N_1 \exp(\gamma t), & q_2(t) = N_2\exp(g(t)), \end{array} \quad (1.15)$$

provides a pair of *generalised* upper and lower solutions of (1.1-1.2). Since $(D_i(x)\phi_{ix} + C_i(x)\phi_i)_x = 0$ for $i = 1, 2$, the necessary boundary inequalities defined in Pao (1992) are satisfied. Condition (1.9a) holds provided

$$-\dot{g}(t)\frac{1}{k}e^{-g(t)}\phi_1 \ge (a-b)\left(\frac{a}{\lambda\phi_{1\,\min}} + \frac{1}{k}e^{-g(t)}\right)\phi_1 - \lambda\left(\frac{a}{\lambda\phi_{1\,\min}} + \frac{1}{k}e^{-g(t)}\right)\phi_1 I + aI,$$

for all C^0 functions I with $\underline{I} \le I \le \overline{I}$. This is true if

$$-\dot{g}(t) \ge k(a-b)\frac{a}{\lambda\phi_{1\,\min}}e^{g(t)} - \lambda\underline{I} + (a-b),$$

This is true for all $x \in \Omega$ and $t \in (0, \infty)$ provided (1.11) and (1.14) hold. Condition (1.10a) holds provided $\gamma + c \ge \lambda S$, for all C^0 functions S with $\underline{S} \le S \le \overline{S}$. This inequality is satisfied for all $x \in \Omega$ and $t \in (0, \infty)$ if (1.13) holds.

Condition (1.9b) holds if

$$\beta\frac{a}{\lambda\phi_{1\,\max}}e^{-\beta t}\phi_1 \le (a-b)\frac{a}{\lambda\phi_{1\,\max}}(1-e^{-\beta t})\phi_1 - \lambda\frac{a}{\lambda\phi_{1\,\max}}(1-e^{-\beta t})\phi_1 I + aI,$$

all C^0 functions I with $\underline{I} \le I \le \overline{I}$, which, in turn, is satisfied if

$$\beta\frac{a}{\lambda\phi_{1\,\max}}e^{-\beta t} \le (a-b)\frac{a}{\lambda\phi_{1\,\max}}(1-e^{-\beta t}) + \frac{a}{\phi_{1\,\max}}e^{-\beta t}\underline{I}.$$

This inequality holds provided $\beta \le (a-b)e^{\beta t} - (a-b) + \lambda N_2 e^{g(t)}\phi_2$, which is true if (1.12) holds.

Finally, condition (1.10b) is satisfied if $\dot{g}(t) \le \lambda S - c$, for all C^0 functions S with $\underline{S} \le S \le \overline{S}$. The latter inequality holds in turn provided

$$ar - c - ae^{-\beta t} \le a\frac{\phi_1}{\phi_{1\,\max}} - c - a\frac{\phi_1}{\phi_{1\,\max}}e^{-\beta t},$$

which is true for all $x \in \Omega$ and $t \in (0, \infty)$.

Hence applying the existence–comparison theorem, see Pao (1992, theorem 9.2, p. 436), for continuous initial data (S_0, I_0) such that $S_0 > 0$ and (1.8) holds, given suitable positive constants β, γ, N_1, N_2 and k so that

$$(0, N_2\exp(\frac{a}{\beta})) \le (S_0, I_0) \le \left(\frac{a}{\lambda} + \frac{a}{\beta k}\phi_1, N_1\phi_2\right),$$

equation (1.1-1.2) has a unique solution $(S(x,t), I(x,t)) \in C^0(\overline{D}_T) \times C^0(\overline{D}_T)$ provided $N_1 > N_2$ and (1.11-1.14) hold. The result now follows since $p_1(t) \to a/(\lambda\phi_{1\,\min})$, $p_2(t) \to a/(\lambda\phi_{1\,\max})$ and $q_1(t), q_2(t) \to \infty$ as $t \to \infty$. □

According to proposition 1.1, in the case where the birth rate is larger than both natural and disease induced death rates, the total population will become arbitrarily large. However, the number of susceptibles stays bounded while the infection level grows without bound.

Since the terms representing disease-dynamics in (1.1) do not form a *quasi-monotone* function, in order to prove proposition 1.1 we have constructed a pair of *generalised* upper and lower solutions. The spatially homogeneous extensions of the solutions of the corresponding ODE (equation (1.6)) cannot be used in order to form a comparison function pair for (1.1) as the necessary boundary inequalities as set out in (Pao, 1992) are not satisfied by such a function. Additionally, proposition 1.1 requires the initial data (S_0, I_0) to be sufficiently large, in a suitable sense, and therefore this result does not cover the cases where either S_0 or I_0 has support which is a proper subset of Ω.

It is also worth commenting that the proposition provides the existence of solutions only for continuous initial data, whereas a simple argument using semigroup theory (Henry, 1981) shows that solutions exist with initial data in $L^2(\Omega) \times L^2(\Omega)$.

2. Case III: A Bifurcation Problem

In the final case, we assume that the birth rate is greater than the natural death rate, but less than the disease induced mortality rate, that is $b < a < c$. In order to simplify some of the following, we introduce a change of variables and define functions u and v by

$$S = u\phi_1 \text{ and } I = v\phi_2,$$

where ϕ_i is defined above. After this transformation, (1.4) is seen to be equivalent to the following Neumann boundary value problem

$$\begin{array}{rcll} -\mathcal{L}_1 u &=& (a-b)u\phi_1 - \lambda uv\phi_1\phi_2 + av\phi_2, & x \in \Omega, \\ -\mathcal{L}_2 v &=& \lambda uv\phi_1\phi_2 - cv\phi_2, & x \in \Omega, \\ 0 &=& u_x = v_x, & x \in \partial\Omega, \end{array} \tag{2.1}$$

where $\mathcal{L}_i : C^2(\Omega) \to C^0(\overline{\Omega})$ are the continuous, linear operators defined by

$$\mathcal{L}_i u := (D_i(x)\phi_i u_x)_x, \qquad (i = 1, 2). \tag{2.2}$$

Since $\phi_i(x) \geq \phi_{i\,\min} > 0$ it is clear that each $\mathcal{L}_i$ is uniformly elliptic, it is also self-dual with respect to the usual L^2 dual-pairing between $C^0(\overline{\Omega})$ and $C^2(\Omega)$ as defined in Zeidler (1995). Moreover, each mapping is *Fredholm of index 0*, so that each has a null-space of finite dimension, d say, and a closed range whose codimension equals d.

Remark 1. Throughout the following we shall define the continuous linear operator $\mathcal{L} : C_0^2(\Omega) \to C^0(\overline{\Omega})$ by

$$\mathcal{L}v = \mathcal{L}_2 v - c\phi_2 v.$$

Let us note that if $c \notin \sigma(\mathrm{L}_2)$ then $\mathcal{L}$ has a continuous inverse $\mathcal{L}^{-1} : C^0(\overline{\Omega}) \to C_0^2(\Omega)$ (the latter space incorporating the Neumann boundary conditions).

