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by

Ivano Primi, Angela Stevens, and Juan J.L. Velazquez

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PATTERN FORMING INSTABILITIES DRIVEN BY NON-DIFFUSIVE INTERACTION

I. Primi¹, A. Stevens² and J. J. L. Velázquez³

Abstract

Analogous to the analysis of minimal conditions for the formation of Turing patterns or diffusion driven instabilities, in this paper we discuss minimal conditions for a class of kinetic equations with mass conservation, which form patterns with a characteristic wavelength. The related linearized systems are analyzed and the minimal number of equations is derived, which is needed to obtain specific patterns.

1 Introduction

Pattern formation is ubiquitous in biological and chemical systems. To be able to distinguish between the possible underlying mechanisms driving these patterns and their related function, is an important aim for a better understanding and for experimental control. Patterns generated by diffusive instabilities are by now quite well understood. In his pioneering work (cf. [24]) Turing proved, that for chemical reactions of activator and inhibitor type, diffusion can drive an otherwise stable system towards pattern formation with a characteristic wavelength or characteristic time period. This idea of diffusive morphogens or Turing instabilities has later been applied to many pattern forming biological systems (cf. [12, 18], [19]), to name only a few of the many references.

A main part of Turing's analysis was devoted to linearized reaction-diffusion systems. This is often sufficient in order to obtain estimates on the basic quantitative features of the observed patterns, like their characteristic wavelength; or in the case of dynamic patterns, their speed of propagation. The linearized analysis, however, predicts exponential growth of the chemical, respectively morphogen concentrations. The picture can be completed if saturating chemical kinetics are assumed.

 $^{^1{\}rm Universit\"{a}t}$ Heidelberg, Angewandte Mathematik und Bio
Quant, INF 267, D-69120 Heidelberg, Germany (ivano.primi@uni-hd.de)

 $^{^2{\}rm Universit\"{a}t}$ Heidelberg, Angewandte Mathematik und BioQuant, INF 267, D-69120 Heidelberg, Germany (angela.stevens@uni-hd.de)

³ICMAT (CSIC-UAM-UC3M-UCM), Facultad de Ciencias Matemáticas, Universidad Complutense, Madrid 28040, Spain (velazque@mat.ucm.es)

There are, however, structure forming processes in biology where diffusive signals do not seem to play the major role. An example for this are for instance the counter migrating rippling waves that occur before the final aggregation of myxobacteria, [6]. These are assumed to result from local cell-cell interactions. Also in a number of signaling processes within tissues local exchange of signals seems to play a major role.

From a mathematical point of view examples for systems, where the patterns result from local interactions, are kinetic equations of the type

$$\partial_t f(t, x, c) + U(c) \cdot \partial_x f(t, x, c) + \partial_c \left[K \left[f(t, x, c) \right] \right] = 0. \tag{1.1}$$

Here $\{c\}$ denotes a set of internal variables characterizing the state of the cells. For cell movement in one spatial dimension this would also include the direction of motion (right or left). In higher spatial dimensions $\{c\}$ might indicate cell orientation. Further variables like e.g. chemical/cell concentrations and the fraction of occupied receptors could also be included. The set $\{c\}$ can be continuous or discrete. In the discrete case the operator ∂_c must be replaced by a suitable "discrete divergence operator" whose meaning will be specified later.

The function f(t, x, c) can be thought of as the cell density in the state space (t, x, c). The operator K[f(t, x, c)] in (1.1) is an additive or integral operator, in general non-linear, which describes the cell fluxes with respect to the internal variables $\{c\}$. The most distinctive feature of this operator is, that it acts on the densities $f(t, x, \cdot)$ in a local manner. So the values of $K[f(t, x, \cdot)]$ are depending on the values of $f(t, x, \cdot)$ at point x only. Some examples for equations of type (1.1) being used as models for pattern formation in biology can be found in [7], [8], [9], [10], [11], [15] [17], [21]. Sometimes more general models which include noise and diffusion are considered. Further examples for equations of type (1.1) will be described in detail later.

Mathematically, model (1.1) is rather different from the parabolic systems considered by Turing. In particular, linearization around a homogeneous state does not provide any specific wavelength, if the space of internal variables $\{c\}$ contains only two elements (cf. [17])). However, systems more general than (1.1), which yield specific wavelengths for such type of linearizations have been discussed by several authors. For instance, in [14] examples of systems with a structure similar to (1.1) are given, but which contain an additional diffusive factors in the spatial variable x that exhibits nontrivial patterns. On the other hand, in [2] examples are discussed, where besides the terms like in (1.1), an additional delay term occurs, which also produces nontrivial patterns near homogeneous states. It is then natural to ask if it is possible to obtain examples for systems of type (1.1) which yield non trivial patterns near homogeneous solutions, where neither diffusion nor explicit delays are responsible for pattern formation.

In this paper we will provide sufficient conditions for equations of form (1.1) that are able to select a wavelength in a similar way as it happens in Turing

systems. This means that the linearized system already shows this behavior. In order to obtain pattern formation, both types of systems need a minimal complexity. In the case of Turing systems at least two different species are necessary. For the systems considered in this paper, we need at least three equations to obtain nontrivial patterns on the linearized level. If the interactions between the cells are assumed to satisfy additional symmetry assumptions, at least four equations are needed.

In [13], Turing like instabilities for

$$a_{t} + \Gamma a_{x} = M (b - a) + \frac{1}{2} f (a + b)$$

$$b_{t} - \Gamma b_{x} = M (a - b) + \frac{1}{2} f (a + b)$$
(1.2)

were studied, with

$$\begin{split} a &= \left(\begin{array}{c} \alpha_1 \\ \alpha_2 \end{array} \right) \;,\; b = \left(\begin{array}{c} \beta_1 \\ \beta_2 \end{array} \right) \;\; \Gamma = \left(\begin{array}{c} \gamma_1 & 0 \\ 0 & \gamma_2 \end{array} \right) \;,\; M = \left(\begin{array}{c} \mu_1 & 0 \\ 0 & \mu_2 \end{array} \right) \;,\\ f\left(u \right) &= \left(\begin{array}{c} f_1 \left(u_1, u_2 \right) \\ f_2 \left(u_1, u_2 \right) \end{array} \right) \end{split}$$

A key feature of (1.2) is that the reactions between the species generally change the total concentration $\int \sum_{i=1}^{2} (\alpha_i + \beta_i) dx$. Therefore (1.2) is not of type (1.1), where the total concentration $\int \int f(t, x, c) dxdc$ is preserved.

In [13] several types of instabilities for the system (1.2) are considered. Among them a kind of hyperbolic version of Turing's instability. An intuitive explanation for this is as follows. Consider the following asymptotic limit for the solutions of (1.2)

$$||M|| \to \infty$$
, $||\Gamma|| \to \infty$, $M^{-1}\Gamma^2 \to D$,

where $\|\cdot\|$ denotes a typical matrix norm and $D=\begin{pmatrix}d_1&0\\0&d_2\end{pmatrix}$ with $d_1,d_2>0$. Formally, solutions which have a characteristic wavelength larger than $\frac{1}{\sqrt{\|M\|}}$ can be approximated by solutions of the parabolic system

$$u_t = Du_{xx} + f(u) \quad \text{with} \quad u = a + b . \tag{1.3}$$

System (1.3) can exhibit instabilities near homogeneous equilibria, according to the Turing mechanism. Therefore, solutions of a suitable linearization of this model near a homogeneous steady state yield pattern formation with a specific wavelength of order one. Since solutions of (1.2) with large enough wavelengths can be approximated by solutions of (1.3), one can expect instabilities analogous to the ones obtained by Turing for problem (1.2) under suitable assumptions on M and D. This is the case even if the dispersion relations associated to the last system are very different from the ones for (1.3) for very large wavelengths due to the change of character of the problem from hyperbolic to parabolic.

The instabilities we consider in the present paper for conservation laws of type (1.1) are rather different. The resulting patterns are not stationary solutions but traveling waves with a characteristic wavelength and wave velocity. In [13] sets of parameters are studied which yield Hopf bifurcations for (1.2). However, it is not clear from the analysis in [13] if a characteristic wavelength can be obtained for the solutions associated to such bifurcations.

The plan of this paper is as follows. In Section 2 we give a precise definition of what we call a pattern forming system in the present context. In Section 3 we briefly discuss some of Turing's results. In Section 4 we study the pattern forming properties of equations of type (1.1). In Subsection 4.2 we recall a situation for which pattern formation can not be decided upon the analysis on the linearized level. In Subsection 4.3 and the following subsections necessary conditions for patterns with a defined wavelength are given on the linearized level. In Section 5 minimal models for rippling of myxobacteria are discussed, without the assumption of the existence of an internal clock or delays. Also, natural conditions can be given for the increasing wavelength of the rippling pattern in experiments with mixtures of wildtype and mutant cells, as well as the loss of the rippling phenomenon when too many mutants are present.

2 Pattern Forming Equations

We will restrict our analysis to linearized equations. So in abstract terms we are interested in problems of the form

$$u_t = Au (2.1)$$

where A is a linear operator, invariant under spatial translations $x \to x + a$, $x \in \mathbb{R}^N$, $a \in \mathbb{R}^N$, acting in a suitable functional space. The function $x \to u$ (x,t) maps \mathbb{R}^N into some functional space X, describing the variables needed to characterize a "macroscopic" region [x, x + dx]. Typically X will include variables measuring chemical concentrations, internal cell variables, cell orientations and others. We will restrict ourselves to the class of operators which for any fixed vector $k \in \mathbb{R}^N$ can be written as

$$A\left(e^{ikx}V\right)=\left[M\left(k\right)V\right]e^{ikx}\ ,\ V\in X\ ,$$

where M(k) is a linear operator acting on X. We can then look for solutions of (2.1) of the form

$$u = e^{\omega t + ikx} V$$
.

where V is a eigenfunction of

$$\omega V = M(k) \cdot V \tag{2.2}$$

Typically, under some general compactness assumptions, the eigenvalues of (2.2) are a discrete set of values for each $k \in \mathbb{R}^N$, e.g. $\{\omega_1(k), \omega_2(k), \ldots\}$. Given a perturbation $u(x,0) = u_0(x) = V_0 e^{ikx}$ with wave number k we obtain its corresponding growth rate by

$$\Omega(k) \equiv \max_{j} \left\{ \operatorname{Re} \left(\omega_{j}(k) \right) \right\} . \tag{2.3}$$

We use the following definition for a pattern generating system in the present context

Definition 1 Equation (2.1) is said to generates patterns, if there exists a set of non-zero real numbers such that

$$\max_{k \in \mathbb{R}^{N} \setminus \{k_{01}, \dots, k_{0l}\}} \Omega(k) < \Omega(k_{0,i}) , i = 1, \dots, \ell$$

$$\Omega(k_{0,i}) = \Omega(k_{0,j}) , \text{ for all } i, j = 1, \dots, \ell$$
(2.4)

$$\Omega(k_{0,i}) = \Omega(k_{0,i})$$
, for all $i, j = 1, ..., \ell$ (2.5)

If (2.4) is satisfied, then solutions of (2.1) with suitable initial data develop patterns with wavelength $\lambda_i = \frac{2\pi}{k_{0,i}}$.

These patterns can also have oscillatory parts if $\operatorname{Im}(\omega_{\ell}(k_{0,i})) \neq 0$ for some $i=1,...,\ell$. Then we will say that (2.1) generates oscillatory patterns.

If (2.4) and (2.5) are satisfied for any $|k| \ge \delta > 0$, then we will say that equation (2.1) generates oscillatory patterns for wavelengths smaller than $\frac{2\pi}{\delta}$.

If $\operatorname{Im}(\omega_{\ell}(k_{0,i})) = 0$ for every $i = 1,...,\ell$ we will say that (2.1) generates stationary patterns.

3 Turing Instabilities

Let us briefly recall the classical instability results derived by Turing (cf. [24]) for reaction-diffusion systems within the above mentioned terminology. Although Turing's paper contains also problems in higher spatial dimensions, we restrict ourselves to the one-dimensional analysis. For this case in [24] the patternforming properties of equations of type

$$\partial_t u = \begin{pmatrix} D_1 & 0 & 0 & 0 & 0 \\ 0 & D_2 & 0 & 0 & 0 \\ 0 & 0 & . & 0 & 0 \\ 0 & 0 & 0 & . & 0 \\ 0 & 0 & 0 & 0 & D_N \end{pmatrix} \partial_x^2 u + A u \tag{3.1}$$

was studied. Here u = u(x,t) is a function with values in \mathbb{R}^N , $D_i > 0$ for i=1,...,N, and A is a real $N\times N$ matrix. Denote the set of such matrices by $M_N(\mathbb{R})$. System (3.1) is typically obtained from the linearization of a reactiondiffusion system without cross-diffusion terms near a homogeneous state.

Theorem 2 (Turing, cf. [24]).

- For N=1 equation (3.1) does not generate patterns for any $A \in \mathbb{R}$ in the sense of Definition 1.
- Let N=2, $A=\begin{pmatrix} a_{1,1} & a_{1,2} \\ a_{2,1} & a_{2,2} \end{pmatrix}$ and $D=\begin{pmatrix} D_1 & 0 \\ 0 & D_2 \end{pmatrix}$. Then system (3.1) generates stationary patterns in the sense of Definition 1 if

$$a_{11} + a_{22} < 0$$
 and $detA > 0$,
 $a_{11}D_2 + a_{22}D_1 > 2\sqrt{D_1D_2detA} > 0$. (3.2)

On the other hand, equation (3.1) does not generate oscillatory patterns for any choice of $A \in M_2(\mathbb{R})$.

• Let N=3. Then there exists an open set of matrices $A \in M_3(\mathbb{R})$ such that equation (3.1) generates oscillatory patterns.

Remark 3 Several results for Turing-like instabilities, also by Turing himself, have been derived in bounded domains with periodic or Neumann boundary conditions. Here we consider equations in the whole space. Thus the discrete character of the spectrum of the operators does not have to be taken into account.

Linear reaction-diffusion equations can generate nontrivial patterns with specific wavelengths, if at least two chemical species are involved. Moreover, patterns with nontrivial characteristic length and time scales can be generated, if at least three chemical species involved.

It is well known that conditions (3.2) can be interpreted by the interplay between a short range acting chemical activator and a long range acting inhibitor, where the diffusion coefficient of the inhibitor is larger than the one of the activator.

4 Pattern Formation Without Diffusive Interactions

First we define the general framework for our analysis. We will study some of the pattern formating properties of equations of type

$$\partial_t f(t, x, c) + U(c) \cdot \partial_x f(t, x, c) + \partial_c [L[f]](t, x, c) = 0, \qquad (4.1)$$

where f is the concentration of "cells" in the state $\{c\}$ at a given time t, and L is a linear operator acting on f as explained in the introduction. Let the space of states be measurable and $\mu\left(\cdot\right)$ be a suitable related measure. Equations of type (4.1) naturally arise when systems of the form (1.1) are linearized around a spatially homogeneous ("patternless") state. The set $\{c\}$ can be continuous or discrete. In the discrete case the differential operator ∂_c has to be replaced

by a suitable discrete derivative. This will be explained in examples later. In general, we will assume that the operator ∂_c is a kind of "flux", i.e.

$$\partial_{c}g\left(t,x,c\right) = -\int K\left(c,c'\right)g\left(t,x,c'\right)d\mu\left(c'\right) + \int K\left(c',c\right)g\left(t,x,c\right)d\mu\left(c'\right) \ .$$

In the discrete case such operators reduce to finite sums. Their most relevant property is preservation of mass

$$\int \partial_{c}g\left(t,x,c\right)d\mu\left(c\right) = -\int \int K\left(c,c'\right)g\left(t,x,c'\right)d\mu\left(c'\right)d\mu\left(c\right)$$
$$+\int \int K\left(c',c\right)g\left(t,x,c\right)d\mu\left(c'\right)d\mu\left(c\right) = 0.$$

Therefore, these interactions locally preserve

$$\int f(t,x,c) d\mu(c) .$$

Now we consider some simple examples. Suppose that the space of internal states $\{c\}$ is the real line and let μ be the classical Lebesgue measure $d\mu$ (c)=dc. Let

$$K(c,c') = \frac{1}{h}\delta_0 (c - c' - h) ,$$

where δ_0 is the Dirac measure. Then

$$\partial_c g(t, x, c) = -\frac{g(t, x, c - h)}{h} + \frac{g(t, x, c)}{h}.$$

Define

$$L[f](t, x, c) = a(c) f(t, x, c)$$
 (4.2)

for a suitable function a(c). Then

$$\partial_{c} \left(L\left[f\right] \left(t,x,c\right) \right) = -\frac{a\left(c-h\right) f\left(t,x,c-h\right)}{h} + \frac{a\left(c\right) f\left(t,x,c\right)}{h}\;,$$

and for $h \to 0$ we obtain

$$\partial_{c}g\left(t,x,c\right) = \frac{\partial}{\partial c}\left[a\left(c\right)g\left(t,x,c\right)\right]$$
.

Therefore (4.1) becomes

$$\partial_{t} f(t, x, c) + U(c) \cdot \partial_{x} f(t, x, c) + \frac{\partial}{\partial c} [a(c) f(t, x, c)] = 0$$
.

This equation naturally arises, when studying stage structured models with spatial dynamics. See for instance in [7], [8]. Some general references for modeling

and analysis of stage/age structured populations are for instance [4], [5], [20], [23], and [22].

A typical choice of internal variables is a discrete set

$$\{c\} = \{s_1, s_2, s_3, ..., s_N\}.$$

Define the "shift operator"

$$\tau_{+}(s_{k}) = s_{k+1}$$
, for $k = 1, ..., N$ and define $s_{N+1} = s_{1}$.

The discrete derivative $\tilde{\partial}_c$ will then be defined by

$$\tilde{\partial}_{c}g\left(x,c\right) \equiv g\left(x,\tau_{+}\left(c\right)\right) - g\left(x,c\right). \tag{4.3}$$

On the other hand L[f] is defined as in (4.2). So (4.1) becomes

$$\partial_t f\left(t,x,c\right) + U\left(c\right) \cdot \partial_x f\left(t,x,c\right) + a\left(\tau_+\left(c\right)\right) f\left(t,x,\tau_+\left(c\right)\right) - a\left(c\right) f\left(t,x,c\right) = 0.$$

Since the set $\{c\}$ is discrete, this equation is a finite dimensional system of equations for N variables, namely

$$f(t, x, s_1), f(t, x, s_2), ..., f(t, x, s_N)$$
.

Models of type (1.1) and (4.1) naturally arise when modeling systems of cells which interact via direct contact and not by means of any diffusive chemical. The transport of information between different spatial regions for the models discussed here is purely due to the cell motion.

In [13] Turing like instabilities for equations without diffusive interactions were studied. However, the interactions in (4.1), unlike the "chemical reactions" in [13], preserve the number of "cells" which are involved. Thus pattern formation occurs solely due to cell interaction and does not relate to growth and death processes.

4.1 A Model Problem

Here we describe a class of models whose linearization yields problems of type (4.1). Although we do not aim for detailed biological modeling at this stage, the problems considered are motivated by the intriguing counter migrating wave-like patterns observed before the final aggregation of myxobacteria (cf. [6]). During an alignment process and before final self-organization the bacteria move in opposite directions and reverse their direction of motion, mainly due to contact with counter migrating cells. As a result, characteristic counter-migrating concentration waves occur. A major question is, if such patterns can result from purely local interaction of the bacteria or rather not.

Of course, the instabilities described in the following can also arise in other biological or physical contexts. But for simplicity we stick with the basic phenomenon of rippling in myxobacteria here.

