

Diffusive logistic equations with indefinite weights: population models in disrupted environments

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Synopsis

The dynamics of a population inhabiting a strongly heterogeneous environment are modelled by diffusive logistic equations of the form $u_t = d \Delta u + [m(x) - cu]u$ in $\Omega \times (0, \infty)$, where u represents the population density, $c, d > 0$ are constants describing the limiting effects of crowding and the diffusion rate of the population, respectively, and $m(x)$ describes the local growth rate of the population. If the environment Ω is bounded and is surrounded by uninhabitable regions, then $u = 0$ on $\partial\Omega \times (0, \infty)$. The growth rate $m(x)$ is positive on favourable habitats and negative on unfavourable ones. The object of the analysis is to determine how the spatial arrangement of favourable and unfavourable habitats affects the population being modelled. The models are shown to possess a unique, stable, positive steady state (implying persistence for the population) provided $1/d > \lambda_1^+(m)$, where $\lambda_1^+(m)$ is the principle positive eigenvalue for the problem $-\Delta\phi = \lambda m(x)\phi$ in Ω , $\phi = 0$ on $\partial\Omega$. Analysis of how $\lambda_1^+(m)$ depends on m indicates that environments with favourable and unfavourable habitats closely intermingled are worse for the population than those containing large regions of uniformly favourable habitat. In the limit as the diffusion rate $d \downarrow 0$, the solutions tend toward the positive part of $m(x)/c$, and if m is discontinuous develop interior transition layers. The analysis uses bifurcation and continuation methods, the variational characterisation of eigenvalues, upper and lower solution techniques, and singular perturbation theory.

1. Introduction

The subject of our investigation is a class of diffusive logistic equations which model population dynamics in environments with strong spatial heterogeneity. We represent that spatial heterogeneity by taking the coefficient describing the intrinsic rate of growth in the population at low densities to be positive in some regions and negative in others. The object of our investigation is to determine how variations in the spatial distribution of these favourable and unfavourable habitats affect the predictions of the model. We are especially interested in comparing situations where the total sizes of the favourable and unfavourable regions are fixed but the spatial arrangement of those regions is allowed to vary. The fundamental biological question that we address, and partially answer, is: which arrangements are best for the population, and which are worst? We also provide a framework for the analysis of related problems arising in conservation and pest control. Our approach is to observe that whether a model predicts persistence or extinction for the population it describes is determined by the nature of its steady states, and then to analyse those steady states.

To perform the basic qualitative analysis, we use methods from multiparameter bifurcation theory, singular perturbation theory, and partial differential equations. As is frequently the case, we find that the heart of the problem lies in questions of linear spectral theory. It turns out that most of the quantitative and

many of the qualitative aspects of the analysis depend crucially on the size of the first positive eigenvalue for a linear elliptic problem with a sign indefinite weight. Therefore our efforts have largely been devoted to understanding how the distribution of regions of positivity and negativity for the weight function affects that eigenvalue, and most of our new theoretical results deal with such questions. Our analysis shows that the models we consider predict persistence for a population if its diffusion rate is below a certain critical value depending on the coefficient describing the growth rate, and extinction if the diffusion rate is above that value. The way that the critical value depends on the growth rate coefficient seems to be rather subtle and complicated; but roughly, the critical value will tend to be smaller in situations where favourable and unfavourable habitats are closely intermingled, and larger when the favourable region consists of a relatively small number of relatively large isolated components.

The models we analyse most completely are of the form

$$\begin{aligned} u_t &= d \Delta u + [m(x) - cu]u && \text{in } \Omega \times (0, \infty), \\ u(x, 0) &= u_0(x) \geq 0 && \text{for } x \in \Omega, \\ u(x, t) &= 0 && \text{on } \partial\Omega \times (0, \infty), \end{aligned} \tag{1.1}$$

where $\Omega \subseteq \mathbf{R}^n$ is a bounded domain, c and d are positive constants, and $m(x) \in L^\infty(\Omega)$ is positive on a set of positive measure, but generally not on all of Ω . We discuss our motivation and some of the modelling process leading to (1.1) later, but the basic interpretation of the various terms in (1.1) is that u represents the population density of a species inhabiting a region Ω which is surrounded by a completely inhospitable region where the population density is zero. The members of the population are assumed to move about Ω via a "random walk" process, which is modelled by the diffusive term $d \Delta$; here d represents the diffusion rate, so for larger values of d the population spreads more rapidly than for smaller values of d . The local rate of change in the population density is described by the density dependent term $m(x) - cu$. In this term, $m(x)$ describes the rate at which the population would grow or decline at the location x in the absence of crowding or limitations on the availability of resources. The sign of $m(x)$ will be positive on favourable habitats and negative on unfavourable ones. The term $-cu$ describes the effects of crowding on the growth rate of the population; these effects are assumed to be independent of those determining the growth rate at low densities. The size of the constant c describes the strength of the crowding effects. Many of our results are still valid for somewhat more general nonlinearities which behave qualitatively like $[m(x) - cu]u$. We describe the appropriate class of nonlinearities at the end of Section 2.

In some cases a more realistic assumption about the region Ω would be that it is surrounded by a region that is unable to sustain a population but which is not so inhospitable that the population density outside Ω is driven to zero immediately. That modelling assumption would lead to boundary conditions of the third or Robin type, namely $\gamma u + \partial u / \partial n = 0$ on $\partial\Omega$, where $\gamma > 0$ is a constant and $\partial u / \partial n$ is the outer normal derivative of u ; see, for example, [3]. We do not consider that case here for several reasons. Firstly, we are primarily interested in the effects of variations of the habitat inside Ω rather than boundary effects, and

we expect that any type of dissipative boundary conditions should give qualitatively similar results. Secondly, our choice of Dirichlet boundary conditions allows us to use various known mathematical techniques rather than spending time on technicalities which are really tangential to the main thrust of our work. We shall consider the question of more general boundary conditions elsewhere.

To study (1.1), we show that it admits a unique positive steady state which is a global attractor for nonnegative nontrivial solutions, provided that d is sufficiently small, so that the population persists, and that the solution $u \equiv 0$ is a global attractor for nonnegative solutions if d is large, so that the population tends to extinction. The steady state problem

$$\begin{aligned} -d \Delta u &= m(x)u - cu^2 \text{ in } \Omega, \\ u &= 0 \text{ on } \partial\Omega \end{aligned} \tag{1.2}$$

may be considered from the viewpoint of bifurcation theory with respect to one or more parameters; we use the single parameter d and the pair $(d, m(x))$ and apply results of Rabinowitz [40] and Alexander and Antman [1], respectively, to analyse the parameter dependence of (1.2). We find (among other things) that (1.2) has a unique positive solution which is an attractor for nonnegative, nontrivial solutions of (1.1) provided that $d < 1/\lambda_1^+(m)$, and no positive solutions if $d > 1/\lambda_1^+(m)$, where $\lambda_1^+(m)$ is the smallest positive eigenvalue for the problem

$$\begin{aligned} -\Delta \phi &= \lambda m(x)\phi \text{ in } \Omega, \\ \phi &= 0 \text{ on } \partial\Omega. \end{aligned} \tag{1.3}$$

That the problem (1.3) has such an eigenvalue even though $m(x)$ may change sign in Ω follows from results of Manes and Micheletti [36], among others. Eigenvalue problems with indefinite weights have been widely studied; see [4, 6, 9, 13, 16, 17, 21, 30, 32, 36, 39]. However, the results are mostly either qualitative in nature or not sharp enough for our purposes, so we have devoted most of our analytic efforts to deciding how variations in $m(x)$ affect $\lambda_1^+(m)$.

Our main results regarding the dependence of $\lambda_1^+(m)$ on m are given in Section 3. In addition to their relevance in the present applied setting, they are also of some independent mathematical interest. The fundamental result is Theorem 3.1. It allows us to distinguish classes of growth rates $m(x)$ within which any given species can be driven to extinction by an appropriate choice of m from those classes for which any species with a sufficiently low diffusion rate will persist, independently of how m is chosen within the class. The theorem states that for a sequence of weights $\{m_j(x)\}$ to have a sequence of smallest positive eigenvalues $\{\lambda_1^+(m_j)\}$ with $\lim_{j \rightarrow \infty} \lambda_1^+(m_j) = \infty$, it is necessary and sufficient that $\limsup_{j \rightarrow \infty} \int_{\Omega} m_j \psi \leq 0$ for all $\psi \in L^1(\Omega)$ with $\psi \geq 0$ almost everywhere. If we apply the result with $\psi \equiv 1$, it follows that if a class \mathcal{M} of weights satisfies $\int_{\Omega} m \geq m_0 > 0$ for all m in the class, then the set of associated principal eigenvalues $\{\lambda_1^+(m)\}$ is bounded. Thus, if m is constrained to lie in such a class and if $d < 1/\sup\{\lambda(m) : m \in \mathcal{M}\}$, then no matter how $m \in \mathcal{M}$ is chosen, (1.1) admits a globally attracting positive steady state and hence implies persistence for the population it models. In addition to Theorem 3.1, we obtain some fairly sharp estimates for $\lambda_1^+(m)$, especially in the case of one space dimension. In Theorem 3.5 we show that if

$\Omega = (0, \pi)$, $E \subseteq \Omega$ is measurable with $|E| > |\Omega \setminus E|$, and $m = \chi_E - \chi_{\Omega \setminus E}$, then we have

$$\lambda_1^+(\chi_E - \chi_{\Omega \setminus E}) \leq \pi^2/[|E| - |\Omega \setminus E|]^2.$$

Theorem 3.6 gives some new lower bounds for $\lambda(m)$, which imply that for $\Omega = (0, \pi)$ we have $\lambda_1^+(\sin(jx)) \rightarrow \infty$ with order j as $j \rightarrow \infty$. In principle, it should be possible to extract such information from the estimates of Gossez and Lami Dozo [21], but applying the methods of [21] in practice seems to present some difficulties. Finally, we show in Theorem 3.9 that if we restrict m to a class $\mathcal{M} = \{m \in L^\infty(\Omega) : \int_\Omega m = m_0 \text{ and } -m_1 \leq m(x) \leq m_2\}$, where m_0, m_1 , and m_2 are positive constants, then there exists a weight $\bar{m} = m_2\chi_E - m_1\chi_{\Omega \setminus E}$ for some subset $E \subseteq \Omega$ such that $\bar{m} \in \mathcal{M}$ and $\lambda_1^+(\bar{m}) = \inf \{\lambda_1^+(m) : m \in \mathcal{M}\}$. If we view m as control for $\lambda_1^+(m)$, we may interpret the result as saying that there exists an optimal control for minimising $\lambda_1^+(m)$ and that the control may be assumed to be of “bang-bang” type.

In Section 4 we obtain various bounds and asymptotic results for solutions to (1.2) and (1.1). We give a bound on the L^1 norm for a solution of (1.2) when $d < 1/\lambda_1^+(m)$; since the solution represents a population density, the L^1 norm measures the total size of the population. We then use some results from singular perturbation theory, especially as treated by DeSanti [14] to give some fairly mild conditions under which the positive solution to (1.2) tends toward m_+ , the positive part of m , as $d \downarrow 0$. If m is the difference of two characteristic functions, this produces interior transition layers. We also estimate the rate of decline toward extinction of a population modelled by (1.1) when $d > 1/\lambda_1^+(m)$.

We now return to the biological considerations which underlie the model given by (1.1) and which follow from the model's predictions. Our interest in models such as (1.1) is motivated by two types of ecological questions, each of which is in a sense the converse of the other. The first can be called the “roach-proofing” problem: suppose that we wish to exterminate some pest population, but only have enough pesticide to treat some fraction of the infested region. How should the pesticide be distributed over the region to have the greatest negative impact on the pest population? Conversely, if some desirable species inhabits a region in which the environment is being polluted or destroyed and we can only preserve part of the environment as a refuge, how should the refuge be arranged geographically to best protect and maintain the population? Such questions have been widely studied, but not usually via the type of differential equations models which have been used so often and effectively in other areas of mathematical ecology. Some work in that direction has been done by Aronson, Ludwig and Weinberger [3], but they consider only regions which are strips, and assume that within a given strip the growth rate is a constant. The corresponding case of spatially homogeneous but temporally varying environments has been studied from that viewpoint by T. Hallam and his co-workers in [22–28], and our investigations were inspired partly by that work. Another source of our inspiration lies in some questions posed by L. Gross on how the spatial distribution of susceptible and resistant strains of crop plants would affect the crop yield in the presence of a pathogenic organism. Our model (1.1) could be viewed as a simplified formulation of the population dynamics of the pathogen in

such a situation. Our results provide a starting point and framework for the application of ideas from the theory of differential equations to the spatially heterogeneous situation. Ultimately, it would be desirable to allow both spatial and temporal variations in the environment, but that situation presents some serious technical difficulties requiring further analysis.

