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The evolution of dispersal rates in a heterogeneous time-periodic environment

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Abstract. A reaction-diffusion model for the evolution of dispersal rates is considered in which there is both spatial heterogeneity and temporal periodicity. The model is restricted to two phenotypes because of technical difficulties, but a wide range of mathematical techniques and computational effort are needed to obtain useful answers. We find that the question of selection is a great deal richer than in the autonomous case, where the phenotype with the lowest diffusion is selected for. In the current model either the lower or higher diffuser rate may be selected, or there may be coexistence of phenotypes. The paper raises several open questions and suggests in particular that a mutation-selection multi-phenotypic model would repay study.

1. Introduction

It has now become well accepted that it is essential to include the spatial environment in ecological, evolutionary and/or genetic models (see [24, 36] for a variety of perspectives and references). However, as soon as a spatial component is introduced into the analysis, it becomes important to understand dispersal within the environment and in particular the mechanisms for the evolution of dispersal rates. Within the biological literature one can find the following claims:

1. Spatial heterogeneities occur at all scales of the environment [20].
2. Spatial variation that is temporally constant tends to reduce dispersal rates [4, 18, 25].
3. Temporal changes in the environment tend to lead to higher dispersal rates [4, 18, 37].
4. If habitats fluctuate both spatially and temporally, then the interaction between the two determines the optimal dispersal rate [4]; alternatively there is the claim that it can lead to coexistence of phenotypes with differing dispersal rates [25].

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The most direct way of incorporating the first point, and the path that we shall follow, is to view space as a continuous variable. Having made this choice, the purpose of this paper is to present a mathematically tractable model which permits precise formulations of claims 2-4, and then to examine to what extent they are valid.

Up to this point we have been deliberately vague as to our definition of dispersal. Obviously organisms have developed a wide variety of dispersal mechanisms and no single model will be able to capture all of them. Since we wish to understand as clearly as possible the mechanism behind the evolution of dispersal rates we have chosen the simplest dispersal model consistent with a continuous spatial variable, namely diffusion. Furthermore, since our goal is to understand how spatial and temporal heterogeneity in and of themselves have an evolutionary impact we have used a haploid model of a species where the only phenotypic difference is the diffusion rate. Finally, we assume that the evolution is driven by competition and that the local fitness is density dependent.

With this in mind, consider 2 phenotypes of a species with densities $u(x,t)$ and $v(x,t)$ at the point x in the smooth bounded domain $\Omega \subset \mathbb{R}^n$ at time t. The phenotypes u and v have diffusion rates μ and ν respectively where it is assumed that

$$0 < \mu \leq \nu.$$

Thus, u always represents the phenotype with the slower dispersal rate. Since the phenotypes are taken to be identical in all other aspects, they both experience the same per-capita rate of increase $a(x,t)$ though a is allowed to change smoothly in space and time. For the sake of simplicity of exposition we assume a logistic growth function and, of course, intraspecific competition. Thus, the set of equations we will consider take the form

$$\begin{aligned} \frac{\partial u}{\partial t} &= \mu \Delta u + (a(x,t) - u - v)u, \\ \frac{\partial v}{\partial t} &= \nu \Delta v + (a(x,t) - u - v)v, \quad x \in \Omega,\ t > 0. \end{aligned} \tag{1.1}$$

Again, to avoid the introduction of extraneous events we impose Neumann boundary conditions

$$\frac{\partial u}{\partial n} = 0, \quad \frac{\partial v}{\partial n} = 0 \qquad \text{on } \partial\Omega,\ t > 0, \tag{1.2}$$

where n is the unit outward normal to $\partial\Omega$; this corresponds to the assumption that there is no migration across the physical boundary of the region.

We begin by returning to the first claim that spatial heterogeneities occur on all levels. In particular, we interpret this in two ways. Given a fixed spatial domain there is either no minimal size on which the environment should be viewed as homogeneous; or, perhaps more reasonably, the size of the homogeneous regions is small as compared to the size of the entire domain. In the first case, a continuous model is necessary, and in the second, the continuous model should be viewed as an approximation to a high dimensional system consisting of many different homogeneous regions.

A considerable body of literature on the evolution of dispersal has appeared in the last few years. A significant portion of the theoretical work that led to the above mentioned claims are based on patch models, and an extensive list of references may be found in the reviews [18,4,8] and in the papers [6,17,25,37] for example. We therefore wish to enquire to what extent this class of model is related to the reaction-diffusion model (1.1). In the setting of a patch model, the environment is essentially viewed as a collection of distinct patches and dispersal is taken to be movement between the patches. This leads to a system of ordinary differential equations, or more typically to a system of maps (perhaps because the latter are more tractable numerically) discrete in both space and time. These models are notoriously intractable analytically, and in our view this makes it difficult to obtain convincing results concerning the effect of variation in the parameters and indeed the structure of the models themselves. Furthermore, in our view the patch models are quite different from (1.1). Indeed, it is well known that the approximation of continuous evolution equations via discretization in time and/or space is a delicate issue. In particular, it is not uncommon for a coarse discretization, e.g. a patch model with few patches, to exhibit more solutions than the limiting system, in our case the reaction diffusion system. Perhaps the simplest example of this phenomena is the logistic map $x \mapsto ax(1-x)$ which can be obtained via a coarse Euler approximation to the corresponding differential equation $\dot{x} = x(1-x)$. For appropriate values of a the map exhibits chaotic dynamics, thus an infinite number of distinct solutions, while the dynamics of the differential equation is trivial.

Unfortunately, just choosing more patches does not necessarily overcome this problem. High dimensional systems provide better approximations only if the migration matrix incorporates appropriate scalings in space and time (see [27] for such an analysis in the context of genetics). Because such scalings rapidly lead to mathematically intractable systems, this is often not done, in which case the spatial structure of the problem is not explicitly represented in the limiting system (see [1] for a more complete discussion).

Given the above mentioned difficulty of studying high dimensional patch systems which approximate spatially explicit models, one cannot expect that the corresponding partial differential equations should be easy to analyze. Fortunately though the reaction diffusion system (1.1). is sufficiently tractable to allow us to investigate rigorously the effect of simultaneous spatial and temporal fluctuations in the habitat on dispersal rates. Our main aim is then to make a contribution to the study of the rather difficult issues raised in Claim 4, and we outline our approach and some of our main results in Subsection 1.3. However, we first consider Claims 2 and 3 as these are important limiting cases which provide perspective on our results. To simplify the discussion we will assume that the initial conditions for solutions to (1.1) are continuous nonnegative functions, that is

$$u(\cdot,0) = u_0, \quad v(\cdot,0) = v_0 \tag{1.3}$$

where $(u_0, v_0) \in C(\bar{\Omega}) \times C(\bar{\Omega})$ and $u_0, v_0 \geq 0$.

1.1. Spatially heterogeneous but temporally homogeneous

When the environment is time independent, that is $a(x) = a(x,t)$ for all $t \in \mathbb{R}$, rather strong results may be proved [11,5], see Appendix A for details. However, here we shall outline the principal conclusion in biological terms. *It is the case that in a very strong sense, and under very clear conditions on a, the phenotype with the slowest dispersal rate will be selected.* Specifically, coexistence between phenotypes of differing diffusion rates is impossible, and if two phenotypes of differing diffusion rates are present, then the phenotype with the faster diffusion rate is driven to extinction. This is in agreement with Claim 2.

It is tempting to argue that this result follows from the fact that through diffusion individuals are, in effect, moving into areas in which their fitness is reduced. In our view this argument is on its own rather unconvincing, and we are not able to provide a proof of the result along these lines. This is unfortunate, since it is conceivable that such an argument could be applied to understanding the global dynamics of an arbitrary number of phenotypes differentiated only by their diffusion rate.

On the mathematical side, the above assertion, formulated precisely in Theorem 7.1, rests on two important points. The first is that in the time independent case, the principle eigenvalue (which is the one that determines stability) is a monotone function of the diffusion rate. The second is that with only two phenotypes the system is monotone and therefore the global dynamics can be ascertained. Unfortunately, this monotonicity is lost for systems representing three or more phenotypes and so it remains an open question whether Theorem 7.1 can be extended.

1.2. Spatially homogeneous but temporally heterogeneous

The simplest interpretation of the third claim is that temporal heterogeneity can have an effect on dispersal rates even when the environment is spatially homogeneous. This is certainly possible as is shown by the interesting Hamilton, May, Commins patch model discussed in detail in [18]. However, it is probable that often Claim 3 is implicitly rather that a small spatially heterogeneous perturbation imposed on the temporal heterogeneity causes an increase in dispersal rate.

Let us start investigating the situation when the environment is periodic but spatially constant, that is $a(x,t) = a(t)$ for all $x \in \Omega$. The periodicity of a is assumed for the sake of simplicity, but note that the much more general class of almost periodic functions can be dealt with in a similar manner. We refer the reader to Appendix A for additional remarks about this point and for the precise statement of a theorem on which the following is based. *With the environment as assumed above, for any nonnegative initial conditions u_0, v_0, the solution (u, v) of (1.1) -(1.3)) tends to a spatially homogeneous solution $(u^*(t), v^*(t))$ as $t \to \infty$.* One can also show that each such limit solution $(u^*(t), v^*(t))$ is stable, hence spatially heterogeneous perturbations die out. This is in contrast with patch models [1] which permit solutions in which different patches support different numbers of individuals at a given time instant.

Returning to the question of dispersal rates, consider any spatially homogeneous solution $u^*(t)/v^*(t)$ with $v^*(0) \neq 0$. From (1.1) we then obtain $dw/dt = 0$, where $w(t) = u^*(t)/v^*(t)$. That is, the ratio of u^* to v^* is constant in time, and there is no selection on the dispersal rate.

On the other hand, suppose an additional spatial perturbation is imposed on the environment. Then the analysis in Section 3.2, in particular (3.5), suggests that there may be selection for either lower or higher dispersal rate. We summarize these observations as follows.

Conclusion 1. *Temporal variability in the absence of spatial heterogeneity does not select for or against dispersal. However, an additional small spatio-temporal change in the environment may cause either selection for or against dispersal.*

It is worth speculating why this conclusion is at odds with the perceptions of the biological community. Another way of stating this conclusion is that temporal variability has a neutral effect on dispersal rates. Thus, small perturbations to the model could lead to dramatic changes in the asymptotic states and hence the selection for faster or slower diffusion. In many of the models which examine dispersal rates against fluctuations in the environment the populations have distinguishing features beyond just their dispersal rates; for further discussion see for example [18, 6, 26, 7, 21, 8]. It is conceivable that it is the interaction of these distinguishing features and the time variability that has raised the idea that temporal changes lead to higher dispersal rates. After all, as will be made clear in this paper, the interaction between temporal and spatial variability can lead to a variety of outcomes.

In conclusion, it is worth noting in view of what follows that the above shows that spatial homogeneity is a somewhat degenerate assumption in the context of our model. For there is a family of homogeneous periodic solutions (u^*, v^*) with positive components which attracts all solutions (u, v) with positive initial conditions. Thus for any non-trivial initial conditions one gets coexistence asymptotically. This contrasts with the situation described in section 1.1 and with that which follows.

1.3. Spatially and temporally heterogeneous

In this subsection we summarize the main body of our investigation, which is the analysis of system (1.1) when a is allowed to have an arbitrary dependence on space but is periodic in time. We remark that if more generally an arbitrary dependence on time is allowed, the analysis is likely to be considerably more difficult.