We also remark that if α is an eigenvalue of the operator L_2 then $\alpha \leq 0$. To see this, consider $L_2 I = \alpha I$ and set $I = v\phi_2$, now test the resulting equation $\alpha v\phi_2 = (D_2 v_x \phi_2)_x$ with v to give

$$\alpha \int_\Omega \phi_2 v^2 dx = -\int_\Omega D_2 \phi_2 v_x^2 dx.$$

In this section we demonstrate the existence of non–negative solutions of (2.1) for $b < a < c$, by seeking secondary bifurcations from the line of solutions $(u, v) = (k, 0)$, where k is any constant. First we define the following spaces

$$X := \{u \in C^2(\Omega) : u_x = 0 \text{ on } \partial\Omega\}, \quad Y := C^0(\overline{\Omega}),$$

and

$$Z := \{u \in L^2(\Omega) : \int_\Omega u(x)dx = 0\} = \langle 1 \rangle^\perp .$$

We shall also make use of the Banach spaces $X_Z := X \cap Z$ and $Y_Z := Y \cap Z$, noting that we may decompose each $u \in X$ into its L^2-orthogonal parts:

$$u = k + \hat{u} \in \langle 1 \rangle \oplus X_Z,$$

where $k \in \mathbb{R}$. Here, we identify $\mathbb{R}$ with the space of constant functions which we denote by $\langle 1 \rangle$. In what follows, we shall also set

$$a = b + \mu,$$

where $\mu \in \mathbb{R}$. Let us now define the restricted operators

$$\hat{\mathcal{L}}_i := \mathcal{L}_i|_{X_Z} : X_Z \to Y_Z, \qquad i = 1, 2, \tag{2.3}$$

which are isomorphisms, with bounded linear inverses $\hat{\mathcal{L}}_i^{-1} : Y_Z \to X_Z$.

Solving (2.1) is then equivalent to the following bifurcation problem, with $(\mu, \hat{u}, v, k) \in \mathbb{R} \times X_Z \times X \times \mathbb{R}$:

$$\begin{array}{rcll} -\hat{\mathcal{L}}_1 \hat{u} &=& \mu(k + \hat{u})\phi_1 - \lambda(k + \hat{u})v\phi_1\phi_2 + (b + \mu)v\phi_2, & x \in \Omega, \\ -\mathcal{L}_2 v &=& \lambda(k + \hat{u})v\phi_1\phi_2 - cv\phi_2, & x \in \Omega, \\ 0 &=& u_x = v_x, & x \in \partial\Omega, \end{array} \tag{2.4}$$

where $k \in \mathbb{R}$ is now the bifurcation parameter. We also define bounded, linear projections $P : L^2 \to Z$ and $Q : L^2 \to \mathbb{R}$ ($\cong \langle 1 \rangle$) by

$$P[n] = n - \int_\Omega n dx \quad \text{and} \quad Q[n] = \int_\Omega n dx.$$

Using these projection mappings, the system (2.4) is then equivalent to

$$\begin{array}{rcll} 0 &=& \mu Q[(k+\hat{u})\phi_1] - \lambda Q[(k+\hat{u})\phi_1 v\phi_2] + (b+\mu)Q[v\phi_2], & x \in \Omega, \\ -\hat{\mathcal{L}}_1 \hat{u} &=& \mu P[(k+\hat{u})\phi_1] - \lambda P[(k+\hat{u})\phi_1 v\phi_2] + (b+\mu)P[v\phi_2], & x \in \Omega, \\ -\mathcal{L}_2 v &=& \lambda(k+\hat{u})\phi_1 v\phi_2 - cv\phi_2, & x \in \Omega, \\ 0 &=& \hat{u}_x = v_x, & x \in \partial\Omega, \end{array} \tag{2.5}$$

which we can write as an analytic map of Banach spaces $F : \mathbb{R} \times X_Z \times X \times \mathbb{R} \to \mathbb{R} \times Y_Z \times Y$, and we denote this

$$F(\mathbf{w}, k) = \mathbf{0}, \tag{2.6}$$

with $\mathbf{w} = (\mu, \hat{u}, v)$, where F is given by

$$F(\mathbf{w}, k) = \begin{pmatrix} \mu Q[(k+\hat{u})\phi_1] - \lambda Q[(k+\hat{u})\phi_1 v\phi_2] + (b+\mu)Q[v\phi_2] \\ \hat{\mathcal{L}}_1 \hat{u} + \mu P[(k+\hat{u})\phi_1] - \lambda P[(k+\hat{u})\phi_1 v\phi_2] + (b+\mu)P[v\phi_2] \\ \mathcal{L}_2 v + \lambda(k+\hat{u})\phi_1 v\phi_2 - cv\phi_2 \end{pmatrix}. \tag{2.7}$$

In order to prove the existence of local bifurcation from the *vertical branch* of solutions to (2.5) at $a = b$, we shall need the following preliminary lemma on the existence of eigenfunctions for an *indefinite* elliptic eigenproblem.

Lemma 2.1. *Let $\Phi, \Psi \in C^1(\Omega)$ be strictly positive functions on $\overline{\Omega}$ and let $L : C^2(\Omega) \to C^0(\overline{\Omega})$ be the operator $Lu = (\Phi(x)u_x)_x$ where Neumann boundary conditions apply on $\partial\Omega$. Now, let $c, \lambda > 0$ and consider the principal Neumann eigenproblem*

$$-Lw = \Phi w(\lambda k \Psi - c), \qquad \int_\Omega w^2 = 1, w > 0, \tag{2.8}$$

where k is the eigenvalue. Then for each $c, \lambda > 0$ there is a unique positive value of k, $k = k^*$, and a unique positive eigenfunction, $w = w^*$, which satisfies (2.8).

Proof. We shall use a proof similar to one used in Affrouzi & Brown (1999). Consider the augmented principle eigenvalue problem

$$-Lw - \Phi w(\lambda k \Psi - c) = \mu w, \qquad \int_\Omega w^2 = 1, w > 0. \tag{2.9}$$

It is clear that if $\mu = \mu_{\lambda,c}(k) = 0$ then we have a solution of (2.8). However, there is the variational characterisation of μ:

$$\mu(k) = \inf\left\{ \int \Phi w_x^2 - \Phi(\lambda k \Psi - c)w^2 dx : w \in H^1(\Omega), \int_\Omega w^2 dx = 1 \right\}.$$

For each fixed $w \in H^1(\Omega)$, it follows that

$$\mu(k) \le \int \Phi w_x^2 - \lambda k \int \Phi \Psi w^2 + c \int \Phi w^2 dx, \tag{2.10}$$

and therefore $\lim_{k\to+\infty}\mu(k) = -\infty$ as $\Phi\Psi > 0$. However, since $k \mapsto \int \Phi w_x^2 - \Phi(\lambda k\Psi - c)w^2dx$ is affine and the infimum over an affine family of functions is a concave function, we see that $\mu(k)$ is concave and therefore continuous. However, it is clear that $\mu(0) \geq 0$ and $\mu(0) = 0$ cannot occur because $c > 0$, whence $\mu(0) > 0$. The intermediate value theorem thus provides the solution k^* and the uniqueness is a consequence of the concavity of μ. □