Logistic equations have long been used as models in population dynamics; their use dates back at least to the work of Verhulst [44, 45] in the mid-nineteenth century. Recently there has been considerable interest in models which allow for spatial variations in population density and represent the movements of members of the population by the type of random walks occurring in Brownian motion. These models typically have the form

$$u_t = d \Delta u + f(u)u, \quad (1.4)$$

where $f(u)$ is typically positive for small positive values of u and negative for larger ones. The classical Verhulst dynamics use $f(u) = r - cu$ with r denoting the growth rate at low density and $K = r/c$ denoting the carrying capacity of the environment. Detailed discussions of the development and use of models such as ordinary differential equations of logistic type and reaction-diffusion equations of the form (1.4) are given by Hallam and Levin respectively in [22] and [34]; models such as (1.4) are also discussed in [15, 43], among many other references. The extent to which mathematical models in biology are realistic depictions of reality has frequently been a topic of debate. That is not surprising; life is complicated, and any model simple enough to analyse at all must necessarily be limited in its scope. However, models such as (1.4) are widely regarded as being at least qualitatively correct descriptions of some species in some situations. In [21–27], Hallam *et al.* consider models for population dynamics in stressed environments which include as a special case

$$u_t = (r(t) - cu)u. \quad (1.5)$$

Our model (1.1) combines features of (1.4) and (1.5). Since we are primarily concerned with the effects of spatial variations in the growth rate $m(x)$, we have chosen to use the simplest reasonable representations for diffusion and the effects of crowding, and have assumed that the diffusion rate and the strength of crowding effects are independent of spatial variations in the basic growth rate. (Most of the results in Sections 2 and 3 of this paper can be extended to more general types of diffusion and dynamics.)

As noted, the basic ecological content of our results is that for a species with a given rate of diffusion, the worst environments are those where favourable and unfavourable regions are closely intermingled, producing “cancellation” effects, and the best are those where the favourable regions are relatively large and few in number. This conclusion has significant implications for the design of wildlife refuges. It suggests that a small number of large preserves will provide better protection for a species modelled by (1.1) than many small ones, and if the preserves are too small and too closely intermingled with regions where the environment has been damaged, they may not effectively protect the species from extinction. Similar conclusions have been drawn by other investigators using other methods; for example in the work of Newmark [38] or in some of the

discussions in the book of Frankel and Soulé [19]. Newmark uses the theory of island biogeography, which was developed by MacArthur and Wilson [35] and is described by Levin [35] as being a major alternative to reaction–diffusion models for studying the effects of the geometry of the habitat on the dynamics of a population. One advantage of our approach is that it allows us to concentrate on a single species; island biogeography describes the relationship between the size of a region and the number of different species it will support. Since our models are for a population rather than a community, they operate at one level of complexity lower than does island biogeography. It should be noted that there are situations in which neither island biogeography nor our models give an appropriate viewpoint for refuge design; for example, species which are adapted to transitional habitats rather than habitats near equilibrium seem to be difficult to model from these viewpoints. (We remark that our approach *does* give information even if a population is not near an equilibrium, provided that the environment is essentially constant. That is because the nature of the set of possible equilibria effectively determines the qualitative aspects of the dynamics of the model.) Although models such as (1.1) may not be universally applicable, they are well within the mainstream of current approaches to mathematical ecology, and questions of conservation are important enough that providing a new perspective for their study seems to us a worthy endeavour.

There are various possible extensions and refinements to our work which could broaden its range of applicability, and various connections with other mathematical problems of current interest. One obvious type of extension would be to consider environments which vary in both time and space and species whose movements are not modelled accurately by Brownian motion. A particular example would be a population subject to drift, due either to effects of winds and currents or to the response of the population to chemical gradients in the environment. Examining the types of models discussed in [22] and [34] we find that a rather wide range of situations would be modelled by equations of the form

$$u_t = \nabla \cdot (d(x, t) \nabla u) + \vec{b}(x, t) \cdot \nabla u + [m(x, t) - f(x, t, u)]ug(u), \quad (1.6)$$

where $d \geq 0$, $|f(x, t, u)| \leq f_0 |u|$ with $f(x, t, u)$ positive for u large, and g is positive and smooth for positive u with $g(0) = 1$. Unfortunately such models are too general to be amenable to our techniques. Our results depend on the analysis of steady states, and use the variation characterisation of eigenvalues of the linearisation of the operator on the right-hand side of (1.1). Unless the right-hand side of (1.6) is constant or at least periodic in t , the idea of a steady state does not make too much sense. By using results of Beltramo and Hess [4] or Hess and Kato [32] we could extend the results of Section 2 to problems of the form

$$u_t = \nabla \cdot d(x, t) \nabla u + \vec{b}(x, t) \cdot \nabla u + [m(x, t) - cu]u, \quad (1.7)$$

with d , \vec{b} , and m either constant or periodic in t , d positive, and all coefficients Hölder continuous. We cannot extend the results of Section 3 to that case because they use the variational formulation for eigenvalues of a self-adjoint elliptic operator. Also, the variational approach allows us to consider $m \in L^\infty(\Omega)$; it is an open question whether the results of Hess and Kato for the nonself-adjoint case extend to weights that are not continuous. (Nussbaum [39] has a

version of the results in [32] under weakened regularity assumptions but still requires m to be continuous.) Hence, one natural class of questions is that of extending our results to nonselfadjoint operators. (A case of particular applied interest would be where the terms d and \vec{b} are related to m . Such a situation would arise if the negative regions for m represented areas polluted by a toxin which the population can sense or which affects the diffusion rate of the population.) Another natural direction to take in the analysis is to try to view m not simply as a parameter, as we do, but as a control (in the sense of control theory), and ask to what extent the system is controllable, whether or not there are optimal controls and if so whether a “bang-bang” principle applies, and so on. Theorems 3.1 and 3.9 provide some information on these questions, but much remains to be done. Yet another direction would be to consider more than one species. Models for communities are discussed in [8, 10, 22, 34, 43] and the references therein. Analysing such models in our context would require extending the results of Section 3 to systems with indefinite weights. Many of the results used in Section 2 have been extended to certain types of linear systems with indefinite weights by the first co-author in joint research with K. Schmitt [9] (see also [30]), but much remains to be done. (In fact, the limitations of the results in [8] are due largely to limitations of existing spectral theory for linear systems.)

As a final introductory remark, we note that eigenvalue problems with indefinite weights also arise in population genetics, and that models of the form $u_t = -d \Delta u + m(x)f(u)$, where m can change sign, have been studied from that viewpoint in [18, 42]. The results are somewhat related to ours but differ considerably in detail and interpretation; we mention them mostly for completeness.

2. A qualitative overview

In this section, we describe the basic existence, uniqueness, and stability properties of the positive steady-state solutions to (1.1). To this end, consider

$$\left. \begin{aligned} -d \Delta u &= m(x)u - cu^2 && \text{in } \Omega, \\ u &= 0 && \text{on } \partial\Omega. \end{aligned} \right\} \quad (2.1)$$

We assume $m(x) \in L^\infty(\Omega)$ and that c is a positive constant. Let A denote the inverse of $-\Delta$ subject to zero Dirichlet boundary data. Then A is a continuous map from $L^p(\Omega)$ into $W^{2,p}(\Omega) \cap W_0^{1,p}(\Omega)$, $p \in (1, \infty)$, and $W^{2,p}(\Omega) \cap W_0^{1,p}(\Omega)$ embeds compactly into $C_0^{1+\alpha}(\bar{\Omega})$, $0 < \alpha < 1$, for sufficiently large p . (See [19], for example.) Consequently, (2.1) is equivalent to an equation of the form

$$e = \lambda(Le + H(e)), \quad (2.2)$$

where $e \in C_0^0(\bar{\Omega})$, $L: C_0^0(\bar{\Omega}) \rightarrow C_0^0(\bar{\Omega})$ is compact and linear, $H: C_0^0(\bar{\Omega}) \rightarrow C_0^0(\bar{\Omega})$ is completely continuous with $\lim_{e \rightarrow 0} (H(e)/\|e\|) = 0$, and $\lambda = 1/d$. (We are thinking of $e = u$.) As a result, (2.1) is amenable to description via the methods of bifurcation theory.

Therefore, let us now consider the linearisation about 0 of (2.1), namely

$$\left. \begin{aligned} -d \Delta z &= m(x)z && \text{in } \Omega, \\ z &= 0 && \text{on } \partial\Omega. \end{aligned} \right\} \quad (2.3)$$

If the sets $\Omega^+ = \{x \in \Omega: m(x) > 0\}$ and $\Omega^- = \{x \in \Omega: m(x) < 0\}$ both have positive measure, the eigenvalue problem

$$\left. \begin{aligned} -\Delta z &= \lambda m(x)z && \text{in } \Omega, \\ z &= 0 && \text{on } \partial\Omega, \end{aligned} \right\} \quad (2.4)$$

has a doubly infinite sequence of eigenvalues

$$\dots \leq \lambda_3^- \leq \lambda_2^- \leq \lambda_1^- < 0 < \lambda_1^+ \leq \lambda_2^+ \leq \lambda_3^+ \leq \dots,$$

with variational characterisations

$$\frac{1}{\lambda_n^+} = \sup_{F_n} \inf \left\{ \int_{\Omega} m u^2: \sum_{i=1}^N \int_{\Omega} \left(\frac{\partial u}{\partial x_i} \right)^2 = 1, u \in F_n \right\},$$

$$\frac{1}{\lambda_n^-} = \inf_{F_n} \sup \left\{ \int_{\Omega} m u^2: \sum_{i=1}^N \int_{\Omega} \left(\frac{\partial u}{\partial x_i} \right)^2 = 1, u \in F_n \right\},$$

where F_n varies over all n -dimensional subspaces of $H_0^1(\Omega)$ (see [13]). Moreover, the theorem of Manes and Micheletti [36] guarantees that λ_1^+ is algebraically simple viewed as a characteristic value of $e = \lambda A(me)$ and that the eigenspace corresponding to λ_1^+ is $\langle \phi \rangle$, where $\phi \in C_0^{1+\alpha}(\bar{\Omega})$ is such that $\phi(x) > 0$ in Ω and $\partial\phi/\partial\eta(x) < 0$ on $\partial\Omega$. In addition, if $\bar{m} \in L^\infty(\Omega)$ is such that $m(x) \leq \bar{m}(x)$ almost everywhere in Ω , then $\lambda_1^+(m) \geq \lambda_1^+(\bar{m})$. (If the inequality is strict on a set of positive measure, then $\lambda_1^+(m) > \lambda_1^+(\bar{m})$.)

The Rabinowitz bifurcation theorem [40] may now be employed to assert the existence of an unbounded continuum \mathcal{C} of positive solutions to

$$\left. \begin{aligned} -\Delta u &= \lambda(m(x)u - cu^2) && \text{in } \Omega, \\ u &= 0 && \text{on } \partial\Omega, \end{aligned} \right\} \quad (2.5)$$

in $\mathbf{R} \times C_0^0(\bar{\Omega})$ emanating from $(\lambda_1^+(m), 0)$. In fact, all such solutions (λ, u) are such that $u \in C_0^{1+\alpha}(\bar{\Omega})$, $u(x) > 0$ in Ω , and $\partial u/\partial\eta < 0$ on $\partial\Omega$ (i.e. u is strictly positive).

To see that such is the case, recall from the Rabinowitz theory that the simplicity of $\lambda_1^+(m)$ guarantees that the continuum of solutions emanating from $(\lambda_1^+(m), 0)$ in $\mathbf{R} \times C_0^0(\bar{\Omega})$ can be expressed as the union of two subcontinua which intersect at $(\lambda_1^+(m), 0)$. Moreover, these subcontinua either intersect outside a small neighbourhood of $(\lambda_1^+(m), 0)$ or both satisfy the global Rabinowitz alternatives. Since (2.2) may be viewed as an equation in $C_0^1(\bar{\Omega})$ with maintenance of the compactness properties of L and H , the Crandall–Rabinowitz local bifurcation theorem [12] and the strict positivity of ϕ from Manes–Micheletti distinguish these subcontinua locally as being the strictly positive and the strictly negative solutions to (2.5). The strong maximum principle for weak solutions ([20, Theorem 8.19]) guarantees global preservation of strict positivity and of strict negativity, and that (2.5) has no nontrivial solutions for $\lambda = 0$.