Thus we will recast (1.1) in the form

$$\begin{aligned} \frac{\partial u}{\partial t} &= \mu\Delta u + (a(x,\omega t) - u - v)u, \\ \frac{\partial v}{\partial t} &= \nu\Delta v + (a(x,\omega t) - u - v)v, \quad x \in \Omega,\ t > 0 \end{aligned} \tag{1.4}$$

where $\omega > 0$ represents the frequency of the periodic oscillation. Rescaling the time variable of (1.4) leads to

$$\begin{aligned} \omega\frac{\partial u}{\partial t} &= \mu\Delta u + (a(x,t) - u - v)u, \\ \omega\frac{\partial v}{\partial t} &= \nu\Delta v + (a(x,t) - u - v)v, \quad x \in \Omega,\ t > 0. \end{aligned} \tag{1.5}$$

We impose the following assumption which is a standing hypothesis for the remainder of this paper:

(H) a is a continuous function on $\bar{\Omega} \times \mathbb{R}$ and it is 1-periodic in t. Furthermore, $\omega > 0$ and $0 < \mu \leq \nu$ (usually, it is assumed that $\mu < \nu$).

Before continuing we make a few remarks on the mathematical setting of the problem. We make it a **standing convention** that Neumann boundary conditions are imposed on solutions of all parabolic equations considered in the paper. The initial conditions for problem (1.5) are assumed to lie in $X := C(\bar{\Omega}) \times C(\bar{\Omega})$. By solutions of (1.5), (1.2), we understand mild solutions, that is solutions of the corresponding variation of constant formula (see [12, 23]). If a is Hölder continuous, then these are classical solutions. When referring to periodic solutions of (1.5), we mean, unless stated otherwise, solutions that are 1-periodic in t.

It is within the context of this model that we have investigated the relationship between dispersal rates and spatial and temporal heterogeneity, and been able to draw the following conclusions for our model with two phenotypes.

Conclusion 2. *For a given spatio-temporal heterogeneous environment, there need not be an optimal dispersal rate ('optimal' being used here in the sense of 'selected for').*

As is shown in Section 4 under certain conditions on $a(x, t)$ and μ sufficiently small we are able to prove the existence of an asymptotically stable periodic solution in which both variables u and v are positive. Furthermore, our numerical investigations suggest that this is a fairly common phenomenon. We discuss this issue further in Section 6.

As is pointed out in the review article of Gaines and Johnson [18] there are few empirical tests for the evolution of dispersal. However, this conclusion adds yet another difficulty to such an undertaking. Measuring precise dispersal rates of a population is extremely difficult. Since in our model we are assuming that the only phenotypic difference between individuals are their dispersal rates it is difficult to imagine how an experimentalist would be able to distinguish between individuals with different dispersal rates and errors in measuring the rate. In particular, this result suggests that averaging of measurements between different individuals requires justification.

Conclusion 3. *A given spatio-temporal heterogeneous environment can select for the higher dispersal rate.*

Given the results in the settings of only spatial variability or only temporal variability, this result is somewhat surprising since it indicates that interaction between spatial and temporal changes can completely reverse the effects of spatial heterogeneity alone. In particular, Theorem 5.2 states that under certain conditions the global attractor for the set of positive initial conditions is a periodic solution $(0, v^*(x, t))$. Thus the phenotype with the slower diffusion rate is driven to extinction.

Conclusion 4. *Given any spatio temporal heterogeneous environment, if the frequency of oscillation ω is too large or too small then the phenotype displaying the higher dispersal rate is driven to extinction.*

The precise formulation of this conclusion can be found in Theorem 5.3, however the point that needs to be made is that this reinforces our feeling that the assertion that temporal variability selects for dispersal must be used cautiously. In fact, our numerical simulations suggest that given a fixed $a(x, t)$ if there is a range of frequencies ω for which either one has coexistence of both phenotypes or one has selection of the faster diffuser, then it is rather narrow; there is what might tentatively be described as a 'tuning' in operation. We return to this point in Section 6.

1.4. Outline of contents

Sections 2-5 consist of a theoretical and numerical examination of asymptotic (large time) behavior of the system (1.6), with the aim of discovering the conditions under which one or the other of the phenotypes is selected or coexistence of phenotypes holds. Since the periodic-parabolic problem is considerably more difficult than the corresponding problem considered in [5], a wide range of mathematical techniques needs to be used. For example, in order to resolve the large ν behavior, we employ (an extension of) a shadow-system lemma in [9], and to understand the dynamics when $\omega \to \infty$ we rely on the method of averaging. We also construct a number of classes of examples to show that certain types of behavior can arise. The investigation throws up a number of open problems.

In Section 2 we examine the principal eigenvalue of a scalar periodic-parabolic problem, focusing on its dependence on the diffusion coefficient. We also make some remarks on its dependence on frequency. Both theoretical and computational results are obtained, which extend the discussion in [13] and make a contribution towards obtaining a broader view of the behavior of the periodic-parabolic eigenvalue. In Section 3, we consider semitrivial periodic solutions, by which we mean time-periodic solutions (u, v) of (1.5) with $u \geq 0$, $v \geq 0$ and with exactly one of the components identically equal to zero. We discuss stability properties of such solutions under various assumptions on the parameters. For easy reference, these results are summarized in a table at the end of the section.

In Section 4, we address the problem of coexistence. Thus we deal with the question whether a stable periodic solution with both components positive may exist. We give sufficient conditions for this to happen. Using an explicit example, we also indicate how a coexistence solution can appear and disappear via bifurcations at semitrivial periodic solutions.

In Section 5, we describe the global dynamics of (1.4). At present we are only able to do this in a few special cases, where the global attractor turns out to be one of the semitrivial periodic solutions. We indicate basic problems that one has to face when attempting more general results.

Finally, in Section 6, we pick out a number of particular points of interest which have arisen during this investigation and discuss some of the biological implications.

2. The principal eigenvalue

A central notion in our investigation is that of the principal eigenvalue of a linear periodic-parabolic operator. In this section we recall some of its basic properties which are used throughout the paper. We then study in some detail the dependence of the eigenvalue on the diffusion coefficient. The main result says that, in contrast to the time-independent problem, the principal eigenvalue may not be monotone in the diffusion coefficient. This observation will help us to construct examples of problems (1.5) demonstrating interesting phenomena that do not occur in autonomous equations. We conclude with some remarks on the dependence of the eigenvalue on the frequency ω. This section is crucial for an understanding of the later analysis. However, in order not to interrupt the outline of the investigation, we put the proofs of technical results in Appendix B.

Consider the eigenvalue problem

$$\omega \frac{\partial \phi}{\partial t} - \rho \Delta \phi - h(x,t)\phi = \lambda \phi, \qquad x \in \Omega,\ t \in \mathbb{R} \tag{2.1}$$

where ω, ρ are positive constants and h is a continuous function that is 1-periodic in t. Recall, that by our standing convention, a zero Neumann boundary condition is imposed on ϕ.

The *principal eigenvalue* of (2.1) is a real number λ such that (2.1) has a positive 1-periodic solution. It is known (see [13]) that such a value exists, that it is unique and that the corresponding 1-periodic solution ϕ is unique up to a scalar multiple. The eigenvalues of (2.1) can equivalently be discussed in terms of the period-1 map (that is, the Poincaré map) $\Pi : C(\bar{\Omega}) \to C(\bar{\Omega})$ of the equation

$$\omega \frac{\partial \phi}{\partial t} - \rho \Delta \phi - h(x,t)\phi = 0, \qquad x \in \Omega,\ t > 0. \tag{2.2}$$

In particular, if λ is the principal eigenvalue of (2.1), then $e^{-\lambda}$ is an eigenvalue of Π with a positive eigenfunction. By the Krein-Rutman theorem, it is an algebraically simple eigenvalue, it is greater than the modulus of any other eigenvalue, and no other eigenvalue has a nonnegative eigenfunction. Furthermore, $e^{-\lambda}$ is an eigenvalue of the adjoint operator Π^* whose eigenvector is a nonnegative functional. As a consequence one deduces that λ is the principal eigenvalue of the adjoint problem

$$-\omega \frac{\partial \psi}{\partial t} - \rho \Delta \psi - h(x,t)\psi = \lambda \psi, \qquad x \in \Omega,\ t \in \mathbb{R}. \tag{2.3}$$

(Note that upon time reversal, this becomes a regular periodic-parabolic equation.) See [13] for more details on principal eigenvalues.

We denote by $\lambda(h, \rho)$ the principal eigenvalue of (2.1). By standard results on perturbation of simple eigenvalues (see [22]), $\lambda(h, \rho)$ is a smooth function of $\rho \in (0, \infty)$ and $h \in C(\bar{\Omega} \times [0, 1])$.

We next examine monotonicity properties of $\rho \mapsto \lambda(h, \rho)$. There appears to be a significant difference, crucial in our study, between autonomous and time-periodic equations. When h is independent of t, $\lambda(h, \rho)$ is increasing in ρ, but this may no longer be true in the time periodic case. We state the results precisely.

Theorem 2.1. *If h is independent of t and it is not constant then $\rho \mapsto \lambda(h, \rho)$ is an increasing function:*

$$D_\rho \lambda(h, \rho) > 0 \quad (\rho \in (0, \infty)),$$

where D_ρ denotes the partial derivative with respect to ρ.

In the next theorem and at other places below we frequently use the following notation for the temporal and spatial averages of a function $h : \bar{\Omega} \times \mathbb{R} \to \mathbb{R}$.

$$\hat{h}(x) = \int_0^1 h(x, t)dt$$
$$\bar{h}(t) = \frac{1}{|\Omega|} \int_\Omega h(x, t)dx.$$

We say that a function $h(x, t)$ is spatially homogeneous (or spatially constant) if $h(x, t) = h(y, t)$ for any x, y, t.

Theorem 2.2. *Let $h(x, t) = \hat{h}(x) + \gamma H(x, t)$, where $\gamma \in \mathbb{R}$ (and $\hat{H} \equiv 0$), and suppose that h lies in one of the following classes of functions.*

(a) $\hat{h}$ is constant, and h is not spatially homogeneous.
(b) $\hat{h}(x) \le 0$ $(x \in \bar{\Omega})$, $\int_0^1 \max_{x \in \bar{\Omega}} H(x, t)\, dt > 0$, and γ is large.

Then the following two statements hold.

(i) $D_\rho \lambda(h, \rho) < 0$ for some $\rho > 0$,
(ii) $\lambda(h, \rho_1) = \lambda(h, \rho_2)$ for some $0 < \rho_1 < \rho_2$.

In the autonomous case, $\lambda(h, \rho)$ is the principal eigenvalue of a formally self-adjoint elliptic operator, hence one can use its variational characterization. This can be employed to prove the monotonicity property stated in Theorem 2.1 (see [5]). Alternatively, one can compute the derivative directly using Lemma 2.3 below. An intriguing observation [15] which complements (b) above is that, under weak conditions on h, $\lambda(h, \rho) < \lambda(\hat{h}, \rho)$. That is, effectively independent of the environment, the principal periodic-parabolic eigenvalue is less than the principal eigenvalue for the elliptic problem.

The time-periodic problem does not have a variational structure. Although $\lambda(h, \rho)$ can be shown to be monotone with respect to h, as in the autonomous case, it may in general fail to be monotone in ρ. In fact, Theorem 2.2 shows that it is not monotone for a large class of functions. Figure 1 illustrates this in a special case.

We proceed by stating two preparatory results; their proofs are given in Appendix B. In the first one we compute the derivative of $\lambda(h, \rho)$.