Consider cell, which exist in two different states 1 and 2, and move along a one dimensional axis. Let u_i, v_i denote the densities of cells which move towards the right, respectively the left, with internal state i=1,2. First, the cells change their state e.g. from 1 to 2. Then, in a second step, they reverse their direction of motion. The most characteristic feature of this mechanism is the presence of an intermediate state for the cells before they reorient. This can be interpreted e.g. by the local transfer of a signal during cell interaction, bringing the cell to an excited state or preparing to switch the motor for movement itself, before it reverses its direction. We are interested in the minimal mathematical features such a model must have, to be able to account for nontrivial patterns. The four cellular states then evolve according to the following transition

$$u_1 \rightarrow u_2 \rightarrow v_1 \rightarrow v_2 \rightarrow u_1$$
.

Translating the previously described kinetics into a system of differential equations, we obtain

$$(u_1)_t + (u_1)_x = S_2(u_1, u_2, v_1, v_2) - T_1(u_1, u_2, v_1, v_2)$$

$$(4.4)$$

$$(u_2)_t + (u_2)_x = T_1(u_1, u_2, v_1, v_2) - T_2(u_1, u_2, v_1, v_2)$$

$$(4.5)$$

$$(v_1)_t - (v_1)_x = T_2(u_1, u_2, v_1, v_2) - S_1(u_1, u_2, v_1, v_2)$$

$$(4.6)$$

$$(v_2)_t - (v_2)_x = S_1(u_1, u_2, v_1, v_2) - S_2(u_1, u_2, v_1, v_2).$$

$$(4.7)$$

In order to further simplify the functional dependences, we assume that the system is invariant under the change of variables

$$(x, u_i, v_i) \to (-x, v_i, u_i)$$
, $i = 1, 2$. (4.8)

As a consequence

$$T_i(u_1, u_2, v_1, v_2) = S_i(v_1, v_2, u_1, u_2)$$
, $i = 1, 2$.

And (4.4)-(4.7) can be rewritten as

$$(u_1)_t + (u_1)_x = T_2(v_1, v_2, u_1, u_2) - T_1(u_1, u_2, v_1, v_2)$$

$$(4.9)$$

$$(u_2)_t + (u_2)_x = T_1(u_1, u_2, v_1, v_2) - T_2(u_1, u_2, v_1, v_2)$$

$$(4.10)$$

$$(v_1)_t - (v_1)_x = T_2(u_1, u_2, v_1, v_2) - T_1(v_1, v_2, u_1, u_2)$$

$$(4.11)$$

$$(v_2)_t - (v_2)_x = T_1(v_1, v_2, u_1, u_2) - T_2(v_1, v_2, u_1, u_2)$$
 (4.12)

We will now study systems of type (4.1), which are obtained by linearizing systems of type (4.9)-(4.12) around a homogeneous equilibrium, having the same values for u_1 , v_1 and u_2 , v_2 . Thus there exists a solution for the algebraic system

$$T_1(u_{1,0}, u_{2,0}, u_{1,0}, u_{2,0}) = T_2(u_{1,0}, u_{2,0}, u_{1,0}, u_{2,0})$$
 (4.13)

For generic functions T_1 , T_2 a curve of stationary states solving (4.13) in the plane $(u_{1,0}, u_{2,0})$ is to be expected. This is a major difference in comparison with Turing instabilities, where only an isolated non-zero homogeneous steady state

occurs. This continuum of steady states relates to the fact that the individual cell populations may have different total cell densities. Moreover, prescribing the total cell density $\sigma \equiv (u_1 + u_2 + v_1 + v_2)$, an additional equation is obtained, namely $u_{1,0} + u_{2,0} = \frac{\sigma}{2}$. So the homogeneous steady state can be determined uniquely. Under our symmetry condition the total cell density is given by

$$n_0 = 2\left(u_{1,0} + u_{2,0}\right) \ . \tag{4.14}$$

If n_0 is fixed we must solve (4.13) with the constraint (4.14). For generic functions T_1 , T_2 we can expect this problem to have a unique solution, at least locally near $u_{1,0} = u_{2,0}$. The stationary values for u_1 , u_2 , v_1 , v_2 are assumed to fulfill

$$u_1 = v_1 = u_{1,0}$$
 , $u_2 = v_2 = u_{2,0}$.

This symmetry assumption is reasonable due to (4.8). As a consequence

$$\frac{\partial T_{\ell}}{\partial u_{i}} \Big(u_{1,0}, u_{2,0}, u_{1,0}, u_{2,0} \Big) = \frac{\partial T_{\ell}}{\partial v_{i}} \Big(u_{1,0}, u_{2,0}, u_{1,0}, u_{2,0} \Big) . \tag{4.15}$$

Define $T_{\ell,j} \equiv \partial_j T_\ell$ $(u_{1,0}, u_{2,0}, u_{1,0}, u_{2,0})$, where j = 1, 2 denotes derivatives with respect to u_1 , u_2 and k = 3, 4 denotes derivatives with respect to v_1 , v_2 . Using (4.15), the linearization of (4.4)-(4.7) becomes

$$(\varphi_1)_t + (\varphi_1)_x = (T_{2,3} - T_{1,1}) \varphi_1 + (T_{2,4} - T_{1,2}) \varphi_2 + (T_{2,1} - T_{1,3}) \psi_1 + (T_{2,2} - T_{1,4}) \psi_2$$
(4.16)

$$(\varphi_2)_t + (\varphi_2)_x = (T_{1,1} - T_{2,1}) \varphi_1 + (T_{1,2} - T_{2,2}) \varphi_2 + (T_{1,3} - T_{2,3}) \psi_1 + (T_{1,4} - T_{2,4}) \psi_2$$

$$+ (T_{1,3} - T_{2,3}) \psi_1 + (T_{1,4} - T_{2,4}) \psi_2$$

$$(\psi_1)_t - (\psi_1)_x = (T_{2,1} - T_{1,3}) \varphi_1 + (T_{2,2} - T_{1,4}) \varphi_2$$

$$(4.17)$$

$$+ (T_{2,3} - T_{1,1}) \psi_1 + (T_{2,4} - T_{1,2}) \psi_2$$

$$(\psi_2)_t - (\psi_2)_x = (T_{1,3} - T_{2,3}) \varphi_1 + (T_{1,4} - T_{2,4}) \varphi_2$$

$$+ (T_{1,1} - T_{2,1}) \psi_1 + (T_{1,2} - T_{2,2}) \psi_2$$

$$(4.18)$$

with $u_i = u_{i,0} + \varphi_i$, $v_i = v_{i,0} + \psi_i$, i = 1, 2 and $|\varphi_i| << u_{i,0}$, $|\psi_i| << v_{i,0}$. Problem (4.16)-(4.19) is of type (4.1), with a point measure $d\mu(c)$ containing four elements $\{c\} \equiv \left\{ \begin{pmatrix} 1 \\ + \end{pmatrix}, \begin{pmatrix} 2 \\ + \end{pmatrix}, \begin{pmatrix} 1 \\ - \end{pmatrix}, \begin{pmatrix} 2 \\ - \end{pmatrix} \right\}$. In the following we analyze systems of type (4.16)-(4.19) and variations, which yield oscillatory patterns. Systems having some analogies with (4.4)-(4.7) but include time-

delays have been considered in [2]. More precisely, models of the form

 $(u_1)_t + (u_1)_x = f_l(x - v\tau, t - \tau) - f_r(x, t)$ (4.20)

$$(u_2)_t + (u_2)_x = f_l(x,t) - f_l(x - v\tau, t - \tau)$$
(4.21)

$$(v_1)_{t} - (v_1)_{\tau} = f_r (x + v\tau, t - \tau) - f_l (x, t)$$

$$(4.22)$$

$$(v_2)_t - (v_2)_r = f_r(x, t) - f_r(x + v\tau, t - \tau)$$
(4.23)

were studied, where f_r , f_l are suitable functions of the variables u_1 , u_2 , v_1 , v_2 . In [2] it was shown that the linearization of (4.20)-(4.23) around an homogeneous solution generates oscillatory patterns in the sense of Definition 1. One of the major differences between systems (4.4)-(4.7) and (4.20)-(4.23) is the presence of the delay τ in the second model, that might be interpreted as an "internal clock" or refractory time. The main result of our paper is to show that the structure of the nonlinearities in (4.4)-(4.7) is rich enough to generate oscillatory patterns without including delay terms in the equation. Further mathematical models for pattern formation in myxobacteria can be found in [1] and [3], to only name a few references.

4.2 The Non-Pattern Forming Case

First we recall some of the results derived in [17] and relate these to the case N=1 in Theorem 2. Consider a system with two internal variables $\{c\}$ denoted by + and -. To connect with the notation in [17], we write

$$f(x, +, t) = u_{+}(x, t)$$
, $f(x, -, t) = u_{-}(x, t)$, $U(+) = U_{+}$, $U(-) = U_{-}$.

The most general local operator L[f] in (4.1) is of the form

$$\begin{pmatrix} L[f]_+ \\ L[f]_- \end{pmatrix} = \begin{pmatrix} a_{1,1} & a_{1,2} \\ a_{2,1} & a_{2,2} \end{pmatrix} \begin{pmatrix} u_+ \\ u_- \end{pmatrix}$$

with $a_{i,j} \in \mathbb{R}$ for $i, j \in \{1, 2\}$. The "discrete derivative" operator (4.3) then becomes

$$\begin{pmatrix} (\partial_c g)_+ \\ (\partial_c g)_- \end{pmatrix} = \begin{pmatrix} (g)_+ - (g)_- \\ (g)_- - (g)_\perp \end{pmatrix} .$$

Therefore, (4.1) reduces to

$$\begin{pmatrix} \partial_t u_+ \\ \partial_t u_- \end{pmatrix} + \begin{pmatrix} U_+ \partial_x u_+ \\ U_- \partial_x u_- \end{pmatrix} = \begin{pmatrix} a_{1,1} u_+ + a_{1,2} u_- \\ a_{2,1} u_+ + a_{2,2} u_- \end{pmatrix} - \begin{pmatrix} a_{2,1} u_+ + a_{2,2} u_- \\ a_{1,1} u_+ + a_{1,2} u_- \end{pmatrix}$$

Making the change of variables $x \to x - \frac{U_+ + U_-}{2}t$, we can assume w.l.o.g. that $U_+ = -U_- \equiv U$. Such a transformation does not change the non-pattern or pattern forming behavior of the system. Also, the characteristic wave length of the patterns, if existent, does not change. However, any standing pattern could change to a traveling wave type of pattern or vice versa. We will assume that the system under consideration has the form

$$\begin{pmatrix} \partial_t u_+ \\ \partial_t u_- \end{pmatrix} + \begin{pmatrix} U \partial_x u_+ \\ -U \partial_x u_- \end{pmatrix} + \begin{pmatrix} T & -S \\ -T & S \end{pmatrix} \begin{pmatrix} u_+ \\ u_- \end{pmatrix} = 0 \tag{4.24}$$

with
$$T \equiv -a_{1,1} + a_{2,1}$$
, $S \equiv -a_{2,2} + a_{1,2}$. (4.25)

Systems of type (4.24) were obtained in [17] from

$$\begin{pmatrix} \partial_{t}u_{+} \\ \partial_{t}u_{-} \end{pmatrix} + \begin{pmatrix} U\partial_{x}u_{+} \\ -U\partial_{x}u_{-} \end{pmatrix} = \begin{pmatrix} -\lambda\left(u_{+}, u_{-}\right)u_{+} + \lambda\left(u_{-}, u_{+}\right)u_{-} \\ -\lambda\left(u_{-}, u_{+}\right)u_{-} + \lambda\left(u_{+}, u_{-}\right)u_{+} \end{pmatrix}$$
(4.26)

for a general class of functions λ by linearization around homogeneous stationary solutions. System (4.26) is a simplified version of (4.16)-(4.19) for a problem with two internal states. The following result obtained in [17], will now be restated in the above given terminology.

Theorem 4 ([17]) The linear system (4.24) does not generate patterns in the sense of Definition 1 for any choice of $U, T, S \in \mathbb{R}$.

Proof. W.l.o.g. assume $U \neq 0$, otherwise $\omega = \omega(k)$ in (2.3) is independent on k. The dispersion relation associated to (4.24) can be computed by solving

$$\det \left(\begin{array}{cc} \omega + ikU + T & -S \\ -T & \omega - ikU + S \end{array} \right) = 0 ,$$

or equivalently $(\omega)^2 + k^2U^2 + (T+S)\omega + ikU(S-T) = 0$. Then

$$\omega_{\pm} = \frac{1}{2} \left[-(T+S) \pm \left[(T+S)^2 - 4 \left(ikU(S-T) + k^2 U^2 \right) \right]^{\frac{1}{2}} \right] .$$

In order to analyze the behavior of $\Omega(k) = \max\{\operatorname{Re}(\omega_{+}(k)), \operatorname{Re}(\omega_{-}(k))\}\$ it is sufficient to study

$$h(k) \equiv \operatorname{Re} \left\{ \left[(T+S)^2 - 4 \left(ikU(S-T) + k^2U^2 \right) \right]^{\frac{1}{2}} \right\}$$
$$= \operatorname{Re} \left\{ \sqrt{(a^2 - b^2k^2) + cik} \right\} ,$$

with $a^2 \equiv (T+S)^2$, $b^2 \equiv 4U^2$, $c=-4U\,(S-T)=4U\,(T-S)$, and $\sqrt{\cdot}$ being the complex root with positive real part. By symmetry $h\,(k)=h\,(-k)$. We will show that $h\,(k)$ is monotone in $[0,\infty)$. Using again symmetry, we can restrict our analysis to the case $c\geq 0$. Since $U\neq 0$ we have $b^2>0$. Notice that

$$h(k) = \sqrt[4]{(a^2 - b^2 k^2)^2 + c^2 k^2} \cos\left(\frac{1}{2}\arctan\left(\frac{ck}{(a^2 - b^2 k^2)}\right)\right)$$

where $\arctan(\cdot) \in [0, \pi]$. Therefore $h(k) \geq 0$. Elementary trigonometric calculations yield

$$h(k) = \sqrt[4]{(a^2 - b^2 k^2)^2 + c^2 k^2} \sqrt{\frac{1 + \cos\left(\arctan\left(\frac{ck}{(a^2 - b^2 k^2)}\right)\right)}{2}}$$

with $\cos(\cdot) \in [0, \pi]$. Thus after some computations we obtain

$$h\left(k\right) = \frac{1}{\sqrt{2}}\sqrt{H\left(k\right)} ,$$

where

$$H(k) \equiv \sqrt{(a^2 - b^2 k^2)^2 + c^2 k^2} + (a^2 - b^2 k^2)$$
.

In order to check the monotonicity for H(k) we calculate

$$\begin{split} &\frac{dH\left(k\right)}{dk} \\ &= \frac{k}{\sqrt{\left(a^2 - b^2 k^2\right)^2 + c^2 k^2}} \left(-2b^2 \left(a^2 - b^2 k^2\right) + c^2 - 2b^2 \sqrt{\left(a^2 - b^2 k^2\right)^2 + c^2 k^2} \right) \\ &= \frac{k}{\sqrt{\left(a^2 - b^2 k^2\right)^2 + c^2 k^2}} \left(c^2 - 2b^2 H\left(k\right) \right) \; , \; \text{and} \; H\left(0\right) = 2a^2 \; . \end{split}$$

So H(k) is increasing if $4a^2b^2 < c^2$, and decreasing if $4a^2b^2 > c^2$. If $4a^2b^2 = c^2$, H(k) is constant. Thus $H(\cdot)$ and also h(k) are monotone, and our theorem follows.

4.3 The Pattern Forming Case

In this subsection we study a particular class of equations of type (4.1), namely

$$\partial_t f + U \cdot \partial_x f + DAf = 0 , \qquad (4.27)$$

where

$$D = \begin{pmatrix} 1 & 0 & \dots & -1 \\ -1 & 1 & \dots & 0 \\ & \dots & \dots \\ 0 & \dots & -1 & 1 \end{pmatrix}, U = \begin{pmatrix} U_1 & 0 & \dots & 0 \\ 0 & U_2 & \dots & 0 \\ & \dots & \dots \\ 0 & \dots & 0 & U_N \end{pmatrix}$$
(4.28)

and A is a square matrix in $M(\mathbb{R}^N)$. For this problem the space of "internal cell states" $\{c\}$ is the set of integers $\{1, 2, ..., N\}$. It would be natural to assume certain symmetry conditions for U, A, and positivity for all or some of the coefficients of A. However, first we will begin our analysis with generic matrices A and U. The dispersion relation associated to (4.27) solves

$$zw + ikU \cdot w + DAw = 0 \tag{4.29}$$

Here and in the following we often omit the identity matrix in arithmetic expression with scalar quantities and matrices.

In the subsequent arguments the following properties of the matrix DA will be relevant.

Proposition 5 Let D be given as in (4.28). Then, the matrix DA has a zero eigenvalue. Moreover

$$\vec{b} = (1, \cdots, 1)^t \tag{4.30}$$

is an element of the kernel of $(DA)^T$, which is the transposed matrix of DA.

Proof. We have $\det(DA) = \det(D) \det(A) = 0$ since $\det D = 0$. Therefore $0 \in \sigma(DA)$. Since $D^Tb = 0$,

$$(DA)^T b = A^T D^T b = A^T (0) = 0.$$
 (4.31)

Thus $b \in \ker ((DA)^T)$.

4.4 Case 1: Nondegenerate U and non-symmetric A.

Definition 6 We will call the matrix U in (4.28) nondegenerate, if $U_i \neq U_j$ for $i \neq j$.

In this subsection we show how to obtain a class of matrices A for which (4.27) exhibits nontrivial patterns when U is nondegenerate. The key idea is to choose $A = A_0 + \varepsilon M$, where A_0 yields a "hyperbolic" dispersion relation for (4.27). Thus the most unstable part of the spectrum of A_0 is contained in the imaginary axis. The matrix εM will then be chosen as a small perturbation of A_0 that will change such a part of the spectrum to a curve yielding pattern formation properties in the sense defined before. More precisely, we assume the following

Assumption 1) The set of eigenvectors with zero eigenvalue of DA_0 is the linear subspace generated by $e_1 = (1, 0, \dots, 0)^t$. The eigenvectors of DA_0 are a basis of \mathbb{R}^N . Moreover $U_1 \neq 0$.

As a consequence, the set of solutions of the family of eigenvalue problems

$$zw + ikU \cdot w + DA_0w = 0 \quad , \quad k \in \mathbb{R}$$
 (4.32)

contains the straight line $\{z = -ikU_1\}$. This means that the spectrum associated to A_0 is "hyperbolic".

Assumption 2) All solutions of (4.32) which are not contained in $\{z = -ikU_1\}$ are located in the half-plane $\{\operatorname{Re}(z) < -\nu_0\}$ for some $\nu_0 > 0$.

Remark: For convenience we have chosen e_1 as distinguished eigenvector for DA_0 from the canonical basis of \mathbb{R}^N . But e_1 cannot be rotated without modifying the matrix U. Thus we do not have the most general choice of matrices A_0

yielding hyperbolic behavior. The main goal of this paper is to find examples for instabilities. It would be interesting though to classify the matrices A_0 , which yield hyperbolic behavior for the spectrum.

The condition $U_1 \neq 0$ is essential, since without a characteristic speed it would not be possible to obtain a characteristic wavelength. W.l.o.g. $U_1 > 0$. To avoid lengthy calculations involving Jordan canonical forms the assumption that the eigenvectors of DA_0 are a basis of \mathbb{R}^N is convenient.

Now we analyze the dispersion relation associated to (4.29) for

$$A = A_0 + \varepsilon M \tag{4.33}$$

where $\varepsilon > 0$ is small and M will be defined later. The spectrum of (4.29) can be computed in a perturbative manner and the following lemma yields a preliminary estimate of its position.