Consequently, the subcontinua intersect only at $(\lambda_1^+(m), 0)$, and the subcontinuum of positive solutions satisfies the global Rabinowitz alternatives. Since there are no positive eigenvalues of (2.4) other than $\lambda_1^+(m)$ which admit a positive eigenfunction, the continuum of positive solutions must be unbounded.

Notice that if

$$-\Delta u = \lambda(m(x) - cu)u,$$

then $\lambda = \lambda_1^+(m(x) - cu) > \lambda_1^+(m(x))$. Consequently, the projection of \mathcal{C} into \mathbf{R} is contained in $(\lambda_1^+(m(x)), \infty)$.

Suppose now that $l = \left(\text{ess sup}_{\Omega} m^+(x)\right) / c > 0$ and that for some $(\lambda, u) \in \mathcal{C}$, $u(x_0) > l$ for some $x_0 \in \Omega$. Let Ω' be the connected component of $\{x \in \Omega : u(x) > l\}$ which contains x_0 . Then $u(x) > l$ on Ω' and $u(x) = l$ on $\partial\Omega'$. Hence

$$\begin{aligned} \Delta(u - l) &= \lambda u(cu - m(x)) \quad \text{in } \Omega', \\ u - l &= 0 \quad \text{on } \partial\Omega'. \end{aligned}$$

The maximum principle implies that $u - l \leq 0$ in Ω' , a contradiction. Consequently, for any (λ, u) lying on \mathcal{C} , $\|u\|_{\infty} \leq \left(\text{ess sup}_{\Omega} m^+(x)\right) / c$. It follows readily that the image of the projection of \mathcal{C} into \mathbf{R} is $(\lambda_1^+(m), \infty)$.

In fact, \mathcal{C} is actually an arc. To see that this is so, suppose that for some $\lambda > \lambda_1^+(m)$, (2.5) has positive solutions u_1 and u_2 . Then $v = u_1$ is a positive solution to

$$\begin{aligned} -\Delta v + \lambda(cu_1 - m(x))v &= \sigma v \quad \text{in } \Omega, \\ v &= 0 \quad \text{on } \partial\Omega, \end{aligned}$$

with $\sigma = 0$, while $w = u_1 - u_2$ solves

$$\begin{aligned} -\Delta w + \lambda(c(u_1 + u_2) - m(x))w &= \alpha w \quad \text{in } \Omega, \\ w &= 0 \quad \text{on } \partial\Omega, \end{aligned}$$

with $\alpha = 0$. Since v is positive, 0 is the principal eigenvalue of the operator $-\Delta + \lambda(cu_1 - m(x))$ on Ω , subject to zero Dirichlet boundary conditions. Since $u_2 > 0$, all the eigenvalues of $-\Delta + \lambda(c(u_1 + u_2) - m(x))$ on Ω , subject to zero Dirichlet boundary data, must be positive, a contradiction. Hence \mathcal{C} is an arc.

Moreover, the points on \mathcal{C} are globally asymptotically stable when considered as steady-state solutions to (1.1). To see the local asymptotic stability, let $\lambda \in (\lambda_1^+(m), \infty)$. As in [30], the principle of linearised stability obtains and consequently we need only show that if $F(w) = -\Delta w - \lambda m(x)w + \lambda cw^2$, then the first eigenvalue of

$$\left. \begin{aligned} F'(u)\phi &= \mu\phi \quad \text{in } \Omega, \\ \phi &= 0 \quad \text{on } \partial\Omega, \end{aligned} \right\} \tag{2.6}$$

is positive, where $(\lambda, u) \in \mathcal{C}$. Now (2.6) becomes

$$\begin{aligned} -\Delta\phi - \lambda m(x)\phi + 2\lambda cu\phi &= \mu\phi \quad \text{in } \Omega, \\ \phi &= 0 \quad \text{on } \partial\Omega. \end{aligned}$$

Since $v = u > 0$ solves

$$\begin{aligned} -\Delta v - \lambda m(x)v + \lambda cuv &= 0 \quad \text{in } \Omega, \\ v &= 0 \quad \text{on } \partial\Omega, \end{aligned}$$

and $2\lambda cu - \lambda m(x) > \lambda cu - \lambda m(x)$, $\mu > 0$, establishing the result.

To infer that the unique positive solution to (2.5) is in fact the global attractor for nontrivial negative initial data in $W^{1,2}(\Omega)$, we observe that the nonlinearity is such that the maximum principle can be applied to compare any nonnegative solution to (1.1) with a sufficiently large constant. Consequently, as in [29] or [43], orbits exist for all time and are bounded. We may now view (1.1) as a dynamical system on $W^{1,2}(\Omega)$ with

$$V(\phi) = \int_{\Omega} \left[\frac{1}{2} |\nabla \phi|^2 - m(x) \frac{\phi^2}{2} + c \frac{\phi^3}{3} \right]$$

as a Lyapunov function.

Then, as in [29, Section 5.3], the ω -limit set for (1.1) consists of equilibrium points. The only nonnegative solutions to (2.5) are u and 0. Since $\lambda \in (\lambda_1^+(m), \infty)$, it follows from the proof of Proposition 3 in [32] and the principle of linearised stability as in [31] that 0 is unstable. Consequently, the global asymptotic stability follows from the local asymptotic stability. We should note that in case $\lambda < \lambda_1^+(m)$, the trivial solution is the only nonnegative solution to (2.5) and hence is globally asymptotically stable as a solution to (1.1) for nonnegative initial data in $W^{1,2}(\Omega)$. (Since any initial data in $L^\infty(\Omega)$ will produce a local solution which is in $W^{1,2}(\Omega)$ for any small, positive value for t , and the equation is autonomous, this requirement imposes no real restriction.)

Summarising, we have the following result.

THEOREM 2.1. *Let $m \in L^\infty(\Omega)$ be such that $\{x \in \Omega: m(x) > 0\}$ has positive measure. Let $\lambda_1^+(m) > 0$ be the unique eigenvalue for (2.4) admitting a strictly positive eigenfunction in $C_0^{1+\alpha}(\bar{\Omega})$. Then (2.1) has a unique strictly positive (i.e. $u(x) > 0$ in Ω and $(\partial u / \partial \eta)(x) < 0$ on $\partial\Omega$) solution in $C_0^{1+\alpha}(\bar{\Omega})$ for all $d \in (0, [\lambda_1^+(m)]^{-1})$. Moreover, for each fixed $d \in (0, [\lambda_1^+(m)]^{-1})$, this solution is globally asymptotically stable when viewed as a steady-state solution to (1.1).*

It is also instructive to view (2.1) as a multiparameter nonlinear eigenvalue problem with $(d, m) \in \mathbf{R} \times L^\infty(\Omega)$ as parameters. (Compare, for example, [1].) To this end, we have the following result.

THEOREM 2.2. *Let $D = \{(d, m) \in \mathbf{R}^+ \times L^\infty(\Omega): (2.1) \text{ has a positive solution}\}$. Then the map $(d, m) \rightarrow u(d, m)$ is a differentiable map from D into $C_0^{1+\alpha}(\bar{\Omega})$.*

Proof. Let $G: W^{2,p}(\Omega) \cap W_0^{1,p}(\Omega) \times [\mathbf{R} \times L^\infty(\Omega)] \rightarrow L^p(\Omega)$ be given by $G(u, d, m) = -d \Delta u - m(x)u + cu^2$. Suppose that $(d_0, m_0) \in \mathbf{R}^+ \times L^\infty(\Omega)$ and $u_0 \in C_0^{1+\alpha}(\bar{\Omega})$ are such that $G(u_0, d_0, m_0) = 0$ and u_0 is strictly positive. $(\partial G / \partial u)(u_0, d_0, m_0)$ is invertible by standard elliptic theory [20] provided 0 is not an eigenvalue of $(\partial G / \partial u)(u_0, d_0, m_0)$. Since $(\partial G / \partial u)(u_0, d_0, m_0)w = -d_0 \Delta w - m_0(x)w + 2cu_0w$, the relevant eigenvalue problem is

$$\begin{aligned} -d_0 \Delta w - m_0(x)w + 2cu_0w &= \mu w \quad \text{in } \Omega, \\ w &= 0 \quad \text{on } \partial\Omega. \end{aligned}$$

As in the proof of the stability assertion for Theorem 2.1, $\mu > 0$. Consequently, the result follows from the implicit function theorem and the fact that $W^{2,p}(\Omega) \cap W_0^{1,p}(\Omega)$ embeds into $C_0^{1+\alpha}(\bar{\Omega})$ [20]. \square

The results of this section extend to more general equations than (1.1), (2.1). If we consider the problem

$$\left. \begin{aligned} u_t &= d \Delta u + f(x, u)u \quad \text{in } \Omega \times (0, \infty), \\ u(x, 0) &= u_0(x) \geq 0 \quad \text{on } \Omega, \\ u &= 0 \quad \text{on } \partial\Omega \times (0, \infty), \end{aligned} \right\} \quad (2.7)$$

and the corresponding steady-state problem

$$\left. \begin{aligned} 0 &= d \Delta u + f(x, u)u \quad \text{in } \Omega, \\ u &= 0 \quad \text{on } \partial\Omega, \end{aligned} \right\} \quad (2.8)$$

then applying the methods of this section yields the following result, which we state without proof.

THEOREM 2.3. *Suppose that $f: \bar{\Omega} \times \mathbf{R} \rightarrow \mathbf{R}$ is a measurable function satisfying the following conditions:*

- (i) $f(x, \alpha) \in L^\infty(\bar{\Omega})$ with $\|f(x, \alpha)\|_\infty \leq K(r)$ for each $\alpha \in [-r, r]$, where $K: [0, \infty) \rightarrow \mathbf{R}^+$ is some nondecreasing function;
- (ii) $(\partial f / \partial \alpha)(x, \alpha)$ is a measurable function on $\bar{\Omega} \times \mathbf{R}$ which is continuous in α for any fixed $x \in \Omega$ and which belongs to $L^\infty(\bar{\Omega})$ for each fixed α when viewed as a function of x , with $\|(\partial f / \partial \alpha)(x, \alpha)\|_\infty \leq K(r)$ for all $\alpha \in [-r, r]$, where again $K: [0, \infty) \rightarrow \mathbf{R}^+$ is nondecreasing;
- (iii) $(\partial f / \partial \alpha)(x, \alpha) \leq 0$ for $\alpha \geq 0$, with strict inequality for $\alpha > 0$;
- (iv) $f(x, \alpha) \leq 0$ for $\alpha \geq l > 0$, for all $x \in \bar{\Omega}$;
- (v) $\{x: f(x, 0) > 0\}$ has positive measure.

Then (2.8) has a unique strictly positive solution in $C_0^{1+\alpha}(\bar{\Omega})$ for all $d \in (0, [\lambda_1^+(f(x, 0))]^{-1})$. Moreover, for each fixed $d \in (0, [\lambda_1^+(f(x, 0))]^{-1})$, this solution is globally asymptotically stable when viewed as a steady-state solution to (2.7).

Finally, we conclude this section with two remarks. The first concerns the choice of $C_0^0(\bar{\Omega})$ as the underlying Banach space in the proof of Theorem 2.1. We use the fact that $\|u\|_\infty \leq \left(\text{ess sup}_{x \in \bar{\Omega}} m^+(x) \right) / c$ for all positive solutions to (2.5) in conjunction with the fact that the continuum \mathcal{C} of positive solutions to (2.5) is unbounded to conclude that \mathcal{C} is unbounded in λ ; i.e. there is $(\lambda, u) \in \mathcal{C}$ for all $\lambda > \lambda_1^+(m)$. This argument is not possible in general if the C^0 norm is replaced by the C^α or C^1 norm. Indeed uniform C^α or C^1 boundedness implies precompactness in the C^0 topology by the Ascoli–Arzela theorem. However, when m is discontinuous, it is frequently the case that $u(\lambda)$ tends pointwise to a discontinuous function as $\lambda \rightarrow +\infty (d \rightarrow 0^+)$, as we demonstrate using singular perturbation techniques in Section 4.