Lemma 2.3. *One has*

$$D_\rho \lambda(h, \rho) = \int_0^1 \int_\Omega \nabla \phi_\rho(x, t) \cdot \nabla \psi_\rho(x, t) dx dt, \tag{2.4}$$

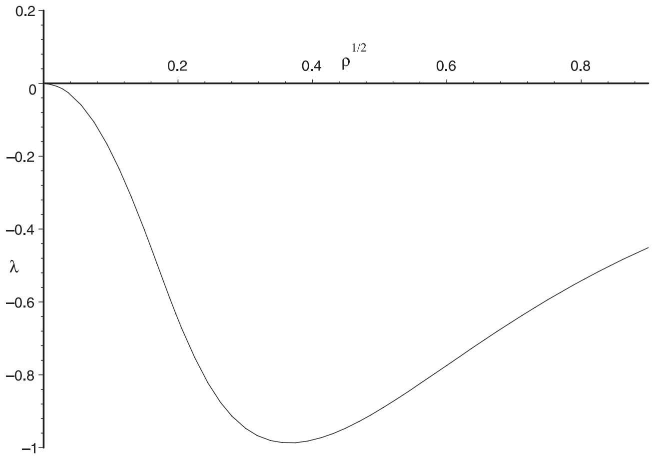

Fig. 1. The eigenvalue $\lambda(h, \rho)$ as a function of $\rho^{1/2}$ for $h(x, t) = 4 \sin 2\pi t \cos \pi x$ and $\omega = 0.25$.

where $\phi_\rho(x, t)$ *is the positive solution of* (2.1) *(with* $\lambda = \lambda(h, \rho)$*) with normalization*

$$\frac{1}{|\Omega|} \int_\Omega \phi_\rho^2(\cdot, 0) = 1, \tag{2.5}$$

and $\psi_\rho(x, t)$ *is the positive 1-periodic solution of* (2.3) *with normalization*

$$\int_\Omega \phi_\rho(x, 0)\psi_\rho(x, 0)dx = 1. \tag{2.6}$$

This lemma easily implies the conclusion of Theorem 2.1. Indeed, if h is independent of t, the adjoint eigenfunction ψ is a positive scalar multiple of ϕ (and they are both independent of t). Hence (2.4) gives $D_\rho\lambda(h, \rho) > 0$. Below, we shall use Lemma 2.3 again when discussing the dependence of the principal eigenvalue on ω.

Lemma 2.4. *The following statements hold*

(a) $\lambda(h, \rho) \le -\hat{\hat{h}} \quad (\rho \in (0, \infty))$ *with strict inequality if* h *is not spatially homogeneous.*
(b) $\lim_{\rho\to\infty} \lambda(h, \rho) = -\hat{\hat{h}}$.
(c) $\lim_{\rho\to 0} \lambda(h, \rho) = -\max_{x\in\bar{\Omega}} \hat{h}(x)$.

Proof of Theorem 2.2 (a) Clearly from Lemma 2.4(b),(c)

$$\lim_{\rho\to 0} \lambda(h, \rho) = -\hat{\hat{h}} = \lim_{\rho\to\infty} \lambda(h, \rho).$$

The result follows from Lemma 2.4(a).

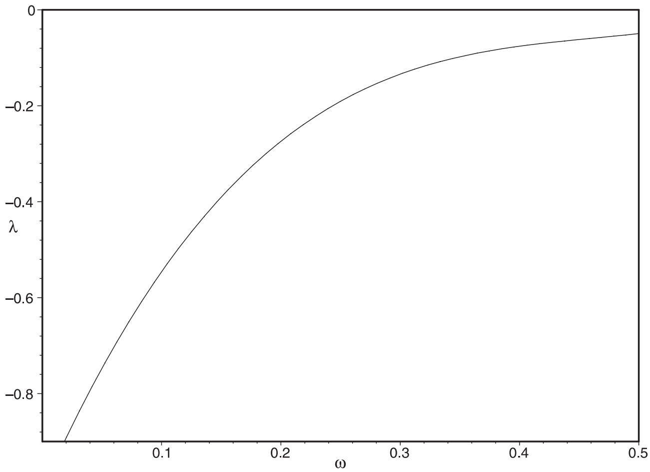

Fig. 2. The eigenvalue $\lambda(h, \rho)$ plotted against ω for $h(x, t) = 2 \sin 2\pi t \cos \pi x$ and $\rho = 0.05$.

(b) The idea is to use [13, Lemma 15.4]; the reader is warned of possible confusion resulting from the different role played by λ there. Also, $\hat{h}$ must be incorporated in the elliptic operator $\mathcal{A}$ [13, pp. 34, 38] by putting $a_0 = -\hat{h}(x)$.

Fix some $\rho_0 > 0$. Then by the lemma referred to above we may choose γ so large that $\lambda(h, \rho_0) < 0$. By Lemma 2.4, $\lambda(h, \rho_0)$ has nonnegative limits as $\rho \to 0$ and $\rho \to \infty$, and the result follows. □

An interesting question, both for its own sake and also for its implications in the biological problem, concerns the role of the frequency ω and we conclude the section with some remarks on it.

Suppose that a formal expansion of the principal eigenvalue in negative powers of ω is carried out; the details are somewhat tedious and we shall omit them here. For the case $\hat{h} = 0$, with h not spatially homogeneous, one finds that to order ω^{-1}, $\nabla\phi = -\nabla\psi$. It then follows from Lemma 2.3 that for any fixed ρ and large enough ω, $D_\rho\lambda(h, \rho) < 0$. This provides another range of examples for which the conclusions of Theorem 2.2 hold. It does not appear to be easy to obtain further analytical results of this nature. Some numerical calculations have been carried out for a case where $\hat{h} \equiv 0$, and these suggest that $\lambda(h, \rho)$ is an increasing function of ω and tends to a finite negative limit as $\omega \to 0$, see Fig. 2. This conclusion is supported for $\lambda(\epsilon h, \rho)$ when ϵ is small by using an expansion technique. However, a proof of the general result is not available.

3. Semitrivial periodic solutions and their stability

In this section we examine the semitrivial periodic solutions of (1.5), i.e. those 1-periodic solutions with one of the components u, v equal to zero and the other component positive. Obviously, the nonzero component of a semitrivial periodic solution is a solution of a scalar logistic equation. We examine that equation in

Subsection 3.1. In Subsections 3.2 and 3.3, we separately consider the stability of the *slow diffuser* and *fast diffuser* by which we mean semitrivial periodic solutions of the form $(u, 0)$ and $(0, v)$, respectively.

In the whole of this section we assume the standing hypotheses given in the introduction (Ω is a smooth bounded domain, $a(x, t)$ is a continuous function that is 1-periodic in t and zero Neumann boundary conditions are assumed with parabolic equations throughout).

We use the notion of linear stability of periodic solutions as in [13]: a periodic solution (u, v) of (1.5) is *linearly stable* if all eigenvalues of the period map of the linear variational equation

$$\begin{aligned} \omega \frac{\partial \bar{u}}{\partial t} &= \mu \Delta \bar{u} + (a(x,t) - u - v)\bar{u} - u(\bar{u} + \bar{v}), \\ \omega \frac{\partial \bar{v}}{\partial t} &= \nu \Delta \bar{v} + (a(x,t) - u - v)\bar{v} - v(\bar{u} + \bar{v}), \quad x \in \Omega,\ t > 0, \end{aligned} \tag{3.1}$$

(under Neumann boundary conditions) have modulus less than 1. If at least one eigenvalue has modulus greater than 1, the periodic solution (u, v) is said to be *linearly unstable*. We remark that the period maps that we discuss are always compact (since Ω is bounded) and therefore their spectrum consists entirely of eigenvalues and the point 0. For different types of equation, the linear stability is understood in an analogous way. Of course, when the principal eigenvalue of the linearization is defined, its sign determines the linear stability. This applies in particular to scalar equations to be discussed in the Subsection 3.1.

If a periodic solution (u, v) is linearly stable, then it is *asymptotically stable* in the sense that $(u(\cdot, 0), v(\cdot, 0))$ is an asymptotically stable fixed point of the period map $F : X \mapsto X$ of (1.5) (recall that X = $C(\bar{\Omega}) \times C(\bar{\Omega})$).

Conversely, a linearly unstable periodic solution is not stable. For a semitrivial periodic solution (u, v) this can be made more specific. If it is linearly unstable, then $(u(\cdot, 0), v(\cdot, 0))$ is an unstable fixed point for the restriction $F|_{X^+}$ of the period map to the positively invariant cone $X_+ = \{(u, v) : u \geq 0, v \geq 0\}$. This follows from the competitive structure of (1.5) (see [13, Sect. IV.33] for details).

3.1. *The logistic equation*

Let $(\tilde{u}, \tilde{v})$ be a semitrivial periodic solution of (1.5). For definiteness assume that $\tilde{v} = 0$, the other case can be treated in a similar way. Then $\tilde{u}$ is a solution of the equation

$$\omega \frac{\partial u}{\partial t} = \mu \Delta u + (a(x,t) - u)u, \quad x \in \Omega,\ t > 0. \tag{3.2}$$

From the previous section we recall that $\lambda(h, \rho)$ is the principal eigenvalue of (2.1). With $h = a$ and $\rho = \mu$, (2.1) is the linearization of (3.2) around $u = 0$. Thus the conditions $\lambda(a, \mu) < 0$ in the following proposition means that the trivial solution of (3.2) is linearly unstable. A sufficient, but by no means necessary, condition for this is $\hat{\hat{a}} > 0$, see Lemma 2.4.

Proposition 3.1. *A positive 1-periodic solution* $\tilde{u}$ *of* (3.2) *exists if and only if* $\lambda(a, \mu) < 0$*. If the solution exists then it is unique, linearly stable, that is,* $\lambda(a - 2\tilde{u}, \mu) > 0$*, and globally attractive, that is, any positive solution* u *of* (3.2) *satisfies*

$$\|u(\cdot, t) - \tilde{u}(\cdot, t)\|_{L^\infty(\Omega)} \to 0 \text{ as } t \to \infty.$$

See [13, Sect. III.28] for the proof.

Proposition 3.1 in particular implies that $\tilde{u}(\cdot, 0)$ is a nondegenerate fixed point of the period-1 map of (3.2). Therefore, by the implicit function theorem, $\tilde{u}(\cdot, 0)$ depends smoothly on the parameters in the equation. This statement will be made more precise when needed.

We next characterize the stability of semitrivial periodic solutions relative to system (1.5).

Lemma 3.2. *Assume* $\lambda(a, \mu) < 0$ *so that there exists a unique semi-trivial periodic solution* $(\tilde{u}, 0)$ *of* (1.5)*. Then this periodic solution is linearly stable, respectively linearly unstable if* $\lambda(a - \tilde{u}, \nu) > 0$*, respectively* $\lambda(a - \tilde{u}, \nu) < 0$*. Analogous statements hold for the semitrivial periodic solution* $(0, \tilde{v})$ *if* $\lambda(a, \nu) > 0$.