From this lemma it follows that for each positive c and λ the indefinite-weight eigenproblem

$$-\mathcal{L}_2 v = v\phi_2(\lambda k\phi_1 - c), \tag{2.11}$$

(where k is the eigenvalue and $\phi_2(\lambda k\phi_1 - c)$ is the weight) has a unique positive eigenfunction $v = \nu^*$ with eigenvalue $k = k^*$. This will allow us to demonstrate that the nonlinear elliptic problem (1.3) has a unique branch of positive solutions bifurcating from the vertical solution branch which exists $a = b$. This is essentially done in the following result which shows that there is a solution of (2.5) bifurcating from the line of trivial solutions $(\mu, \hat{u}, v, k) = (0, 0, 0, k)$.

Theorem 2.2. *There exists a neighbourhood $N \subset \mathbb{R}$ containing* 0 *and analytic functions*

$$\hat{u} : N \to X_Z, \qquad v : N \to X \quad \text{and} \quad k : N \to \mathbb{R}$$

with $\hat{u}(0) = 0, v(0) = 0, k(0) = k^*$ which is an analytically parameterised branch of non-trivial solutions of (2.5), bifurcating from $(\hat{u}, v, \mu, k) = (0, 0, 0, k^*)$. Each element $(\mu, \hat{u}(\mu), v(\mu), k(\mu))$ on this branch corresponds to a non-trivial, positive solution $(a - b, u, v) = (\mu, k(\mu) + \hat{u}(\mu), v(\mu)) \in \mathbb{R}_+ \times X_+ \times X_+$ of (2.1).

Proof. It is clear that $(\mu, \hat{u}, v) = (0, 0, 0)$ is a solution of (2.5). Linearising (2.5) around $\mathbf{w} = (\mu, \hat{u}, v) = (0, 0, 0)$ and seeking a simple null–space of the linearised problem, we seek a non-trivial solution to the linear equation

$$d_{\mathbf{w}}F((0, 0, 0), k)(h_1, h_2, h_3)^T = (0, 0, 0)^T,$$

with $(h_1, h_2, h_3) \in \mathbb{R} \times X_Z \times X$. Writing this in full, we need to find a non–trivial solution of

$$0 = h_1 kQ[\phi_1] - \lambda kQ[\phi_1 h_3\phi_2] + bQ[h_3\phi_2], \tag{2.12}$$
$$-\hat{\mathcal{L}}_1 h_2 = h_1 kP[\phi_1] - \lambda kP[\phi_1 h_3\phi_2] + bP[h_3\phi_2], \tag{2.13}$$
$$-\mathcal{L}_2 h_3 = h_3(\lambda k\phi_1\phi_2 - c\phi_2). \tag{2.14}$$

Applying lemma 2.1 to (2.14), it follows that there exists a non-zero solution, h_3, to (2.14) when $k = k^*$ from lemma 2.1.

Integrating (2.14) we obtain $\lambda k^* \int_\Omega \phi_1\phi_2 h_3 dx = c\int_\Omega h_3\phi_2 dx$, which we use in (2.12) in order to obtain $h_1 = (c - b)Q[h_3\phi_2]/(k^*Q[\phi_1])$. Finally, substituting the values of h_1, h_3 and k^* into (2.13) there remains to solve the linear equation

$$-\hat{\mathcal{L}}_1 h_2 = f(x) \tag{2.15}$$

for h_2, where $f(x) = P[h_1 k^*\phi_1 - \lambda k^*\phi_1 h_3\phi_2 + bh_3\phi_2]$. Since $f(x) \in Y_Z$ and $\hat{\mathcal{L}}_1 : X_Z \to Y_Z$ is an isomorphism, there is a non–trivial solution, $h_2 \in X_Z$, to (2.15).

We have thus shown that $d_w F((0,0,0),k^*)$ has a one dimensional null space,

$$\mathrm{N}(d_{\mathbf{w}} F((0,0,0),k^*) = \left\langle (h_1,h_2,h_3)^T \right\rangle,$$

and to conclude the proof we apply the bifurcation from a simple eigenvalue theorem (Ambrosetti & Prodi 1995). Hence, there remains to show that

$$d^2_{k,\mathbf{w}} F((0,0,0),k^*)(h_1,h_2,h_3)^T \notin \mathrm{R}(d_{\mathbf{w}} F((0,0,0),k^*)). \tag{2.16}$$

Suppose, seeking a contradiction, that there exists a $(\mu,\hat{u},v) \in \mathbb{R} \times X_Z \times X$ such that

$$d_{\mathbf{w}} F((0,0,0),k^*)(\mu,\hat{u},v)^T = d^2_{k,\mathbf{w}} F((0,0,0),k^*)(h_1,h_2,h_3)^T,$$

which is the system

$$\begin{aligned} Q[(\lambda k^*\phi_1 - b)\phi_2 v] - \mu k^* Q[\phi_1] &= Q[\lambda\phi_1\phi_2 h_3 - h_1\phi_1], \\ \hat{\mathcal{L}}_1\hat{u} + P[(\lambda k^*\phi_1 - b)\phi_2 v] - \mu k^* P[\phi_1] &= P[\lambda\phi_1\phi_2 h_3 - h_1\phi_1], \\ \mathcal{L}_2 v - (\lambda k^*\phi_1 - c)\phi_2 v &= -\lambda\phi_1\phi_2 h_3. \end{aligned} \tag{2.17}$$

Since the operator $\mathcal{L}_2 : X \to Y$ is self dual with respect to the usual L^2-dual pairing of X and Y, for $v \in X$ to be a solution of (2.17) we require

$$\begin{aligned} -\lambda \int_\Omega \phi_1\phi_2 h_3^2 dx &= \int_\Omega (\mathcal{L}_2 v - (\lambda k^*\phi_1 - c)\phi_2 v) h_3 dx \\ &= \int_\Omega v(\mathcal{L}_2 h_3 - (\lambda k^*\phi_1 - c)\phi_2 h_3) dx = 0 \end{aligned}$$

by definition of h_3. Since $h_3^2\phi_1\phi_2 > 0$ on $\overline{\Omega}$ we have a contradiction and the result follows. □

We now state the main result of this section.

Theorem 2.3. *Fix c and b with $c > b > 0$ and $\lambda > 0$, then there is an $\eta \in (0, c-b)$ and analytic functions $S : (b, b+\eta) \to C^2$ and $I : (b, b+\eta) \to C^2$ such that $(S(a), I(a))$ is a positive solution of (1.3) for each $a \in (b, b+\eta)$. Moreover, taking convergence in the C^2 sense there results*

$$S(a) \to k^*\phi_1 \text{ and } I(a) \to 0$$

as $a \searrow b$ where k^* is an eigenvalue of the eigenproblem (2.11).