Lemma 7 Suppose that A_0 satisfies Assumptions 1) and 2). Let A be given by (4.33). Then, there exist positive constants $C = C(A_0, M)$, β and ε_0 , independent of ε , such that for each $k \in \mathbb{R}$ and $|\varepsilon| \leq \varepsilon_0$ the spectrum associated to problem (4.29) consists of

- (i) an eigenvalue $z_1 = z_1(k)$ satisfying $|\operatorname{Re}(z_1)| \leq C\varepsilon^{\beta}$.
- (ii) at most (N-1) eigenvalues located in the half-plane $\{\operatorname{Re}(z)<-\nu_0+C\varepsilon^\beta\}$.

Proof. This result follows from classical perturbation theory of eigenvalue problems as it can be found e.g. in [16]. For the uniformicity estimates for the change of eigenvalues as $|k| \to \infty$, let $\rho_+(B)$ denote the subset of the complex plane such that the inverse matrix $(B+zI)^{-1}$ exists. Due to Assumptions 1) and 2) we have

$$\{z \in \mathbb{C} : \operatorname{Re}(z) > -\nu_0 \text{ and } z \neq -ikU_1\} \subset \rho_+ (ikU + DA_0)$$
 (4.34)

Moreover, using for a matrix B that $B^{-1} = \frac{(Adj(B))^T}{\det(B)}$ and the fact that the numbers of zeros of the determinant of a $N \times N$ -matrix is less or equal than N it follows that

$$\left\| (zI + ikU + DA_0)^{-1} \right\| \le \frac{L(R_1, R_2)}{\left| \text{dist} (z, \partial \rho_+ (ikU + DA_0)) \right|^N} , \tag{4.35}$$

for $|k| \leq R_1$, $|z| \leq R_2$, where $L = L(R_1, R_2)$ is a constant independent of k and z. For $R_2 > ik ||U|| + ||DA||$ we obtain that $z \in \rho_+$ (ikU + DA).

Let $|z| \leq R_2$, Re $(z) > -\nu_0 + C\varepsilon^{\frac{1}{N}}$ or $|\text{Re}(z)| > C\varepsilon^{\frac{1}{N}}$, where C is a constant to be determined. We then compute by Neumann series

$$(zI + ikU + DA)^{-1} = \left(\sum_{n=0}^{\infty} (-1)^n \left[\varepsilon (zI + ikU + DA_0)^{-1} DM \right]^n \right) (zI + ikU + DA_0)^{-1}$$

which converges for $\|\varepsilon (zI + ikU + DA_0)^{-1} DM\| < 1$. Using (4.34), (4.35) and the constraints for the values of z one obtains

$$\left\| \varepsilon \left(zI + ikU + DA_0 \right)^{-1} DM \right\| \leq \frac{L\left(R_1, R_2 \right) \left\| DM \right\| \varepsilon}{\left| C\varepsilon^{\frac{1}{N}} \right|^N} = \left(\frac{L\left(R \right) \left\| DM \right\|}{C^N} \right) < 1 ,$$

for $C > (L(R_1, R_2) ||DM||)^{1/N}$. Since the spectrum of the matrices depends continuously on the parameters, we obtain the properties (i) and (ii) for $|k| \le R_1$, $|z| \le R_2$.

In order to prove our Lemma for $|k| > R_1$ we rewrite (4.29) as

$$\frac{z}{ik}w + U \cdot w + \frac{1}{ik}DAw = 0. (4.36)$$

Then, if |k| is large enough, (4.36) becomes a perturbation of the eigenvalue problem for U. It is well known that the eigenvalues of (4.36) are analytic functions w.r.t. the perturbation parameter. So

$$\frac{z_j}{ik} = -U_j + f_j\left(\frac{1}{ik}\right) , j = 1, ..., N ,$$
 (4.37)

where the $f_j(\cdot)$ are differentiable in a neighborhood of the origin of coordinates (cf. [16], p. 82, Theorem 2.3). Moreover

$$f_j(\zeta) \sim \lambda_j(DA)\zeta + O(|\zeta|^2) \text{ as } \zeta \to 0,$$
 (4.38)

where λ_j (DA) are the eigenvalues of the projection of the matrix DA onto the subspace of eigenvectors associated to a given eigenvalue U_j (cf. [16]). In particular, such eigenvalues are roots of polynomials with maximal degree N. Therefore

$$|\lambda_j(DA) - \lambda_j(DA_0)| \le C\varepsilon^{\frac{1}{N}},$$
 (4.39)

where C depends on the norms of U, A and M. Due to Assumptions 1) and 2) the λ_j (DA_0) are either zero, or their real part is smaller than $-\nu_0$. Then, using (4.37)-(4.39) for $|k| > R_1$, we obtain (i) and (ii) of our Lemma for large values of |k| and the previous estimates for $|k| \le R_1$.

Due to Lemma 7 we have for small ε , that the only relevant eigenvalue for the pattern formation properties of (4.27) is contained in the strip $|\text{Re}(z_1)| \leq C\varepsilon^{\beta}$. This eigenvalue can be obtained as a perturbation of the eigenvalue $z = -ikU_1$ of problem (4.29). To compute the asymptotics of this eigenvalue for $\varepsilon \to 0$ we will use classical perturbation methods for eigenvalue problems.

First we introduce some notation. Let $\langle \cdot, \cdot \rangle$ denote the scalar product in \mathbb{R}^N , let B^T denote the transposed matrix of B and let span (a, b, ..., z) denote the linear subspace of \mathbb{R}^N generated by the vectors a, b, ..., z.

Lemma 8 Let A_0 satisfy Assumptions 1) and 2). Then, for each $k \in \mathbb{R}$ there exists a unique vector $e_1^T = e_1^T(k) \in \mathbb{C}^N$, which solves the linear system

$$\left[-ikU_1 + ikU + (DA_0)^T \right] e_1^T = 0 (4.40)$$

and with

$$\langle e_1^T, e_1 \rangle = 1 . (4.41)$$

Proof. Assumptions 1) and 2) imply that for each $k \in \mathbb{R}$, $\ker(-ikU_1 + ikU + DA_0) = \operatorname{span}(e_1)$. Therefore

rank
$$(-ikU_1 + ikU + DA_0) = \text{rank} \left(-ikU_1 + ikU + (DA_0)^T\right) = N - 1.$$

So there exists a vector $w = w(k) \in \mathbb{C}^N$ such that $\ker\left(-ikU_1 + ikU + (DA_0)^T\right) = \operatorname{span}(w)$. To obtain a unique e_1^T solving (4.40), (4.41) with $e_1^T = Cw$ for some $C \in \mathbb{R}$ when $\langle w, e_1 \rangle \neq 0$, we notice that, due to Assumption 1)

with coefficients $t_{i,j} = t_{i,j}(k)$. Due to Assumption 2) the characteristic polynomial of this matrix has a simple root at $\zeta = 0$. Therefore

$$\det \begin{pmatrix} t_{2,2} & t_{2,3} & \dots & t_{2,N} \\ \dots & \dots & \dots & \dots \\ \dots & \dots & \dots & \dots \\ t_{N,2} & t_{N,3} & \dots & t_{N,N} \end{pmatrix} \neq 0.$$
 (4.42)

Thus when solving

$$\left[-ikU_1 + ikU + (DA_0)^T \right] w = 0$$

the first component of w can be chosen as a free parameter w_1 . In particular, for $w_1 = 1$, and $e_1^T = w$ we obtain the desired solution of problem (4.40), (4.41).

Now we can compute the asymptotics of the eigenvalue of (4.29) as a perturbation of $z = -ikU_1$.

Proposition 9 Let A_0 satisfy Assumptions 1) and 2). Let A be defined as in (4.33) and $e_1^T = e_1^T(k)$ as in Lemma 8. Then, there exist positive constants C, ε_0 which depend on $\|A_0\|$, $\|M\|$ but are independent of k and ε , such that

for each $0 \le \varepsilon \le \varepsilon_0$ the spectrum associated to problem (4.29) consists of one eigenvalue $z_1 = z_1(k)$ satisfying

$$\left| z_1 + ikU_1 + \varepsilon \left\langle e_1^T, DM e_1 \right\rangle \right| \le \frac{C\varepsilon^2}{1 + |k|} \tag{4.43}$$

and at most (N-1) eigenvalues which are contained in the half plane

$$\operatorname{Re}\left(z\right) \le -\frac{\nu_0}{2} \ . \tag{4.44}$$

Proof. Estimate (4.44) is a consequence of Lemma 7, (ii). To obtain (4.43) suppose that $|k| \leq R$ for some constant R > 0. General perturbation theory for eigenvalues of matrices ensures that

$$z = -ikU_1 + \theta \tag{4.45}$$

$$w = e_1 + r (4.46)$$

where $\theta = \theta (k, \varepsilon)$ and $r = r (k, \varepsilon)$ are small for $\varepsilon \to 0$. Plugging this into (4.29) and using Assumptions 1) and 2) we obtain

$$-ikU_1r + \theta e_1 + \theta r + ikUr + DA_0r + \varepsilon DMe_1 + \varepsilon DMr = 0. \tag{4.47}$$

Assume, w.l.o.g. that the eigenvector w satisfies $\langle e_1^T, w \rangle = 1$. Then (4.41) and (4.45) yield

$$\langle e_1^T, r \rangle = 0 . (4.48)$$

Therefore, multiplying (4.47) by e_1^T and using (4.48) it follows

$$\theta + \varepsilon \langle e_1^T, DM e_1 \rangle + \varepsilon \langle e_1^T, DM r \rangle = 0. \tag{4.49}$$

Neglecting quadratic terms we obtain the following approximation

$$\theta \sim -\varepsilon \langle e_1^T, DM e_1 \rangle$$
 as $\varepsilon \to 0$. (4.50)

This gives the leading order term in the asymptotic expansion (4.43). The error term for $|k| \leq R$ can be obtained by classical perturbation theory for eigenvalue problems (cf. [16]). To obtain (4.43) for $|k| \geq R$ we rewrite (4.29) as

$$\frac{z}{ik}w + \left(U + \frac{DA_0}{ik}\right) \cdot w + \frac{\varepsilon}{ik}DM \cdot w = 0. \tag{4.51}$$

The correction of the eigenvalue of problem (4.51) for $\varepsilon = 0$, $\frac{z}{ik} = -U_1$ can be computed perturbatively, similar as above. Arguing like in the proof of Lemma 7 it follows that

$$\frac{z}{ik} = -U_1 - \frac{\varepsilon}{ik} \left\langle e_1^T, DM e_1 \right\rangle + O\left(\frac{\varepsilon^2}{|k|^2}\right)$$

for $\varepsilon \to 0$, uniformly for $|k| \ge 1$. Thus (4.43) follows.

To understand the pattern forming properties of (4.27) for small ε we use Proposition 9 and study

$$\eta(k) \equiv -\langle e_1^T, DM e_1 \rangle . \tag{4.52}$$

To prove that (4.27) shows pattern formation in the sense of Definition 1, we show that $\eta(k)$ reaches its maximum at a discrete set of values $k_{0,i} \neq 0$. Since $\eta(k)$ is analytic this property will be a consequence of

Proposition 10 Under Assumptions 1) and 2), the asymptotics of η (k) defined in (4.52) are given by

$$\eta(k) \sim -\langle e_1, DM e_1 \rangle \quad \text{for} \quad |k| \to \infty$$
(4.53)

$$\eta\left(k\right) \sim -ik\left\langle \psi_{0}, DMe_{1}\right\rangle - k^{2}\left\langle \psi_{1}, DMe_{1}\right\rangle + \dots \text{ for } |k| \to 0.$$
 (4.54)

Here ψ_0 and ψ_1 are unique solutions of

$$(U - U_1) b + (DA_0)^T \psi_0 = 0 , \langle \psi_0, e_1 \rangle = 0$$
 (4.55)

$$-(U - U_1) \psi_0 + (DA_0)^T \psi_1 = 0 , \quad \langle \psi_1, e_1 \rangle = 0$$
 (4.56)

with b as in (4.30).

Proof. Due to (4.52) the problem reduces to deriving the asymptotic behavior of the vector e_1^T which solves (4.40), (4.41). To show (4.53) for $|k| \to \infty$ problem (4.40), (4.41) can be approximated by using the fact that under suitable normalization conditions solutions of linear systems of equations depend continuously on their parameters. So we can approximate the solutions of (4.40), (4.41) by the solutions of

$$[-iU_1 + iU]e_1^T = 0 , \langle e_1^T, e_1 \rangle = 1.$$
 (4.57)

Since the matrix U is diagonal and nondegenerate, both equations in (4.57) are solved for $e_1^T = e_1$. Therefore $\lim_{|k| \to \infty} e_1^T = e_1$. Then (4.53) follows from (4.50).

For $k \to 0$ the asymptotics of $\eta(k)$ can again be computed by perturbative methods. Consider (4.40), (4.41) as perturbation of

$$(DA_0)^T e_1^T = 0$$
$$\langle e_1^T, e_1 \rangle = 1$$

which is solved, due to (4.31), by $e_1^T = b$. Assume

$$e_1^T = b + ik\psi_0 + k^2\psi_1 + \dots {4.58}$$

$$\langle \psi_0, e_1 \rangle = \langle \psi_1, e_1 \rangle = \dots = 0 \tag{4.59}$$

where ψ_0 , ψ_1 ,... will be determined later. Plugging (4.58) into (4.40) and separating terms with the same powers of k we obtain

$$(DA_0)^T \psi_0 + (U - U_1) b = 0$$

$$(DA_0)^T \psi_1 - (U - U_1) \psi_0 = 0.$$
(4.60)

Equations (4.60) combined with the normalization conditions (4.59) can be solved due to (4.42) and since $\langle b, (u-u_1)e_1 \rangle = 0$. Plugging (4.58) into (4.52) we obtain (4.54), since $D^Tb = 0$. So

$$\langle b, DM e_1 \rangle = \langle D^T b, M e_1 \rangle = 0. \tag{4.61}$$

The convergence of the series in (4.58) can be shown by using (4.42) and standard perturbation theory, [16]

Now we can formulate the main result of this subsection.

Theorem 11 Suppose that A_0 satisfies Assumptions 1) and 2). Let A be given as in (4.33), with M satisfying

$$\langle e_1, DM e_1 \rangle \ge 0 \quad , \quad \langle \psi_1, DM e_1 \rangle < 0 \quad , \tag{4.62}$$

where ψ_1 is as in (4.55), (4.56). Then, for $\varepsilon > 0$ small enough, system (4.27) generates oscillatory patterns in the sense of Definition 1.

Proof. The asymptotics (4.53), (4.54) as well as (4.62) imply that $\operatorname{Re}(\eta(k))$ has a global maximum in \mathbb{R} for some bounded set of values $k_{0,i} \in \mathbb{R} \setminus \{0\}$. On the other hand, $\eta(k)$ is analytic w.r.t. k and therefore the set of points where $\operatorname{Re}(\eta(k))$ achieves its maximum is finite. Using the asymptotic formulas (4.43), it follows that $\operatorname{Re}(z_1(k))$ reaches its maximum for some set of values $k_{0,i} \in \mathbb{R} \setminus \{0\}$, if $\varepsilon > 0$ is small enough. Since $z_1(k)$ is contained in the set of zeros of an analytic function, this maximum is achieved in a finite number of points. On the other hand, since for such a point $k_{0,i} \neq 0$, it follows from (4.43) that $\operatorname{Im}(z_1(k_{0,i})) \neq 0$, if ε is small enough. Thus the result follows.

The key problem now is to show the existence of matrices A_0 , M which satisfy the properties of Theorem 11.

The case N=3. First we describe the assumptions for the matrices U, A_0 , M in Theorem 11 if the internal sets of variables contain three elements. Let

$$U = \begin{pmatrix} U_1 & 0 & 0 \\ 0 & U_2 & 0 \\ 0 & 0 & U_3 \end{pmatrix} , U_i \neq U_j \text{ if } i \neq j , D = \begin{pmatrix} 1 & 0 & -1 \\ -1 & 1 & 0 \\ 0 & -1 & 1 \end{pmatrix}$$

$$A_0 = \begin{pmatrix} a_{1,1} & a_{1,2} & a_{1,3} \\ a_{2,1} & a_{2,2} & a_{2,3} \\ a_{3,1} & a_{3,2} & a_{3,3} \end{pmatrix} , M = \begin{pmatrix} m_{1,1} & m_{1,2} & m_{1,3} \\ m_{2,1} & m_{2,2} & m_{2,3} \\ m_{3,1} & m_{3,2} & m_{3,3} \end{pmatrix} .$$

Then

$$DA_0 = \begin{pmatrix} a_{1,1} - a_{3,1} & a_{1,2} - a_{3,2} & a_{1,3} - a_{3,3} \\ -a_{1,1} + a_{2,1} & -a_{1,2} + a_{2,2} & -a_{1,3} + a_{2,3} \\ -a_{2,1} + a_{3,1} & -a_{2,2} + a_{3,2} & -a_{2,3} + a_{3,3} \end{pmatrix}.$$

Assumption $DA_0e_1 = 0$ implies

$$a_{1,1} - a_{3,1} = a_{1,1} - a_{2,1} = a_{2,1} - a_{3,1} = 0$$
,

thus

$$a_{1,1} = a_{2,1} = a_{3,1} (4.63)$$

and

$$DA_0 = \begin{pmatrix} 0 & a_{1,2} - a_{3,2} & a_{1,3} - a_{3,3} \\ 0 & -a_{1,2} + a_{2,2} & -a_{1,3} + a_{2,3} \\ 0 & -a_{2,2} + a_{3,2} & -a_{2,3} + a_{3,3} \end{pmatrix}$$
(4.64)

In order to fulfill the second condition of Assumption 1) the matrix

$$B = \begin{pmatrix} -a_{1,2} + a_{2,2} & -a_{1,3} + a_{2,3} \\ -a_{2,2} + a_{3,2} & -a_{2,3} + a_{3,3} \end{pmatrix}$$
(4.65)

must be diagonalizable. A sufficient condition for this is to have different eigenvalues, or respectively, that the polynomial

$$\det \begin{pmatrix} -a_{1,2} + a_{2,2} - x & -a_{1,3} + a_{2,3} \\ -a_{2,2} + a_{3,2} & -a_{2,3} + a_{3,3} - x \end{pmatrix} \equiv P(x)$$
 (4.66)

must have different non-vanishing roots. This is the case if

$$(a_{1,2} + a_{2,3} - a_{2,2} - a_{3,3})^{2} - 4(a_{1,2}a_{2,3} - a_{1,2}a_{3,3} - a_{2,3}a_{3,2} + a_{2,2}a_{3,3} - a_{1,3}a_{2,2} + a_{1,3}a_{3,2}) \neq 0$$

$$a_{1,2}a_{2,3} - a_{1,2}a_{3,3} - a_{2,3}a_{3,2} + a_{2,2}a_{3,3} - a_{1,3}a_{2,2} + a_{1,3}a_{3,2} \neq 0$$

$$(4.67)$$

Therefore, Assumption 1) reduces to (4.63), (4.67), (4.68), if N=3. In this case Assumption 2) reduces to the following. Let B be given as in (4.65).