Proof. For $(u, v) = (\tilde{u}, 0)$, the linearization (3.1) simplifies to the triangular system

$$\begin{aligned} \omega \frac{\partial \bar{u}}{\partial t} &= \mu \Delta \bar{u} + [a(x, t) - 2\tilde{u}]\bar{u} - \tilde{u}\bar{v}, \\ \omega \frac{\partial \bar{v}}{\partial t} &= \nu \Delta \bar{v} + [a(x, t) - \tilde{u}]\bar{v}. \end{aligned} \tag{3.3}$$

Let Π be the period map of this system. It is easy to see that if γ is an eigenvalue of Π then it is either an eigenvalue of the period map of the second equation (if the eigenfunction has a nonzero v-component) or an eigenvalue of the period map of

$$\omega \frac{\partial \bar{u}}{\partial t} = \mu \Delta \bar{u} + [a(x, t) - 2\tilde{u}]\bar{u}. \tag{3.4}$$

Equation (3.4) is the linearization of the logistic equation at its positive solution, hence, by Proposition 3.1, all eigenvalues of the period map of (3.4) lie inside the unit circle. The linear stability of $(\tilde{u}, 0)$ is therefore determined by the principal eigenvalue of the second equation and we obtain the linear stability and instability criteria as in the lemma. □

3.2. Slow diffuser

In this subsection we give various conditions on the stability and instability of the semitrivial periodic solution $(\tilde{u}, 0)$, provided it exists. For the sake of simplicity, we usually make the assumption $\hat{\hat{a}} > 0$ which guarantees that both semitrivial periodic solutions exist for all values of the parameters. In several cases this assumption can be relaxed, but we will not consider this question here.

The reader may find it instructive to look at the following special example first. Take the one-dimensional domain $\Omega = (0, 1)$ and let

$$a(x, t) = 1 + \epsilon q(x, t),$$

where q can be expanded in the double Fourier series

$$q(x,t) = \sum_{m,n=0,m+n\neq 0}^{\infty} \cos m\pi x(a_{mn}\cos 2\pi nt + b_{mn}\sin 2\pi nt).$$

Then one can show formally, that for small ϵ,

$$\lambda(a-\tilde{u},\nu) = (\nu-\mu)\epsilon^2\pi^2\Bigg\{\frac{\mu}{2\nu}\sum_{m=1}^{\infty}\frac{m^2}{(1+\mu m^2\pi^2)^2}a_{m0}^2 + \frac{1}{4}\sum_{m,n\geq 1}^{\infty}\frac{m^2(\mu\nu m^4\pi^2-4n^2\omega^2)(a_{mn}^2+b_{mn}^2)}{[\pi^2\nu^2m^4+4n^2\omega^2][(1+\mu m^2\pi^2)^2+4n^2\pi^2\omega^2]}\Bigg\} + O(\epsilon^3). \tag{3.5}$$

Of course, we recover $\lambda(a-\tilde{v},\mu)$ by interchanging μ and ν. From this formula one can find several relations between the parameters that give $\lambda(a-\tilde{u},\nu) > 0$ or $\lambda(a-\tilde{u},\nu) < 0$. It turns out that the estimates of λ give a fairly reliable guide to the general case in many circumstances, even for ϵ as large as 1 or 2. We give rigorous proofs of the stability results is some limit situations, assuming that one of the parameters is small or large. Other cases will be treated numerically.

In the assertions below the parameters not explicitly mentioned are assumed to be fixed and may enter the indicated estimates. For example, the statement "a condition holds for ω small enough" should be interpreted as saying that the condition holds for $\omega < C$ where the constant C may depend on a, μ and ν.

Lemma 3.3. *Assume that $\bar{\hat{a}} > 0$, so that the semitrivial periodic solution $(\tilde{u},0)$ exists for any $0<\mu<\nu$ and $\omega > 0$. Further assume that $\hat{a}$ is not constant. Then $\lambda(a-\tilde{u},\nu) > 0$, that is $(\tilde{u},0)$ is linearly stable, in each of the following cases:*

(a) $\bar{a}(t) > 0$ $(t\in[0,1])$, *a is of class C^1 and ω is small enough,*
(b) *ω is large enough,*
(c) *ν is large enough,*
(d) $\sup_{x,t}|a(x,t)-\hat{a}(x)|$ *is small enough.*

Proof. (a) Consider the family of elliptic problems obtained formally by setting $\omega = 0$ in (3.2)

$$0 = \mu\Delta u + (a(x,t)-u)u, \quad x\in\Omega, \tag{3.6}$$

(as always we assume Neumann boundary conditions). One can view (3.6) as the stationary equation for the following autonomous logistic equation with artificial time s and parameter t:

$$\frac{\partial u}{\partial s} = \mu\Delta u + (a(x,t)-u)u, \quad x\in\Omega,\ s>0. \tag{3.7}$$

The assumption $\bar{a}(t) > 0$ implies that for any t, equation (3.7) has a positive linearly stable periodic solution $u_0(\cdot,t)$. This periodic solution is unique, by Lemma 3.1, hence, by the periodicity of a, $u_0(x,t)$ is 1-periodic in t. It follows (see [34]) that for ω sufficiently small, there exists a linearly stable 1-periodic solution u_ω of (3.2) that satisfies

$$\|u_\omega - u_0\|_{L^\infty(\Omega\times(0,1))} \to 0 \text{ as } \omega \to 0. \tag{3.8}$$

This property in particular implies that u_ω is positive for small ω, hence, by uniqueness, $u_\omega = \tilde{u}$.

We next claim that $\lambda(a-u_0,\nu) > 0$, which, combined with (3.8) and continuity of $\lambda(h,\nu)$ in $h \in C(\bar{\Omega}\times[0,1])$, implies that $\lambda(a-u_\omega,\nu) > 0$ for small ω.

To prove the claim, let $\lambda(t)$ and $\psi_0(\cdot,t) > 0$ be the principal eigenvalue and L^2-normalized eigenfunction of the elliptic eigenvalue problem

$$\nu\Delta w + (a(x,t) - u_0(x,t) + \lambda)w = 0. \tag{3.9}$$

Clearly, $\lambda(t)$ and $\psi_0(\cdot,t)$ are 1-periodic in t. The sign of $\lambda(t)$ determines the linear stability of the slow diffuser $(u_0,0)$ of the artificial system

$$\begin{aligned} \omega\frac{\partial u}{\partial s} &= \mu\Delta u + (a(x,t) - u - v)u, \\ \omega\frac{\partial v}{\partial s} &= \nu\Delta v + (a(x,t) - u - v)v, \quad x\in\Omega,\ s>0, \end{aligned} \tag{3.10}$$

(cf. Lemma 3.2). Since this system is autonomous for each t, we have $\lambda(t) > 0$ as proved in [5]. By continuity and periodicity, $\inf_t \lambda(t) > 0$.

Now, we are assuming that a is of class C^1. Thus u_0 is of class C^1, by the implicit function theorem, and consequently, $\psi_0(\cdot,t)$ is of class C^1. Further, $w = \psi_0(\cdot,t)$ satisfies

$$\omega w_t - \nu\Delta w - (a(x,t) - u_0(x,t))w = \omega w_t + \lambda(t)w.$$

If ω is sufficiently small, the right-hand side of this equation is positive. Since the equation has a positive 1-periodic solution $\psi_0(\cdot,t)$, the principal eigenvalue of the operator on the left-hand side is necessarily positive, that is, $\lambda(a-u_0,\nu) > 0$ (see [13, Theorem 16.6 and Remark 16.7]). This completes the proof of (a).

(b) The result is based on the method of averaging (see [10] and references therein for a general background). We first compare the logistic equation in the following rescaled form

$$\frac{\partial u}{\partial t} = \mu\Delta u + (a(x,\omega t) - u)u, \quad x\in\Omega,\ t>0, \tag{3.11}$$

with the corresponding averaged equation

$$\frac{\partial u}{\partial t} = \mu\Delta u + (\hat{a}(x) - u)u, \quad x\in\Omega,\ t>0. \tag{3.12}$$

As $\hat{\hat{a}}$ is assumed positive, (3.12) has a unique positive periodic solution u_0 and this periodic solution is linearly stable. Therefore, for ω sufficiently large there is a $1/\omega$-periodic solution u_ω of (3.11) such that

$$\sup_t \|u_\omega(\cdot,t) - u_0\|_{L^\infty(\Omega)} \to 0 \text{ as } \omega\to\infty \tag{3.13}$$

(see [12, Exercise 2, Sect. 7.5]). This in particular implies that for large ω, u_ω is the unique positive solution of (3.11).

We next consider the linear equation

$$v_t = \nu\Delta v - (a(x,\omega t) - u_\omega(x,\omega t))v \quad x \in \Omega,\ t > 0, \tag{3.14}$$

which determines the stability of the fast diffuser (see Lemma 3.2), and compare it with the following autonomous equation

$$v_t = \nu\Delta v - (\hat{a}(x) - u_0(x))v \quad x \in \Omega,\ t > 0. \tag{3.15}$$

By (3.13), $\hat{u}_\omega \to u_0$ in $C(\bar{\Omega})$. Further,

$$\int_0^1 (a(x,\omega t) - \hat{a}(x))dt \to 0, \quad \int_0^1 (u_\omega(x,\omega t) - u_0(x))dt \to 0$$

in $C(\bar{\Omega})$ as $\omega \to \infty$. Therefore [12, Theorem 7.5.2] applies in the present situation (cf. [12, Sect. 7.5, Example 1]) and it asserts that the evolution operators of (3.14) and (3.15) are close to one another, uniformly on compact time intervals, if ω sufficiently large. Now, there is an $r > 0$ such that for any $\tau > 0$, the eigenvalues of the time-τ map of the autonomous equation (3.15) are contained in the circle of radius $e^{-r\tau}$ (the slow diffuser $(u_0, 0)$ is linearly stable in the autonomous case by [5]). Hence the same is true of the time-τ map of (3.14), uniformly for τ in any compact interval in $(0,\infty)$, if ω is large enough. This clearly implies the assertion (b).

(c) The (positive) function $\tilde{u}$ satisfies (3.2). Divide that equation by u and integrate over $\Omega \times (0, 1)$ obtaining

$$(a - \tilde{u})\hat{} = -\mu \int_{\bar{\Omega}} \int_0^1 \frac{|\nabla \tilde{u}|^2}{\tilde{u}^2} < 0.$$

The assertion now follows from Lemma 2.4 on taking $h = a - \tilde{u}$.

(d) The autonomous equation (3.12) has a unique solution u_0 and this solution is a hyperbolic equilibrium. With $\sup_{x,t} |a(x,t) - \hat{a}(x)|$ small, (3.1) is a small perturbation of (3.12), hence its unique positive periodic solution $\tilde{u}$ is close to u_0. This further implies that $\lambda(a - \tilde{u}, \nu)$ is close to the principal eigenvalue of

$$\omega v_t = \nu\Delta v + (\hat{a}(x) - u_0(x))v + \lambda v.$$

The latter being positive (the slow diffuser is linearly stable in the autonomous case), we obtain $\lambda(a - \tilde{u}, \nu) > 0$. □

The situation that occurs under any of the above conditions (a)-(d) is similar to that in the autonomous case, where the slow diffuser is always stable. However, under certain other conditions, which we now consider, the stability is reversed with $(\tilde{u}, 0)$ *unstable*.

Lemma 3.4. *Assume* $a \in C^2(\bar{\Omega} \times [0,1])$, $\hat{a}(x) > 0$ $(x \in \bar{\Omega})$ *and*

$$\frac{\partial a(x,t)}{\partial n} = 0 \ \ (x \in \partial\Omega,\ \ t \in [0,1]). \tag{3.16}$$

Further assume that

$$a(x,t) \not\equiv c(x)e^{d(t)} + d(t) \tag{3.17}$$

for any functions $c(x)$, $d(t)$. *Then for* μ *sufficiently small,* $\lambda(a - \tilde{u}, \nu) < 0$.

The assumptions $a \in C^2(\bar{\Omega} \times [0,1])$ and (3.16) can be relaxed, but this would only burden the proof with additional technicalities.

Proof. Consider the formal limit of (3.2) when $\mu \to 0$:

$$\omega \frac{\partial u}{\partial t} = (a(x,t) - u)u. \tag{3.18}$$

The assumption $\hat{a} > 0$ implies that for each $x \in \bar{\Omega}$ there is a unique positive and linearly stable 1-periodic solution $p(x,t)$ of the ODE (3.18). As a is of class C^2, so is $p(x,t)$.