The second of the two remarks is a simple observation regarding scaling of the solutions. Namely, if $u \in C_0^{1+\alpha}(\bar{\Omega})$ is a strictly positive solution of (2.1), then

$U = cu/\|m\|_\infty$ is a strictly positive solution of

$$\begin{aligned} -\left(\frac{d}{\|m\|_\infty}\right)\Delta w &= \frac{m(x)}{\|m\|_\infty} w - w^2 && \text{in } \Omega, \\ w &= 0 && \text{on } \partial\Omega. \end{aligned}$$

Consequently, there is no loss of generality in assuming for the remainder of the paper that $\|m\|_\infty \leq 1$ and $c = 1$. It also follows that if γ is a positive constant, $\lambda_1^+(\gamma m) = \lambda_1^+(m)/\gamma$.

3. The location and behaviour of eigenvalues

To apply the results of the last section in a meaningful way to the problem of analysing the effects of distribution of good and bad environmental patches on a population, it is crucial to obtain estimates of the first eigenvalue of the problem

$$\left. \begin{aligned} -\Delta\phi &= \lambda m(x)\phi && \text{in } \Omega, \\ \phi &= 0 && \text{on } \partial\Omega. \end{aligned} \right\} \quad (3.1)$$

We shall assume throughout this section that $m(x) \in L^\infty(\Omega)$ with $\|m\|_\infty \leq 1$ and $m(x) > 0$ on a set of positive measure. As noted, under these conditions the problem (3.1) has a principal positive eigenvalue $\lambda_1^+(m)$. As in the case of positive, regular weights, $\lambda_1^+(m)$ is monotone in m in the sense that if $m_1 \leq m_2$ then $\lambda_1^+(m_1) \leq \lambda_1^+(m_2)$. However, this type of qualitative information is not sufficient for our purposes, since we wish to compare weight functions which may not be ordered in such a way. Specifically, we are interested in the basic biological question: given a class of weights reflecting some natural restrictions on the environment, such as fixed sizes for the favourable and unfavourable regions, which sorts of weights describe the best environments for the population, and which sorts describe the worst? More generally, how does the distribution (as opposed to size) of the favourable and unfavourable regions affect the population? These biological questions lead to mathematical ones such as how $\lambda_1^+(\chi_E - \chi_{\Omega \setminus E})$ varies with $E \subseteq \Omega$ if the measure of E is fixed. There are various results in the literature giving estimates for some or all of the eigenvalues of (3.1) (e.g. [16, 21, 39]), but those estimates do not immediately yield the type of information we need. Hence we shall derive some properties and estimates of $\lambda_1^+(m)$. Our first result will give a criterion for deciding if a given class of admissible weights m contains a sequence $\{m_j\}$ such that $\lambda_1^+(m_j) \rightarrow \infty$ as $j \rightarrow \infty$. If such a sequence $\{m_j\}$ exists, the results of the previous section show that for fixed diffusion coefficient d , we may force the nonexistence of positive steady states for (1.1), and hence the extinction of the population which (1.1) describes, by choosing $m = m_j$ for j sufficiently large. On the other hand, if for all m in a class of admissible weights we have $\lambda_1^+(m) \leq \Lambda_1$, then if $d < 1/\Lambda_1$ the population will persist, no matter how we choose m in the class. Hence, the distinction between the two cases is fundamental for our application. Once we have established the basic qualitative result, we discuss the special case where $n = 1$, Ω is an interval and $|m(x)| = 1$ almost everywhere, and obtain some rather specific quantitative estimates. Finally, we return to the general setting and discuss some approaches

to estimating $\lambda_1^+(m)$, and show that within some biologically reasonable classes of weights, there exist “most favourable” choices.

A basis result for our analysis is a version of the variational characterisation of $\lambda_1^+(m)$ given in [13, 36] and stated in Section 2:

$$\lambda_1^+(m) = \inf \left\{ \int_{\Omega} |\nabla \phi|^2 / \int_{\Omega} m\phi^2 : \phi \in W_0^{1,2}(\Omega), \int_{\Omega} m\phi^2 > 0 \right\}. \tag{3.2}$$

Our basic result is as follows.

THEOREM 3.1. *Suppose that for $j = 1, 2, \dots$, $m_j \in L^\infty(\Omega)$ with $\|m_j\|_\infty \leq 1$ and $m_j(x) > 0$ on a set of positive measure. To have $\lambda_1^+(m_j) \rightarrow \infty$ as $j \rightarrow \infty$, it is necessary and sufficient that*

$$\limsup_{j \rightarrow \infty} \int_{\Omega} m_j \psi \leq 0 \text{ for all } \psi \in L^1(\Omega) \text{ with } \psi \geq 0 \text{ a.e.} \tag{3.3}$$

Proof. To show the sufficiency of (3.3) we use an argument suggested by our colleague Alan Lazer [33]. Suppose that (3.3) holds but $\lambda_1^+(m_j) \not\rightarrow \infty$. Choose a subsequence of $\{\lambda_1^+(m_j)\}$ which is bounded and reindex that bounded subsequence as $\lambda_1^+(m_k)$. Let $\phi_k \in W_0^{1,2}(\Omega)$ be the eigenfunction of (3.1) corresponding to $\lambda_1^+(m_k)$, normalised so that $\int_{\Omega} |\nabla \phi_k|^2 = 1$. We have

$$1 = \int_{\Omega} |\nabla \phi_k|^2 = \lambda_1^+(m_k) \int_{\Omega} m_k \phi_k^2. \tag{3.4}$$

The normalisation of ϕ_k implies that the sequence $\{\phi_k\}$ is uniformly bounded in $W_0^{1,2}(\Omega)$, and the Sobolev embedding theorem then implies that $\{\phi_k\}$ is uniformly bounded and has a convergent subsequence in $L^2(\Omega)$ since $W_0^{1,2}(\Omega)$ embeds compactly in $L^2(\Omega)$. Again reindexing, let us denote that subsequence as $\{\phi_l\}$, with $\phi_l \rightarrow \phi$ in $L^2(\Omega)$ as $l \rightarrow \infty$. We must, by our choice of subsequences, have $\lambda_1^+(m_l)$ bounded as $l \rightarrow \infty$. However, (3.4) yields

$$1 = \lambda_1^+(m_l) \int_{\Omega} m_l (\phi_l^2 - \phi^2) + \lambda_1^+(m_l) \int_{\Omega} m_l \phi^2. \tag{3.5}$$

As $l \rightarrow \infty$, the first integral in (3.5) goes to zero since $\|m_l\|_\infty \leq 1$, $\|\phi_l\|_2$ is bounded, and $\phi_l \rightarrow \phi$ in $L^2(\Omega)$. The second integral has a nonpositive lim sup as $l \rightarrow \infty$ by (3.3), so taking the lim sup as $l \rightarrow \infty$ in (3.5) yields $1 \leq 0$, a contradiction. Hence, if (3.3) holds we must have $\lambda_1^+(m_j) \rightarrow \infty$ as $j \rightarrow \infty$.

To see the necessity of (3.3), suppose that for some $\psi \in L^1(\Omega)$ with $\psi \geq 0$ almost everywhere, we have $\limsup_{j \rightarrow \infty} \int_{\Omega} m_j \psi = 2\varepsilon_0 > 0$. Then we must have a subsequence $\{m_k\}$ for which $\int_{\Omega} m_k \psi \geq \varepsilon_0 > 0$. Also, $\sqrt{\psi}$ is well defined in $L^2(\Omega)$. Thus, for any $\varepsilon > 0$, there exists $\phi \in C_0^\infty(\Omega)$ such that $\|\sqrt{\psi} - \phi\|_2 < \varepsilon$, so

$$\begin{aligned} \left| \int_{\Omega} m_k (\psi - \phi^2) \right| &\leq \|m_k\|_\infty \int_{\Omega} (|\sqrt{\psi} - \phi|)(|\sqrt{\psi} + \phi|) \\ &\leq \|\sqrt{\psi} - \phi\|_2 \|\sqrt{\psi} + \phi\|_2 \\ &\leq \varepsilon(2\|\psi\|_1^{1/2} + \varepsilon). \end{aligned}$$

Choosing ε so that $\varepsilon(2\|\psi\|_1^{1/2} + \varepsilon) \leq \varepsilon_0/2$ and making the corresponding choice of ϕ , we have

$$\int m_k \phi^2 = \int m_k \psi + \int m_k (\phi^2 - \psi) \geq \varepsilon_0/2 > 0,$$

so by (3.2),

$$\lambda_1^+(m_k) \leq \frac{\int_{\Omega} |\nabla \phi|^2}{\int_{\Omega} m_k \phi^2} \leq (2/\varepsilon_0) \int_{\Omega} |\nabla \phi|^2. \quad (3.6)$$

Since ϕ does not depend on k , (3.6) provides an upper bound for $\lambda_1^+(m_k)$, and hence it is impossible to have $\lambda_1^+(m_j) \rightarrow \infty$.

Remarks 3.2. If we let $\psi = 1$ in (3.3) we see that to have $\lambda_1^+(m_j) \rightarrow \infty$ we must have $\limsup \int_{\Omega} m_j \leq 0$; so if we impose a condition which implies $\int_{\Omega} m \geq m_0 > 0$ (e.g. $\int_{\Omega} m_+ \geq m_0 + \int_{\Omega} m_-$, or $m = \chi_E - \chi_{\Omega \setminus E}$ with $|E| \geq m_0 + |\Omega \setminus E|$) then the set of principal eigenvalues for weights m in that class will be bounded above.

Since the characterisation in [36] for $\lambda_1^-(m)$ corresponding to (3.2) implies that $\lambda_1^-(m) = -\lambda_1^+(-m)$, we have $\lambda_1^-(m_j) \rightarrow -\infty$ as $j \rightarrow \infty$ if and only if $\liminf_{j \rightarrow \infty} \int m_j \psi \geq 0$ for $\psi \in L^1(\Omega)$ with $\psi \geq 0$ almost everywhere. Then by writing $\psi = \psi^+ - \psi^-$ with ψ^+, ψ^- nonnegative almost everywhere, we obtain from Theorem 3.1 the following.

COROLLARY 3.3. *Suppose that for $j = 1, 2, \dots$, $m_j \in L^\infty(\Omega)$ with $\|m_j\|_\infty \leq 1$ and with the sets where $m_j > 0$ and $m_j < 0$ both having positive measure for each j . A necessary and sufficient condition for $|\lambda_1^\pm(m_j)| \rightarrow \infty$ as $j \rightarrow \infty$ is that*

$$\int_{\Omega} m_j \psi \rightarrow 0 \quad \text{as } j \rightarrow \infty \text{ for any } \psi \in L^1(\Omega). \quad (3.7)$$

Note that (3.7) says the weights m_j must satisfy a type of Riemann–Lebesgue lemma; that will be the case, for example, for $\Omega = (0, 1)$ and $m_j(x) = \sin(\alpha_j x)$ with $\alpha_j \rightarrow \infty$ as $j \rightarrow \infty$. In that sense, Theorem 3.1 and Corollary 3.3 assert that having $\lambda_1^+(m)$ large is roughly equivalent to having m negative or highly oscillatory on Ω , and that having $|\lambda_1^\pm(m)|$ both large requires m to be near zero or highly oscillatory. Further, if $\mathcal{M} \subseteq \{m \in L^\infty(\Omega) : \int_{\Omega} m \geq m_0 > 0, |m| \leq 1\}$, for some constant m_0 , then there must exist a constant $\Lambda_0 < \infty$ such that $\lambda_1^+(m) \leq \Lambda_0$ for $m \in \mathcal{M}$, since otherwise we could choose a sequence $m_j \in \mathcal{M}$ such that $\limsup_{j \rightarrow \infty} \int m_j > 0$ but $\lambda_1^+(m_j) \rightarrow \infty$, in contradiction to Theorem 3.1. On the other hand, Theorem 3.1 shows that in some classes of weights there is none reflecting an environment that is “worst” for the population. For example, if $N = 1$, $\Omega = (0, \pi)$, and $\mathcal{M} = \{\sin \alpha x : \alpha > 0\}$, then for each $m \in \mathcal{M}$, $\lambda_1^+(m)$ is finite, but $\sup_{m \in \mathcal{M}} \lambda_1^+(m) = \infty$, so the supremum is never attained. Thus, Theorem 3.1 is of fundamental importance for two reasons: it provides insight into the qualitative aspects of the dependence of $\lambda_1^+(m)$ on m , and it shows that the question “which environment in a given class is worst?” will not always have an answer.

We now turn to the case where $N = 1$ and take $\Omega = (a, b)$. In this situation we can make the conclusions of Theorem 3.1 quantitatively precise. We shall have need of the following lemma. (Compare [13], Proposition 1.12B.)