The roots of
$$\det \left(zI + ik \begin{pmatrix} U_2 & 0 \\ 0 & U_3 \end{pmatrix} + B \right) = 0$$
 are located in the half-plane $\{ \operatorname{Re}(z) \le -\nu_0 \}$ for some $\nu_0 > 0$. (4.69)

Choose M such that (4.61), (4.62) hold. Due to (4.59) we have

$$\psi_1 = (0, \psi_{1,2}, \psi_{1,3})^t \tag{4.70}$$

for suitable numbers $\psi_{1,2}$, $\psi_{1,3}$. On the other hand

$$DM = \begin{pmatrix} m_{1,1} - m_{3,1} & m_{1,2} - m_{3,2} & m_{1,3} - m_{3,3} \\ -m_{1,1} + m_{2,1} & -m_{1,2} + m_{2,2} & -m_{1,3} + m_{2,3} \\ -m_{2,1} + m_{3,1} & -m_{2,2} + m_{3,2} & -m_{2,3} + m_{3,3} \end{pmatrix}.$$

Then, (4.62) reduces to

$$m_{1,1} - m_{3,1} \ge 0$$
 and (4.71)
 $\langle \psi_1, DM e_1 \rangle = [\psi_{1,2} - \psi_{1,3}] (m_{2,1} - m_{1,1}) + \psi_{1,3} (m_{3,1} - m_{1,1}) < 0$.

In order to show the existence of a matrix M satisfying the conditions (4.71), we only need to have $\psi_{1,2} \neq \psi_{1,3}$. The vector ψ_1 is defined by (4.59), (4.60) and can be expressed in terms of the matrices U and A. The result is not giving very much insight though. So it is more convenient to give specific values of U, A_0 and M satisfying (4.63), (4.67), (4.68), (4.69), (4.71). Let D be given as before and

$$U = \begin{pmatrix} 1 & 0 & 0 \\ 0 & 2 & 0 \\ 0 & 0 & 3 \end{pmatrix} , A_0 = \begin{pmatrix} a & 1 & 0 \\ a & 2 & 1 \\ a & 0 & 2 \end{pmatrix}$$
 (4.72)

with arbitrary a > 0. Then

$$DA_0 = \left(\begin{array}{ccc} 0 & 1 & -2 \\ 0 & 1 & 1 \\ 0 & -2 & 1 \end{array}\right)$$

and (4.60) reduce to

$$\begin{pmatrix} 1 & -2 \\ 1 & 1 \end{pmatrix} \begin{pmatrix} \psi_{0,2} \\ \psi_{0,3} \end{pmatrix} + \begin{pmatrix} 1 \\ 2 \end{pmatrix} = 0$$
$$\begin{pmatrix} 1 & -2 \\ 1 & 1 \end{pmatrix} \begin{pmatrix} \psi_{1,2} \\ \psi_{1,3} \end{pmatrix} - \begin{pmatrix} \psi_{0,2} \\ 2\psi_{0,3} \end{pmatrix} = 0.$$

So

$$\begin{pmatrix} \psi_{0,2} \\ \psi_{0,3} \end{pmatrix} = \begin{pmatrix} -\frac{5}{3} \\ -\frac{1}{3} \end{pmatrix} , \quad \begin{pmatrix} \psi_{1,2} \\ \psi_{1,3} \end{pmatrix} = \begin{pmatrix} -1 \\ \frac{1}{3} \end{pmatrix} . \tag{4.73}$$

Using (4.71) these conditions further reduce to

$$4(m_{1,1}-m_{2,1})<(m_{1,1}-m_{3,1})$$
 and $m_{1,1}-m_{3,1}\geq 0$.

There are infinitely many different choices for M which yield this inequalities.

If A_0 is given by (4.72), then the polynomial defined in (4.66) equals

$$P(x) = \det \begin{pmatrix} 1-x & 1 \\ -2 & 1-x \end{pmatrix} = x^2 - 2x + 3.$$

So (4.67) and (4.68) are automatically satisfied. It remains to check (4.69). We have

$$\det \left(z \begin{pmatrix} 1 & 0 \\ 0 & 1 \end{pmatrix} + ik \begin{pmatrix} 2 & 0 \\ 0 & 3 \end{pmatrix} + \begin{pmatrix} 1 & 1 \\ -2 & 1 \end{pmatrix} \right)$$
$$= z^2 + 2z - 6k^2 + 3 + i (5zk + 5k) \equiv Q(z, k)$$

and the roots of Q(z, k) are given by

$$z = -1 - \frac{5}{2}ik \pm \frac{1}{2}\sqrt{(-8-k^2)}$$
.

Since the real part of these roots is -1, we obtain (4.69). Let

$$M = \begin{pmatrix} 2 & 0 & 0 \\ 1.95 & 0 & 0 \\ 1 & 0 & 0 \end{pmatrix} \tag{4.74}$$

Then the dispersion relation consists in finding the roots of the polynomial

$$\det(z + ikU + DA) = 0 \tag{4.75}$$

for D as in (4.4), U, A_0 as in (4.72) with a=0.5, and $A=A_0+\varepsilon M$ for $\varepsilon=0.01$, which are calculated numerically for given $k\in\mathbb{R}$ with respect to the variable z. Figure 1 shows the branch with the largest real part. All other roots have negative real parts.

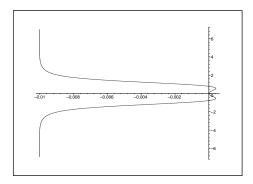


Figure 1: Plot of the root with the largest real part of (4.75) close to the imaginary axis for D as in (4.4), U, A_0 as in (4.72), with a = 0.5, M as in (4.74), $A = A_0 + \varepsilon M$, and $\varepsilon = 0.01$.

The case N=2. Assumptions 1) and 2) as well as (4.62) cannot be satisfied if N=2 as expected from the results in [17], (cf. Theorem 4). In this a case we have

$$A_0 = \begin{pmatrix} a_{1,1} & a_{1,2} \\ a_{2,1} & a_{2,2} \end{pmatrix} , M = \begin{pmatrix} m_{1,1} & m_{1,2} \\ m_{2,1} & m_{2,2} \end{pmatrix}$$

$$D = \begin{pmatrix} 1 & -1 \\ -1 & 1 \end{pmatrix} , U = \begin{pmatrix} U_1 & 0 \\ 0 & U_2 \end{pmatrix}$$

Since $DA_0e_1=0$ it follows that $a_{1,1}=a_{2,1}$. Condition (4.62), which is $\langle e_1,DMe_1\rangle \geq 0$, implies $m_{1,1}-m_{2,1}\geq 0$. Condition $\langle \psi_1,DMe_1\rangle < 0$ results in

$$\frac{(U_2 - U_1)^2}{(a_{1,2} - a_{2,2})^2} (m_{1,1} - m_{2,1}) < 0$$

by using (4.55), (4.56). Therefore, $(m_{1,1} - m_{2,1}) < 0$, which is a contradiction. Thus the assumptions for pattern formation in Theorem 11 cannot be satisfied for N = 2. The inequalities required impose a minimal degree of complexity for system (4.27), or, more precisely, the need for at least three different variables.

4.5 Examples with reflection-symmetry and nondegenerate matrix U.

In this subsection we will study systems of the form (4.27) which fulfill some symmetry properties, which naturally arise in models for pattern formation in myxobacteria.

Assume that N=2n is an even number and that f in (4.27) is of the form

$$f = \begin{pmatrix} \varphi \\ \psi \end{pmatrix}$$
 , φ , $\psi \in \mathbb{R}^n$.

Further assume that system (4.27) is invariant under the transformation

$$(x, \varphi, \psi) \to (-x, \psi, \varphi)$$
 (4.76)

Due to this invariance and by explicit calculations it can be seen that the matrices U and A must have the form

$$U = \begin{pmatrix} V & 0 \\ 0 & -V \end{pmatrix} , A = \begin{pmatrix} Y & Z \\ Z & Y \end{pmatrix} , \tag{4.77}$$

and D is as usual. Here V,Y,Z are $n\times n$ matrices. To check the formulas for U and A, it is convenient to write $A=\begin{pmatrix} Y_1&Z_1\\Z_2&Y_2 \end{pmatrix}$ and use

$$\begin{pmatrix} 0 & I \\ I & 0 \end{pmatrix} \begin{pmatrix} \psi \\ \varphi \end{pmatrix} = \begin{pmatrix} \varphi \\ \psi \end{pmatrix} \tag{4.78}$$

$$\begin{pmatrix} 0 & I \\ I & 0 \end{pmatrix} \begin{pmatrix} V & 0 \\ 0 & -V \end{pmatrix} = -\begin{pmatrix} V & 0 \\ 0 & -V \end{pmatrix} \begin{pmatrix} 0 & I \\ I & 0 \end{pmatrix}$$
(4.79)

$$\begin{pmatrix} 0 & I \\ I & 0 \end{pmatrix} \begin{pmatrix} Y_1 & Z_1 \\ Z_2 & Y_2 \end{pmatrix} = \begin{pmatrix} Y_2 & Z_2 \\ Z_1 & Y_1 \end{pmatrix} \begin{pmatrix} 0 & I \\ I & 0 \end{pmatrix} . \tag{4.80}$$

On the other hand, we can rewrite D as

$$D = \begin{pmatrix} 1 & 0 & \dots & \dots & -1 \\ -1 & 1 & 0 & \dots & 0 \\ & \dots & & \dots & \\ 0 & \dots & -1 & 1 & 0 \\ 0 & \dots & 0 & -1 & 1 \end{pmatrix} = \begin{pmatrix} \sigma & \lambda \\ \lambda & \sigma \end{pmatrix}$$
(4.81)

where σ and λ are $n \times n$ matrices with

$$\sigma \equiv \left(\begin{array}{ccccc} 1 & 0 & \dots & & 0 \\ -1 & 1 & 0 & \dots & 0 \\ & \dots & & \dots & \\ 0 & \dots & -1 & 1 & 0 \\ 0 & \dots & 0 & -1 & 1 \end{array} \right) \quad , \quad \lambda \equiv \left(\begin{array}{cccccc} 0 & 0 & \dots & 0 & -1 \\ 0 & 0 & \dots & 0 & -1 \\ & \dots & & \dots & & \\ 0 & 0 & \dots & 0 & 0 \\ 0 & 0 & \dots & 0 & 0 \end{array} \right) \; .$$

Then

$$\begin{pmatrix} 0 & I \\ I & 0 \end{pmatrix} D = \begin{pmatrix} 0 & I \\ I & 0 \end{pmatrix} \begin{pmatrix} \sigma & \lambda \\ \lambda & \sigma \end{pmatrix}$$
$$= \begin{pmatrix} \sigma & \lambda \\ \lambda & \sigma \end{pmatrix} \begin{pmatrix} 0 & I \\ I & 0 \end{pmatrix} = D \begin{pmatrix} 0 & I \\ I & 0 \end{pmatrix}. \tag{4.82}$$

Applying the transformation (4.76) to system (4.27) we obtain

$$\partial_t \left(\begin{array}{c} \psi \\ \varphi \end{array} \right) - \left(\begin{array}{cc} V & 0 \\ 0 & -V \end{array} \right) \cdot \partial_x \left(\begin{array}{c} \psi \\ \varphi \end{array} \right) + D \left(\begin{array}{cc} Y_1 & Z_1 \\ Z_2 & Y_2 \end{array} \right) \left(\begin{array}{c} \psi \\ \varphi \end{array} \right) = 0 \; .$$

Multiplying this formula by $\begin{pmatrix} 0 & I \\ I & 0 \end{pmatrix}$ and using (4.78)-(4.82) we get

$$\partial_t \begin{pmatrix} \varphi \\ \psi \end{pmatrix} + \begin{pmatrix} V & 0 \\ 0 & -V \end{pmatrix} \cdot \partial_x \begin{pmatrix} \varphi \\ \psi \end{pmatrix} + D \begin{pmatrix} Y_2 & Z_2 \\ Z_1 & Y_1 \end{pmatrix} \begin{pmatrix} \varphi \\ \psi \end{pmatrix} = 0 . \quad (4.83)$$

This equation is equivalent to (4.27) if

$$D \left(\begin{array}{cc} Y_1 & Z_1 \\ Z_2 & Y_2 \end{array} \right) = D \left(\begin{array}{cc} Y_2 & Z_2 \\ Z_1 & Y_1 \end{array} \right) \ ,$$

respectively $Y_2 = Y_1 + G$, $Z_2 = Z_1 + H$, where

$$D\begin{pmatrix} G & H \\ -H & -G \end{pmatrix} = \begin{pmatrix} \sigma & \lambda \\ \lambda & \sigma \end{pmatrix} \begin{pmatrix} G & H \\ -H & -G \end{pmatrix} = 0.$$

Since under this assumption the matrices G and H do not appear in the equation, we can assume $Y_2 = Y_1 \equiv Y$, $Z_2 = Z_1 \equiv Z$, which yields the second equation of (4.77). Further on, we assume in this subsection that the matrix V is non degenerate. Under these symmetry assumptions the eigenvalue problem (4.29) reduces to

$$z \begin{pmatrix} w_1 \\ w_2 \end{pmatrix} + ik \begin{pmatrix} V & 0 \\ 0 & -V \end{pmatrix} \begin{pmatrix} w_1 \\ w_2 \end{pmatrix} + \begin{pmatrix} P & Q \\ Q & P \end{pmatrix} \begin{pmatrix} w_1 \\ w_2 \end{pmatrix} = 0 , \quad (4.84)$$

where $P = \sigma Y + \lambda Z$, $Q = \sigma Z + \lambda Y$. Our goal is to study the eigenvalue problem (4.84) as a perturbation of a problem which is as "hyperbolic" as possible. Let

$$A = A_0 + \varepsilon M \tag{4.85}$$

$$M = \begin{pmatrix} m & n \\ n & m \end{pmatrix} , \begin{pmatrix} \Theta & \Lambda \\ \Lambda & \Theta \end{pmatrix} = DM$$

$$A_0 = \begin{pmatrix} Y_0 & Z_0 \\ Z_0 & Y_0 \end{pmatrix} , \begin{pmatrix} P_0 & Q_0 \\ Q_0 & P_0 \end{pmatrix} = DA_0 .$$

$$(4.86)$$

Assuming $\varepsilon = 0$, (4.84) reduces to

$$z \begin{pmatrix} w_1 \\ w_2 \end{pmatrix} + ik \begin{pmatrix} V & 0 \\ 0 & -V \end{pmatrix} \begin{pmatrix} w_1 \\ w_2 \end{pmatrix} + \begin{pmatrix} P_0 & Q_0 \\ Q_0 & P_0 \end{pmatrix} \begin{pmatrix} w_1 \\ w_2 \end{pmatrix} = 0. \quad (4.87)$$

Notice that Assumptions 1) and 2) in Subsection 4.4 cannot be satisfied for the eigenvalue problem (4.87), since due to the symmetry assumptions, some of the eigenvalues are degenerate. Indeed, suppose that DA_0 has an eigenvector with

zero eigenvalue $\begin{pmatrix} e_1 \\ 0 \end{pmatrix}$. This is equivalent to $P_0e_1=0$, $Q_0e_1=0$. Due to the symmetry of DA_0 we have

$$DA_0 \left(\begin{array}{c} 0 \\ e_1 \end{array} \right) = 0 \ .$$

So the kernel of DA_0 has at least dimension 2. Therefore, if A satisfies the symmetry conditions above, the assumptions defining the "hyperbolic" character of the problem (4.27) with $A = A_0$ have to be modified. Instead of Assumptions 1) and 2) we need in this case

Assumption 3) The kernel of DA_0 is the subspace generated by the vectors $\begin{pmatrix} e_1 \\ 0 \end{pmatrix}$, $\begin{pmatrix} 0 \\ e_1 \end{pmatrix}$. In particular $P_0e_1 = Q_0e_1 = 0$.

> As a consequence the set of solutions of the eigenvalue problem (4.87) contains the lines $\{z=-ikV_1, z=ikV_1, k\in\mathbb{R}\}$. Further we need

Assumption 4) All other solutions of the eigenvalue problem (4.87) are included in the half plane $\{\operatorname{Re}(z) \leq -\nu_0\}$ for some $\nu_0 > 0$.

> Now we can study the spectrum of (4.87) for A given is as in (4.85), $0 < \varepsilon < 1$ and M satisfying the symmetry assumptions in (4.86). Then the analog to Lemma 7 is

> **Lemma 12** Suppose that the matrix A_0 satisfies Assumptions 3) and 4). Let A be given by (4.85). Then there exist positive constants $C = C(A_0, M)$, β and ε_0 independent of ε such that for each $k \in \mathbb{R}$ and $|\varepsilon| \leq \varepsilon_0$ the spectrum associated to problem (4.84) consists of

- (i) Two eigenvalues $z_1 = z_1(k)$, $z_2 = z_2(k)$ satisfying $|\operatorname{Re}(z_1)| \le C\varepsilon^{\beta}$.
- (ii) At most (N-2) eigenvalues contained in the half-plane $\{\operatorname{Re}(z) < -\nu_0 + C\varepsilon^{\beta}\}.$

Proof. The proof is identical to the proof of Lemma 7, since the arguments given there do not use the non-degeneracy of the matrix U.

Using perturbative methods, we now compute the changes of the part of the spectrum of (4.87) contained in the lines $\{z=-ikV_1\ ,\ z=ikV_1\ ,\ k\in\mathbb{R}\}$ for $\varepsilon\to 0$. Due to the degeneracy of these eigenvalues for k=0, this computation has to be done in a slightly different manner in comparison to the case for non-degenerate matrices. The following analog of Lemma 8 holds

Lemma 13 Suppose that A_0 satisfies Assumptions 3) and 4). Then, for each $k \in \mathbb{R}$ there exist vectors $v_1^T(k)$, $v_2^T(k)$ solving the adjoint problems

$$zv_1^T(k) + ik \begin{pmatrix} V & 0 \\ 0 & -V \end{pmatrix} v_1^T(k) + \begin{pmatrix} P_0^T & Q_0^T \\ Q_0^T & P_0^T \end{pmatrix} v_1^T(k) = 0$$
 (4.88)

$$z = -ikV_1$$

$$zv_{2}^{T}(k) + ik \begin{pmatrix} V & 0 \\ 0 & -V \end{pmatrix} v_{2}^{T}(k) + \begin{pmatrix} P_{0}^{T} & Q_{0}^{T} \\ Q_{0}^{T} & P_{0}^{T} \end{pmatrix} v_{2}^{T}(k) = 0$$

$$z = ikV_{1}$$
(4.89)

and satisfying the normalization conditions

$$\left\langle v_1^T\left(k\right), \left(\begin{array}{c} e_1 \\ 0 \end{array}\right) \right\rangle = \left\langle v_2^T\left(k\right), \left(\begin{array}{c} 0 \\ e_1 \end{array}\right) \right\rangle = 1 \ . \tag{4.90}$$

Proof. The proof is basically identical to the proof of Lemma 8. The only essential difference is, that for k=0 the subspace of solutions that solve the eigenvalue problem (4.87) with z=0 is of dimension two. Therefore, the solution of the adjoint problem is two dimensional, and arguing as in Lemma 8, the basis of eigenfunctions $v_1^T(0)$, $v_2^T(0)$ can be chosen such that they satisfy the normalization conditions (4.90), [16].

Arguing as in the proof of Proposition 9, we can now compute the changes of the eigenvalues $\{z = \pm ikV_1\}$.