(a) *Global analytic bifurcation*

In this section we show that the local bifurcation obtained above gives rise to a global bifurcation and there a several approaches that one could employ. In Stuart (1985) and Davidson (1999) the authors use nodal properties of solutions to show that the linearisation operator, which in our case is $d_{\mathbf{w}} F(\mathbf{w}, k)$, is a bijection for all $\mathbf{w}$ and k. If we were able to prove *hyperbolicity* of $d_{\mathbf{w}} F(\mathbf{w}, k)$ for each $\mathbf{w}$ and k, then the existence of a locally stable, global branch of solutions would follow.

Despite strong numerical evidence that the non-trivial branch of solutions of (1.3) is stable for all $a \in (b, c)$, we have been unable to prove this.

One should like to apply the global results given in Kielhöfer (1984), which is an extension of the results of Krasnoselskii (1964) and Crandall & Rabinowitz (1971), in order to obtain the global existence of non-trivial equilibria. In this reference the author proves the existence of global solution branches in bifurcation problems based on the topological degree for C^2 proper mappings of Fredholm index zero, which includes an arbitrary dependence of the nonlinearity on the parameter; this is not a feature of the work of Crandall *et al.* However, because the formulation of our bifurcation problem (2.5) is somewhat cumbersome and because it is not clear that the results of Kielhöfer (1984) are applicable (because F must be a proper mapping according to Theorem 4.5 of Kielhöfer (1984) and this property is not an obvious one), a cleaner approach to the problem at hand is to use the theory of global bifurcation for analytic mappings developed in Dancer (1973) and Buffoni *et al.* (2001).

Lemma 2.4. *If $\lambda > 0, c > b > 0$ then (1.3-1.4) has solutions with $I(x) > 0$ for all $x \in \overline{\Omega}$ only for $a \in (b, c)$. If $a \in (b, c)$ and (S, I) is a solution of (1.3-1.4) with $I > 0$ then*

$$\|S\|_{L^\infty} \geq \frac{c}{\lambda}.$$

If $a = b$ then non-negative solutions to (1.3) have the form $(S, I) = (k\phi_1, 0)$ for any $k \geq 0$.

Proof. Integrate the first equation in (1.3) over Ω to give $(a-b)\int S + (a-c)\int I = 0$ and the first and last parts follow. Integrating the second equation in (1.3) yields $c\int I dx = \lambda \int SI dx \leq \lambda \|S\|_{L^\infty} \int I dx$. □

We now define $\mathcal{Z} = \mathbb{R} \times X_Z \times X$ and the open set $U \subset \mathcal{Z} \times \mathbb{R}$ by

$$U = \{(\mathbf{w}, k) = (\hat{u}, v, \mu, k) \in \mathcal{Z} \times \mathbb{R} : v > 0,\ \|\phi_1(k + \hat{u})\|_{C^0} > c/(2\lambda),\ 0 < \mu < c - b\}, \tag{2.18}$$

$\Sigma = \{(\mathbf{w}, k) \in U : F(\mathbf{w}, k) = 0\}$ and $\Sigma_R = \{(\mathbf{w}, k) \in U : F(\mathbf{w}, k) = 0, d_{\mathbf{w}}F(\mathbf{w}, k) \in \mathrm{Iso}(X, Y)\}$. Moreover, let C be the maximal, connected subset of Σ which contains the point $(\mathbf{w}, k) = (\mathbf{0}, k^*) := (0, 0, 0, k^*) \in \mathcal{Z} \times \mathbb{R}$ in its closure (in $\mathcal{Z} \times \mathbb{R}$, noting that $(\mathbf{0}, k^*) \notin U$).

We continue with the following preparatory lemma.

Lemma 2.5. *Suppose that $c > b > 0$ then the following hold.*

1. *The mapping $F : \mathbb{R} \times X_Z \times X \times \mathbb{R} \to \mathbb{R} \times Y_Z \times Y$ is an analytic mapping and $d_{\mathbf{w}}F(\mathbf{w}, k) \in BL(X, Y)$ is* Fredholm of index 0 *for each $(\mathbf{w}, k)$.*

2. *The set Σ_R contains a maximal, analytically parameterised curve of solutions $\mathcal{A}$ such that $\overline{\mathcal{A}}$ contains the point $(\mathbf{w}, k) = (\mathbf{0}, k^*) \notin U$.*

3. *Any bounded set in Σ has compact closure (in $\mathcal{Z} \times \mathbb{R}$).*

4. *Suppose that $(\mathbf{w}_n, k_n) \subset \overline{\Sigma_R} \cap U$ is some convergent sequence such that $(\mathbf{w}_n, k_n) \to (\mathbf{w}', k') \notin U$ and $\sup_n(\|\mathbf{w}_n\|_{C^0} + |k_n|) < \infty$, then $(\mathbf{w}', k') = (\mathbf{0}, k^*)$.*

Proof. For the first part it suffices to show (see, for instance, Taylor (1996)) that the linearisation $d_{\mathbf{w}}F(\mathbf{w},k)$ is a compact perturbation of a Fredholm mapping of index 0. To this end, we remark that one can write the given derivative as a multiplicative, and therefore compact perturbation of the operator matrix

$$-\begin{pmatrix} 0 & 0 & 0 \\ 0 & \hat{\mathcal{L}}_1 & 0 \\ 0 & 0 & \mathcal{L}_2 \end{pmatrix} \in BL(\mathbb{R}\times X_Z \times X, \mathbb{R}\times Y_Z \times Y).$$

Since this is Fredholm of index 0 the first part follows.

From theorem 2.3, it follows that Σ_R contains a (locally) analytically parameterised curve of solutions, A say. Now define $\mathcal{A}$ to be the maximal path-connected subset of Σ_R which contains A.

The third part follows from the continuity of the inverse mappings

$$(\hat{\mathcal{L}}_1)^{-1} \in BL(Y_Z, X_Z) \quad \text{and} \quad \mathcal{L}^{-1} \in BL(Y, X),$$

where, we recall, $\mathcal{L}v = \mathcal{L}_2 v - c\phi_2 v$ and the compactness of the embeddings $X_Z \hookrightarrow Y_Z, X \hookrightarrow Y$.