LEMMA 3.4. Suppose that $\{m_n\}_{n=1}^\infty \subseteq L^\infty(a, b)$ and $m \in L^\infty(a, b)$ are such that the sets $\Omega_n = \{x \in \Omega: m_n(x) > 0\}$ and $\Omega = \{x \in \Omega: m(x) > 0\}$ all have positive measure. Suppose furthermore that $\lim_{n \rightarrow \infty} \int_a^b |m_n - m| = 0$ (i.e. that $m_n \rightarrow m$ in the topology of $L^1(a, b)$ as $n \rightarrow \infty$). Then $\lambda_1^+(m_n) \rightarrow \lambda_1^+(m)$ as $n \rightarrow \infty$.

Proof. By the definition of weak solutions in $W_0^{1,2}(a, b)$, $\frac{1}{\lambda_1^+(m_n)} = \int_a^b m_n \phi_n^2$ if $-\phi_n'' = \lambda_1^+(m_n) m_n \phi_n$ and $\int_a^b (\phi_n')^2 = 1$. Similarly, $\frac{1}{\lambda_1^+(m)} = \int_a^b m \phi^2$, where $-\phi'' = \lambda_1^+(m) m \phi$ and $\int_a^b (\phi')^2 = 1$. Also, since $\int_a^b (\phi')^2 = \int_a^b (\phi_n')^2 = 1$, ϕ and ϕ_n are absolutely continuous and satisfy $\max \{\|\phi\|_{L^\infty(a,b)}^2, \|\phi_n\|_{L^\infty(a,b)}^2\} \leq b - a$ by the Cauchy-Schwarz inequality. Since (3.2) implies that $\frac{1}{\lambda_1^+(m_n)} = \sup \left\{ \int_a^b m_n f^2: f \in W_0^{1,2}(a, b) \text{ and } \int_a^b (f')^2 = 1 \right\}$ and $\frac{1}{\lambda_1^+(m)} = \sup \left\{ \int_a^b m f^2: f \in W_0^{1,2}(a, b) \text{ and } \int_a^b (f')^2 = 1 \right\}$, $\int_a^b m \phi^2 - \int_a^b m_n \phi_n^2 \leq \int_a^b (m - m_n) \phi^2$ and $\int_a^b m_n \phi_n^2 - \int_a^b m \phi^2 \leq \int_a^b (m_n - m) \phi_n^2$. Consequently,

$$\left| \frac{1}{\lambda_1^+(m_n)} - \frac{1}{\lambda_1^+(m)} \right| \leq [\max \{\|\phi^2\|_{L^\infty(a,b)}, \|\phi_n^2\|_{L^\infty(a,b)}\}] \cdot \|m_n - m\|_{L^1(a,b)},$$

and the result is immediate. \square

It is also immediate that the weaker result of Lemma 3.4 with L^∞ instead of L^1 convergence on $\{m_n\}$ is a corollary to Lemma 3.4. More significantly, we may now prove the following.

THEOREM 3.5. Let $(a, b) = (0, \pi)$ and let E be a measurable subset of $(0, \pi)$ such that $|E| > |(0, \pi) \setminus E|$, where $|\cdot|$ denotes Lebesgue measure. Then $\lambda_1^+(\chi_E - \chi_{(0,\pi) \setminus E}) < (\pi / (|E| - |(0, \pi) \setminus E|))^2$.

Proof. By standard measure theory [41] and Lemma 3.4, it suffices to consider only the case where E is a finite union of intervals. Therefore, let $E = \bigcup_{i=1}^R [a_{2i-1}, a_{2i}]$, where $0 \leq a_1 < a_2 < \dots < a_{2R} \leq \pi$. Let f be a normalised positive solution to

$$\begin{aligned} -f'' &= \lambda_1^+(\chi_E - \chi_{(0,\pi) \setminus E})(\chi_E - \chi_{(0,\pi) \setminus E})f \quad \text{in } (0, \pi) \\ f(0) &= 0 = f(\pi). \end{aligned}$$

Then, for $i = 1, 2, \dots, R$, there are unique $A_i > 0$ and θ_i so that $f(x) = A_i \sin(\alpha x - \theta_i)$ and $f'(x) = \alpha A_i \cos(\alpha x - \theta_i)$ for all $x \in [a_{2i-1}, a_{2i}]$ where $\alpha = (\lambda_1^+(\chi_E - \chi_{(0,\pi) \setminus E}))^{1/2}$ and $\alpha x - \theta_i \in [0, \pi]$ for all $x \in [a_{2i-1}, a_{2i}]$.

Let us now fix $i \in \{1, 2, \dots, R - 1\}$ and consider the interval $[a_{2i}, a_{2(i+1)-1}] = [a_{2i}, a_{2i+1}]$. Since f is necessarily continuously differentiable on $[0, \pi]$, it follows

that

$$\alpha a_{2i} - \theta_i = \cot^{-1} \left(\frac{f'(a_{2i})}{\alpha f(a_{2i})} \right)$$

and

$$\alpha a_{2i+1} - \theta_{i+1} = \cot^{-1} \left(\frac{f'(a_{2i+1})}{\alpha f(a_{2i+1})} \right).$$

Now define $g: [a_{2i}, a_{2i+1}] \rightarrow \mathbf{R}$ by

$$g(x) = \cot^{-1} \left(\frac{f'(x)}{\alpha f(x)} \right).$$

Then g is continuous on $[a_{2i}, a_{2i+1}]$ and differentiable on (a_{2i}, a_{2i+1}) . Since $\theta_i = a_{2i} - g(a_{2i})$ and $\theta_{i+1} = \alpha a_{2i+1} - g(a_{2i+1})$,

$$\begin{aligned} \theta_{i+1} - \theta_i &= \alpha(a_{2i+1} - a_{2i}) - [g(a_{2i+1}) - g(a_{2i})] \\ &= (\alpha - g'(b_i))(a_{2i+1} - a_{2i}), \end{aligned}$$

where $b_i \in (a_{2i}, a_{2i+1})$ by the Mean Value Theorem. Since $f'' = \alpha^2 f$ on (a_{2i}, a_{2i+1}) ,

$$g'(b_i) = -\alpha \left\{ \frac{\alpha^2 f^2(b_i) - [f'(b_i)]^2}{\alpha^2 f^2(b_i) + [f'(b_i)]^2} \right\}.$$

Hence

$$\theta_{i+1} - \theta_i = \alpha \left[1 - \frac{\alpha^2 f^2(b_i) - [f'(b_i)]^2}{\alpha^2 f^2(b_i) + [f'(b_i)]^2} \right] (a_{2i+1} - a_{2i}) < 2\alpha (a_{2i+1} - a_{2i}).$$

As a consequence,

$$\begin{aligned} \theta_R &= \left(\sum_{i=1}^{R-1} (\theta_{i+1} - \theta_i) \right) + \theta_1 \\ &< 2\alpha \sum_{i=1}^{R-1} (a_{2i+1} - a_{2i}) + \alpha a_1 \end{aligned} \quad (3.8)$$

as $0 \leq \alpha a_1 - \theta_1$. Since $\alpha a_{2R} - \theta_R \leq \pi$, (3.8) implies

$$\alpha a_{2R} - 2\alpha \sum_{i=1}^{R-1} (a_{2i+1} - a_{2i}) - \alpha a_1 < \pi. \quad (3.9)$$

Observe that (3.9) may be rewritten

$$\alpha \sum_{i=1}^R (a_{2i} - a_{2i-1}) - \alpha \sum_{i=1}^{R-1} (a_{2i+1} - a_{2i}) < \pi.$$

Hence

$$\alpha \left[\sum_{i=1}^R (a_{2i} - a_{2i-1}) - \left(\sum_{i=1}^{R-1} (a_{2i-1} - a_{2i}) + a_1 + (\pi - a_{2R}) \right) \right] < \pi.$$

But since $|E| = \sum_{i=1}^R (a_{2i} - a_{2i-1})$ and $|(0, \pi) \setminus E| = \sum_{i=1}^{R-1} (a_{2i+1} - a_{2i}) + a_1 + (\pi - a_{2R})$, the result is established.

A remark is now in order. Suppose that E is as in the proof of Theorem 3.5; i.e. $E = \bigcup_{i=1}^R [a_{2i-1}, a_{2i}]$, where $0 \leq a_1 < a_2 < \dots < a_{2R} \leq \pi$. Then if $\alpha^2 = \lambda_1^+(\chi_E - \chi_{[0,\pi] \setminus E})$, $\alpha^2 < (\pi/a_{2i} - a_{2i-1})^2$ for $i = 1, 2, \dots, R$. To see that such is the case, recall that an eigenfunction restricted to $[a_{2i-1}, a_{2i}]$ can be expressed in the form $A_{\pm} \sin(\alpha x - \theta_i)$, where $\alpha x - \theta_i \in [0, \pi]$ for $x \in [a_{2i-1}, a_{2i}]$. More generally, suppose that Ω' is a subdomain of $\Omega \subseteq \mathbb{R}^n$ such that $m(x) > 0$ for $x \in \Omega'$. Let $f \in W_0^{1,2}(\Omega')$ be such that $\int_{\Omega'} |\nabla f|^2 = 1$. If we extend f to $\bar{f} \in W_0^{1,2}(\Omega)$ by

$$\bar{f}(x) = \begin{cases} f(x), & x \in \Omega', \\ 0, & x \in \Omega \setminus \Omega', \end{cases}$$

then $\int_{\Omega} |\nabla \bar{f}|^2 = \int_{\Omega'} |\nabla f|^2 = 1$. Consequently, $\int_{\Omega'} m f^2 = \int_{\Omega} m \bar{f}^2 \leq \frac{1}{\lambda_1^+(m)}$, and so $\lambda_1^+(m) \leq \lambda_1^+(m|_{\Omega'})$. Another remark, of a more specific nature, is that the analysis in Theorem 3.5 also applies to the case where $N = 1$, $\Omega = (0, \pi)$, and $E \subseteq (0, \pi)$ is measurable with $m_1 |E| > m_2 |\Omega \setminus E|$ where $m_1, m_2 \in (0, 1)$, and we wish to bound $\lambda_1^+(m_1 \chi_E - m_2 \chi_{\Omega \setminus E})$. The corresponding estimate is

$$\lambda_1^+(m_1 \chi_E - m_2 \chi_{\Omega \setminus E}) \leq \frac{m_1 \pi^2}{(m_1 |E| - m_2 |\Omega \setminus E|)^2}.$$

Theorem 3.5 and the remarks following the proof of that theorem give upper bounds for $\lambda_1^+(m)$. The following result gives some lower bounds. Some of the ideas used in the proof were suggested by A. B. Mingarelli [37] or M. H. Protter.

THEOREM 3.6. *Suppose that $m \in L^\infty(\Omega)$, with $\|m\|_\infty \leq 1$ and $m(x) > 0$ on a set of positive measure. Let M be any solution of $\Delta M = m$ in Ω , and let $M_1 = \sup(M)$, $M_2 = \text{ess sup}(-Mm)$.*

(i) *If $M_2 > 0$, then*

$$\lambda_1^+(m) \geq \frac{-M_1 \lambda_1^+(1) + [M_1^2 \lambda_1^+(1)^2 + 2M_2 \lambda_1^+(1)]^{\frac{1}{2}}}{2M_2} = \frac{1}{M_1 + [M_1^2 + 2M_2/\lambda_1^+(1)]^{\frac{1}{2}}}.$$

(ii) *If $M_2 \leq 0$, then $\lambda_1^+(m) \geq \frac{1}{2}M_1$.*

Remark 3.7. If $M_1 < 0$, then $M < 0$ in Ω , so $-m(x)M(x) > 0$ on a set of positive measure and hence $M_2 > 0$. Observe that no boundary conditions are imposed on M , so we may add any harmonic function to M and our theorem will still apply. Thus, we can control the sign of M_1 . Roughly, the size of M_1 and M_2 decreases as m becomes more oscillatory, since in solving $\Delta M = m$, oscillations in m tend to be cancelled. This can be seen most readily in the one-dimensional case, in which $M = \int^x \int^s m(r) dr ds$. We give an example after the proof of the result.