Proposition 14 Suppose that A_0 satisfies Assumptions 3) and 4), that A is given as in (4.85) and $v_1^T = v_1^T(k)$, $v_2^T = v_2^T(k)$ are as given in Lemma 8. Here we additionally assume that $|k| \ge \delta > 0$. Then, there exist positive constants C, ε_0 depending on $||A_0||$, ||M||, δ , but independent of k and ε , such that for each $0 \le \varepsilon \le \varepsilon_0$ the spectrum associated to problem (4.29) consists of two eigenvalues $z_1 = z_1(k)$, $z_2 = z_2(k)$ satisfying

$$|z_1 + ikV_1 - \varepsilon\theta_1| + |z_2 - ikV_1 - \varepsilon\theta_2| \le \frac{C\varepsilon^2}{1 + |k|}, \quad where$$
 (4.91)

$$\theta_{1} = -\left\langle v_{1}^{T}(k), \begin{pmatrix} \Theta & \Lambda \\ \Lambda & \Theta \end{pmatrix} \begin{pmatrix} e_{1} \\ 0 \end{pmatrix} \right\rangle$$

$$\theta_{2} = -\left\langle v_{2}^{T}(k), \begin{pmatrix} \Theta & \Lambda \\ \Lambda & \Theta \end{pmatrix} \begin{pmatrix} 0 \\ e_{1} \end{pmatrix} \right\rangle$$

$$(4.92)$$

and at most (N-2) eigenvalues are contained in the half plane

$$\operatorname{Re}\left(z\right) \le -\frac{\nu_0}{2} \ . \tag{4.93}$$

Proof. The argument is basically the same as for Proposition 9. Consider solutions of (4.84) in the perturbative form

$$z_1 = -ikV_1 + \varepsilon\theta_1 + \dots$$
, $z_2 = ikV_1 + \varepsilon\theta_2 + \dots$

with eigenvectors

$$v_1 = \begin{pmatrix} e_1 \\ 0 \end{pmatrix} + \varepsilon Z_1 + \dots , \quad v_2 = \begin{pmatrix} 0 \\ e_1 \end{pmatrix} + \varepsilon Z_2 + \dots .$$

Plugging these formulas into (4.84), using $P_0e_1 = Q_0e_1 = 0$, and neglecting quadratic terms in ε we obtain

$$\theta_{1} \begin{pmatrix} e_{1} \\ 0 \end{pmatrix} - ikV_{1}Z_{1} + ik \begin{pmatrix} V & 0 \\ 0 & -V \end{pmatrix} Z_{1} + \begin{pmatrix} P_{0} & Q_{0} \\ Q_{0} & P_{0} \end{pmatrix} Z_{1} + \varepsilon \begin{pmatrix} \Theta & \Lambda \\ \Lambda & \Theta \end{pmatrix} \begin{pmatrix} e_{1} \\ 0 \end{pmatrix} = 0$$

$$(4.94)$$

$$\theta_{2} \begin{pmatrix} 0 \\ e_{1} \end{pmatrix} + ikV_{1}Z_{2} + ik \begin{pmatrix} V & 0 \\ 0 & -V \end{pmatrix} Z_{2} + \begin{pmatrix} P_{0} & Q_{0} \\ Q_{0} & P_{0} \end{pmatrix} Z_{2} + \varepsilon \begin{pmatrix} \Theta & \Lambda \\ \Lambda & \Theta \end{pmatrix} \begin{pmatrix} 0 \\ e_{1} \end{pmatrix} = 0$$

$$(4.95)$$

Taking the scalar product of (4.94), respectively (4.95), with v_1^T, v_2^T as given in Lemma 13, we obtain

$$z_1 \sim -ikV_1 + \varepsilon\theta_1$$
, $z_2 \sim ikV_1 + \varepsilon\theta_2$

with θ_1, θ_2 as given in (4.92). This provides the terms of leading order in (4.91). The error terms can be estimated as in the proof of Proposition 9. Finally (4.93) follows from Lemma 12. \blacksquare

To obtain sufficient conditions for pattern formation, we analyze the asymptotics as $|k| \to 0$ and $|k| \to \infty$ for the functions θ_1 and θ_2 . We need the following auxiliary result

Lemma 15 Suppose that A_0 satisfies Assumption 3). Then, there exists a basis of $\ker ((DA_0)^T)$ given by two vectors $\{b_1, b_2\}$, which satisfy

$$\left\langle \begin{pmatrix} e_1 \\ 0 \end{pmatrix}, b_1 \right\rangle = \left\langle \begin{pmatrix} 0 \\ e_1 \end{pmatrix}, b_2 \right\rangle = 1$$

$$\left\langle \begin{pmatrix} e_1 \\ 0 \end{pmatrix}, b_2 \right\rangle = \left\langle \begin{pmatrix} 0 \\ e_1 \end{pmatrix}, b_1 \right\rangle = 0 \tag{4.96}$$

$$b_2 = \begin{pmatrix} 0 & I \\ I & 0 \end{pmatrix} b_1 \tag{4.97}$$

Proof. Assumption 3) implies dim ker $((DA_0)^T)$ = dim ker (DA_0) = 2. The two unique vectors b_1 , b_2 satisfying (4.96) can be found like in the proof of Lemma 8. Relation (4.97) follows from the identity

$$\begin{pmatrix} 0 & I \\ I & 0 \end{pmatrix} \begin{pmatrix} P_0^T & Q_0^T \\ Q_0^T & P_0^T \end{pmatrix} \begin{pmatrix} 0 & I \\ I & 0 \end{pmatrix} = \begin{pmatrix} P_0^T & Q_0^T \\ Q_0^T & P_0^T \end{pmatrix}. \tag{4.98}$$

Now we can compute the asymptotics of θ_1 and θ_2

Proposition 16 Under Assumptions 3) and 4) the asymptotics of θ_1 (k) and θ_2 (k) defined in (4.92) for $|\mathbf{k}| \to \infty$ and $|\mathbf{k}| \to 0$ are given by

$$\theta_1 \sim \langle e_1, \Theta e_1 \rangle$$
 , $\theta_2 \sim \langle e_1, \Theta e_1 \rangle$ for $|k| \to \infty$. (4.99)

For $k \to 0$ we have

$$\theta_{1} = \left\langle \begin{bmatrix} b_{1} + ik\psi_{1,0} + k^{2}\psi_{1,1} \end{bmatrix}, \begin{pmatrix} \Theta & \Lambda \\ \Lambda & \Theta \end{pmatrix} \begin{pmatrix} e_{1} \\ 0 \end{pmatrix} \right\rangle$$

$$= \left\langle b_{1}, \begin{pmatrix} \Theta e_{1} \\ \Lambda e_{1} \end{pmatrix} \right\rangle + ik\left\langle \psi_{1,0}, \begin{pmatrix} \Theta e_{1} \\ \Lambda e_{1} \end{pmatrix} \right\rangle + k^{2}\left\langle \psi_{1,1}, \begin{pmatrix} \Theta e_{1} \\ \Lambda e_{1} \end{pmatrix} \right\rangle + \dots$$

$$(4.100)$$

$$\theta_{2} = \left\langle b_{1}, \begin{pmatrix} \Theta e_{1} \\ \Lambda e_{1} \end{pmatrix} \right\rangle - ik \left\langle \psi_{1,0}, \begin{pmatrix} \Theta e_{1} \\ \Lambda e_{1} \end{pmatrix} \right\rangle + k^{2} \left\langle \psi_{1,1}, \begin{pmatrix} \Theta e_{1} \\ \Lambda e_{1} \end{pmatrix} \right\rangle + \dots$$

$$(4.101)$$

where $\psi_{1,0}$, and $\psi_{1,1}$ are the unique solutions of

$$-V_1 b_1 + \begin{pmatrix} V & 0 \\ 0 & -V \end{pmatrix} b_1 + \begin{pmatrix} P_0^T & Q_0^T \\ Q_0^T & P_0^T \end{pmatrix} \psi_{1,0} = 0$$
 (4.102)

$$V_1 \psi_{1,0} - \begin{pmatrix} V & 0 \\ 0 & -V \end{pmatrix} \psi_{1,0} + \begin{pmatrix} P_0^T & Q_0^T \\ Q_0^T & P_0^T \end{pmatrix} \psi_{1,1} = 0$$
 (4.103)

$$\left\langle \left(\begin{array}{c} e_1 \\ 0 \end{array}\right), \psi_{1,0} \right\rangle = \left\langle \left(\begin{array}{c} 0 \\ e_1 \end{array}\right), \psi_{1,0} \right\rangle = 0 \tag{4.104}$$

$$\left\langle \left(\begin{array}{c} e_1 \\ 0 \end{array} \right), \psi_{1,1} \right\rangle = \left\langle \left(\begin{array}{c} 0 \\ e_1 \end{array} \right), \psi_{1,1} \right\rangle = 0 \tag{4.105}$$

and b_1 is as in Lemma 15.

Proof. Arguing similarly as in the proof of Proposition 10, we obtain

$$v_1^T(k) \sim \begin{pmatrix} e_1 \\ 0 \end{pmatrix}$$
 as $|k| \to \infty$, $v_2^T(k) \sim \begin{pmatrix} 0 \\ e_1 \end{pmatrix}$ as $|k| \to \infty$.

Thus (4.99) follows. To compute the asymptotics of θ_1 , θ_2 as $|k| \to 0$ we expand $v_1^T(k)$, $v_2^T(k)$ which solve (4.88), (4.89) as power series

$$v_1^T(k) = \alpha_{1,1}b_1 + \alpha_{1,2}b_2 + ik\psi_{1,0} + k^2\psi_{1,1} + \dots$$
 (4.106)

$$v_2^T(k) = \alpha_{2,1}b_1 + \alpha_{2,2}b_2 + ik\psi_{2,0} + k^2\psi_{2,1} + \dots$$
 (4.107)

where the coefficients $\alpha_{i,j}$ must be determined. Plugging (4.106) into (4.88) and using that $z = -ikV_1$ we obtain

$$-ikV_{1} (\alpha_{1,1}b_{1} + \alpha_{1,2}b_{2}) + k^{2}V_{1}\psi_{1,0} + ik \begin{pmatrix} V & 0 \\ 0 & -V \end{pmatrix} (\alpha_{1,1}b_{1} + \alpha_{1,2}b_{2})$$

$$-k^{2} \begin{pmatrix} V & 0 \\ 0 & -V \end{pmatrix} \psi_{1,0} + \begin{pmatrix} P_{0}^{T} & Q_{0}^{T} \\ Q_{0}^{T} & P_{0}^{T} \end{pmatrix} (ik\psi_{1,0} + k^{2}\psi_{1,1}) = O(k^{3})$$

Separating the terms with powers k and multiplying them by $\begin{pmatrix} e_1 \\ 0 \end{pmatrix}$, $\begin{pmatrix} 0 \\ e_1 \end{pmatrix}$ we obtain a set of compatibility conditions.

$$-V_{1}\left(\alpha_{1,1}\left\langle \begin{pmatrix} e_{1} \\ 0 \end{pmatrix}, b_{1}\right\rangle + \alpha_{1,2}\left\langle \begin{pmatrix} e_{1} \\ 0 \end{pmatrix}, b_{2}\right\rangle \right)$$

$$+ (e_{1}, 0)\begin{pmatrix} V & 0 \\ 0 & -V \end{pmatrix}(\alpha_{1,1}b_{1} + \alpha_{1,2}b_{2}) = 0$$

$$-V_{1}\left(\alpha_{1,1}\left\langle \begin{pmatrix} 0 \\ e_{1} \end{pmatrix}, b_{1}\right\rangle + \alpha_{1,2}\left\langle \begin{pmatrix} 0 \\ e_{1} \end{pmatrix}, b_{2}\right\rangle \right)$$

$$+ (0, e_{1})\begin{pmatrix} V & 0 \\ 0 & -V \end{pmatrix}(\alpha_{1,1}b_{1} + \alpha_{1,2}b_{2}) = 0.$$

Using the normalization conditions (4.96) as well as $V^T = V$ and $V_1 \neq 0$, it follows that

$$-\alpha_{1,1}V_1 + V_1 \left\langle \begin{pmatrix} e_1 \\ 0 \end{pmatrix}, (\alpha_{1,1}b_1 + \alpha_{1,2}b_2) \right\rangle = 0$$

$$-\alpha_{1,2}V_1 - V_1 \left\langle \begin{pmatrix} 0 \\ e_1 \end{pmatrix}, (\alpha_{1,1}b_1 + \alpha_{1,2}b_2) \right\rangle = 0 ,$$

respectively $-\alpha_{1,1}V_1 + \alpha_{1,1}V_1 = 0$, $-\alpha_{1,2}V_1 - \alpha_{1,2}V_1 = 0$, therefore $\alpha_{1,2} = 0$. On the other hand, taking the limit $k \to 0$ in (4.90) we obtain $\alpha_{1,1} = 1$. Imposing the additional normalization conditions (4.104) we have a unique solution for (4.102). The compatibility conditions required for solving (4.103) are satisfied, namely

$$\left\langle \left(\begin{array}{c} e_1 \\ 0 \end{array} \right), V_1 \psi_{1,0} - \left(\begin{array}{cc} V & 0 \\ 0 & -V \end{array} \right) \psi_{1,0} \right\rangle$$
$$= \left\langle \left(\begin{array}{c} 0 \\ e_1 \end{array} \right), V_1 \psi_{1,0} - \left(\begin{array}{cc} V & 0 \\ 0 & -V \end{array} \right) \psi_{1,0} \right\rangle = 0.$$

Imposing the compatibility conditions (4.105) we can solve (4.103) uniquely. In a similar manner, plugging (4.107) into (4.89) we obtain

$$V_{1} \left[\alpha_{2,1}b_{1} + \alpha_{2,2}b_{2}\right] + \begin{pmatrix} V & 0 \\ 0 & -V \end{pmatrix} \left[\alpha_{2,1}b_{1} + \alpha_{2,2}b_{2}\right] + \begin{pmatrix} P_{0}^{T} & Q_{0}^{T} \\ Q_{0}^{T} & P_{0}^{T} \end{pmatrix} \psi_{2,0} = 0$$

$$(4.108)$$

$$-V_1 \psi_{2,0} - \begin{pmatrix} V & 0 \\ 0 & -V \end{pmatrix} \psi_{2,0} + \begin{pmatrix} P_0^T & Q_0^T \\ Q_0^T & P_0^T \end{pmatrix} \psi_{2,1} = 0$$
 (4.109)

Multiplying by $\begin{pmatrix} e_1 \\ 0 \end{pmatrix}$, $\begin{pmatrix} 0 \\ e_1 \end{pmatrix}$ and using (4.90) we obtain, as in the previous case, that $\alpha_{2,1}=0$, $\alpha_{2,2}=1$. Thus we can uniquely solve systems (4.108), (4.109) by imposing the normalization conditions

$$\left\langle \left(\begin{array}{c} e_1 \\ 0 \end{array} \right), \psi_{2,0} \right\rangle = \left\langle \left(\begin{array}{c} 0 \\ e_1 \end{array} \right), \psi_{2,0} \right\rangle = 0$$

$$\left\langle \left(\begin{array}{c} e_1 \\ 0 \end{array} \right), \psi_{2,1} \right\rangle = \left\langle \left(\begin{array}{c} 0 \\ e_1 \end{array} \right), \psi_{2,1} \right\rangle = 0.$$

To summarize, for $|k| \to \infty$ we obtained the asymptotics (4.99). Using (4.92), (4.106), (4.107) we obtain the asymptotics (4.100) for $|k| \to 0$. With a similar argument we obtain for $k \to 0$ that

$$\theta_{2} = \left\langle \begin{bmatrix} b_{2} + ik\psi_{2,0} + k^{2}\psi_{2,1} \end{bmatrix}, \begin{pmatrix} \Theta & \Lambda \\ \Lambda & \Theta \end{pmatrix} \begin{pmatrix} 0 \\ e_{1} \end{pmatrix} \right\rangle$$

$$= \left\langle b_{2}, \begin{pmatrix} \Lambda e_{1} \\ \Theta e_{1} \end{pmatrix} \right\rangle + ik \left\langle \psi_{2,0}, \begin{pmatrix} \Lambda e_{1} \\ \Theta e_{1} \end{pmatrix} \right\rangle + k^{2} \left\langle \psi_{2,1}, \begin{pmatrix} \Lambda e_{1} \\ \Theta e_{1} \end{pmatrix} \right\rangle + \dots$$

$$(4.110)$$

Using (4.97) we get

$$\psi_{2,0} = - \begin{pmatrix} 0 & I \\ I & 0 \end{pmatrix} \psi_{1,0}$$
 , $\psi_{2,1} = \begin{pmatrix} 0 & I \\ I & 0 \end{pmatrix} \psi_{1,1}$.

With this expression we can transform (4.110) into (4.101).

Remark 17 There is a crucial difference between the asymptotics (4.100), (4.101) in Proposition 16 and the asymptotics (4.54) in Proposition 10. In the later case the zero's order term in the expansion (4.54) vanishes due (4.61). In the case of Proposition 16 the term $\left\langle b_1, \begin{pmatrix} \Theta e_1 \\ \Lambda e_1 \end{pmatrix} \right\rangle$ does not necessarily vanish.

Now we can finally formulate some sufficient conditions for pattern formation under the symmetry assumption (4.76).

Theorem 18 Let $\delta > 0$. Suppose that U, A satisfy (4.77) and A_0 satisfies Assumptions 3) and 4). Let A be given as in (4.85) with $\varepsilon > 0$ sufficiently small. Let $\psi_{1,0}$, $\psi_{1,1}$ be the unique solutions of (4.88)-(4.90) and b_1 be given

as in Lemma 15. Then, system (4.27) has oscillatory patterns with wavelength smaller than $\frac{2\pi}{\delta}$ in the sense of Definition 1, if the following conditions are fulfilled

$$\left\langle b_1, \left(\begin{array}{c} \Theta e_1 \\ \Lambda e_1 \end{array} \right) \right\rangle = 0 \ , \ \left\langle e_1, \Theta e_1 \right\rangle \leq 0 \ , \ \left\langle \psi_{1,1}, \left(\begin{array}{c} \Theta e_1 \\ \Lambda e_1 \end{array} \right) \right\rangle > 0 \ .$$
 (4.111)

Example: N=4, n=2. Here we give a specific example of matrices U, A satisfying the hypothesis of Theorem 18. Consider matrices satisfying (4.77). These have the form

$$V = \begin{pmatrix} V_1 & 0 \\ 0 & V_2 \end{pmatrix} , V_1 \neq V_2 , U = \begin{pmatrix} V_1 & 0 & 0 & 0 \\ 0 & V_2 & 0 & 0 \\ 0 & 0 & -V_1 & 0 \\ 0 & 0 & 0 & -V_2 \end{pmatrix} , (4.112)$$

$$D = \begin{pmatrix} 1 & 0 & 0 & -1 \\ -1 & 1 & 0 & 0 \\ 0 & -1 & 1 & 0 \\ 0 & 0 & -1 & 1 \end{pmatrix} , A_0 = \begin{pmatrix} y_{1,1} & y_{1,2} & z_{1,1} & z_{1,2} \\ y_{2,1} & y_{2,2} & z_{2,1} & z_{2,2} \\ z_{1,1} & z_{1,2} & y_{1,1} & y_{1,2} \\ z_{2,1} & z_{2,2} & y_{2,1} & y_{2,2} \end{pmatrix} . (4.113)$$

Then

$$DA_0 = \begin{pmatrix} y_{1,1} - z_{2,1} & y_{1,2} - z_{2,2} & z_{1,1} - y_{2,1} & z_{1,2} - y_{2,2} \\ -y_{1,1} + y_{2,1} & -y_{1,2} + y_{2,2} & -z_{1,1} + z_{2,1} & -z_{1,2} + z_{2,2} \\ z_{1,1} - y_{2,1} & z_{1,2} - y_{2,2} & y_{1,1} - z_{2,1} & y_{1,2} - z_{2,2} \\ -z_{1,1} + z_{2,1} & -z_{1,2} + z_{2,2} & -y_{1,1} + y_{2,1} & -y_{1,2} + y_{2,2} \end{pmatrix}.$$

Assumption 3) implies that $y_{1,1}=z_{2,1}$, $y_{1,1}=y_{2,1}$, $z_{1,1}=y_{2,1}$, $z_{1,1}=z_{2,1}$ and the matrix DA_0 reduces to

$$DA_0 = \begin{pmatrix} 0 & y_{1,2} - z_{2,2} & 0 & z_{1,2} - y_{2,2} \\ 0 & -y_{1,2} + y_{2,2} & 0 & -z_{1,2} + z_{2,2} \\ 0 & z_{1,2} - y_{2,2} & 0 & y_{1,2} - z_{2,2} \\ 0 & -z_{1,2} + z_{2,2} & 0 & -y_{1,2} + y_{2,2} \end{pmatrix}.$$

Now we can compute b_1 , b_2 as in Lemma 15. These vectors solve

$$(y_{1,2} - z_{2,2}) b_{i,1} + (-y_{1,2} + y_{2,2}) b_{i,2} + (z_{1,2} - y_{2,2}) b_{i,3} + (-z_{1,2} + z_{2,2}) b_{i,4} = 0$$
 (4.114)

$$(z_{1,2} - y_{2,2}) b_{i,1} + (-z_{1,2} + z_{2,2}) b_{i,2} + (y_{1,2} - z_{2,2}) b_{i,3} + (-y_{1,2} + y_{2,2}) b_{i,4} = 0 ,$$

$$(4.115)$$

where $b_i=(b_{i,1},b_{i,2},b_{i,3},b_{i,4})^t$. Notice that (4.96) yields $b_{1,1}=1$, $b_{1,3}=0$, $b_{2,3}=1$, $b_{2,1}=0$. Thus system (4.114), (4.115) reduces to

$$(-y_{1,2} + y_{2,2}) b_{1,2} + (-z_{1,2} + z_{2,2}) b_{1,4} = -(y_{1,2} - z_{2,2})$$

$$(4.116)$$

$$(-z_{1,2} + z_{2,2}) b_{1,2} + (-y_{1,2} + y_{2,2}) b_{1,4} = -(z_{1,2} - y_{2,2})$$

$$(4.117)$$

$$(-y_{1,2} + y_{2,2}) b_{2,2} + (-z_{1,2} + z_{2,2}) b_{2,4} = -(z_{1,2} - y_{2,2})$$

$$(-z_{1,2} + z_{2,2}) b_{2,2} + (-y_{1,2} + y_{2,2}) b_{2,4} = -(y_{1,2} - z_{2,2})$$

Notice that $b_{2,2} = b_{1,4}$, $b_{2,4} = b_{1,2}$. Therefore the solutions obtained this way satisfy (4.97) and the problem reduces to the system of equations (4.116), (4.117). In order to solve this system we have to $\operatorname{assume}(-y_{1,2} + y_{2,2})^2 \neq (-z_{1,2} + z_{2,2})^2$. Then the vectors b_1 , b_2 are given by

$$b_1 = (1, b_{1,2}, 0, b_{1,4})^t$$
, $b_2 = (0, b_{1,4}, 1, b_{1,2})^t$.