To prove the final part, suppose that $(\mathbf{w}_n, k_n) = (\hat{u}_n, v_n, \mu_n, k_n) \to (\hat{u}', v', \mu', k')$. Since $0 < \mu_n < c-b$ then $0 \le \mu' \le c-b$. If $\mu' = c-b$ then lemma 2.4 is contradicted and if v' is non-positive then the maximum principle is violated, so suppose that $0 < \mu' < c-b$. Since $\|\phi_1(k_n + \hat{u}_n)\|_{C^0} \ge c/\lambda$ from lemma 2.4, it follows that $\|\phi_1(k' + \hat{u}')\|_{C^0} \ge c/\lambda > c/(2\lambda)$ which contradicts the fact that the limit of this sequence is not in U. It follows that we must have $\mu' = 0$, whence $S' = \phi_1(k' + \hat{u}')$ and $I' = \phi_2 v'$ provides a solution of (1.3) with $a = b$. From lemma 2.4 we must have $v' = 0$ and $S' = k'\phi_1$ where k' is to be determined, so that $\hat{u}' = 0$ and therefore k' is a bifurcation point from the trivial branch of solutions to (2.6) into U. However, a necessary condition for this to hold is that $d_{\mathbf{w}}F(\mathbf{0}, k') \in BL(\mathbb{R}\times X_Z \times \mathbb{R}, \mathbb{R}\times Y_Z \times Y)$ has a zero eigenvalue. This in turn implies that (2.14), that is (2.11), has a non-negative eigenfunction at $k = k'$. Since $k = k^*$ is the *unique* eigenvalue of (2.11) corresponding to a non-negative eigenfunction, it follows that $k' = k^*$. □

From Buffoni *et al.* (2001) we obtain the following information.

Theorem 2.6. *The set $C \subset \Sigma$ is unbounded.*

Proof. This follow immediately from theorem 7.3 part (iv) from Buffoni *et al.* (2001, p. 45) where lemma 2.5 verifies hypotheses C1-C8 of this reference, and the functional ν required to verify C6 is given by the norm $\|\mathbf{w}\| + |k|$. □

Corollary 2.7. *The set C contains a* bifurcation at infinity *in $\mathcal{Z}\times\mathbb{R}$ in the sense that there is a sequence $(\mathbf{w}_n, \mu_n) \subset C$ such that $\|\mathbf{w}_n\|_{C^0} \to \infty$ as $n \to \infty$, where $0 < \mu_n < c-b$.*

According to the real-analytic bifurcation theory of Buffoni *et al.* (2001) the continuum C in the statement of theorem 2.6 actually contains an unbounded set which is path-connected (see theorems 7.3 and 7.4 of Buffoni *et al.* (2001)); this is a stronger conclusion than the global results to be found in Kielhöfer (1984) which, if applicable, could only assert that C is unbounded. Furthermore, with regard to the asymptotic properties of C we would like to be able to demonstrate that the bifurcation at infinity in corollary 2.7 occurs in such a way that the sequence μ_n satisfies $\mu_n \nearrow c - b$ as $n \to \infty$. While numerical experiments given later in the paper indicate this to be the case, we have been unable to prove this in general.

Remark 2. *One can extend all of the above results to the case $d \geq 2$ with Ω a domain in $\mathbb{R}^d$ by replacing the C^k-spaces in the statement of each result with its corresponding Hölder space, $C^{k,\alpha}$ with $0 < \alpha < 1$. The only additional assumption required is that $\partial\Omega$ is a $C^{2,\alpha}$, codimension-1, orientable submanifold of $\mathbb{R}^d$. In this case, the functions ϕ_1 and ϕ_2 are the principal eigenfunctions of the operators $-L_1$ and $-L_2$.*

3. Matched Asymptotics of the Global Branch

In the previous section we demonstrated the existence of a vertical branch of solutions to (1.3) bifurcating from the trivial branch at the bifurcation point $a = b$. In addition, we have shown for $b < a < c$ that there exists a secondary global branch of non–trivial solutions of (1.3) emanating from the vertical branch $(S, I) = (k\phi_1, 0)$ at the bifurcation point $k = k^*$. In this section we obtain formal asymptotic properties of the solutions on the global branch C for values of a near c. To this end, we rewrite (1.3-1.4) by employing the following rescaling

$$S = \frac{c}{\lambda}\tilde{S} \quad \text{and} \quad I = \frac{c(a-b)}{\lambda(c-a)}\tilde{I},$$

set $c - a = \epsilon$ and then remove the tildes for clarity. The system (1.3-1.4) can then be written as the singularly perturbed boundary-value problem

$$\begin{aligned} -\epsilon L_1 S &= (c - b - \epsilon)(\epsilon S + cI - \epsilon I - cSI), \\ -L_2 I &= cI(S-1), \qquad\qquad\qquad\qquad x \in \Omega, \\ 0 &= D_1(x)S_x + C_1(x)S = D_2(x)I_x + C_2(x)I, \qquad x \in \partial\Omega. \end{aligned} \tag{3.1}$$

We assume that $0 < \epsilon \ll 1$ and analyse the solutions of (3.1) in the $a \to c$ limit, that is $\epsilon \to 0$. We use well-known singular perturbation theory (Murray 1984) to obtain an approximation to the true solution of (3.1) valid for small ϵ.

(i) *Outer solution*

Let us begin by seeking a solution of (3.1) in the form

$$S_{\text{out}} = S_0 + \epsilon S_1 + O(\epsilon^2) \text{ and } I = I_0 + \epsilon I_1 + O(\epsilon^2). \tag{3.2}$$

Substituting these expressions into (3.1) and equating the coefficients of powers of ϵ we obtain the following at $O(1)$:

$$0 = c(c-b)I_0(1 - S_0), \qquad x \in \Omega, \tag{3.3}$$

$$-L_2 I_0 = cI_0(S_0 - 1), \qquad x \in \Omega, \tag{3.4}$$

together with boundary conditions

$$D_1(x)S_{0x} + C_1(x)S_0 = 0, \qquad x \in \partial\Omega, \tag{3.5}$$

$$D_2(x)I_{0x} + C_2(x)I_0 = 0, \qquad x \in \partial\Omega. \tag{3.6}$$

It is easy to see that we must take $S_0 = 1$ and $I_0 = B\phi_2(x)$, where B is a constant to be determined and $\phi_2(x)$ is defined above. The function I_0 clearly satisfies the necessary boundary conditions (3.6) although S_0 satisfies (3.4) but not the boundary conditions. Thus we anticipate that for small ϵ, the S component of the solution of (3.1) will undergo a rapid change in value in a small neighbourhood of the boundary of Ω.