We claim that for each μ sufficiently small, the positive solution $u = u_\mu$ of (3.2) exists and satisfies

$$\|u_\mu - p\|_{L^\infty(\Omega\times(0,1))} \to 0 \text{ as } \mu \searrow 0. \tag{3.19}$$

Assume for the moment that the claim is true. Then $\lambda(\nu, a - u_\mu)$ approaches $\lambda(\nu, a-p)$, as $\mu \searrow 0$. The assertion of the lemma follows because $\lambda(\nu, a-p) < 0$, as we now show. Let ψ be a positive eigenfunction, corresponding to the principal eigenvalue $\lambda = \lambda(\nu, a - p)$, of the problem

$$\omega\psi_t - \nu\Delta\psi - (a(x,t) - p(x,t))\psi = \lambda\psi. \tag{3.20}$$

Dividing this equation by ψ and integrating by parts we obtain

$$\lambda(\nu, a-p) = -\nu \int_0^1 \int_\Omega \frac{|\nabla\psi|^2}{\psi^2} - \int_0^1 \int_\Omega (a-p).$$

By (3.18) and the periodicity of p,

$$\int_0^1 \int_\Omega (a-p) = \int_\Omega \int_0^1 \frac{p_t}{p} = 0$$

Further we have $\nabla\psi \not\equiv 0$ for otherwise (3.20) implies that $a - p$ is spatially homogeneous and then (3.18) leads to a contradiction with (3.17). We conclude that, indeed, $\lambda(\nu, a - p) < 0$.

It remains to prove the claim. Since p is linearly stable, an application of the implicit function theorem shows that there is a $\delta_0 > 0$ such that for any $\delta \in (-\delta_0, \delta_0)$ and $x \in \bar{\Omega}$ there exist linearly stable 1-periodic solutions $p_\delta^\pm$ of the equations

$$\omega \frac{\partial u}{\partial t} = u(a(x,t) - u) \pm \delta. \tag{3.21}$$

Strictly speaking, when applying the implicit function theorem, one only obtains a δ_0 depending on x, but using a compactness argument it is easy to see that it can be chosen independent of x. Clearly, $p_\delta^\pm(x,t)$ are of class C^2 in x, t, δ and we have

$$\|p_\delta - p\|_{L^\infty(\Omega\times(0,1))} \to 0 \text{ as } \delta \to 0. \tag{3.22}$$

In particular, $p_\delta^\pm$ are positive (by choice of δ_0 smaller if necessary). We next verify the following properties:

(A) $\frac{\partial p_\delta^\pm}{\partial n} = 0$ on $\partial\Omega$,
(B) $p_\delta^- < p_\delta^+$ if $\delta > 0$,
(C) For any $\delta \in (0, \delta_0)$ there exists an $m_0 = m_0(\delta)$ such that for $0 < \mu < m_0$ the function $p_\delta^-(x,t)$ is a subsolution and $p_\delta^+(x,t)$ is a supersolution of (3.2).

To verify (A), we differentiate (3.21) with respect to x, in the normal direction. Using (3.16), we obtain the following equation for $v = \partial p_\delta^\pm/\partial n$ at any point $x \in \partial\Omega$:

$$\omega v_t = (a(x,t) - 2p_\delta^\pm(x,t))v. \tag{3.23}$$

Since this is the linearization of (3.21) along the linearly stable solution $p_\delta^+(x,t)$, its only 1-periodic solution is $v \equiv 0$. This implies (A).

Differentiating (3.21) with respect to δ, we obtain a linear nonhomogeneous equation for $D_\delta p_\delta^+$. This equation and the periodicity of p_δ^+ yields $D_\delta p_\delta^+ > 0$. Since $p_0^\pm = p$, (B) follows.

Finally, for a fixed $\delta > 0$ we have

$$\omega\frac{\partial p_\delta^+}{\partial t} - \mu\Delta p_\delta^+ - (a(x,t) - p_\delta^+)p_\delta^+ = \mu\Delta p_\delta^+ + \delta, \quad x \in \Omega,\ t \in \mathbb{R}.$$

The right-hand side is positive if μ is small enough, hence p_δ^+ is a supersolution. Similarly one shows that p_δ^- is a subsolution.

Using (A) – (C) one proves, employing the monotonicity method for competitive systems (see [13]), that there exists a periodic solution u of (3.2) satisfying $0 < p_\delta^- < u < p_\delta^+$. By uniqueness, this periodic solution coincides with u_μ. Property (3.19) now follows from (3.22). □

Lemma 3.5. *There exist a smooth function $a(x,t)$, 1-periodic in t, with the following property. For some $\mu > 0$ the positive solution $\tilde{u}$ of (3.2) exists, and $D_\nu\lambda(a-\tilde{u},\nu)|_{\nu=\mu} < 0$. In particular, $\lambda(a-\tilde{u},\nu) < 0$ for ν sufficiently close to μ (and greater than μ).*

Proof. Choose h and ρ such that statement (i) of Theorem 2.2 holds. Without affecting this property, we may assume, replacing h by $h + const$, if necessary, that $\lambda(h,\rho) = 0$. Let $\phi > 0$ be the corresponding eigenfunction of (2.1). Set $\mu = \rho$, and $a(x,t) = h(x,t) + \phi(x,t)$. Then $\tilde{u} = \phi$ is a positive solution of the logistic equation (3.2), and for any ν we have $\lambda(a-\tilde{u},\nu) = \lambda(h,\nu)$. This implies $D_\nu\lambda(a-\tilde{u},\nu)|_{\nu=\mu} < 0$. Next observe that $\lambda(a-\tilde{u},\mu) = 0$ (indeed, with $h = a-\tilde{u}$ and $\rho = \mu$, $\tilde{u}$ is a positive eigenfunction of (2.1) with eigenvalue $\lambda = 0$). Hence, $\lambda(a-\tilde{u},\nu) < 0$ for $\nu > \mu$, $\nu \approx \mu$. □

Lemma 3.4 shows that, for a large class of a, $(\tilde{u}, 0)$ is unstable for μ small. Lemma 3.5 has a different flavor and proves that an a exists such that $(\tilde{u}, 0)$ is unstable even for μ very near ν with $\mu < \nu$. We remark that there is another set of conditions ensuring this, which is suggested by the large ω expansion discussed at the end of Section 2, namely that $\hat{a} \equiv 0$ and ω is large enough.

3.3. Fast diffuser

We next examine the stability of the fast diffuser $(0, \tilde{v})$, $\tilde{v} > 0$. Again, in the statements below parameters not mentioned explicitly are assumed to be fixed.

In the autonomous case, the fast diffuser is always unstable. The next lemma gives a few other conditions for this to be the case.

Lemma 3.6. *Assume that $\hat{\hat{a}} > 0$ and that $\hat{a}$ is not constant. Then $\lambda(a - \tilde{v}, \mu) < 0$, that is , $(0, \tilde{v})$ is linearly unstable, in each of the following cases*

(a) $\bar{a}(t) > 0$ $(t \in [0, 1])$, *a is of class C^1 and ω is small enough,*
(b) *ω is large enough,*
(c) *ν is large enough,*
(d) $\sup_{x,t} |a(x, t) - \hat{a}(x)|$ *is small enough.*

If ω, ν and a are fixed such that $\max_{x \in \bar{\Omega}} (a - \tilde{v})\hat{}(x) > 0$ *(this condition does not involve μ), then $\lambda(a - \tilde{v}, \mu) < 0$ also in the case*

(e) *μ is sufficiently small.*

The hypothesis $\max_{x \in \bar{\Omega}} (a - \tilde{v})\hat{}(x) > 0$ *is satisfied if ν is sufficiently large.*

The proofs of (a), (b) and (d) are analogous to the proofs of the corresponding statements of Lemma 3.3 and are omitted.

For the proof of (c) we need the following preliminary result on the behavior of the fast diffuser when $\nu \to \infty$. For future purposes, we state a more general result dealing with any periodic solution.

Lemma 3.7. *Assume that $\hat{\hat{a}} > 0$. Let $\nu_k > 0$ be a sequence approaching ∞ and let (u_k, v_k) be an periodic solution of* (1.5) *with $\nu = \nu_k$ such that $u_k \geq 0$, $v_k \geq 0$. Then the sequence $\{(u_k, v_k)\}$ is relatively compact in $C(\bar{\Omega} \times [0, 1])$ and the limit of any of its convergent subsequences is a 1-periodic solution (u^*, v^*) of the shadow system:*

$$\begin{aligned} \omega u_t &= \mu \Delta u + (a(x, t) - u - \zeta)u, \\ \omega \zeta_t &= (\bar{a} - \bar{u} - \zeta)\zeta \qquad\qquad x \in \Omega, t > 0. \end{aligned} \tag{3.24}$$

Proof. The result is essentially proved in [9], however a few modifications are necessary. We give some details. For $\nu \geq \mu$ let A_ν denote the unbounded closed operator on $Y = C(\bar{\Omega})$ defined by

$$D(A_\nu) = \{u \in \bigcap_{p \geq 1} W^{2,p}(\bar{\Omega}) : \frac{\partial u}{\partial n} = 0, \text{ on } \partial\Omega, \quad \Delta u \in Y\},$$
$$A_\nu u = \nu \Delta u \quad (u \in D(A_\nu)).$$

Then A_ν generates an analytic semigroup $e^{A_\nu t}$ on Y and we have the following estimate (see [23, Sect. 3.1.5])

$$\|e^{A_\nu t}u\|_{Y^{1/2}} \leq Mt^{-1/2}\|u\|_Y, \quad (u \in Y, t > 0). \tag{3.25}$$

Here $Y^{1/2}$ stands for a Banach space (a fractional power space) compactly imbedded in Y, and M is a constant independent of ν (one chooses a constant for $\nu = \mu$ and scales time to find a ν-independent constant). Moreover, on the invariant space

$$Y^\perp := \{u \in Y : \bar{u} = 0\},$$

the spectrum of A_ν consists of positive eigenvalues, therefore we have the estimates (see [12,23])

$$\begin{aligned} \|e^{A_\nu t}w\|_Y &\leq Ke^{-\nu rt}\|w\|_Y, && (w \in Y^\perp, t > 0), \\ \|e^{A_\nu t}w\|_{Y^{1/2}} &\leq Ke^{-\nu rt}t^{-1/2}\|w\|_Y, && (w \in Y^\perp, t > 0), \end{aligned} \tag{3.26}$$

where $K, r > 0$ are independent of ν (using the scaling of t again). Now, as in [5], the maximum principle implies that the periodic solutions (u_k, v_k) are uniformly bounded in $X = Y \times Y$:

$$\max \{\|u_\nu\|_{L^\infty(\Omega\times(0,1))}, \|v_\nu\|_{L^\infty(\Omega\times(0,1))}\} \leq \max_{x,t}\ a(x,t). \tag{3.27}$$

Thus along the solutions (u_k, v_k) the nonlinearities in (1.5) are uniformly bounded in X. By (3.25), a standard estimate using the variation of constants implies that $(u_k(\cdot, 1), v_k(\cdot, 1))$ (which is the same as $(u_k(\cdot, 0), v_k(\cdot, 0))$, by periodicity) is bounded in $Y^{1/2} \times Y^{1/2}$, hence relatively compact in X. The assertion can now be proved using the estimates (3.26) and the estimates in Lemma 1 of [9]. □

Proof of Lemma 3.6 (c) (d). It follows from Lemma 3.7 that as $\nu \to \infty$, the semitrivial periodic solution $(0, \tilde{v})$ approaches the function $(0, \zeta)$, where ζ is a 1-periodic solution of the equation

$$\omega\zeta_t = (\hat{a} - \zeta)\zeta.$$

It is easy to see that $\tilde{v}$ cannot converge to 0 (since there is a uniform subsolution), hence $\zeta(t) > 0$. The last equation then gives $(\hat{a} - \hat{\zeta})^- = 0$. As a is not spatially constant, Lemma 2.4(a) implies that $\lambda(a - \zeta, \mu) < 0$. Therefore, by continuity of λ in the first argument, we also have $\lambda(a - \tilde{v}, \mu) < 0$ if ν is large enough. This proves (c).