Proof. Suppose that ϕ is the eigenfunction corresponding to $\lambda_1^+(m)$, normalised via $\int_{\Omega} |\nabla \phi|^2 = 1$. Since $M \in W^{2,p}(\Omega)$ and $\phi \in W^{2,p}(\Omega) \cap W_0^{1,p}(\Omega)$ for any p via standard elliptic theory, we may use the following version of Green's formula, in which the boundary integrals are zero and derivatives are interpreted

in the appropriate weak sense:

$$\begin{aligned}
 0 &= \int_{\partial\Omega} [M(\partial\phi^2/\partial n) - \phi^2 \partial M/\partial n] \\
 &= \int_{\Omega} [M \Delta\phi^2 - \phi^2 \Delta M] \\
 &= \int 2M\phi \Delta\phi + 2M |\nabla\phi|^2 - \int m\phi^2. \tag{3.10}
 \end{aligned}$$

Also, we have $\Delta\phi + \lambda_1^+(m)m\phi = 0$, so that our normalisation of ϕ implies $1 = \int |\nabla\phi|^2 = \lambda_1^+(m) \int m\phi^2$; since $\phi \in W_0^{1,2}(\Omega)$, we have $\lambda_1^+(1) \int \phi^2 \leq \int |\nabla\phi|^2 = 1$. Multiplying (3.10) by $\lambda_1^+(m)$ and using the above properties of ϕ yields

$$1 = \lambda_1^+(m) \int m\phi^2 = -2\lambda_1^+(m)^2 \int_{\Omega} Mm\phi^2 + 2\lambda_1^+(m) \int_{\Omega} M |\nabla\phi|^2. \tag{3.11}$$

If M_2 is positive, (3.11) implies $1 \leq [(2\lambda_1^+(m)^2 M_2/\lambda_1^+(1)) + 2\lambda_1^+(m)M_1]$, so that $2M_2\lambda_1^+(m)^2 + 2M_1\lambda_1^+(1)\lambda_1^+(m) - \lambda_1^+(1) \geq 0$ and $\lambda_1^+(m)$ must be at least as large as the positive root of the quadratic $2M_2\lambda^2 + 2M_1\lambda_1^+(1)\lambda - \lambda_1^+(1) = 0$; calculating that root gives the estimate (i). If $M_2 \leq 0$, then (3.11) yields $1 \leq 2\lambda_1^+(m)M_1$, which implies (ii).

EXAMPLE 3.8. Suppose that $\Omega = (0, \pi)$ and $m = \sin nx$. Then $\lambda_1^+(1) = 1$, and we may choose $M = -\sin nx/n^2$. Then $M_1 = M_2 = 1/n^2$, so $\lambda_1^+(\sin nx) \geq n^2/(1 + [1 + (2n^2)]^{\frac{1}{2}})$, and for $n \geq 1$, $\lambda_1^+(\sin nx) \geq n/(1 + \sqrt{3})$. Thus, as $n \rightarrow \infty$, $\lambda_1^+(\sin nx) \rightarrow \infty$ with order at least n .

We began this section with a theorem which implies, among other things, that in some situations there is no ‘‘worst’’ environment in a given class. We end the section by showing that for at least one biologically reasonable set of constraints on the environment, there is always at least one ‘‘best’’ environment.

THEOREM 3.9. Let $\mathcal{M} = \{m(x) \in L^\infty(\Omega) : -m_2 \leq m(x) \leq m_1 \text{ almost everywhere in } \Omega, m(x) > 0 \text{ on a set of positive measure and } \int_{\Omega} m = m_0\}$, where m_0, m_1 , and m_2 are constants with m_1 and m_2 positive and $-m_2|\Omega| < m_0 \leq m_1|\Omega|$ (so that \mathcal{M} is nonempty). Then there exists a measurable set $E \subseteq \Omega$ such that $\bar{m} \equiv m_1\chi_E - m_2\chi_{\Omega \setminus E} \in \mathcal{M}$, and $\lambda_1^+(\bar{m}) = \inf \{\lambda_1^+(m) : m \in \mathcal{M}\}$.

Proof. Given $\phi \in L^2(\Omega)$, let $E_\alpha(\phi) = \{x \in \Omega : \phi^2(x) > \alpha\}$. If $\phi \neq 0$ outside a set of measure zero, the restrictions on m_0, m_1 , and m_2 imply that we can choose α so that

$$|E_\alpha| m_1 - |\Omega \setminus E_\alpha| m_2 = m_0. \tag{3.12}$$

If $\phi = 0$ on a set of positive measure, it may be the case that $|E_0| m_1 - |\Omega \setminus E_0| m_2 < m_0$. In that case, choose \bar{E}_0 to be any fixed measurable subset of Ω with $E_0 \subseteq \bar{E}_0$ and $|\bar{E}_0| m_1 - |\Omega \setminus \bar{E}_0| m_2 = m_0$. If we can choose α so that (3.12) holds, define $\bar{m}(\phi) = m_1\chi_{E_\alpha} - m_2\chi_{\Omega \setminus E_\alpha}$. If we cannot so choose α , then define $\bar{m}(\phi) = m_1\chi_{\bar{E}_0} - m_2\chi_{\Omega \setminus \bar{E}_0}$. In either case, $\bar{m}(\phi) \in \mathcal{M}$. Also, we have in the first case, for

any $m \in \mathcal{M}$,

$$\begin{aligned} \int_{\Omega} [\bar{m}(\phi) - m] \phi^2 &= \int_{E_{\alpha}} (m_1 - m) \phi^2 + \int_{\Omega \setminus E_{\alpha}} (-m_2 - m) \phi^2 \\ &\geq \alpha \int_{E_{\alpha}} (m_1 - m) - \alpha \int_{\Omega \setminus E_{\alpha}} (m_2 + m) \\ &= \alpha \int_{\Omega} [\bar{m}(\phi) - m] = 0, \end{aligned}$$

since $\phi^2 > \alpha$ on E_{α} and $\phi^2 \leq \alpha$ on $\Omega \setminus E_{\alpha}$. In the second case, $\int_{\Omega} [\bar{m}(\phi) - m] \phi^2 = \int_{E_0} (m_1 - m) \phi^2 \geq 0$. Thus in either case, we have $\int_{\Omega} \bar{m}(\phi) \phi^2 \geq \int_{\Omega} m \phi^2$ for all $m \in \mathcal{M}$. Suppose now that $m \in \mathcal{M}$ is given and that $\phi \in W_0^{1,2}(\Omega)$ is the eigenfunction corresponding to $\lambda_1^+(m)$. Then we have $\int_{\Omega} m \phi^2 > 0$, and thus $\int_{\Omega} \bar{m}(\phi) \phi^2 > 0$. Hence,

$$\begin{aligned} \lambda_1^+(\bar{m}(\phi)) &= \inf_{\substack{\psi \in W_0^{1,2}(\Omega) \\ \int_{\Omega} \psi^2 > 0}} \frac{\int_{\Omega} |\nabla \psi|^2}{\int_{\Omega} \bar{m}(\phi) \psi^2} \\ &\leq \frac{\int_{\Omega} |\nabla \phi|^2}{\int_{\Omega} \bar{m}(\phi) \phi^2} \leq \frac{\int_{\Omega} |\nabla \phi|^2}{\int_{\Omega} m \phi^2} = \lambda_1^+(m). \end{aligned} \quad (3.13)$$

It follows that $\lambda_0 \equiv \inf \{ \lambda_1^+(m) : m \in \mathcal{M} \} = \inf \{ \lambda_1^+(m_1 \chi_E - m_2 \chi_{\Omega \setminus E}) : E \subseteq \Omega \text{ is measurable, with } m_1 |E| - m_2 |\Omega \setminus E| = m_0 \}$. (This infimum is positive, as $\lambda_1^+(m) \geq \lambda_1^+(m_1)$ for $m \in \mathcal{M}$.) To see that the infimum is attained, choose a sequence of weights $m_n \in \mathcal{M}$ such that $\lambda_1^+(m_n) \downarrow \lambda_0$ as $n \rightarrow \infty$, and let ϕ_n be the eigenfunction for $\lambda_1^+(m_n)$ normalised by $\sup_{\Omega} \phi_n = 1$. Then we have $-\Delta \phi_n = \lambda_1^+(m_n) m_n \phi_n$ in Ω ,

$\phi_n = 0$ on $\partial\Omega$, with $\{ \lambda_1^+(m_n) m_n \phi_n \}$ uniformly bounded in $L^{\infty}(\Omega)$. Hence, by standard elliptic theory, $\{ \phi_n \}$ is uniformly bounded in $W^{2,p}(\Omega) \cap W_0^{1,p}(\Omega)$ for any $p \in [1, \infty)$. Since $W^{2,p}(\Omega) \hookrightarrow C^{1+\alpha}(\bar{\Omega})$ compactly for p sufficiently large, we may choose a subsequence, which by reindexing we may still call $\{ \phi_n \}$, such that as $n \rightarrow \infty$, $\phi_n \rightarrow \phi_{\infty}$ in $C^{1+\alpha}(\bar{\Omega})$ for some $\phi_{\infty} \in C^{1+\alpha}(\bar{\Omega})$. Since the convergence is in $C^{1+\alpha}(\bar{\Omega})$, we have $\phi_{\infty} = 0$ on $\partial\Omega$ and $\sup_{\Omega} \phi_{\infty} = 1$, so that $\phi_{\infty} \not\equiv 0$. Also,

$C^{1+\alpha}(\bar{\Omega}) \hookrightarrow W^{1,2}(\Omega)$, so we have $\lim_{n \rightarrow \infty} \int_{\Omega} |\nabla \phi_n|^2 = \int_{\Omega} |\nabla \phi_{\infty}|^2$, and $\int_{\Omega} |\nabla \phi_{\infty}|^2 \neq 0$

since $\phi_{\infty} \not\equiv 0$. Let $\psi_n = \phi_n / (\int_{\Omega} |\nabla \phi_n|^2)^{\frac{1}{2}}$ and $\psi_{\infty} = \phi_{\infty} / (\int_{\Omega} |\nabla \phi_{\infty}|^2)^{\frac{1}{2}}$. Then $\psi_n \rightarrow \psi_{\infty}$ in $C^{1+\alpha}(\bar{\Omega})$, and $\int_{\Omega} |\nabla \psi_n|^2 = \int_{\Omega} |\nabla \psi_{\infty}|^2 = 1$. Hence $\int_{\Omega} m_n \psi_n^2 = 1 / \lambda_1^+(m_n)$. Recall that in general, if $\psi \in W_0^{1,2}(\Omega)$ with $\int_{\Omega} |\nabla \psi|^2 = 1$ then $\int_{\Omega} m \psi^2 \leq 1 / \lambda_1^+(m)$. We can now construct the weight for which the infimum in the class \mathcal{M} is attained. Our choice is $m = \bar{m}(\psi_{\infty})$, which by our construction is a function of the form $m_1 \chi_E - m_2 \chi_{\Omega \setminus E}$ and belongs to \mathcal{M} . To see that $\lambda_1^+(\bar{m}(\psi_{\infty})) = \lambda_0$, observe that $1/\lambda_0 \geq 1/\lambda_1^+(\bar{m}(\psi_{\infty})) \geq \int_{\Omega} \bar{m}(\psi_{\infty}) \psi_{\infty}^2 \geq \int_{\Omega} m_n \psi_n^2$ for any n . Thus

$$1/\lambda_0 \geq 1/\lambda_1^+(\bar{m}(\psi_{\infty})) \geq \int_{\Omega} m_n \psi_n^2 = \int_{\Omega} m_n \psi_n^2 + \int_{\Omega} m_n (\psi_{\infty}^2 - \psi_n^2). \quad (3.14)$$

As $n \rightarrow \infty$, $\int_{\Omega} m_n \psi_n^2 = 1/\lambda_1^+(m_n) \rightarrow 1/\lambda_0$ by our choice of $\{m_n\}$, and since $|m_n| \leq m_1 + m_2$ for all n and $\psi_n \rightarrow \psi_{\infty}$ in $C^{1+\alpha}(\bar{\Omega})$, we may take the limit as $n \rightarrow \infty$ in (3.14) to obtain $1/\lambda_0 \geq 1/\lambda_1^+(\bar{m}(\psi_{\infty})) \geq 1/\lambda_0$, so $\lambda_0 \equiv \inf \{ \lambda_1^+(m) : m \in \mathcal{M} \} = \lambda_1^+(\bar{m}(\psi_{\infty}))$ as desired.

Remark 3.10. If we view $m(x)$ as a control on $\lambda_1^+(m)$ and we consider a control that minimises $\lambda_1^+(m)$ to be optimal, then Theorem 3.9 says that an optimal control exists, and is “bang-bang”.

The proof of Theorem 3.9 is based on the idea of looking at rearrangements of the weight m . Combining this idea with Schwarz symmetrisation, it is fairly easy to see that if we specify $|\Omega|$ rather than Ω , but impose the same conditions on m as in the theorem, the lowest value of $\lambda_1^+(m)$ occurs when Ω is a ball and $m = m_1\chi_E - m_2\chi_{\Omega \setminus E}$, where $E \subseteq \Omega$ is also a ball, concentric with Ω , with radius such that $m_1|E| - m_2|\Omega \setminus E| = m_0$. This fact was pointed out to us by H. F. Weinberger [46].