Due to the normalization conditions (4.104) the vectors $\psi_{1.0}$, $\psi_{1.1}$ satisfy

$$\psi_{1,0} = (0, \psi_{1,0,2}, 0, \psi_{1,0,4})^t$$
, $\psi_{1,1} = (0, \psi_{1,1,2}, 0, \psi_{1,1,4})$

and

Defining

$$L \equiv \left(\begin{array}{cc} (-y_{1,2} + y_{2,2}) & (-z_{1,2} + z_{2,2}) \\ (-z_{1,2} + z_{2,2}) & (-y_{1,2} + y_{2,2}) \end{array} \right)$$

these systems, as well as (4.116), (4.117) can be written in the form

$$L\begin{pmatrix} b_{1,2} \\ b_{1,4} \end{pmatrix} = -\begin{pmatrix} y_{1,2} - z_{2,2} \\ z_{1,2} - y_{2,2} \end{pmatrix} =: w$$

$$L\begin{pmatrix} \psi_{1,0,2} \\ \psi_{1,0,4} \end{pmatrix} + \begin{pmatrix} V_2 - V_1 & 0 \\ 0 & -(V_1 + V_2) \end{pmatrix} \begin{pmatrix} b_{1,2} \\ b_{1,4} \end{pmatrix} = 0$$

$$L\begin{pmatrix} \psi_{1,1,2} \\ \psi_{1,1,4} \end{pmatrix} - \begin{pmatrix} V_2 - V_1 & 0 \\ 0 & -(V_1 + V_2) \end{pmatrix} \begin{pmatrix} \psi_{1,0,2} \\ \psi_{1,0,4} \end{pmatrix} = 0.$$

On the other hand

$$M = \begin{pmatrix} m_{1,1} & m_{1,2} & n_{1,1} & n_{1,2} \\ m_{2,1} & m_{2,2} & n_{2,1} & n_{2,2} \\ n_{1,1} & n_{1,2} & m_{1,1} & m_{1,2} \\ n_{2,1} & n_{2,2} & m_{2,1} & m_{2,2} \end{pmatrix} ,$$

$$DM = \begin{pmatrix} m_{1,1} - n_{2,1} & m_{1,2} - n_{2,2} & n_{1,1} - m_{2,1} & n_{1,2} - m_{2,2} \\ -m_{1,1} + m_{2,1} & -m_{1,2} + m_{2,2} & -n_{1,1} + n_{2,1} & -n_{1,2} + n_{2,2} \\ n_{1,1} - m_{2,1} & n_{1,2} - m_{2,2} & m_{1,1} - n_{2,1} & m_{1,2} - n_{2,2} \\ -n_{1,1} + n_{2,1} & -n_{1,2} + n_{2,2} & -m_{1,1} + m_{2,1} & -m_{1,2} + m_{2,2} \end{pmatrix}$$

$$= \begin{pmatrix} \Theta & \Lambda \\ \Lambda & \Theta \end{pmatrix}.$$

Then

$$\Theta e_1 = \left(\begin{array}{c} m_{1,1} - n_{2,1} \\ -m_{1,1} + m_{2,1} \end{array} \right) \quad , \quad \Lambda e_1 = \left(\begin{array}{c} n_{1,1} - m_{2,1} \\ -n_{1,1} + n_{2,1} \end{array} \right) \ .$$

The sufficient conditions for pattern formation, (4.111), then reduce to

$$(m_{1,1} - n_{2,1}) + b_{1,2} (-m_{1,1} + m_{2,1}) + b_{1,4} (-n_{1,1} + n_{2,1}) = 0$$

$$m_{1,1} - n_{2,1} \le 0$$

$$\psi_{1,1,2} (m_{1,1} - n_{2,1}) + \psi_{1,1,4} (-n_{1,1} + n_{2,1}) > 0$$

Therefore, as in the previous case, we need the linear independence of $(b_{1,2}, b_{1,4})^t$, $(\psi_{1,1,2}, \psi_{1,1,4})^t$.

As a specific example we can chose

$$L = \begin{pmatrix} 2 & -1 \\ -1 & 2 \end{pmatrix} = \begin{pmatrix} (-y_{1,2} + y_{2,2}) & (-z_{1,2} + z_{2,2}) \\ (-z_{1,2} + z_{2,2}) & (-y_{1,2} + y_{2,2}) \end{pmatrix} ,$$

$$y_{1,2} - y_{2,2} = -2$$
, $z_{1,2} - z_{2,2} = 1$, $z_{2,2} - y_{1,2} = a$.

Thus $z_{1,2} - y_{1,2} = 1 + a$, $z_{1,2} - y_{2,2} = -1 + a$.

$$w = \begin{pmatrix} a \\ 1 - a \end{pmatrix} = - \begin{pmatrix} y_{1,2} - z_{2,2} \\ z_{1,2} - y_{2,2} \end{pmatrix}$$

$$R = \begin{pmatrix} -1 & 0 \\ 0 & -3 \end{pmatrix} = \begin{pmatrix} V_2 - V_1 & 0 \\ 0 & -(V_1 + V_2) \end{pmatrix}$$

with $V_1 = 2, V_2 = 1$.

$$\begin{pmatrix} b_{1,2} \\ b_{1,4} \end{pmatrix} = L^{-1}w = \begin{pmatrix} \frac{1}{3}a + \frac{1}{3} \\ -\frac{1}{3}a + \frac{2}{3} \end{pmatrix}$$

$$\begin{pmatrix} \psi_{1,1,2} \\ \psi_{1,1,4} \end{pmatrix} = -L^{-1}RL^{-1}RL^{-1}w = \begin{pmatrix} \frac{17}{27}a - \frac{55}{27} \\ \frac{31}{27}a - \frac{86}{27} \end{pmatrix}$$

and the desired condition is satisfied.

On the other hand, Assumption 4) requires that the rest of the spectrum of

$$zw + ikU \cdot w + DA_0w = 0 , k \in \mathbb{R}$$
 (4.118)

is below a half plane contained in $\{\operatorname{Re}(z)<0\}$. The spectrum reduces to the roots of

$$\det \left(\begin{array}{cccc} z + ikV_1 & y_{1,2} - z_{2,2} & 0 & z_{1,2} - y_{2,2} \\ 0 & -y_{1,2} + y_{2,2} + (z + ikV_2) & 0 & -z_{1,2} + z_{2,2} \\ 0 & z_{1,2} - y_{2,2} & z - ikV_1 & y_{1,2} - z_{2,2} \\ 0 & -z_{1,2} + z_{2,2} & 0 & -y_{1,2} + y_{2,2} + (z - ikV_2) \end{array} \right)$$

=0, respectively

$$(z+ikV_1)(z-ikV_1) \det \begin{pmatrix} (y_{2,2}-y_{1,2})+(z+ikV_2) & (z_{2,2}-z_{1,2}) \\ (z_{2,2}-z_{1,2}) & (y_{2,2}-y_{1,2})+(z-ikV_2) \end{pmatrix}$$

Therefore we have to solve

$$(y_{2,2} - y_{1,2})^2 + 2(y_{2,2} - y_{1,2})z + z^2 + k^2V_2^2 - (z_{2,2} - z_{1,2})^2 = 0$$

whose solutions are

$$z = -(y_{2,2} - y_{1,2}) \pm \left[(y_{2,2} - y_{1,2})^2 - (y_{2,2} - y_{1,2})^2 + (z_{2,2} - z_{1,2})^2 - k^2 V_2^2 \right]^{\frac{1}{2}}$$

= $-(y_{2,2} - y_{1,2}) \pm \left[(z_{2,2} - z_{1,2})^2 - k^2 V_2^2 \right]^{\frac{1}{2}}$.

Then, if $|z_{2,2}-z_{1,2}| < (y_{2,2}-y_{1,2})$ we obtain the desired condition. Summarizing, we choose

$$y_{1,2} - y_{2,2} = -2$$
, $z_{1,2} - z_{2,2} = 1$, $z_{2,2} - y_{1,2} = a$, $z_{1,2} - y_{2,2} = -1 + a$.

For instance we can take $y_{2,2}=2.5$, $y_{1,2}=0.5$, $z_{2,2}=0.5+a$, $z_{1,2}=1.5+a$. For a=0 we obtain

$$y_{2,2} = 2.5$$
, $y_{1,2} = 0.5$, $z_{2,2} = 0.5$, $z_{1,2} = 1.5$,

$$y_{1,1} = z_{2,1}$$
 , $y_{1,1} = y_{2,1}$, $z_{1,1} = y_{2,1}$, $z_{1,1} = z_{2,1}$,

$$A_0 = \begin{pmatrix} c & 0.5 & c & 1.5 \\ c & 2.5 & c & 0.5 \\ c & 1.5 & c & 0.5 \\ c & 0.5 & c & 2.5 \end{pmatrix} . \tag{4.119}$$

Then

$$\left(\begin{array}{c} b_{1,2} \\ b_{1,4} \end{array}\right) = \left(\begin{array}{c} \frac{1}{3} \\ -\frac{2}{3} \end{array}\right) \;\;,\;\; \left(\begin{array}{c} \psi_{1,1,2} \\ \psi_{1,1,4} \end{array}\right) = \left(\begin{array}{c} -\frac{55}{27} \\ -\frac{86}{27} \end{array}\right) \;\;.$$

And the conditions for m, n become $m_{2,1}=n_{2,1}-2m_{1,1}+2n_{1,1}$, $86\left(n_{2,1}-n_{1,1}\right)<55\left(n_{2,1}-m_{1,1}\right)$, $m_{1,1}-n_{2,1}\leq0$. For instance for

$$m_{1,1} = 1$$
 , $n_{2,1} = 1.5$, $n_{1,1} = 1.3$, $m_{2,1} = 2.1$

$$M = \begin{pmatrix} 1 & 0 & 1.3 & 0 \\ 2.1 & 0 & 1.5 & 0 \\ 1.3 & 0 & 1 & 0 \\ 1.5 & 0 & 2.1 & 0 \end{pmatrix}$$
 (4.120)

The root with the largest real part of (4.75) for this choice of data and with $\varepsilon=0.001$ can be seen in Figure 2

Note, that the plotted curve does not start at the origin. This is due to some higher order terms, which produce the shift. The effect is rather small though.

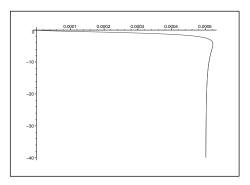


Figure 2: The case N=4. The root with the largest real part of (4.75) close to the imaginary axis for U as in (4.112), with $V_1=2,V_2=1,\,D$ as in (4.113), A_0 as in (4.119) and M as in (4.120). Here $\varepsilon=0.001$.

5 Choices of A_0 , M, which relate to Rippling Dynamics of Myxobacteria

The previous analysis provides a variety of matrices A such that (4.27) is invariant under the transformation $(x, \varphi, \psi) \to (-x, \psi, \varphi)$, and yields oscillatory instabilities in the sense of Definition 1. So far the coefficients of A_0 , M where chosen without any specific application in mind. We have chosen A_0 such that a dispersion relation "as hyperbolic as possible" resulted (cf. Assumptions 3 and 4). Then A_0 was suitably perturbed by a matrix εM .

In this section we will construct two specific examples of systems of type (4.27), where A is a 4×4 matrix satisfying the symmetry conditions (4.77). Here A is obtained by linearizing a system of the form (4.9)-(4.12) with functions T_1 , T_2 satisfying suitable dependencies.

Coming back to the behavior of myxobacteria, which under starvation conditions first align from a basically two-dimensional motion to a one-dimensional axis and then move into two opposite directions, we are interested in how many reasonable types of cells (two are not enough) are needed on the linearized level of analysis to observe counter migrating ripples of cell density waves. The rationale for our example is that the bacteria moving into one direction can be in two different states. The cells pass from a non-excited state to an excited state, which is induced by the cells moving into the opposite direction. First we assume that the cells in the excited state move with slower speed than the non-excited cells. In a second model the excited cells are not moving at all. Similar pattern forming properties can be derived if the speed of the excited cells is larger than the speed of the normal cells, but we omit further details for that case here.

First we show, that if both states of cells move with the same speed, then no pattern formation can be observed in the 4×4 case.

5.1 Degenerate matrices U, symmetric under reflections, do not yield pattern formation near "hyperbolic" 4×4 matrices A.

Here we show that under suitable generic conditions on the coefficients, system (4.27) with 4×4 matrices can not yield patterns in the proximity of "hyperbolic" matrices, if U contains only two opposite velocities and (4.27) is invariant under the transformation $(x, \varphi, \psi) \to (-x, \psi, \varphi)$. To see this, consider $A = A_0 + \varepsilon M$ with

$$A_{0} = \begin{pmatrix} y_{1,1} & y_{1,2} & z_{1,1} & z_{1,2} \\ y_{2,1} & y_{2,2} & z_{2,1} & z_{2,2} \\ z_{1,1} & z_{1,2} & y_{1,1} & y_{1,2} \\ z_{2,1} & z_{2,2} & y_{2,1} & y_{2,2} \end{pmatrix}, M = \begin{pmatrix} m_{1,1} & m_{1,2} & n_{1,1} & n_{1,2} \\ m_{2,1} & m_{2,2} & n_{2,1} & n_{2,2} \\ n_{1,1} & n_{1,2} & m_{1,1} & m_{1,2} \\ n_{2,1} & n_{2,2} & m_{2,1} & m_{2,2} \end{pmatrix}$$

$$(5.1)$$

and
$$U = \begin{pmatrix} V & 0 & 0 & 0 \\ 0 & V & 0 & 0 \\ 0 & 0 & -V & 0 \\ 0 & 0 & 0 & -V \end{pmatrix}$$
 , $D = \begin{pmatrix} 1 & 0 & 0 & -1 \\ -1 & 1 & 0 & 0 \\ 0 & -1 & 1 & 0 \\ 0 & 0 & -1 & 1 \end{pmatrix}$,

where $V \in \mathbb{R}, V \neq 0$ and $\varepsilon > 0$ is small. By rescaling we can assume w.l.o.g. that V = 1.

First we precise the meaning of a hyperbolic matrix.

Definition 19 The matrix A_0 given as in (5.1) is a nonsingular hyperbolic ma-

$$trix \ if \ the \ vectors \left(\begin{array}{c} y_{1,1} \\ y_{2,1} \\ z_{1,1} \\ z_{2,1} \end{array} \right), \ \left(\begin{array}{c} y_{1,2} \\ y_{2,2} \\ z_{1,2} \\ z_{2,2} \end{array} \right) generate \ a \ linear \ subspace \ of \ dimension$$

one and

$$\Delta_1(0) \neq 0 , \qquad (5.2)$$

where

$$\begin{split} \Delta_1(k) & \equiv \det \begin{pmatrix} 2ik + y_{1,1} - z_{2,1} & y_{1,2} - z_{2,2} & z_{1,1} - y_{2,1} \\ -y_{1,1} + y_{2,1} & 2ik - y_{1,2} + y_{2,2} & -z_{1,1} + z_{2,1} \\ z_{1,1} - y_{2,1} & z_{1,2} - y_{2,2} & y_{1,1} - z_{2,1} \end{pmatrix} \\ & + \det \begin{pmatrix} 2ik + y_{1,1} - z_{2,1} & y_{1,2} - z_{2,2} & z_{1,2} - y_{2,2} \\ -y_{1,1} + y_{2,1} & 2ik - y_{1,2} + y_{2,2} & -z_{1,2} + z_{2,2} \\ -z_{1,1} + z_{2,1} & -z_{1,2} + z_{2,2} & -y_{1,2} + y_{2,2} \end{pmatrix} \end{split}$$

Remark 20 Here (5.2) is a technical condition that ensures that the dispersion relation associated to (4.27) can be computed perturbatively for $\varepsilon \to 0$ and is satisfied generically.

The meaning of "hyperbolic" in Definition 19 is, that a large portion of the dispersion relation associated to the evolution problem (4.27), for the matrix $A = A_0$ lies on the imaginary axis as it would be the case for the wave equation. This is a consequence of

Proposition 21 Assume that A_0 is a nonsingular hyperbolic matrix in the sense of Definition 19. Then, there exist two real numbers α_1 , α_2 with $(\alpha_1)^2 + (\alpha_2)^2 \neq 0$ and

$$DA_0 \begin{pmatrix} \alpha_1 \\ \alpha_2 \\ 0 \\ 0 \end{pmatrix} = 0 , DA_0 \begin{pmatrix} 0 \\ 0 \\ \alpha_1 \\ \alpha_2 \end{pmatrix} = 0$$
 (5.3)

The numbers α_1 , α_2 are uniquely determined, up to multiplication by $C \neq 0$. Moreover, for each $k \in \mathbb{R}$ the spectrum of the matrix $-(ikU + DA_0)$ contains the eigenvalues -ik and ik.