Next note that under the hypothesis $\max_{x\in\bar{\Omega}}(a - \tilde{v})\hat{}(x) > 0$, the inequality $\lambda(a - \tilde{v}, \mu) < 0$ follows directly from Lemma 2.4(c). To see that the hypothesis is satisfied for large ν, we use the property $(\hat{a} - \hat{\zeta})^- = 0$ again. Since a is not spatially constant, it clearly implies that $\hat{a}(x) - \hat{\zeta} > 0$ for some x. Therefore, also $(a - \tilde{v})\hat{}(x) > 0$ for this value of x if ν is large enough. □

In the following lemmas the stability of the fast diffuser is opposite to that in the autonomous case.

Lemma 3.8. *Assume that* $\hat{a} \equiv 0$ *but* a *is not spatially homogeneous. Then, the semitrivial periodic solution* $(0, \tilde{v})$ *exists (for any* μ*) and for* μ *sufficiently small one has* $\lambda(a - \tilde{v}, \mu) > 0$*, that is,* $(0, \tilde{v})$ *is linearly stable.*

Proof. We have $\lambda(a, \nu) < 0$ by Lemma 2.4(a), thus the semitrivial periodic solution exists. Take $h = a - \tilde{v}$ and note that $\hat{h}(x) = -\hat{\tilde{v}} < 0$ for every $x \in \bar{\Omega}$. The result follows from Lemma 2.4(c). □

Lemma 3.9. *Let $a(x, t)$ be as in Lemma 3.5. Then, there is a positive constant μ_0 such that if $\mu < \nu$ are both sufficiently close to μ_0 then system* (1.5) *has both semitrivial periodic solutions and*

$$\lambda(a - \tilde{u}, \nu) < 0, \quad \lambda(a - \tilde{v}, \mu) > 0. \tag{3.28}$$

Proof. Let $a(x, t)$ be as in Lemma 3.5. For any $\mu > 0$ let $\tilde{u}_\mu$ denote the positive periodic solution of (3.2), if it exists. By the implicit function theorem, $\tilde{u}_\mu$ exists for an open set of values of μ, and it depends smoothly, in the supremum norm, on μ. Consider the smooth function

$$\beta : (\mu, \nu) \mapsto \lambda(a - \tilde{u}_\mu, \nu).$$

By Lemma 3.5, there is a μ_0 such that

$$D_\nu \lambda(a - \tilde{u}_{\mu_0}, \nu)|_{\nu=\mu_0} < 0. \tag{3.29}$$

It was noted in the proof of Lemma 3.5 that the function β vanishes on the diagonal

$$\lambda(a - \tilde{u}_\mu, \nu) = 0 \text{ for } \mu = \nu.$$

By (3.29) and the implicit function theorem, the diagonal contains all solutions of $\beta(\mu, \nu) = 0$ near (μ_0, μ_0), hence β takes opposite signs on the different sides of the diagonal. This together with (3.29) imply (3.28). □

3.4. Stability table

The following table summarizes some of the stability and instability results proved in this section. We indicate by $+$ and $-$ the linear stability and instability, respectively, of the semitrivial periodic solutions and indicate the lemma where the corresponding result is proved. In all cases, it is assumed that $\mu < \nu$ and $\hat{\bar{a}} > 0$

Table 1.

$a(x,t)$:	μ, ν, ω:	Slow diffuser	Fast diffuser
$\nabla\hat{a} \not\equiv 0$, $\lvert a - \hat{a}\rvert$ small		+ (L 3.3)	− (L 3.6)
$\nabla\hat{a} \not\equiv 0$	ω large	+ (L 3.3)	− (L 3.6)
$\nabla\hat{a} \not\equiv 0$, $\bar{a} > 0$	ω small	+ (L 3.3)	− (L 3.6)
$\nabla\hat{a} \not\equiv 0$	ν large	+ (L 3.3)	− (L 3.6)
Examples of $a(x,t)$	$\mu, \nu \approx \mu_0$	− (L 3.9)	+ (L 3.9)
$\hat{a} > 0$ and additional conditions	ν large, $\mu < \mu_0(\nu)$ with $\mu_0(\nu)$ small	− (L 3.4)	− (L 3.6)
$\hat{a} \equiv 0$, $\nabla a \not\equiv 0$	μ small	?	− (L 3.8)

(so that both semitrivial periodic solutions exist). For simplicity we also assume $a \in C^1$ or $a \in C^2$ where needed (see the lemmas for the precise assumptions).

The most interesting cases are those of simultaneous instability, which will be used to prove coexistence, and of a stable fast diffuser and unstable slow diffuser, which is opposite to the stability in the autonomous case.

4. Coexistence

In this section we discuss *coexistence periodic solutions* of (1.5), that is periodic solutions with both components positive. We first show that under certain conditions on $a(x,t)$ there exists a stable coexistence periodic solution if μ is sufficiently small. The proof is based on the observation that both semitrivial periodic solutions are unstable together with a monotonicity argument. It does not appear to be very easy to obtain more general conditions under which the existence of a stable coexistence periodic solution may be proved. However, formula (3.5) for λ in a small perturbation case suggests that this existence is very common. This is confirmed (without the small perturbation assumption) by computation, a sample set of results being shown in the table below.

We also give an interesting example of a global bifurcation. With the function a depending on a parameter γ, we find a branch of coexistence periodic solutions connecting the fast diffuser (for $\gamma=0$) with the slow diffuser (for $\gamma=1$).

Theorem 4.1. *Let a be as in Lemma 3.4. Then there are $\omega > 0$, $0 < \mu < \nu$ such that* (1.5) *has an asymptotically stable coexistence periodic solution.*

Proof. Note that a function a satisfying the hypotheses of Lemma 3.4 also satisfies the hypotheses of Lemma 3.6. By these two lemmas (more specifically, from Lemma 3.6 we use (e) and the last statement), we can choose ω, μ, ν such that both semitrivial periodic solutions exist and are linearly unstable. Monotonicity method for competitive systems now yields a stable periodic solution (u_c, v_c) satisfying

$$0 < u_c(x,t) < \tilde{u}(x,t) \quad 0 < v_c(x,t) < \tilde{v}(x,t),$$

see [13, Sect. IV.33]. We prove that this stable periodic solution is actually asymptotically stable. It is sufficient to show that $(u_c^0, v_c^0) := (u_c(\cdot,0), v_c(\cdot,0)$ is

Table 2. $a(x,t) = 1.0 + (0.25 + 0.5 \sin 2\pi t) \cos \pi x$. Parameters $\omega = 0.25$, $\nu = 0.1$. Both semitrivial periodic solutions appear to be unstable for all values of μ. Hence there is always a stable coexistence periodic solution.

μ	$\lambda(a-\tilde{u},\nu)$	$\lambda(a-\tilde{v},\mu)$
0.01	−0.0079	−0.037
0.05	−0.00030	−0.0039
0.075	−0.00046	−0.0011
0.095	−0.00016	−0.00018
0.0975	−0.000082	−0.000087

an isolated fixed point of the period map Π of (1.5); its asymptotic stability then follows from a well-know result on monotone maps (see [2], for example).

We employ the fact that Π is a real-analytic map on X (cf. [12]). Using a Lyapunov-Schmidt reduction and continuation one can show that if (the stable fixed point) (u_c^0, v_c^0) is not an isolated fixed point, then there is an unbounded curve of fixed points. See [19,32,38] for results of this type that are easily adapted to the present setting. Now, the existence of an unbounded curve of fixed points is ruled out by an L^∞ a priori bound on periodic solutions of (1.5). This shows that (u_c^0, v_c^0) is isolated and therefore asymptotically stable. □

Theorem 4.2. *There exists a smooth function* $a(x,t,\gamma)$ *of* $x \in \bar{\Omega}, t \in \mathbb{R}, \gamma \in [0,1]$ *that is 1-periodic in* t *and is such that the system* (1.5) *with* $a = a(\cdot,\cdot,\gamma)$ *has a periodic solution* (u_γ, v_γ) *with the following properties:*

(i) $\gamma \mapsto (u_\gamma, v_\gamma) : [0,1] \to C(\bar{\Omega}) \times C(\bar{\Omega})$ *is continuous,*
(ii) $u_\gamma > 0$ *for* $\gamma \in (0,1]$, $v_\gamma > 0$ *for* $\gamma \in [0,1)$,
(iii) $u_0 = 0$, $v_1 = 0$.

Proof. Let h and $\rho_1 < \rho_2$ be as in statement (ii) of Theorem 2.2, that is $\lambda := \lambda(h,\rho_1) = \lambda(h,\rho_2)$. Then there are positive 1-periodic solutions ξ, η of the equations

$$\omega\xi_t = \rho_1\Delta\xi + (h(x,t)+\lambda)\xi,$$
$$\omega\eta_t = \rho_2\Delta\eta + (h(x,t)+\lambda)\eta.$$

These solutions are smooth by parabolic regularity. Set

$$\mu = \rho_1, \quad \nu = \rho_2,$$
$$a(x,t,\gamma) = h(x,t) + \lambda + \gamma\xi + (1-\gamma)\eta,$$
$$u_\gamma = \gamma\xi, \quad v_\gamma = (1-\gamma)\eta.$$

It is easy to verify that these functions have all the properties stated in the theorem. □

5. Global dynamics: examples

In the autonomous case, the fact that there are no coexistence periodic solutions combined with the competitive structure of (1.5) leads to the conclusion that the slow diffuser, if it exists, is the global attractor for solutions in the positive cone

$$X_+ := \{(u,v) \in C(\bar{\Omega}) \times C(\bar{\Omega}) : u > 0, v > 0\}$$

(see [5]). The situation is quite different in the time-periodic case. Indeed, we have seen above that coexistence periodic solutions may occur. The question of how solutions of (1.5) behave for large t is certainly an interesting one, but it will not be addressed here in general. We only give two theorems describing the global dynamics in special cases. In the first one, we show that the dynamics can be "completely opposite" to that in the autonomous case; specifically, the fast diffuser is the global attractor. Then we consider two situations where the slow diffuser is the global attractor. By [5], this is easily seen to be the case when $a(x, t)$ is a small perturbation of a nonconstant autonomous function. In Theorem 5.3 we discuss the more interesting cases of large ω and large ν. In the former case the proof relies on the method of averaging, in the latter case the shadow system is employed.

We use the following standard result on competitive systems (see Section IV.34 in [13]).