Before proceeding, we determine the constant B by equating coefficients at $O(\epsilon)$:

$$\begin{aligned} -L_1 S_0 &= (c-b)S_0 + c(1-S_0)((c-b)I_1 - 1) - (c-b)I_0(1+cS_1), \\ -L_2 I_1 &= c(S_0 I_1 + S_1 I_0) - cI_1, \end{aligned}$$

which yields

$$-C_1'(x) = (c-b) - (c-b)B\phi_2(1+cS_1), \tag{3.7}$$

$$-L_2 I_1 = cB\phi_2 S_1. \tag{3.8}$$

From (3.7) we calculate

$$S_1 = \frac{C_1'(x) + (c-b)(1-B\phi_2)}{c(c-b)B\phi_2}, \tag{3.9}$$

and hence

$$S_{\text{out}} = 1 + \epsilon\frac{C_1'(x) + (c-b)(1-B\phi_2)}{c(c-b)B\phi_2} + O(\epsilon^2).$$

Substituting (3.9) into (3.7) we have

$$-L_2 I_1 = \frac{C_1'(x)}{(c-b)} + 1 - B\phi_2 \;\; =: f(x), \tag{3.10}$$

from where, using a solvability condition of Fredholm-type gives

$$\int_\Omega \phi_2 \left(\frac{C_1'(x)}{(c-b)} + 1 - B\phi_2 \right) dx = 0.$$

To see this, note that a solution to (3.10) can be obtained by writing $I_1 = w\phi_2$ and solving $-\mathcal{L}_2 w = f(x)$. But this requires $\int \phi_2(x) f(x) dx = 0$ as $\mathcal{L}_2$ is self-dual and ϕ_2 spans the null-space of this operator. We may therefore conclude that

$$B = \frac{1}{(c-b)} \frac{\int_\Omega \phi_2 (C_1'(x) + 1) dx}{\int_\Omega \phi_2^2 dx} \tag{3.11}$$

and

$$I(x) = B\phi_2(x) + O(\epsilon), \tag{3.12}$$

with B defined above, is a valid asymptotic expression for the I component of the solution of (3.1).

(ii) *Inner solutions*

Next we construct inner solutions of the S component of the solution of (3.1) which are valid close to the boundaries of Ω at $x=0$ and $x=1$.

Consider first the boundary at $x=0$. Let us define the variable

$$y=\frac{x}{\epsilon^{\alpha}}, \qquad \alpha>0,$$

which stretches out the immediate neighbourhood of $x=0$. It follows that in the small region close to $x=0$, the behaviour of the S component of solutions of (3.1) can be investigated by studying solutions of the following problem

$$\begin{aligned} -\epsilon^{1-2\alpha}D_1S_{yy}-\epsilon^{1-\alpha}(C_1(\epsilon^{\alpha}y)S)_y &= (c-b-\epsilon)(\epsilon S+I(c-\epsilon-cS)), \quad y>0,\\ 0 &= \epsilon^{-\alpha}D_1(\epsilon^{\alpha}y)S_y+C_1(\epsilon^{\alpha}y)S, \qquad y=0. \end{aligned}$$

Using a standard procedure (Murray 1984), we choose $\alpha=\frac{1}{2}$ which gives

$$\begin{aligned} -D_1S_{yy}-\epsilon^{\frac{1}{2}}(C_1S)_y &= (c-b-\epsilon)(\epsilon S+I(c-\epsilon-cS)), \quad y>0,\\ 0 &= D_1S_y+\epsilon^{\frac{1}{2}}C_1S, \qquad y=0. \end{aligned} \tag{3.13}$$

Note that $C_1(x)$ and $I(x)$ are known functions of x and, in terms of the new coordinate, we have $D_1\equiv D_1(\epsilon^{1/2}y), C_1\equiv C_1(\epsilon^{1/2}y)$ and $I\equiv I(\epsilon^{1/2}y)$. Next we set the inner solution at the boundary $x=0$ to be of the form

$$S^0_{\text{in}}=S^0_0+\epsilon^{1/2}S^0_1+o(\epsilon^{1/2}).$$

Substituting into (3.13) we equate the terms of the same power, expressing the functions $D_1(\epsilon^{1/2}y), C_1(\epsilon^{1/2}y)$ and $I(\epsilon^{1/2}y)$ using Taylor's theorem as

$$D_1(\epsilon^{1/2}y)=D_1(0)+\epsilon^{1/2}yD_1'(0)+o(\epsilon^{1/2}), C_1(\epsilon^{1/2}y)=C_1(0)+\epsilon^{1/2}yC_1'(0)+o(\epsilon^{1/2}),$$

and $I(\epsilon^{1/2}y)=B(\phi_2(0)+\epsilon^{1/2}y\phi_2'(0)+o(\epsilon^{1/2}))$.

Equating terms at order $O(1)$ we have

$$-D_1(0)S^0_{0yy}=c(c-b)B(1-S^0_0), \qquad y\in(0,\infty). \tag{3.14}$$

Clearly $S^0_0=1$ solves (3.14) and also satisfies the $O(1)$ boundary condition $S^0_{0y}=0$ at $y=0$. Equating terms of order $O(\epsilon^{1/2})$ we have

$$D_1S^0_{1yy}=c(c-b)BS^0_1, \qquad y\in(0,\infty), \tag{3.15}$$

together with the boundary condition

$$D_1(0)S^0_{1y}+C_1(0)S^0_0=0, \qquad y=0. \tag{3.16}$$

The general solution of (3.15) is of the form

$$S^0_1=Q_1e^{y\sqrt{p}}+Q_2e^{-y\sqrt{p}},$$

where

$$p=\frac{c(c-b)B}{D_1(0)}, \tag{3.17}$$

while Q_1 and Q_2 are constants to be determined. We now perform the matching procedure which, together with boundary conditions (3.16), will determine Q_1 and Q_2. Let

$$\eta = \frac{x}{\gamma(\epsilon)}$$

be considered fixed, where γ is some function such that $\gamma(\epsilon) \to 0$ and $\gamma(\epsilon)\epsilon^{-1/2} \to \infty$ as $\epsilon \to 0$. We now use the matching conditions (Murray 1984)

$$\lim_{\epsilon \to 0} S^0_{\text{in}} \left(\frac{\eta\gamma(\epsilon)}{\epsilon^{1/2}} \right) = \lim_{\epsilon \to 0} S_{\text{out}}(\eta\gamma(\epsilon)),$$

which gives $Q_1 = 0$. Then in order for $S^0_1 = Q_2 e^{-y\sqrt{p}}$ to satisfy (3.16) we need

$$Q_2 = \frac{C_1(0)}{\sqrt{Bc(c-b)D_1(0)}}. \tag{3.18}$$

We conclude that

$$S^0_{\text{in}} = 1 + \epsilon^{1/2} Q_2 e^{-y\sqrt{p}} + o(\epsilon^{1/2})$$

where Q_2 and p are defined in (3.18) and (3.17).