4. Solution estimates

The analysis in Section 2 shows that (1.1) has a positive steady state if and only if $d < 1/\lambda_1^+(m)$. We now consider how the size of the steady state depends on d and m , and how the steady state behaves as $d \downarrow 0$. At the end of the section we briefly discuss the rate of decrease of solutions to (1.1) as $t \rightarrow \infty$ if $d > 1/\lambda_1^+(m)$.

Our first result gives a bound for $\|u\|_1 = \int_{\Omega} u$, which represents the total population being modelled.

THEOREM 4.1. *Suppose that $m \in L^\infty(\Omega)$ with $m(x) > 0$ on a set of positive measure, and that $0 < d < 1/\lambda_1^+(m)$. If u is the positive solution to*

$$\left. \begin{aligned} -d\Delta u &= m(x)u - u^2 && \text{in } \Omega, \\ u &= 0 && \text{on } \partial\Omega, \end{aligned} \right\} \quad (4.1)$$

then

$$\|u\|_1 \leq [1 - d\lambda_1^+(m)] \|m_+\|_3 |\Omega|^{\frac{2}{3}}. \quad (4.2)$$

Proof. Since u is a weak solution of (4.1) in $W_0^{1,2}(\Omega)$, we have $0 < d \int_{\Omega} |\nabla u|^2 + \int_{\Omega} u^3 = \int_{\Omega} mu^2$. Thus, by [35], $\lambda_1^+(m) \int_{\Omega} mu^2 \leq \int_{\Omega} |\nabla u|^2$. Using Hölder's inequality and noting that $\int_{\Omega} mu^2 \leq \int_{\Omega} m_+ u^2$, we have $0 < \|u\|_3^3 = \int_{\Omega} u^3 \leq [1 - d\lambda_1^+(m)] \int_{\Omega} mu^2 \leq [1 - d\lambda_1^+(m)] \|m_+\|_3 \|u^2\|_3$ so that $\|u\|_3 \leq [1 - d\lambda_1^+(m)] \|m_+\|_3$, since $\|u^2\|_3 = \|u\|_3^2$. Since Hölder's inequality also implies $\|u\|_1 \leq \|u\|_3 |\Omega|^{\frac{2}{3}}$, we have (4.2).

Remark 4.2. The bound on u implied by (4.2) decreases as d increases or $\lambda_1^+(m)$ increases.

We now consider the question of how solutions to (4.1) behave as $d \downarrow 0$. That is a singular perturbation problem, and we shall utilise some results from that theory, as developed by DeSanti [14]. For this discussion, we follow the usual convention and write $d = \varepsilon^2$. We shall also use the method of upper and lower solutions. Our approach is to obtain global upper and lower solutions by patching together local upper and lower solutions constructed to satisfy the results of [14], then to compare u with those global upper and lower solutions. For the comparison, we need the following.

LEMMA 4.3. *Suppose that $u, \bar{u} \in W^{1,2}(\Omega) \cap C(\bar{\Omega})$ satisfy (in the weak sense)*

$u \leq \bar{u}$ in Ω , and

$$\left. \begin{aligned} -\varepsilon^2 \Delta u &\leq m(x)u - u^2 && \text{in } \Omega, \\ u &\geq 0 && \text{on } \partial\Omega, \end{aligned} \right\} \quad (4.3)$$

$$\left. \begin{aligned} -\varepsilon^2 \Delta \bar{u} &\geq m(x)\bar{u} - \bar{u}^2 && \text{in } \Omega, \\ \bar{u} &\geq 0 && \text{on } \partial\Omega. \end{aligned} \right\} \quad (4.4)$$

Then (4.1) has a solution u satisfying $u \leq u \leq \bar{u}$. By the uniqueness results of Section 2, if $u \geq 0$, $u \neq 0$, then the positive solution of (4.1) satisfies $u \leq u \leq \bar{u}$.

Discussion 4.4. Lemma 4.3 follows from the maximum principle for weak elliptic differential inequalities in $W^{1,2}(\Omega)$ ([20, Theorems 8.1 and 8.19]) and a rather standard monotone iteration argument (e.g. [2, Theorem 6.1]). Since these ideas are well known, we omit the details of the proof. Some related ideas or results are used in [7, 11, 14]. ([14, Theorem 2.2] is close to our Lemma 4.3 but requires slightly more regularity than is available to us.)

To patch together local upper and lower solutions, we need the following lemma, due to Berestycki and Lions ([5, Lemma 1.1]).

LEMMA 4.5. Suppose that Ω_i is a subdomain of Ω with $\partial\Omega_i$ of class $C^{2+\alpha}$ such that $\bar{\Omega}_i \subseteq \Omega$. Let v denote the outward normal to Ω_i and let $\Omega_2 = \Omega \setminus \Omega_i$. If $v_i \in W^{2,2}(\Omega_i)$, $-\varepsilon^2 \Delta v_i \leq f_i$ on Ω_i with $f_i \in L^1(\Omega_i)$ for $i = 1, 2$, with $v_1 = v_2$ and $\frac{\partial v_1}{\partial v} \leq \frac{\partial v_2}{\partial v}$ on $\partial\Omega_i$, then the function $v = v_i(x)$ for $x \in \Omega_i$ belongs to $W^{1,2}(\Omega)$ and satisfies $-\varepsilon^2 \Delta v \leq f$ in the weak sense on Ω , where $f = f_i(x)$ for $x \in \Omega_i$. Similarly, if $w_i \in W^{2,2}(\Omega_i)$ with $-\varepsilon^2 \Delta w_i \geq f_i$ on Ω_i for $i = 1, 2$ and $w_1 = w_2$, $\frac{\partial w_1}{\partial v} \geq \frac{\partial w_2}{\partial v}$ on $\partial\Omega_i$, then $w = w_i(x)$ for $x \in \Omega_i$ satisfies $-\varepsilon^2 \Delta w \geq f$ in the weak sense.

To analyse our local upper and lower solutions we use a result of De Santi ([14, Theorem 3.1]) (In [14], the result is formulated in \mathbf{R}^2 , but it is noted that it extends to \mathbf{R}^n . Also, the equations in [14] are always written $\varepsilon^2 \Delta u = \dots$, so the notation differs from ours by a minus sign.)

LEMMA 4.6. Consider the problem

$$\left. \begin{aligned} -\varepsilon^2 \Delta w &= k(x, w) && \text{in } \Omega, \\ w &= f(x) && \text{on } \partial\Omega, \end{aligned} \right\} \quad (4.5)$$

where $\Omega \subseteq \mathbf{R}^n$ is a bounded domain with $\partial\Omega$ given by $F(x) = 0$ where $F \in C^1(\mathbf{R}^n)$ and $\nabla F \neq 0$ on $\partial\Omega$, and where $k(x, w) \in C^2(\Omega \times \mathbf{R})$, $f(x) \in C^2(\partial\Omega)$. Let $K(x, w) = \int_0^w k(x, s) ds$ and suppose that there exists $g(x) \in C^2(\Omega)$ such that

- (i) $k(x, g(x)) = 0$ in Ω ,
- (ii) $k_w(x, g(x)) \leq -k_0 < 0$ in Ω for some positive constant k_0 , and
- (iii) $[K(x, w) - K(x, g(x))][f(x) - g(x)] < 0$ for all $w \in (g(x), f(x))$ or $[f(x), g(x)]$ and all $x \in \partial\Omega$.

Then for ε sufficiently small, (4.5) has a classical solution $w = w(x, \varepsilon)$ such that $w(x, \varepsilon) \rightarrow g(x)$ as $\varepsilon \downarrow 0$, uniformly on each closed subset of Ω .

We next must apply Lemma 4.6 to some special cases. First, consider

$$\left. \begin{aligned} -\varepsilon^2 \Delta w &= -m_0 w && \text{in } \Omega, \\ w &= m_1 && \text{on } \partial\Omega, \end{aligned} \right\} \quad (4.6)$$

where $m_0, m_1 > 0$. In the notation of Lemma 4.6, we have $k = -m_0 w$, $g = 0$, $f = m_1$, and $K = -m_0 w^2/2$, and the hypotheses of the lemma are satisfied. Also, (4.6) may be written as $-\varepsilon^2 \Delta w + m_0 w = 0$ in Ω , $w = m_1 > 0$ on $\partial\Omega$, so the maximum principle implies $0 < w < m_1$ on Ω and w has positive outward normal derivative on $\partial\Omega$. By Lemma 4.6, we have $w \rightarrow 0$ uniformly on any closed subset of Ω as $\varepsilon \downarrow 0$, so w shows "boundary layer behaviour" as $\varepsilon \downarrow 0$. Next, consider

$$\left. \begin{aligned} -\varepsilon^2 \Delta w &= m_0 w - w^2 && \text{in } \Omega, \\ w &= 0 && \text{on } \partial\Omega, \end{aligned} \right\} \quad (4.7)$$

where $m_0 > 0$. If $m_0/\varepsilon^2 > \lambda_1^+(1)$ then the results of Section 2 imply that (4.7) has a unique positive solution. In fact, a monotone iteration argument using lower solution $\underline{w} = \delta\phi_1$ with $\delta > 0$ small and $\phi_1 > 0$ the eigenfunction for $\Delta\phi = \lambda_1^+(1)\phi$ in Ω , and upper solution $\bar{w} = \text{constant} > m_0$ shows that the positive solution is the maximal solution, and the maximum principle implies that no solution can be larger than m_0 . Hence, if (4.7) possesses any solution w such that $w \rightarrow m_0$ on arbitrary closed subsets of Ω , then the positive solution must also approach m_0 , necessarily from below. Examining (4.7), we see that if we want to have $w \rightarrow m_0$ we must choose $f = 0$, $g = m_0$; but then, hypothesis (iii) of Lemma 4.6 fails. To overcome that problem, we set $z = m_0 - w$. Then z satisfies

$$\left. \begin{aligned} -\varepsilon^2 \Delta z &= -m_0 z + z^2 && \text{in } \Omega, \\ z &= m_0 && \text{on } \partial\Omega. \end{aligned} \right\} \quad (4.8)$$

Now, choosing $f = m_0$, $g = 0$, the hypotheses of Lemma 4.6 are satisfied, and (4.8) thus has a solution with $z \rightarrow 0$ on closed subsets of Ω as $\varepsilon \downarrow 0$.

We have now collected enough results to analyse an important special case of (4.1), namely that where $m(x) = \chi_E - \chi_{\Omega \setminus E}$ for some subset $E \subseteq \Omega$.

THEOREM 4.7. *Suppose that $\partial\Omega$ is of class $C^{2+\alpha}$ and that $m(x) = \chi_E - \chi_{\Omega \setminus E}$ where E is a finite union of open sets with $\bar{E} \subseteq \Omega$ and ∂E of class $C^{2+\alpha}$. If u_ε denotes the positive solution to (4.1) for a given value of ε , then on any closed subset of E , $u_\varepsilon \rightarrow 1$ uniformly as $\varepsilon \downarrow 0$, while on any closed subset of $\Omega \setminus \bar{E}$, $u_\varepsilon \rightarrow 0$ uniformly as $\varepsilon \downarrow 0$. Hence u_ε develops interior layers at ∂E .*

Proof. It follows from the results of Section 2 (and is well known; see [8, 10]) that for $\varepsilon > 0$ sufficiently small, there is a unique positive solution of $-\varepsilon^2 \Delta v_\varepsilon = v_\varepsilon - v_\varepsilon^2$ on E , $v_\varepsilon = 0$ on ∂E , which is the maximal solution. By Lemma 4.6, $v_\varepsilon \rightarrow 1$ uniformly on closed subsets of E as $\varepsilon \rightarrow 0$. Letting $\Omega_1 = E$, $v_1 = v_\varepsilon$, and $v_2 = 0$, we see that the hypotheses of Lemma 4.5 are satisfied with $f_i = m(x)v_i - v_i^2$ since $m \equiv 1$ on E . Thus, taking $\underline{u}_\varepsilon = v_\varepsilon$ on E , $\underline{u}_\varepsilon = 0$ on $\Omega \setminus E$, we obtain a weak lower solution to (4.1) in the sense of (4.3). By the maximum principle, $\underline{u}_\varepsilon = v_\varepsilon < 1$ on E . To construct an upper solution, we may first solve $-\varepsilon^2 \Delta w_\varepsilon = -w_\varepsilon$ on $\Omega \setminus E$, $w_\varepsilon = 1$ on $\partial(\Omega \setminus E)$. The strong maximum principle implies that $0 < w_\varepsilon < 1$ on $\Omega \setminus E$ and that, moreover, if ν is an inner normal to $\Omega \setminus E$, $\partial w_\varepsilon / \partial \nu < 0$. Since $m(x) = -1$

on $\Omega \setminus E$, $-\varepsilon^2 \Delta w_\varepsilon \geq m(x)w_\varepsilon - w_\varepsilon^2$ on $\Omega \setminus E$. Let $w_1 \equiv 1$ on E and $w_2 = w_\varepsilon$ on $\Omega \setminus E$. The hypotheses of Lemma 4.5 hold, and consequently $\bar{u}_\varepsilon = 1$ on E and $\bar{u}_\varepsilon = w_\varepsilon$ is a weak supersolution to (4.1) in the sense of (4.4). Finally, $\bar{u}_\varepsilon = w_\varepsilon \rightarrow 0$ uniformly on closed subsets of $\Omega \setminus E$ as $\varepsilon \rightarrow 0$ by Lemma 4.6.