Lemma 5.1. *Assume that* (1.5) *has both semitrivial periodic solutions, one of them, say* (u_s, v_s)*, linearly stable, the other one linearly unstable. Further assume that* (1.5) *has no coexistence periodic solution. Then the linearly stable semitrivial periodic solution* (u_s, v_s) *is the global attractor in* X_+*. In other words, for any solution* $(u, v) \in X_+$ *of* (1.5) *one has*

$$\|u(\cdot, t) - u_s(\cdot, t)\|_{L^\infty(\Omega)} \to 0,\ \ \|v(\cdot, t) - v_s(\cdot, t)\|_{L^\infty(\Omega)} \to 0 \text{ as } t \to \infty.$$

Theorem 5.2. *Let* a *be as in Lemma 3.5, that is, for some* $\mu > 0$ *the positive periodic solution* $\tilde{u}$ *of* (3.2) *exists, and* $D_\nu\lambda(a - \tilde{u}, \nu)|_{\nu=\mu} < 0$*. Then, for* $\nu > \mu$ *sufficiently close to* μ *both semitrivial periodic solutions* $(\tilde{u}, 0)$*,* $(0, \tilde{v})$ *of* (1.5) *exist and the fast diffuser* $(0, \tilde{v})$ *is the global attractor in* X_+*.*

Proof. By assumption, there is a $\delta > 0$ such that the condition

$$D_\nu\lambda(h, \nu) < 0 \quad (\nu \in [\mu, \mu + \delta]) \tag{5.1}$$

holds true for $h = a - \tilde{u}$. Since $\lambda(h, \nu)$ is a smooth function of ν and h, there exists a neighborhood U of $a - \tilde{u}$ in $C(\bar{\Omega} \times [0, 1])$ such that (5.1) holds for any $h \in U$.

Now consider system (1.5) with $\nu = \mu$

$$\begin{aligned} \omega \frac{\partial u}{\partial t} &= \mu\Delta u + (a(x, t) - u - v)u, \\ \omega \frac{\partial v}{\partial t} &= \mu\Delta v + (a(x, t) - u - v)v. \end{aligned} \tag{5.2}$$

Adding the equations, we see that $u + v$ satisfies the logistic equation (3.2). Therefore if $(u, v) \not\equiv 0$ is any periodic solution of (5.2) with $u \geq 0$, $v \geq 0$, then necessarily $u + v = \tilde{u}$. Substituting this in the first equation, we further see that if $u \not\equiv 0$ then $\tilde{u}$ and also u are positive eigenfunctions of the same periodic-parabolic eigenvalue problem. Simplicity of the principal eigenvalue implies that u is scalar multiple of $\tilde{u}$ and, consequently, also v is a scalar multiple of $\tilde{u}$. We conclude that all nonzero periodic solutions of (5.2) with nonnegative components are contained on the curve

$$J := \{(\gamma\tilde{u}, (1 - \gamma)\tilde{u}) : \gamma \in [0, 1]\}.$$

The converse is obvious: any element of J is a nonzero periodic solution of (5.2).

We now consider (1.5) with $\nu \approx \mu$ as a small perturbation of (5.2). We show that if $\nu > \mu$ is sufficiently close to μ, then (1.5) has no coexistence periodic solution.

Suppose on the contrary, that for a sequence of values $\nu \searrow \mu$ there exists a coexistence periodic solution (u_ν, v_ν) of (1.5). By the maximum principle, there is a uniform L^∞-bound on (u_ν, v_ν), see (3.27). Using the compactness of the period map, we conclude, passing to a subsequence, if necessary, that (u_ν, v_ν) converges, as $\nu \searrow \mu$, to a periodic solution of (5.2). From the structure of periodic solutions of (5.2) it then follows that $u_\nu + v_\nu$ converges to $\tilde{u}$ or to 0.

In the former case, we find a $\nu > \mu$ so close to μ that $a - u_\nu - v_\nu \in U$, and hence (5.1) holds for $h = a - u_\nu - v_\nu$. In particular,

$$\lambda(a - u_\nu - v_\nu, \mu) < \lambda(a - u_\nu - v_\nu, \nu).$$

On the other hand, since u_μ, u_ν are both positive, by (1.5) we have

$$\lambda(a - u_\nu - v_\nu, \mu) = \lambda(a - u_\nu - v_\nu, \nu) = 0,$$

a contradiction.

In the latter case, $u_\nu + v_\nu \to 0$, we still have $\lambda(a - u_\nu - v_\nu, \mu) = 0$ (by (1.5)), hence, taking the limit, $\lambda(a, \mu) = 0$. But this contradicts the existence of the positive periodic solution $\tilde{u}$, see Proposition 3.1.

These contradictions show that (1.5) has no coexistence periodic solution if ν is close enough to μ. We also know by Lemma 3.9 that if ν is close enough to μ the fast diffuser is stable and the slow diffuser is unstable. The assertion now follows from Lemma 5.1. □

Theorem 5.3. *Assume that $\hat{\bar{a}} > 0$ and that $\hat{a}$ is not constant. Then, both semitrivial periodic solutions exist and the slow diffuser $(\tilde{u}, 0)$ is the global attractor in X_+ in each of the following cases:*

(a) *ν is large enough,*
(b) *ω is large enough.*

(As above, parameters not mentioned are assumed to be fixed.)

Proof. In both cases, the slow diffuser is linearly stable and the fast diffuser is linearly unstable (see Lemmas 3.3, 3.6). By Lemma 5.1, we only need to rule out coexistence periodic solutions.

Consider (a). Assume that there is a sequence $\nu_k \to \infty$ such that (1.5) with $\nu = \nu_k$ has a coexistence periodic solution (u_k, v_k). As in the proof of Theorem 5.2, this means that

$$\lambda(a - u_k - v_k, \mu) = \lambda(a - u_k - v_k, \nu_k) = 0. \tag{5.3}$$

Now by Lemma 3.7, we may assume (passing to a subsequence, if necessary) that (u_k, v_k) converges in $C(\bar{\Omega} \times [0, 1])$ to a 1-periodic solution (u^*, ζ) of the shadow system (3.24). It is easy to check that $a - u^* - \zeta$ cannot be spatially homogeneous, for the first equation in (3.24) would imply that u^* and, consequently a, are spatially homogeneous. Therefore, by Lemma 2.4(a), we have

$$\lambda(a - u^* - \zeta, \mu) < -(\bar{a} - \bar{u^*} - \zeta)\hat{}.$$

Using Remark 1 and the continuity of $\lambda(\cdot,\cdot)$ we now conclude that for large enough k

$$\lambda(a-u_k-v_k,\mu)<\lambda(a-u_k-v_k,\nu_k),$$

contradicting (5.3).

Now consider (b). We again proceed by contradiction. Assume (u_k,v_k) is a sequence of coexistence periodic solutions of (1.5) with $\omega=\omega_k\to\infty$. By the maximum principle, there is a uniform L^∞ a priori bound on (u_k,v_k). Using the rescaled equation (1.4), the periodicity of u_k, v_k, and standard a priori estimates (see for example [23, Section 4.4.3]), we further see that u_k and v_k are uniformly bounded in the Hölder space $C^{\theta,\frac{\theta}{2}}(\bar\Omega\times[0,1])$ for some $\theta>0$. Therefore passing to subsequences, if necessary, we have

$$u_k\to u_\infty \text{ and } v_k\to v_\infty$$

in $C(\bar\Omega,[0,1])$ for some u_∞, v_∞. Moreover, multiplying the first equation in (1.5) by a test function $\varphi\in H_0^2(\Omega)$ and integrating over $\Omega\times(t_1,t_2)$, we obtain

$$\int_\Omega(u_k(x,t_2)-u_k(x,t_1))\varphi(x)\,dx\to 0 \text{ as } \omega_k\to\infty.$$

Hence

$$\int_\Omega(u_\infty(x,t_2)-u_\infty(x,t_1))\varphi(x)\,dx=0$$

for any t_1, t_2 and $\varphi\in H_0^2(\Omega)$, which implies that u_∞ is independent of t. Similarly, v_∞ is independent of t.

We now compare the following two linear problems (assuming Neumann boundary conditions as always).

$$\frac{\partial\xi}{\partial t}=\rho\Delta\xi+[\hat a(x)-u_\infty(x)-v_\infty(x)]\xi, \tag{5.4}$$

and

$$\frac{\partial\eta}{\partial t}=\rho\Delta\eta+[a(x,\omega_k t)-u_k(x,\omega_k t)-v_k(x,\omega_k t)]\eta. \tag{5.5}$$

Applying [12, Theorem 7.5.2], as in the proof of Lemma 3.3, one shows that, as $k\to\infty$, the evolution operator of (5.5) converges in the operator norm of $C(\bar\Omega)$ to the evolution operator of (5.4), uniformly on compact time intervals. In particular, if Π_k denotes the period map of the $\frac{1}{\omega_k}$-periodic problem (5.5) and Π_∞ is the time-1 map of (5.4) then

$$\Pi_k^{[1/\omega_k]}\to\Pi_\infty, \tag{5.6}$$

where $[1/\omega_k]$ is the integer part of $1/\omega_k$. Since (u_k,v_k) is a coexistence periodic solution, we see that for $\rho=\mu$ and $\rho=\nu$, the principal eigenvalue of Π_k is equal to 1. Of course, the principal eigenvalue of $\Pi_k^{[1/\omega_k]}$ is then also equal to 1 and from (5.6) we conclude that the principal eigenvalue of Π_∞ is equal to 1 for both $\rho=\mu$ and $\rho=\nu$. However, by Theorem 2.1, the principal eigenvalue of the autonomous problem (5.4) is increasing in ρ (note that $\hat a-u_\infty-v_\infty$ is not constant, otherwise both u_∞ and v_∞ are constant, consequently a is constant in x). This contradiction rules out coexistence periodic solutions of (1.5) for large ω. □

We finish the section with a few remarks on interesting problems concerning the global dynamics of (1.5).

First we discuss the typical behavior of solutions. As a consequence of abstract results on strongly monotone dynamical systems (see [29,30] or [35]), one obtains the following property. There is an open and dense subset G of X_+ such that any solution of (1.5) emanating from G approaches a solution (u, v) that is k-periodic in t, for some positive integer k, and that is at least linearly neutrally stable. Here "at least linearly neutrally stable" means that the Poincaré map of the (k-periodic) linearized problem (3.1) has all eigenvalues inside or on the unit circle. If the minimal period of a k-solution is greater than 1, it is called a *subharmonic solution*. Thus stable 1-periodic solutions and subharmonic solutions determine the large time behavior of most solutions in X_+.

The problem of the existence of stable subharmonic solutions is of fundamental importance in the study of time-periodic equations that define a monotone dynamical system. In various situations it has been resolved. See [14] for conditions ruling out stable subharmonics and [33,34,3,31] for examples (including time-periodic reaction-diffusion equations) where such solutions do occur. Whether or not (1.5) can have stable subharmonic solutions for some function a, is certainly an interesting nontrivial problem worth further investigation.

A similarly interesting problem is the one of multiplicity of coexistence periodic solutions.

6. Concluding remarks

We comment finally on some points raised by the theoretical and numerical investigation. The first point concerns the rather difficult question of obtaining some intuitive insight into the reason for the difference between the autonomous and periodic cases. One might speculate that the faster phenotype (that is, the one with the higher diffusion coefficient) could be selected as the organism would move more rapidly to spatial regions which are better at any given time. Although this is the most obvious argument, it is open to objection; certainly caution is needed as the slower phenotype is selected both for small *and* large frequencies. From a mathematical point of view, Fig. 1 suggests that there is 'tuning' of the diffusion coefficient to frequency for the eigenvalue of the scalar problem. This leads, as is confirmed by (3.5), to a similar effect for the two phenotype problem. Figure 3 shows that in a more realistic situation, where there are two temporal scales, the picture may be very complex.