Proof. Due Definition 19 there exist α_1 , α_2 as stated in Proposition 21 with

$$\alpha_1 \begin{pmatrix} y_{1,1} \\ y_{2,1} \\ z_{1,1} \\ z_{2,1} \end{pmatrix} + \alpha_2 \begin{pmatrix} y_{1,2} \\ y_{2,2} \\ z_{1,2} \\ z_{2,2} \end{pmatrix} = 0.$$
 (5.4)

On the other hand

$$DA_0 = \left(egin{array}{cccc} y_{1,1} - z_{2,1} & y_{1,2} - z_{2,2} & z_{1,1} - y_{2,1} & z_{1,2} - y_{2,2} \ -y_{1,1} + y_{2,1} & -y_{1,2} + y_{2,2} & -z_{1,1} + z_{2,1} & -z_{1,2} + z_{2,2} \ z_{1,1} - y_{2,1} & z_{1,2} - y_{2,2} & y_{1,1} - z_{2,1} & y_{1,2} - z_{2,2} \ -z_{1,1} + z_{2,1} & -z_{1,2} + z_{2,2} & -y_{1,1} + y_{2,1} & -y_{1,2} + y_{2,2} \end{array}
ight)$$

Formula (5.3) then follows from (5.4). Since
$$U\begin{pmatrix} \alpha_1 \\ \alpha_2 \\ 0 \\ 0 \end{pmatrix} = \begin{pmatrix} \alpha_1 \\ \alpha_2 \\ 0 \\ 0 \end{pmatrix}$$
 and

$$U\begin{pmatrix} 0\\0\\\alpha_1\\\alpha_2 \end{pmatrix} = -\begin{pmatrix} 0\\0\\\alpha_1\\\alpha_2 \end{pmatrix}, \text{ the mentioned properties about the spectrum of}$$
$$-(ikU + DA_0) \text{ follow immediately.} \quad \blacksquare$$

So an additional technical assumption on the matrix A_0 is needed in order to obtain the desired pattern forming properties.

Definition 22 A matrix A_0 is a stable nonsingular hyperbolic matrix, if it is nonsingular hyperbolic and for each $k \in \mathbb{R}$ the spectrum of $-ikU - DA_0$ consists of the eigenvalues -ik, ik and two more eigenvalues contained in the half-plane $\operatorname{Re}(z) < 0$.

Now we can state the main result of this section

Theorem 23 Suppose that A_0 is a stable nonsingular hyperbolic matrix in the sense of Definition 22. Let $A = A_0 + \varepsilon M$. Define

$$\begin{split} \Delta_{1}\left(k\right) & \equiv \det \left(\begin{array}{cccc} 2ik + y_{1,1} - z_{2,1} & y_{1,2} - z_{2,2} & z_{1,1} - y_{2,1} \\ -y_{1,1} + y_{2,1} & 2ik - y_{1,2} + y_{2,2} & -z_{1,1} + z_{2,1} \\ z_{1,1} - y_{2,1} & z_{1,2} - y_{2,2} & y_{1,1} - z_{2,1} \end{array} \right) \\ & + \det \left(\begin{array}{cccc} 2ik + y_{1,1} - z_{2,1} & y_{1,2} - z_{2,2} & z_{1,2} - y_{2,2} \\ -y_{1,1} + y_{2,1} & 2ik - y_{1,2} + y_{2,2} & -z_{1,2} + z_{2,2} \\ -z_{1,1} + z_{2,1} & -z_{1,2} + z_{2,2} & -y_{1,2} + y_{2,2} \end{array} \right) \end{split}$$

$$\Delta_2(k) \equiv$$

$$\det \begin{pmatrix} 2ik+y_{1,1}-z_{2,1} & y_{1,2}-z_{2,2} & z_{1,1}-y_{2,1} & n_{1,2}-m_{2,2} \\ -y_{1,1}+y_{2,1} & 2ik-y_{1,2}+y_{2,2} & -z_{1,1}+z_{2,1} & -n_{1,2}+n_{2,2} \\ z_{1,1}-y_{2,1} & z_{1,2}-y_{2,2} & y_{1,1}-z_{2,1} & m_{1,2}-n_{2,2} \\ -z_{1,1}+z_{2,1} & -z_{1,2}+z_{2,2} & -y_{1,1}+y_{2,1} & -m_{1,2}+m_{2,2} \end{pmatrix}$$

$$+ \det \begin{pmatrix} 2ik+y_{1,1}-z_{2,1} & y_{1,2}-z_{2,2} & n_{1,1}-m_{2,1} & z_{1,2}-y_{2,2} \\ -y_{1,1}+y_{2,1} & 2ik-y_{1,2}+y_{2,2} & -n_{1,1}+n_{2,1} & -z_{1,2}+z_{2,2} \\ z_{1,1}-y_{2,1} & z_{1,2}-y_{2,2} & m_{1,1}-n_{2,1} & y_{1,2}-z_{2,2} \\ -z_{1,1}+z_{2,1} & -z_{1,2}+z_{2,2} & -m_{1,1}+m_{2,1} & -y_{1,2}+y_{2,2} \end{pmatrix}$$

And define functions $P_0(k,a)$, $P_1(k,a)$ by

$$\det\left(\left(ik + a\varepsilon\right) + ikU + DA_0 + \varepsilon DM\right) = P_0\left(k, a\right) + P_1\left(k, a\right)\varepsilon + O\left(\varepsilon^2\right) . \tag{5.5}$$

Then $\Delta_1(k)$, $\Delta_2(k)$ can be written in the form

$$\Delta_1(k) = (2ik) \left[\mu_1 k i + \nu_1 \right] , \quad \Delta_2(k) = (2ik) \left[\mu_2 k i + \nu_2 \right] . \quad (5.6)$$

On the other hand the equation

$$P_0(k,a) + P_1(k,a)\varepsilon = 0 (5.7)$$

defines a function $A(k) = \operatorname{Re}(a)$ that is monotone in case $\mu_1, \mu_2, \nu_1, \nu_2$ as defined in (5.6) satisfy

$$\begin{vmatrix} \mu_1 & \nu_1 \\ \mu_2 & \nu_2 \end{vmatrix} \neq 0. \tag{5.8}$$

Remark 24 The function $\zeta = ik + a\varepsilon$ with a = a(k) defined by (5.7) provides a linear approximation in ε of the eigenvalue $z = z(k, \varepsilon)$ of the eigenvalue problem

$$(z + ikU + DA_0 + \varepsilon DM) v = 0 , \qquad (5.9)$$

such that z = 0 for $\varepsilon = 0$. The fact that the function A(k) is monotone does not imply monotonicity of $\text{Re}(z(k,\varepsilon))$, because classical perturbation theory for

eigenvalue problems just implies $z(k,\varepsilon)=ik+a\varepsilon+O\left(\varepsilon^2\right)$ as $\varepsilon\to0$. The uniformicity of this approximation breaks down in general for $k\to0$, since z(0,0) is a double eigenvalue. Some care is required to show uniformicity of the approximation as $k\to\infty$. Therefore, from Theorem 23 we can only conclude that for the whole eigenvalue problem (5.9) patterns with wavelengths of order one for ε small are absent, if condition (5.8) holds. However, this Theorem does not rule out the onset of patterns with very small, or very large wavelengths for $\varepsilon\to0$ under the condition (5.8). Moreover, if condition (5.8) fails, there could be patterns with wavelengths of order one arising from quadratic terms on ε . Nevertheless, the analysis of such higher order pattern would require the use of methods different from the ones presented in this paper.

Proof. We can expand the left hand side of (5.5) as

$$\det \begin{pmatrix} 2ikI + E & F \\ F & E \end{pmatrix} + O\left(\varepsilon^2\right) , \qquad (5.10)$$

where

$$\begin{split} E &\equiv \left(\begin{array}{ccc} y_{1,1} - z_{2,1} + \varepsilon m_{1,1} - \varepsilon n_{2,1} + a\varepsilon & y_{1,2} - z_{2,2} + \varepsilon m_{1,2} - \varepsilon n_{2,2} \\ -y_{1,1} + y_{2,1} - \varepsilon m_{1,1} + \varepsilon m_{2,1} & -y_{1,2} + y_{2,2} - \varepsilon m_{1,2} + \varepsilon m_{2,2} + a\varepsilon \end{array} \right) \\ F &\equiv \left(\begin{array}{ccc} z_{1,1} - y_{2,1} + \varepsilon n_{1,1} - \varepsilon m_{2,1} & z_{1,2} - y_{2,2} + \varepsilon n_{1,2} - \varepsilon m_{2,2} \\ -z_{1,1} + z_{2,1} - \varepsilon n_{1,1} + \varepsilon n_{2,1} & -z_{1,2} + z_{2,2} - \varepsilon n_{1,2} + \varepsilon n_{2,2} \end{array} \right). \end{split}$$

The first term in (5.10) can be expanded in ε . Arguing as in the proof of Proposition 21 it follows that if $\varepsilon = 0$ the last two columns of (5.10) are linearly dependent, so the determinant vanishes. Therefore, using the multilinearity of the determinant we can rewrite $P_0(k, a)$, $P_1(k, a)$ as

$$P_0(k, a) = 0$$
, $P_1(k, a) = \Delta_1(k) a + \Delta_2(k)$.

Then, the solution of (5.7) yields $a = -\frac{\Delta_2}{\Delta_1}$. Formulas (5.6) are a consequence

of the linear dependence of the vectors
$$\begin{pmatrix} y_{1,1} \\ y_{2,1} \\ z_{1,1} \\ z_{2,1} \end{pmatrix}$$
, $\begin{pmatrix} y_{1,2} \\ y_{2,2} \\ z_{1,2} \\ z_{2,2} \end{pmatrix}$. Due to (5.2) we

have $\nu_1 \neq 0$ and to the leading order

$$a = -\left(\frac{\mu_2 k i + \nu_2}{\mu_1 k i + \nu_1}\right) \text{ and } \operatorname{Re}(a) = \frac{\alpha_2 + \beta_2 k^2}{\alpha_1 + \beta_1 k^2}$$
 (5.11)

for some $\alpha_1, \beta_1, \alpha_2, \beta_2 \in \mathbb{R}$, $\alpha_1 \neq 0$. The right hand side of (5.11) depends monotonically on k, if (5.8) is satisfied, whence our theorem follows.

5.2 Bacteria in the excited state are less motile than in the non-excited state.

We need the matrix U to be nondegenerate. More precisely, assume that

$$U = \begin{pmatrix} 2 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 \\ 0 & 0 & -2 & 0 \\ 0 & 0 & 0 & -1 \end{pmatrix} . \tag{5.12}$$

On the other hand we obtain (4.27) by linearizing (4.9)-(4.12), with A given by

$$A = \begin{pmatrix} T_{1,1} & T_{1,2} & T_{1,3} & T_{1,4} \\ T_{2,1} & T_{2,2} & T_{2,3} & T_{2,4} \\ T_{1,3} & T_{1,4} & T_{1,1} & T_{1,2} \\ T_{2,3} & T_{2,4} & T_{2,1} & T_{2,2} \end{pmatrix} = A_0 + \varepsilon M .$$

Further, we will make the following "reasonable" assumptions

$$T_1 = T_1 \left(u_1 + u_2 + v_1 + v_2, u_1, v_1 + v_2 \right) \tag{5.13}$$

$$T_2 = T_2(u_2)$$
 (5.14)

The bacteria change through the states in the following way: $u_1 \rightarrow u_2 \rightarrow v_1 \rightarrow v_2$. Thus cells of the non-excited type u_1 get excited (i.e. prepare for turning) in dependence of the total cell density, the collisions with counter-migrating cells and by the cell density of their own kind. Turning is then "automatic" and depends on the distribution u_2 itself. Assume, as above, that the eigenvector associated to the eigenvalue (-2ik) for the unperturbed problem $z + ikU + DA_0 = 0$ is $(1,0,0,0)^t$. Then the matrix A_0 has the form (cf. Assumption 3)

$$A_0 = \begin{pmatrix} c & y_{1,2} & c & z_{1,2} \\ c & y_{2,2} & c & z_{2,2} \\ c & z_{1,2} & c & y_{1,2} \\ c & z_{2,2} & c & y_{2,2} \end{pmatrix}$$

for some $c \in \mathbb{R}$. In order to obtain the constraints (5.13), (5.14) and since ε is arbitrary we may assume $c = z_{1,2} = z_{2,2} = 0$. Then

$$A_0 = \left(\begin{array}{cccc} 0 & y_{1,2} & 0 & 0\\ 0 & y_{2,2} & 0 & 0\\ 0 & 0 & 0 & y_{1,2}\\ 0 & 0 & 0 & y_{2,2} \end{array}\right) \ .$$

Due to (5.13), (5.14) we must have

$$M = \left(\begin{array}{cccc} m_{1,1} & m_{1,2} & n_{1,1} & n_{1,1} \\ 0 & m_{2,2} & 0 & 0 \\ n_{1,1} & n_{1,1} & m_{1,1} & m_{1,2} \\ 0 & 0 & 0 & m_{2,2} \end{array} \right) \ .$$

Since we are interested in $A = A_0 + \varepsilon M$ the values of $m_{1,2}$, $m_{2,2}$ can be absorbed in $y_{1,2}$, $y_{2,2}$ respectively. So we chose

$$A_0 = \begin{pmatrix} 0 & y_{1,2} & 0 & 0 \\ 0 & y_{2,2} & 0 & 0 \\ 0 & 0 & 0 & y_{1,2} \\ 0 & 0 & 0 & y_{2,2} \end{pmatrix} , M = \begin{pmatrix} m_{1,1} & 0 & n_{1,1} & n_{1,1} \\ 0 & 0 & 0 & 0 & 0 \\ n_{1,1} & n_{1,1} & m_{1,1} & 0 \\ 0 & 0 & 0 & 0 \end{pmatrix}.$$

The corresponding dispersion relation associated to (4.27) can then be computed by solving

$$\det (z + ikU + DA_0 + \varepsilon DM) = 0. ag{5.15}$$

We compute solutions of (5.15) near the "hyperbolic line" z=-2ik perturbatively. To do this we take an expansion that is uniform on the whole line $k \in \mathbb{R}$

$$z = -2ik + a\varepsilon + \dots$$

Keeping only terms of linear order in ε we obtain

$$a = -m_{1,1} \frac{iy_{2,2}y_{1,2} - 5y_{2,2}k + 4ik^2 + y_{1,2}k - iy_{2,2}^2}{5y_{1,2}k - iy_{1,2}^2 - 5y_{2,2}k + 4ik^2 - iy_{2,2}^2 + 2iy_{2,2}y_{1,2}} .$$

In order to have the remaining part of the spectrum in the region Re(z) < 0 we need

$$y_{1,2} - y_{2,2} < 0. (5.16)$$

Then we get the following asymptotics

$$\begin{split} & \operatorname{Re}\left(a\right) \sim \left(m_{1,1} - n_{1,1}\right) \frac{y_{2,2}}{y_{1,2} - y_{2,2}} - \frac{m_{1,1}y_{1,2} - 9n_{1,1}y_{2,2}}{\left(y_{1,2} - y_{2,2}\right) \left(y_{2,2}^2 + y_{1,2}^2 - 2y_{2,2}y_{1,2}\right)} k^2 + \dots \\ & \text{for} \quad k \to 0 \quad \text{and} \quad \lim_{k \to \infty} a = -m_{1,1} \ . \end{split}$$

Therefore, the following conditions ensure oscillatory pattern formation for (4.27)

$$m_{1,1} = n_{1,1} \; , \; -\frac{m_{1,1}y_{1,2} - 9n_{1,1}y_{2,2}}{(y_{1,2} - y_{2,2})} > 0 \; , \; m_{1,1} > 0 \; .$$

W.l.o.g. assume that $m_{1,1} = n_{1,1} = 1$. Taking into account (5.16), a sufficient condition for pattern formation for small $\varepsilon > 0$ is

$$y_{1,2} - 9y_{2,2} > 0$$
, $y_{2,2} - y_{1,2} > 0$.

A possible choice is $y_{1,2} = -1$, $y_{2,2} = -0.5$. So with

$$A_0 = \begin{pmatrix} 0 & -1 & 0 & 0 \\ 0 & -0.5 & 0 & 0 \\ 0 & 0 & 0 & -1 \\ 0 & 0 & 0 & -0.5 \end{pmatrix} , M = \begin{pmatrix} 1 & 0 & 1 & 1 \\ 0 & 0 & 0 & 0 \\ 1 & 1 & 1 & 0 \\ 0 & 0 & 0 & 0 \end{pmatrix} , \varepsilon > 0$$
 (5.17)

we obtain oscillatory patterns for (4.27). The root with the largest real part corresponding to the dispersion relation for this choice of matrices is shown in Figure 3.

Let us summarize

Theorem 25 The differential equation (4.27) with $A = A_0 + \varepsilon M$, and A_0 , M as in (5.17), U as in (5.12) and $\varepsilon > 0$ sufficiently small generates oscillatory patterns in the sense of Definition 1.

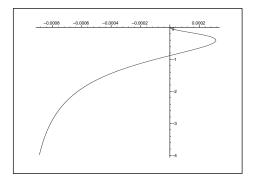


Figure 3: The root with the largest real part for (5.15) close to the imaginary axis for the situation in Theorem 25 with $\varepsilon = 0.001$.

Also other examples were found, where the roles of 1 and 2 in U where exchanged. The conclusion in these cases is the same, including the signs of the coefficients. In all cases, the functions show an inhibitory character for some of the interactions, which seems untypical for the behavior of myxobacteria.

5.3 The cells in the excited state are not moving

We now assume

$$U = \begin{pmatrix} 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & -1 & 0 \\ 0 & 0 & 0 & 0 \end{pmatrix} . \tag{5.18}$$

In this case it is not possible to obtain oscillatory patterns with functional dependences as given in (5.13), (5.14) for the transition rates. We need slightly more detailed dependencies for T_2 , and with these, we can obtain pattern formation without inhibitory effects, which is more realistic in the context of pattern formation in myxobacteria. A first natural generalization, namely

$$T_1 = T_1 (u_1 + u_2 + v_1 + v_2, u_1, v_1 + v_2)$$

$$T_2 = T_2 (u_1 + u_2 + v_1 + v_2, u_2)$$

does also not give oscillatory patters at the linearized level for ε . So we assume

$$T_1 = T_1 (u_1 + u_2 + v_1 + v_2, u_1, v_1, v_2)$$
(5.19)

$$T_2 = T_2 \left(u_1 + u_2 + v_1 + v_2 \right) . {(5.20)}$$

A set of matrices A, A_0, M consistent with this are

$$A_{0} = \begin{pmatrix} c & y_{1,2} & c & z_{1,2} \\ c & c & c & c & c \\ c & z_{1,2} & c & y_{1,2} \\ c & c & c & c & c \end{pmatrix} , M = \begin{pmatrix} m_{1,1} & 0 & n_{1,1} & 0 \\ 0 & 0 & 0 & 0 & 0 \\ n_{1,1} & 0 & m_{1,1} & 0 \\ 0 & 0 & 0 & 0 & 0 \end{pmatrix} , (5.21)$$

$$A = A_0 + \varepsilon M$$
.

We then solve (5.15) near the line of hyperbolicity z = -ik, i.e. we expand

$$z = -ik + a\varepsilon + \dots.$$

The solution of (5.15) to order ε yields

$$a = -k \frac{n_{1,1}c + m_{1,1}y_{1,2} - m_{1,1}c - n_{1,1}z_{1,2} + im_{1,1}k}{-2ck + 2iy_{1,2}c + iz_{1,2}^2 + ik^2 + 2y_{1,2}k - iy_{1,2}^2 - 2iz_{1,2}c}.$$

Then we have the following asymptotic formulas

Re
$$(a) \sim -\frac{1}{(2cy_{1,2} + z_{1,2}^2 - y_{1,2}^2 - 2z_{1,2}c)^2} (-2m_{1,1}cy_{1,2} + m_{1,1}z_{1,2}^2 + m_{1,1}y_{1,2}^2)$$

$$-2m_{1,1}z_{1,2}c + 2n_{1,1}cy_{1,2} - 2n_{1,1}c^2 + 2m_{1,1}c^2 - 2n_{1,1}z_{1,2}y_{1,2} + 2n_{1,1}z_{1,2}c)k^2$$

for $k \to 0$, and $\lim_{k \to \infty} a = -m_{1,1}$.