Since $v_\varepsilon < 1$ on E and $w_\varepsilon > 0$ on $\Omega \setminus E$, we have $0 \leq u_\varepsilon < \bar{u}_\varepsilon$. Applying Lemma 4.3 and the uniqueness of the positive solution of (4.1), we see that $u_\varepsilon \leq u \leq \bar{u}_\varepsilon$ for ε small, and the desired properties of u follow from those of u_ε and \bar{u}_ε .

Let us suppose now that m is not the difference of two characteristic functions, but there exist sets E_1, E_2 satisfying the conditions of Theorem 4.7 with $1 \geq m(x) \geq m_1 > 0$ on E_1 and $-1 \leq m(x) \leq -m_2 < 0$ on E_2 , and with $m \in C^2(E_1 \cup E_2)$. We aim to use the methods employed in the proof of Theorem 4.7 to conclude that the steady state solutions u_ε to (1.1) converge uniformly to $m(x)$ on closed subsets of E_1 and to 0 on closed subsets of E_2 as $\varepsilon \rightarrow 0$. Showing the uniform convergence to 0 on E_2 is relatively straightforward. Let u_ε on E_1 be the unique positive solution to $-\varepsilon^2 \Delta u_\varepsilon = m_1 u_\varepsilon - u_\varepsilon^2$ on E_1 , $u_\varepsilon = 0$ on ∂E_1 , with $u_\varepsilon \equiv 0$ on $\Omega \setminus E_1$; also, let \bar{u}_ε satisfy $-\varepsilon^2 \Delta \bar{u}_\varepsilon = m \bar{u}_\varepsilon$ on E_2 with $\bar{u}_\varepsilon = 1$ on $\Omega \setminus E_2$. Then $0 \leq u_\varepsilon \leq \bar{u}_\varepsilon$, $u_\varepsilon \neq 0$, and by Lemma 4.5 u_ε and \bar{u}_ε are (weak) lower and upper solutions to (4.1), respectively. Lemmas 4.3 and 4.6 are applicable, and we may conclude that $u_\varepsilon \rightarrow 0$ uniformly on closed subsets of E_2 as $\varepsilon \rightarrow 0$. However, on E_1 , we may conclude only that if E' is a closed subset of E_1 and $\alpha > 0$ is given, then $u_\varepsilon(x) > m_1 - \alpha$ for all $x \in E'$ and $0 < \varepsilon < \varepsilon_0$ for a sufficiently small ε_0 .

In order to draw the stronger conclusion that $u_\varepsilon(x) \rightarrow m(x)$ uniformly on closed subsets of E_1 , we prove the following result. The conclusion then follows from a simple compactness argument.

THEOREM 4.8. *Let $x_0 \in E_1$ and let $\alpha > 0$ be given. Then there is an open ball $B_\alpha(x_0)$ about x_0 and an $\varepsilon_{x_0} > 0$ so that $|u_\varepsilon(x) - m(x)| < \alpha$ for all $x \in B_\alpha(x_0)$ and $\varepsilon \in (0, \varepsilon_{x_0})$.*

Proof. Let $\underline{m}_\alpha = m(x_0) - \alpha/4$ and $\bar{m}_\alpha = m(x_0) + \alpha/4$. We will assume that $0 < \underline{m}_\alpha$ and $\bar{m}_\alpha < 1$. If $m(x_0) = 1$, a slight modification in the argument is all that is necessary. Then there is a subdomain $\mathcal{O}_\alpha \subseteq E_2$ with $x_0 \in \mathcal{O}_\alpha$, $\partial \mathcal{O}_\alpha$ sufficiently smooth and $\underline{m}_\alpha \leq m(x) \leq \bar{m}_\alpha$ for all $x \in \mathcal{O}_\alpha$.

Consider the problem

$$\left. \begin{aligned} -\varepsilon^2 \Delta w &= k_\alpha(w) && \text{on } \mathcal{O}_\alpha, \\ w &= 1 && \text{on } \partial \mathcal{O}_\alpha, \end{aligned} \right\} \tag{4.9}$$

where $k_\alpha(w) = \bar{m}_\alpha w - w^2$ for $w \geq \bar{m}_\alpha/2$, $k_\alpha(w) > 0$ for $w < \bar{m}_\alpha/2$ and $k_\alpha \in C^2(\mathbf{R})$. Then by the maximum principle any solution to (4.9) satisfies $\bar{m}_\alpha \leq w \leq 1$ on \mathcal{O}_α since $k_\alpha(w) > 0$ for $w < \bar{m}_\alpha$ and $k_\alpha(w) < 0$ for $w > 1$. Moreover, since $\bar{m}_\alpha \leq w \leq 1$ implies that $-\varepsilon^2 \Delta w \leq 0$, the strong maximum principle implies that $\partial w / \partial \eta > 0$ on $\partial \mathcal{O}_\alpha$ since $w \neq 1$.

We find that $k_\alpha(\bar{m}_\alpha) = 0$, $k'_\alpha(\bar{m}_\alpha) = -\bar{m}_\alpha < 0$, and that if $K_\alpha(w) = \int_0^w k_\alpha(s) ds$, $K'_\alpha(w) = k_\alpha(w) < 0$ for $w \in (\bar{m}_\alpha, 1]$. Consequently, $K_\alpha(w) - K_\alpha(\bar{m}_\alpha) < 0$ if $w \in (\bar{m}_\alpha, 1]$ and Lemma 4.6 is applicable with $f = 1$ and $g = \bar{m}_\alpha$. Hence there exist classical solutions w_ε to (4.9) with $\bar{m}_\alpha \leq w_\varepsilon \leq 1$ on \mathcal{O}_α , $\partial w_\varepsilon / \partial \eta > 0$ on $\partial \mathcal{O}_\alpha$, and w_ε converging uniformly to \bar{m}_α on closed subsets of \mathcal{O}_α . Letting $\bar{u}_\varepsilon = w_\varepsilon$ on \mathcal{O}_α and 1

on $\Omega \setminus \mathcal{O}_\alpha$, $-\varepsilon^2 \Delta \bar{u}_\varepsilon = \bar{m}_\alpha w - w^2 \geq m(x)w - w^2$ on \mathcal{O}_α . Hence Lemma 4.5 implies that \bar{u}_ε is an upper solution for (4.1).

If we solve

$$\begin{aligned} -\varepsilon^2 \Delta v &= m_\alpha v - v^2 && \text{on } \mathcal{O}_\alpha, \\ v &= 0 && \text{on } \partial \mathcal{O}_\alpha, \\ v &> 0 && \text{in } \mathcal{O}_\alpha, \end{aligned}$$

as in (4.7), then there is a solution v_ε which converges uniformly to m_α on closed subsets of \mathcal{O}_α as $\varepsilon \rightarrow 0$. Recalling that $\partial v_\varepsilon / \partial \eta < 0$ on $\partial \mathcal{O}_\alpha$ and $0 < v_\varepsilon < m_\alpha$, we have that $\underline{u}_\varepsilon = v_\varepsilon$ on \mathcal{O}_α and $\underline{u}_\varepsilon = 0$ on $\Omega \setminus \mathcal{O}_\alpha$ is a lower solution to (4.1) by Lemma 4.5 and that $\underline{u}_\varepsilon \leq m_\alpha < \bar{m}_\alpha \leq \bar{u}_\varepsilon$. We may now choose $B_\alpha(x_0)$ to be any closed ball about x_0 properly contained in \mathcal{O}_α . There is an $\varepsilon_{x_0} > 0$ so that $\underline{u}_\varepsilon(x) > m_\alpha - \alpha/4$ and $\bar{u}_\varepsilon(x) < \bar{m}_\alpha + \alpha/4$ for all $x \in B_\alpha(x_0)$ and $\varepsilon \in (0, \varepsilon_{x_0})$. Consequently, $m_\alpha - \alpha/4 < \underline{u}_\varepsilon(x) < \bar{m}_\alpha + \alpha/4$ for $x \in B_\alpha(x_0)$ and $0 < \varepsilon < \varepsilon_{x_0}$. Since $\bar{m}_\alpha + (\alpha/4) - (m_\alpha - \alpha/4) = \alpha$, the theorem is established.

If $\partial E_1 \cap \partial E_2 \neq \emptyset$, then u_ε forms a layer at $\partial E_1 \cap \partial E_2$ as $\varepsilon \rightarrow 0$. If the regions where m is positive are separated from those where m is negative by an open set where m is zero, no layers can be expected. In the one-dimensional case, u must be linear where m is zero, and so for $m = \chi_{E_1} - \chi_{E_2}$ and ε small, we will have u near zero on E_2 , near one on E_1 , and near line segments interpolating between zero and one on $\Omega \setminus (E_1 \cup E_2)$.

So far we have only estimated the size of steady states to (1.1) when $d < 1/\lambda_1^+(m)$. If $d > 1/\lambda_1^+(m)$ then solutions to (1.1) tend to zero as $t \rightarrow \infty$. We can estimate the rate of decay as follows.

THEOREM 4.9. *Suppose that u satisfies*

$$\left. \begin{aligned} u_t &= d \Delta u + mu - u^2 && \text{on } \Omega \times (0, \infty), \\ u &= 0 && \text{on } \partial \Omega \times (0, \infty), \\ u &= u_0 \geq 0 && \text{on } \Omega \times \{0\}, \end{aligned} \right\} \quad (4.10)$$

with $m \in L^\infty(\Omega)$ and $m > 0$ on a set of positive measure. If $d > 1/\lambda_1^+(m)$, then

$$\int_\Omega u(x, t) dx \leq K \exp\{[-d + (1/\lambda_1^+(m))]\lambda_1^+(1)t\} \quad (4.11)$$

where K depends only on u_0 and Ω .

Proof. Let $E(t) = \frac{1}{2} \int_\Omega u^2(x, t) dx$. Then

$$\begin{aligned} E'(t) &= \int_\Omega uu_t dx = d \int_\Omega u \Delta u dx + \int_\Omega mu^2 dx - \int_\Omega u^3 dx \\ &\leq [-d + (1/\lambda_1^+(m))] \int_\Omega |\nabla u|^2 dx - \int_\Omega u^3 dx \\ &\leq [-d + (1/\lambda_1^+(m))]\lambda_1^+(1) \int_\Omega u^2 dx - |\Omega|^{-\frac{1}{2}} \left(\int_\Omega u^2 dx \right)^{\frac{3}{2}}, \end{aligned}$$

so we have

$$\begin{aligned} E'(t) &\leq 2[-d + (1/\lambda_1^+(m))]\lambda_1^+(1)E(t) - 2^{\frac{3}{2}}|\Omega|^{-\frac{1}{2}}E^{\frac{3}{2}}(t) \\ &\leq 2[-d + (1/\lambda_1^+(m))]\lambda_1^+(1)E(t). \end{aligned} \quad (4.12)$$

Thus, $E(t) \leq \exp\{2[-d + (1/\lambda_1^+(m))]\lambda_1^+(1)t\}E(0)$ and since $\int_{\Omega} u dx \leq |\Omega|^{\frac{1}{2}}(\int_{\Omega} u^2 dx)^{\frac{1}{2}} = 2^{\frac{1}{2}}|\Omega|^{\frac{1}{2}}E^{\frac{1}{2}}(t)$, (4.11) follows.

Remark 4.10. The estimate (4.12) may actually give faster decay for u than is implied by (4.11), at least when u is large; however, the last term in (4.12) becomes negligible when u is close to zero.

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