A particularly interesting issue is that of determining how selection operates when there are several phenotypes and mutation. For the autonomous case it is known [5] that the slowest phenotype is selected; in this special sense we shall say that the lowest rate is 'optimal'. Further, of course a stable polymorphism is impossible. The periodic, multi-phenotype model is a great deal more difficult to analyze. However, it is clear from the 2-phenotype case that the situation is more complex. For our model, coexistence is certainly possible, as proved in Section 4, and in other circumstances either the lower or higher rate may be optimal. For a multi-phenotype model with mutation, one might expect that under some circum-

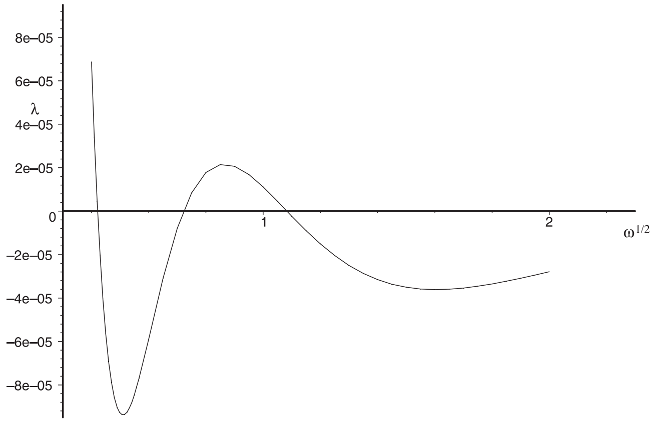

Fig. 3. Here $a(x, t) = 1 + 0.1 \cos \pi x(0.1 + \sin \pi t + 3.2 \sin 24\pi t)$, $\mu = 0.5$, $\nu = 2.0$. $\lambda = \lambda(a - \tilde{u}, \nu)$ is obtained from (3.5); for large ω it is positive. Note that there are two intervals of ω for which λ is negative.

stances there would be an optimal rate whilst under others a polymorphism would be obtained. The point of view taken in adaptive dynamics might be useful here, see [6] and [28] for a discussion of a related model. With the theoretical knowledge currently available, several of the questions in this area would probably have to be tackled numerically.

We close with a few remarks concerning the mathematical side of the investigation. The paper raises a number of interesting open questions. Even for the scalar periodic-parabolic eigenfunction problem, see Section 2, although a great deal is known, there remain questions about basic issues such as the broad qualitative behavior of $\lambda(h, \rho)$ to which answers are not available. For example, how does it behave as a function of ω? Turning next to the coexistence solutions (Section 4), we know that these occur for a wide range of cases, but can there be multiple coexistence solutions? Global questions (Section 5) are often difficult to analyze and we point to some of the issues raised which would repay further study.

7. Appendix A

We give here theorems referred to in the introduction. The first one is concerned with temporally homogeneous equations, as discussed in Subsection 1.2.

Theorem 7.1. *Assume a is sufficiently smooth and independent of t: $a(x, t) = a(x)$. Further assume that either*

(i) $a(x) > 0$ for all $x \in \Omega$, or
(ii) for some $x_0 \in \Omega$, $a(x_0) > 0$ and $0 < \mu < \nu$ are sufficiently small.

Then, there are exactly three nonnegative equilibria for (1.1), (1.2) which take the form:

$$(0, 0), \quad (\tilde{U}(x), 0) \quad \text{and} \quad (0, \tilde{V}(x)).$$

Furthermore, $(\tilde{U}(x), 0)$ *is the global attractor for all solutions of (1.1)–(1.3) with positive initial conditions* u_0, v_0.

The asymptotic stability of the semitrivial equilibrium $(\tilde{U}(x), 0)$ is proved in [11]. The above is a consequence of [5] where n phenotypes and mutation are considered. Further discussion of the literature may be found in these references.

We next consider spatially homogeneous but temporally heterogeneous equations, as discussed in Subsection 1.3. It is reasonable to assume that the temporal change in the environment is bounded and recurrent, though not necessarily periodic. A mathematically tractable but much less restrictive assumption on a than periodicity is almost periodicity, which for completeness we now define. A subset U of $\mathbb{R}$ is said to be relatively dense if there is an $L > 0$ such that $[s, s+L] \cap U \neq \emptyset$ for every $s \in \mathbb{R}$. Let

$$T(a, \epsilon) = \{s : |a(t+s) - a(t)| < \epsilon \quad \text{for all } t \in \mathbb{R}\}.$$

Then, a is almost periodic if for every $\epsilon > 0$, $T(a, \epsilon)$ is relatively dense. It should be noted, especially if one allows for errors in measurements, over any finite time period it is essentially impossible to distinguish an almost periodic and a stochastic fluctuation in the environment.

Under this hypothesis (1.1) reduces to

$$\begin{aligned} \frac{\partial u}{\partial t} &= \mu \Delta u + (a(t) - u - v)u, \\ \frac{\partial v}{\partial t} &= \nu \Delta v + (a(t) - u - v)v, \quad x \in \Omega,\ t > 0. \end{aligned} \tag{7.1}$$

Using a result of G. Hetzer and W. Shen [16, Theorem C] the global dynamics of this system can be described.

Theorem 7.2. *Let* u_0 *and* v_0 *be non-negative continuous functions on* $\bar{\Omega}$ *and let* (u, v) *be a solution of (7.1), (1.2), (1.3). Then, there exists a non-negative spatially homogeneous solution* $(u^*(t), v^*(t))$*, of (7.1), (1.2) such that*

$$\lim_{t\to\infty} ||u(x, t) - u^*(t)|| = 0 \qquad \lim_{t\to\infty} ||v(x, t) - v^*(t)|| = 0.$$

Here $\|\cdot\|$ stands for the supremum norm.

8. Appendix B

In this appendix we give the proofs of Lemmas 2.3, 2.4.

Proof of Lemma 2.3. Since $\exp(-\lambda(h, \rho))$ is a simple eigenvalue of the period map of (2.2), it depends smoothly on ρ, and also the corresponding eigenfunctions, $\phi_\rho(\cdot, 0)$, $\psi_\rho(\cdot, 0)$, normalized as in (2.5), (2.6), are smooth $C(\bar{\Omega})$-valued functions of ρ (see [22]). Consequently, by standard regularity results (see [12]), $\rho \mapsto \phi_\rho$ is a smooth $C^1(\bar{\Omega} \times [0, 1])$-valued map and its derivative $\phi' := D_\rho \phi_\rho$ is a 1-periodic solution of

$$\omega \phi'_t - \rho \Delta \phi' - (h + \lambda)\phi' = \Delta \phi + \lambda' \phi, \tag{8.1}$$

where

$$\lambda' = D_\rho \lambda(h, \rho).$$

Multiplying (8.1) by $\psi_\rho(x, t)$, integrating over $\bar{\Omega} \times [0, 1]$ and rearranging, we obtain (omitting the subscript ρ)

$$\int_0^1 \int_{\bar{\Omega}} \{\omega\phi'_t\psi - \rho\Delta\phi'\psi - h\phi'\psi\} = \iint \Delta\phi\psi + \lambda' \iint \phi\psi.$$

Integrating by parts and using (2.3), one obtains (2.4). □

Proof of Lemma 2.4. Divide (2.1) by (the positive function) ϕ and integrate over $\Omega \times (0, 1)$ to obtain

$$\lambda(h, \rho) = -\rho \int_0^1 \int_\Omega \frac{|\nabla\phi|^2}{\phi^2} - \int_0^1 \int_\Omega h(x, t).$$

This implies (a) (note that $\nabla\phi \not\equiv 0$ if h is not spatially homogeneous).

We prove (b). By the maximum principle, there is a uniform lower bound on $\lambda(h, \rho)$, hence, by (a), $\lambda(h, \rho)$ stays bounded as $\rho \to \infty$.

We normalize ϕ:

$$\frac{1}{|\Omega|} \iint \phi^2 = 1,$$

with the integral over $(0, 1) \times \Omega$.

Multiplying (2.1) by ϕ and integrating, we obtain the equation

$$\rho \iint |\nabla\phi|^2 - \iint (h + \lambda(h, \rho))\phi^2 = 0, \tag{8.2}$$

and it follows that for some constant c_1 independent of ρ,

$$\iint |\nabla\phi|^2 \leq \frac{c_1}{\rho}. \tag{8.3}$$

Let $\Phi = \phi - \bar{\phi}$. Then $\int_\Omega \Phi = 0$ and, by Poincaré's inequality, there is a constant $k > 0$ depending only on Ω such that $\int_\Omega |\nabla\Phi|^2 \geq k \int_\Omega \Phi^2$. With $\nabla\phi = \nabla\Phi$, (8.3) therefore gives

$$\iint |\Phi|^2 \leq \frac{c_1}{k\rho}. \tag{8.4}$$

Now, integrating (2.1) over Ω and substituting $\phi = \bar{\phi} + \Phi$, we obtain

$$\omega\bar{\phi}_t = (\bar{h} + \lambda)\bar{\phi} + g_\rho(t),$$

where, by (8.4), $\int_0^1 |g_\rho(t)|dt = O(1/\rho)$ as $\rho \to \infty$. Using the integrating factor in this first order differential equation, we find that

$$e^{-\frac{1}{\omega}\int_0^t (\bar{h}+\lambda)}\bar{\phi}(t) = \bar{\phi}(0) + O(1/\rho). \tag{8.5}$$

As $\bar{\phi}(1) = \bar{\phi}(0)$, we must have either $(\bar{h} + \lambda)\hat{} \to 0$ or $\bar{\phi}(0) \to 0$, when $\rho \to \infty$. The former gives assertion (b). We show that the latter is impossible. Suppose it holds. Then, by (8.5), also $\bar{\phi}(t) \to 0$, uniformly in $t \in [0, 1]$. But this and (8.3) imply, again by Poincaré's inequality, that

$$\iint \phi^2 \to 0,$$

in contradiction to the normalization of ϕ.

We now prove (c). Rewrite (2.1) in the form

$$\omega \frac{\partial \phi}{\partial t} - \rho \Delta \phi - (h + \lambda_0)\phi = (\lambda - \lambda_0)\phi,$$

where λ_0 is a constant. If $\hat{h}$ is not constant, we may choose λ_0 such that

$$-\max_{x \in \bar{\Omega}} \hat{h} < \lambda_0 < -\hat{\bar{h}}.$$

For any such λ_0 we have $(h + \lambda_0)\hat{\bar{}} < 0$ and

$$\int_0^1 \max_{x \in \Omega}(h + \lambda_0) \geq \max_{x \in \Omega}(h + \lambda_0)\hat{} > 0.$$

Under these conditions, one has $\lambda(h, \rho) - \lambda_0 < 0$ for small enough ρ, as shown in [13, p. 54, Example 17.2]. This implies

$$\limsup_{\rho \to 0} \lambda(h, \rho) \leq -\max_{x \in \bar{\Omega}} \hat{h}.$$

If $\hat{h}$ is constant, the same relation follows from (a).

On the other hand, choosing any $\lambda_0 < -\max_{x \in \bar{\Omega}} \hat{h}$, we have $(h + \lambda_0)\hat{} < 0$ for all x. So by [13, Prop. 17.3], $\lambda(h, \rho) - \lambda_0 > 0$ for small enough ρ.

A combination of the above inequalities proves the result. □

Remark 1. An inspection of the proof of Lemma 2.4(b) reveals that the following stronger statement holds: Assume that for large ρ, $h_\rho(x, t)$ is a continuous function on $\bar{\Omega} \times [0, 1]$ such that $\|h_\rho - h\|_{L^\infty(\Omega \times (0,1))} \to 0$ as $\rho \to \infty$. Then

$$\lim_{\rho \to \infty} \lambda(h_\rho, \rho) = -\hat{\bar{h}}.$$

This is used in the proof of Theorem 5.3.

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