Next we consider the boundary at $x = 1$. Let us define the variable z by

$$z = \frac{1-x}{\epsilon^{1/2}},$$

which stretches the region around $x = 1$. It follows that in the small region close to $x = 1$, the behaviour of the S component of solutions to (3.1) can be investigated by studying solutions of the following problem

$$\begin{aligned} -D_1 S_{zz} + \epsilon^{1/2}(C_1 S)_z &= (c-b-\epsilon)(\epsilon S + I(c-\epsilon-cS)), \quad z > 0, \\ 0 &= D_1 S_z - \epsilon^{1/2} C_1 S, \quad z = 0. \end{aligned} \tag{3.19}$$

Now $D_1(x), C_1(x)$ and $I(x)$, in terms of new coordinate, become $D_1 \equiv D_1(1 - \epsilon^{1/2}z), C_1 \equiv C_1(1-\epsilon^{1/2}z)$ and $I \equiv I(1-\epsilon^{1/2}z)$. We set the inner solution at the boundary $x = 1$ to be of the form

$$S^1_{\text{in}} = S^1_0 + \epsilon^{1/2} S^1_1 + o(\epsilon^{1/2}),$$

and substituting into (3.19) we equate the terms of the same order expressing $D_1(1-\epsilon^{1/2}z), C_1(1-\epsilon^{1/2}z)$ and $I(1-\epsilon^{1/2}z)$, using Taylor's theorem, as $D_1(1-\epsilon^{1/2}z) = D_1(1) - \epsilon^{1/2} z D_1'(1) + o(\epsilon^{1/2}), C_1(1-\epsilon^{1/2}z) = C_1(1) - \epsilon^{1/2} z C_1'(1) + o(\epsilon^{1/2})$ and $I(1-\epsilon^{1/2}z) = B(\phi_2(1) - \epsilon^{1/2} z \phi_2'(1) + o(\epsilon^{1/2}))$. Starting with the lowest order terms at $O(1)$, we have

$$-D_1(1) S^1_{0zz} = c(c-b)B\phi_2(1)(1 - S^1_0), \ z > 0. \tag{3.20}$$

Clearly $S^1_0 = 1$ solves (3.20) and also satisfies the boundary conditions $S^1_{0z} = 0$ at $z = 0$.

Equating terms of order $O(\epsilon^{1/2})$ we have

$$D_1(1) S^1_{1zz} = c(c-b)B\phi_2(1) S^1_1, \ z > 0, \tag{3.21}$$

together with the boundary conditions

$$D_1(1)S^1_{1z} - C_1(1)S^1_0 = 0, \quad z = 0. \tag{3.22}$$

The solution of (3.21) is of the form

$$S^1_1 = R_1 e^{z\sqrt{q}} + R_2 e^{-z\sqrt{q}},$$

where $q = \frac{c(c-b)B\phi_2(1)}{D_1}$ where R_1 and R_2 are constants to be determined.

Performing again the matching procedure, let

$$\mu = \frac{1-x}{\gamma(\epsilon)},$$

for some function γ defined as in the case of the left boundary. Again, the matching condition

$$\lim_{\epsilon\to 0} S^1_{\text{in}}\left(\frac{\mu\gamma(\epsilon)}{\epsilon^{1/2}}\right) = \lim_{\epsilon\to 0} S_{\text{out}}(1-\mu\gamma(\epsilon)),$$

gives $R_1 = 0$. In order for $S^1_1 = R_2 e^{-z\sqrt{q}}$ to satisfy (3.22), we require

$$R_2 = -\frac{C_1(1)}{\sqrt{Bc(c-b)D_1(1)\phi_2(1)}}. \tag{3.23}$$

We have obtained

$$S^1_{\text{in}} = 1 + \epsilon^{1/2} R_2 e^{-z\sqrt{q}} + o(\epsilon^{1/2}),$$

where R_2 is defined above. Having calculated the outer and inner solutions for S we can obtain a uniformly valid asymptotic solution. Adding the inner solutions at each boundary to the outer solution and subtracting the intermediate form which is included twice, we obtain

$$S_{\text{unif}}(x) = S_{\text{out}}(x) + S^0_{\text{in}}\left(\frac{x}{\epsilon^{1/2}}\right) + S^1_{\text{in}}\left(\frac{1-x}{\epsilon^{1/2}}\right) - 2 + o(\epsilon^{1/2}),$$

so that

$$S_{\text{unif}}(x) = 1 + \epsilon^{1/2} Q_2 e^{-\frac{x}{\epsilon^{1/2}}\sqrt{p}} + \epsilon^{1/2} R_2 e^{-\frac{1-x}{\epsilon^{1/2}}\sqrt{q}} + o(\epsilon^{1/2}), \tag{3.24}$$

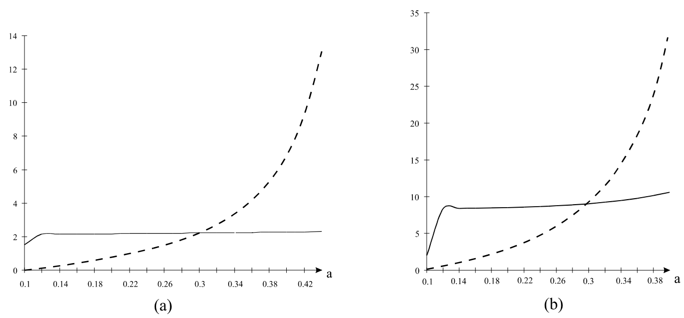
with Q_1 and R_1 defined in (3.18) and (3.23) respectively, while the uniformly valid expansion for I is given by (3.12). We can now obtain a uniformly valid asymptotic expression for the solution of (1.3)

$$\begin{aligned} S(x) &= \frac{c}{\lambda} + \frac{c(c-a)^{1/2}}{\lambda}\Big(Q_2 e^{-\frac{x}{(c-a)^{1/2}}\sqrt{p}} + \\ &\qquad R_2 e^{-\frac{1-x}{(c-a)^{1/2}}\sqrt{q}}\Big) + o((c-a)^{1/2}), \end{aligned} \tag{3.25}$$

$$I(x) = \frac{c(a-b)}{\lambda(c-a)}\frac{\int_\Omega \phi_2(C_1'(x)+1)dx}{(c-b)\int_\Omega \phi_2^2 dx}\phi_2(x) + o((c-a)^{-1}), \tag{3.26}$$

for $x \in \Omega$.

Figure 2. Population levels of susceptible (—) and infected (– – –) groups at steady state. Birth parameter a on horizontal axis and supremum-norm on vertical axis for (a) dumb form (b) furious form.



4. Discussion

In this section we illustrate the findings from the previous sections by simulating the solution of (1.1-1.2) for $b < a < c$, using the NAG library routine D03PCF on the spatial domain $x \in [0, 5]$. Throughout we take D_1 and D_2 to be constants and

$$C_i(x) = C_i \tanh(x - x_D), \qquad (i = 1, 2),$$

where C_i are constants and x_D is the location of the focal point, situated in the centre of the domain $[0, 5]$. Activity around the focal point is represented by the strength of the convection and diffusion coefficients and we assume that only the healthy individuals are involved in the upbringing of offspring. In simulating the behaviour of infected individuals we concentrate on the two extreme forms of disease: *furious* and *dumb*. In each of these two cases we take the following the parameter values $b = 1/10, c = 1/2, \lambda = 1/5$ with $b < a < c$ and

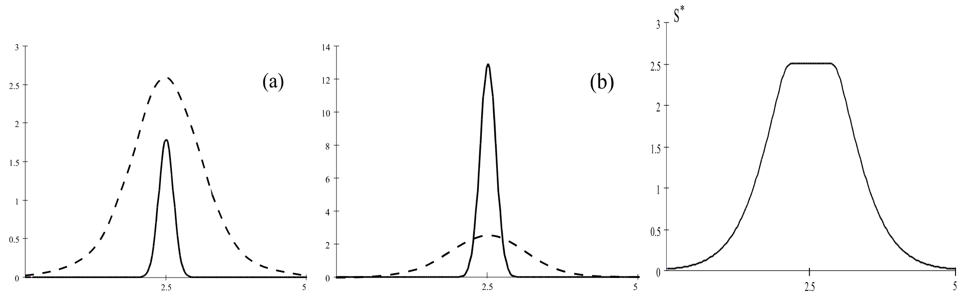
1. dumb: $D_1 = 1, D_2 = 1/20, C_1 = C_2 = 3$
2. furious: $D_1 = 1, D_2 = 4, C_1 = 3, C_2 = 1/100.$

In both cases, we have assumed that the focal point is at the active stage. Susceptible individuals have a strong convective movement which simulates movement to feed offspring but also disperse across the domain to forage.

We are interested in how different disease strains influence the spatial structure of the steady state and its population levels. Let us remark that from an intuitive point of view, the level of infection will increase at a given location provided that the susceptible population is above the threshold level $\frac{c}{\lambda}$ at that point. Therefore we can expect that susceptible individuals will be able to coexist with the disease provided that its levels are at, or below this threshold level in the regions containing infected individuals. We now explore this intuition numerically for different disease strains.

Figure 2 is the bifurcation diagram for (1.3-1.4) in both furious and dumb cases and it illustrates the asymptotic divergence when a nears the mortality rate of infected individuals c. In this diagram the total number of infected individuals at

Figure 3. Steady state solutions for the dumb form of the disease at (a) $a = 15/100$ and (b) $a = 4/10$; S is full line and I broken line. (far-right) S component of the steady state for dumb form of disease at $a = 5 - (0.1)^9$



the steady state increases like $O((c-a)^{-1})$, whereas the total number of susceptibles at steady state is seen to increase much more slowly and asymptotic estimates indicate that this number is bounded.

If we consider the dumb form of disease, then when the value of the birth parameter, a, is close to the natural death rate of susceptible individuals, b, the susceptible levels at steady state are necessarily higher than the infected population levels (see Figure 3(a)). As the birth rate increases (see Figure 3(b)) the total number of infected individuals at steady state eventually becomes larger than the total number of the susceptible individuals. The susceptible population stays at or below the threshold level in those areas where contact with infected individuals is highest, and since the infected individuals suffer from the dumb form of the disease, the highest number of them is situated around the focal point. Therefore the density of the susceptible population is reduced to the threshold level around the focal point, and this is $c/\lambda = 2.5$ (see Figure 3 (c)).

Figure 4 shows the change of steady state solutions for the furious form of the disease as the birth parameter a changes. As in the dumb case, if the value of a is close to the natural death rate of susceptible individuals, the susceptible and infected populations coexist at the steady state level with lower numbers of infecteds than susceptibles. Again, for a near c, the total number of susceptibles is lower than the number of infecteds (see Figure 2(b)). Due to the movement assumptions regarding the furious strain, for a near c the population density of infected individuals at the coexistence steady state is at a very high level and is almost uniformly distributed across the domain (see Figure 4(b)). Moreover, the density of the susceptible population is also uniformly distributed throughout the domain at the threshold value (see Figure 4(a)).

(a) *A further* dumb case

Figure 5 presents some steady state solutions of (1.1-1.2) for various values of birth parameter a, with different movement parameters of susceptible individuals from the two cases above. This could relate to the stage where the activity around the focal point begins to slow down with the offspring reaching adulthood and needing less attention. As a increases, an interesting feature is the spatial structure of the susceptible population. The case when a nears b differs greatly from the

Figure 4. Change of steady state solutions for (a) S and (b) I with respect to the birth parameter a; movement parameter values are $D_1 = 1$, $D_2 = 4$, $C_1 = 3$, $C_2 = 1/100$.

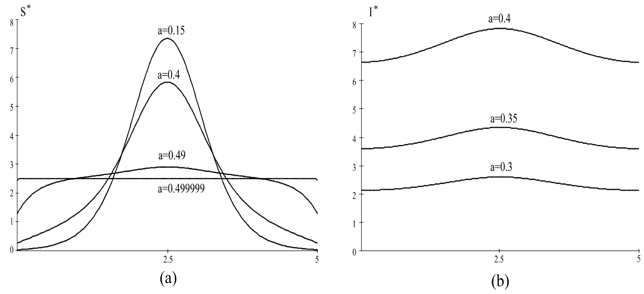
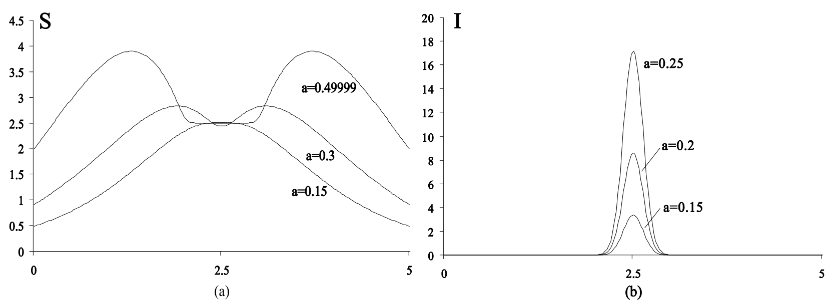


Figure 5. Change of steady state solutions (a) S and (b) I with respect to the birth parameter a; movement parameters are $D_1 = 1/2, D_2 = 1/20, C_1 = 1/2, C_2 = 3$.



case when a is close to c. In the first instance, the susceptible population follows a unimodal distribution with the highest number of individuals situated around the focal point. In the latter case, the structure of the steady state becomes bimodal with two local maxima situated symmetrically about the focal point.

The bi-modal nature of the steady-state in figure 5 is due to the following factors. When a is near c, there is a high concentration of infectivity around the den, so that any susceptible individual there will soon become infected. This follows from the asymptotic form for the infective class at steady-state in equation (3.26). This, in combination with a sufficiently small ratio C_1/D_1 ensures that there is sufficient movement of susceptibles away from the focal point to allow them to flourish in those regions where infection is effectively absent. One can compare this with the far-right diagram in figure 3 where convection to the den is too strong relative to movement via diffusion to allow susceptible individuals to escape the region where infecteds are concentrated.

Finally, we remark that the numerical simulations indicate that the coexistence steady state, whose existence is demonstrated in section 2, is globally attractive when $b < a < c$. In addition, when we used a fine spatial discretisation with a collocation method in *Content* (see Kuznetsov *et al.* (1996)) to continue the branch of steady-states, the software did not report any secondary bifurcations for the movement parameters that we chose.

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