The part of the spectrum of $-(ikU+DA_0)$ not contained in the line $\operatorname{Re}(z)=0$ is given by

$$z = y_{1,2} - 2c + z_{1,2}$$
, $z = -z_{1,2} + y_{1,2}$.

Therefore the following conditions ensure existence of oscillatory patterns for $\varepsilon > 0$ sufficiently small

$$\begin{split} &-2m_{1,1}cy_{1,2}+m_{1,1}z_{1,2}^2+m_{1,1}y_{1,2}^2-2m_{1,1}z_{1,2}c+2n_{1,1}cy_{1,2}-2n_{1,1}c^2\\ &+2m_{1,1}c^2-2n_{1,1}z_{1,2}y_{1,2}+2n_{1,1}z_{1,2}c<0\\ &m_{1,1}>0\ ,\ y_{1,2}-2c+z_{1,2}<0\ ,\ -z_{1,2}+y_{1,2}<0 \end{split}$$

The following choice in (5.21) satisfies all these inequalities

$$c = 1.5$$
, $y_{1,2} = 0.5$, $z_{1,2} = 1$, and $m_{1,1} = 2$, $m_{1,1} = 1$. (5.22)

The form of the root of (5.15) with largest real part for this choice of matrices is given in Figure 4.

In summary we have

Theorem 26 The differential equation (4.27) with $A = A_0 + \varepsilon M$, and A_0 , M as given in (5.21) with coefficients as in (5.22), U given as in (5.18), and $\varepsilon > 0$ sufficiently small, generates oscillatory patterns in the sense of Definition 1.

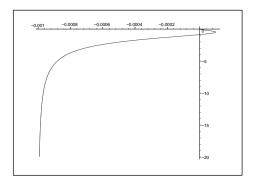


Figure 4: The root with largest real part of (5.15) close to the imaginary axis for the conditions as described in Theorem 26 with $\varepsilon = 0.01$.

5.4 Pattern formation in a symmetric 6×6 system for degenerate U

We have seen before that a generic 4×4 system cannot yield oscillatory patterns near hyperbolic settings if the matrix U contains only two opposite velocities. In this section we will show an example of a 6×6 system, which is invariant under the transformation $(x,\varphi,\psi)\to (-x,\psi,\varphi)$ and yields pattern formation. Let

$$U = \begin{pmatrix} 1 & 0 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & -1 & 0 & 0 \\ 0 & 0 & 0 & 0 & -1 & 0 \\ 0 & 0 & 0 & 0 & 0 & -1 \end{pmatrix} . \tag{5.23}$$

Here

$$D = \left(\begin{array}{cccccc} 1 & 0 & 0 & 0 & 0 & -1 \\ -1 & 1 & 0 & 0 & 0 & 0 \\ 0 & -1 & 1 & 0 & 0 & 0 \\ 0 & 0 & -1 & 1 & 0 & 0 \\ 0 & 0 & 0 & -1 & 1 & 0 \\ 0 & 0 & 0 & 0 & -1 & 1 \end{array}\right).$$

We consider linearizations of systems like (4.9)-(4.12) containing two additional variables (u_3, v_3) . We assume that the transition probabilities are

$$T_1 = T_1 (u_1, v_1 + v_2 + v_3) (5.24)$$

$$T_2 = T_2 (u_2, u_1 + u_2 + u_3 + v_1 + v_2 + v_3)$$
 (5.25)

$$T_3 = T_3(u_3) (5.26)$$

We did not succeed to find simpler functional dependencies than (5.24)-(5.26). In particular replacing (5.25) by $T_2 = T_2(u_2)$ is too simple to generate oscillatory patterns. The linearized matrix A compatible with (5.24)-(5.26) has the form

$$A = \begin{pmatrix} y_{1,1} & 0 & 0 & z_{1,1} & z_{1,1} & z_{1,1} \\ y_{2,1} & y_{2,2} & y_{2,1} & y_{2,1} & y_{2,1} & y_{2,1} \\ 0 & 0 & y_{3,3} & 0 & 0 & 0 \\ z_{1,1} & z_{1,1} & z_{1,1} & y_{1,1} & 0 & 0 \\ y_{2,1} & y_{2,1} & y_{2,1} & y_{2,1} & y_{2,2} & y_{2,1} \\ 0 & 0 & 0 & 0 & 0 & y_{3,3} \end{pmatrix},$$
 (5.27)

with $A = A_0 + \varepsilon M$ where A_0 is "hyperbolic". We assume a particular form of "hyperbolic" behavior, namely

$$DA_0(1,0,0,0,0,0)^t = DA_0(0,0,0,1,0,0)^t = 0$$
 (5.28)

Now (5.28) is satisfied if $y_{1,1} = y_{2,1} = z_{1,1} = 0$. Let

Then $A = A_0 + \varepsilon M$ is of the form (5.27) if

$$M = \begin{pmatrix} m_{1,1} & 0 & 0 & n_{1,1} & n_{1,1} & n_{1,1} \\ m_{2,1} & 0 & m_{2,1} & m_{2,1} & m_{2,1} & m_{2,1} \\ 0 & 0 & 0 & 0 & 0 & 0 \\ n_{1,1} & n_{1,1} & n_{1,1} & m_{1,1} & 0 & 0 \\ m_{2,1} & m_{2,1} & m_{2,1} & m_{2,1} & 0 & m_{2,1} \\ 0 & 0 & 0 & 0 & 0 & 0 \end{pmatrix} .$$
 (5.30)

The spectrum of $-(ikU + DA_0)$ is given by the eigenvalues

$$\{-ik, -ik - y_{2,2}, -ik - y_{3,3}, ik, ik - y_{2,2}, ik - y_{3,3}\}$$
.

Therefore, to obtain that the most unstable branch of the dispersion relation for small ε is a perturbation of $\pm ik$ we have to assume

$$y_{2,2} > 0 , y_{3,3} > 0 .$$
 (5.31)

As before, the dispersion relation associated to (4.27) is given by

$$\det (z + ikU + DA_0 + \varepsilon DM) = 0 , \qquad (5.32)$$

and we can look for perturbative solutions of (5.32) of the form

$$z = ik + a\varepsilon + \dots$$

Solving (5.32) to the leading order in ε we obtain

$$a = -\frac{2km_{1,1}(y_{3,3} + y_{2,2}) + iy_{2,2}y_{3,3}(n_{1,1} - m_{1,1}) + 4ik^2m_{1,1} - 2km_{2,1}y_{3,3}}{-iy_{2,2}y_{3,3} + 2ky_{2,2} + 2ky_{3,3} + 4ik^2} \ .$$

The function a has the following asymptotics

$$a(k) \sim (n_{1,1} - m_{1,1}) - 4 \frac{(n_{1,1} - m_{2,1})y_{2,2}y_{3,3} + n_{1,1}y_{2,2}^2 + (n_{1,1} - m_{2,1})y_{3,3}^2}{y_{2,2}^2 y_{3,3}^2} k^2 + \dots$$
 for $k \to 0$, and $a(k) \to -m_{1,1}$ for $k \to \infty$.

A sufficient condition for oscillatory patterns is then

$$n_{1,1} = m_{1,1} > 0$$

$$-4 \frac{(n_{1,1} - m_{2,1})y_{2,2}y_{3,3} + (n_{1,1} - m_{2,1})y_{3,3}^2 + n_{1,1}y_{2,2}^2}{y_{2,2}^2 y_{3,3}^2} > 0.$$

There are many different choices of coefficients $y_{i,j},\ n_{i,j}$ satisfying these inequalities, e.g.

$$m_{1,1} = n_{1,1} = 1$$
, $y_{2,2} = y_{3,3} = 1$, $m_{2,1} = 4$.

The form of the most unstable branch of the dispersion relation associated to these coefficients is given in Figure 5.

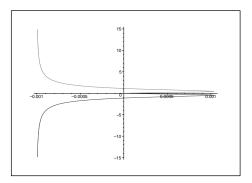


Figure 5: Plot of the root of (5.32) with the largest real part near the imaginary axis for conditions as given in Theorem 27 with $\varepsilon = 0.001$.

To summarize

Theorem 27 The differential equation (4.27) with $A = A_0 + \varepsilon M$, and A_0 , M as in (5.29), (5.30), U as in (5.23) and $\varepsilon > 0$ sufficiently small, generates oscillatory patterns in the sense of Definition 1.

5.5 Transition between oscillatory patterns and absence of patterns in myxobacteria - wildtype and mutants

Pattern formation in biology relates often to certain functional mechanisms. In myxobacteria there is a peculiar phenomenon, that makes it possible to test suggested models for rippling on their reliability. There exist mutants which can be mixed with wildtype populations, that move the way the wildtype does, but which do not produce the signal, which upon contact with counter-migrating bacteria make these bacteria change their orientation. The mutants themselves can receive the signal and thus turn, but they do not induce turning for other bacteria. When mixing these two types of bacteria still rippling patterns occur, but with an increasing number of mutants the wave length of the ripples increases also. For a too large fraction of mutants in the total population, the rippling pattern is finally lost.

We can see all these effects of rippling, increasing of the wavelength of the rippling pattern, and the loss of the rippling phenomenon in the following basic 6×6 model for the wildtype and its naturally extended version for the wildtype-mutant situation. In the wildtype and mutant system a bifurcation for a critical value of the mutant fraction is generated, where the pattern is lost. For this to happen, we exchanged the roles of the dependencies of T_1 and T_2 , in comparison to the model discussed before.

We assume that the bacteria are described by a system with 3 states that can move in opposite spatial directions. So we have the sequence of states

$$u_1 \rightarrow u_2 \rightarrow u_3 \rightarrow v_1 \rightarrow v_2 \rightarrow v_3 \rightarrow u_1$$
.

Then the following set of transition rates (if mutants are absent) can also generate oscillatory patterns and additionally is able to produce the desired bifurcations in the population, when mutants are present

$$T_1 = T_1(\tilde{\sigma}, u_1)$$
 , $T_2 = \lambda_2(v_1 + v_2 + v_3)u_2$, $T_3 = \lambda_3 u_3$, (5.33)

where $\tilde{\sigma} = u_1 + u_2 + u_3 + v_1 + v_2 + v_3$.

So the right moving bacteria of type 1 become type 2 - e.g. excited, respectively able to receive or send the signal to induce turning in other bacteria - in dependence of the total cell density and their own density, for instance, when the total population density is high enough. The bacteria of type 2 become type 3 bacteria - e.g. able to turn - upon contact with counter migrating cells v_i , i = 1, 2, 3. The bacteria of type 3 then turn with a certain probability.

For the model with mutants and wildtype cells we have the following. Since the counter-migrating mutants do not produce the signal, they do not occur in the collision term associated to the rate T_2 . Only wildtype cells produce the signal upon collision, which makes the counter-migrating cells, which receive the signal, turn. Here and in the following we define

$$\sigma = u_1 + u_2 + u_3 + v_1 + v_2 + v_3 + \bar{u}_1 + \bar{u}_2 + \bar{u}_3 + \bar{v}_1 + \bar{v}_2 + \bar{v}_3 ,$$

where \bar{u}_i, \bar{v}_i denote the corresponding concentrations of mutants. Further, we assume

$$T_1 = T_1(\sigma, u_1)$$
 , $T_2 = \lambda_2(v_1 + v_2 + v_3)u_2$, $T_3 = \lambda_3 u_3$

$$\bar{T}_1 = T_1(\sigma, \bar{u}_1)$$
 , $\bar{T}_2 = \lambda_2(v_1 + v_2 + v_3)\bar{u}_2$, $\bar{T}_3 = \lambda_3\bar{u}_3$.

Using our approach to derive coefficients, which yield bifurcations near "hyperbolic" matrices, for functional dependences as in (5.33), we obtain the following choice of coefficients

$$T_{1,\sigma}^{0} + T_{1,u}^{0} = \varepsilon m_{1,1} , T_{1,\sigma}^{0} = \varepsilon m_{1,2} , T_{2,u}^{0} = y_{2,2} ,$$

$$T_{3,u}^{0} = y_{3,3} , T_{1,\xi}^{0} = \varepsilon n_{1,2} .$$

$$(5.34)$$

Here $T_{i,w}^0$ denotes the derivative of the transition coefficient T_i with respect to w evaluated at the corresponding equilibrium values for the system in absence of the wildtype, which means $\alpha = 0$. So only mutants are present.

We will simply use $T_{i,w}$ in case $\alpha \neq 0$. We obtain oscillatory patterns for the following choice of coefficients

$$m_{1,2} = m_{1,1} = 1 (5.35)$$

$$-y_{2,2}y_{3,3} + n_{2,1}y_{3,3}y_{2,2} + n_{2,1}y_{3,3}^2 - y_{2,2}^2 - y_{3,3}^2 > 0 , y_{2,2} > 0 , y_{3,3} > 0$$
 (5.36)

and ε sufficiently small. Condition (5.35) is not strictly needed to generate patterns. However, it is convenient, since then the linear correction to the most unstable branch of the dispersion relation associated to the linearization of model (5.33) vanishes for k=0 up to higher order terms. Since the dispersion relation does not change too much for small values of k, this is practical in order to study bifurcations w.r.t. α and to obtain neutral stability for k=0. Then the change of stability can be associated to transforming the local minimum for k=0 into a local maximum.

An important consequence of (5.34) and (5.35) is that

$$T_{1,u} = 0$$
 for $0 \le \alpha \le r$ and suitable $r < 1$.

Therefore, the function T_1 in (5.33) does not explicitly depend on u_1 . Thus at equilibrium the concentrations of u_2 , \bar{u}_2 , u_3 , \bar{u}_3 take constant values. Notice that u_2 , \bar{u}_2 , u_3 , \bar{u}_3 being constant implies that \bar{u}_1 is negative for $(1 - \alpha)$ small, where α is the fraction of wildtype cells in the system. In order to deal with this problem we will assume

$$T_1 = \lambda_1 \left(\sigma \right) \Psi \left(\frac{u_1}{\sigma^{\beta}} \right) ,$$

where the total cell concentration σ is large and $0 < \beta < 1$. Typically the concentration of u_1 is of order σ , when the total cell density is large. Therefore

 $\Psi\left(\frac{u_1}{\sigma^{\beta}}\right)$ is approximately of order one and thus the transition rate T_1 is basically independent of u_1 and mainly depending on the total cell concentration. In case u_1 is very small, nearly no transition to the next state is happening. Moreover, we assume that

$$\Psi(\xi) \sim \xi \text{ as } \xi \to 0 \text{ and } \Psi(\xi) \sim 1 \text{ as } \xi \to \infty.$$

This type of choice will avoid negative concentrations at equilibrium, since the concentration of mutants will be of order $(1 - \alpha)\sigma$ and then, the function T_1 will approximately be given by the simpler functional dependence

$$T_1 = \lambda_1(\sigma)$$
 for $(1 - \alpha) >> \sigma^{\beta - 1}$,
respectively $(1 - \alpha) >> \sigma^{\beta - 1}$ and $\alpha >> \sigma^{(\beta - 1)}$. (5.37)

We will restrict our analysis to this situation for which we can use (5.37). The homogeneous equilibria for the concentrations of wildtype cells and mutants are characterized by

$$T_1=T_2=T_3$$
 , $\bar{T}_1=\bar{T}_2=\bar{T}_3$, and $u_i=v_i$, $\bar{u}_i=\bar{v}_i$, $i=1,2,3$

as well as

$$u_1 + u_2 + u_3 = \frac{\alpha \sigma}{2}$$
, $\bar{u}_1 + \bar{u}_2 + \bar{u}_3 = \frac{(1 - \alpha) \sigma}{2}$.

The solutions of these equations under approximation (5.37) are

$$u_{2} = \frac{\lambda_{1}\left(\sigma\right)}{\lambda_{2}\left(\frac{\alpha\sigma}{2}\right)} , \ u_{3} = \frac{\lambda_{1}\left(\sigma\right)}{\lambda_{3}} , \ \bar{u}_{2} = \frac{\lambda_{1}\left(\sigma\right)}{\lambda_{2}\left(\frac{\alpha\sigma}{2}\right)} , \ \bar{u}_{3} = \frac{\lambda_{1}\left(\sigma\right)}{\lambda_{3}}$$

$$\begin{split} u_1 &= \frac{\alpha \sigma}{2} - (u_2 + u_3) = \frac{\alpha \sigma}{2} - \frac{\lambda_1 \left(\sigma\right)}{\lambda_2 \left(\frac{\alpha \sigma}{2}\right)} - \frac{\lambda_1 \left(\sigma\right)}{\lambda_3} \\ \bar{u}_1 &= \frac{\left(1 - \alpha\right) \sigma}{2} - (\bar{u}_2 + \bar{u}_3) = \frac{\left(1 - \alpha\right) \sigma}{2} - \frac{\lambda_1 \left(\sigma\right)}{\lambda_2 \left(\frac{\alpha \sigma}{2}\right)} - \frac{\lambda_1 \left(\sigma\right)}{\lambda_3} \;. \end{split}$$

As indicated above, if the λ_i are of order one we have $u_1 \approx \alpha \sigma$ and $\bar{u}_1 \approx (1-\alpha)\sigma$. The linearized problem near the homogeneous states is of the form

$$\partial_t f + \begin{pmatrix} U & 0 \\ 0 & U \end{pmatrix} \partial_x f + \begin{pmatrix} D & 0 \\ 0 & D \end{pmatrix} A f = 0 , \qquad (5.38)$$

where

$$U = \begin{pmatrix} 1 & 0 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & -1 & 0 & 0 \\ 0 & 0 & 0 & 0 & -1 & 0 \\ 0 & 0 & 0 & 0 & 0 & -1 \end{pmatrix} , D = \begin{pmatrix} 1 & 0 & 0 & 0 & 0 & -1 \\ -1 & 1 & 0 & 0 & 0 & 0 \\ 0 & -1 & 1 & 0 & 0 & 0 \\ 0 & 0 & -1 & 1 & 0 & 0 \\ 0 & 0 & 0 & -1 & 1 & 0 \\ 0 & 0 & 0 & 0 & -1 & 1 \end{pmatrix}$$

$$A = \begin{pmatrix} A_1 & A_2 & A_3 & A_3 \\ A_2 & A_1 & A_3 & A_3 \\ \bar{A}_3 & \bar{A}_3 & \bar{A}_1 & \bar{A}_2 \\ \bar{A}_3 & \bar{A}_3 & \bar{A}_2 & \bar{A}_1 \end{pmatrix} \quad \text{with}$$

$$A_{1} = \begin{pmatrix} T_{1,\sigma} & T_{1,\sigma} & T_{1,\sigma} \\ 0 & T_{2,u} & 0 \\ 0 & 0 & T_{3,u} \end{pmatrix} , A_{2} = \begin{pmatrix} T_{1,\sigma} & T_{1,\sigma} & T_{1,\sigma} \\ T_{2,\xi} & T_{2,\xi} & T_{2,\xi} \\ 0 & 0 & 0 \end{pmatrix}$$

$$A_3 = \begin{pmatrix} T_{1,\sigma} & T_{1,\sigma} & T_{1,\sigma} \\ 0 & 0 & 0 \\ 0 & 0 & 0 \end{pmatrix} , \ \bar{A}_1 = \begin{pmatrix} \bar{T}_{1,\sigma} & \bar{T}_{1,\sigma} & \bar{T}_{1,\sigma} \\ 0 & \bar{T}_{2,u} & 0 \\ 0 & 0 & \bar{T}_{3,u} \end{pmatrix}$$

$$\bar{A}_2 = \begin{pmatrix} \bar{T}_{1,\sigma} & \bar{T}_{1,\sigma} & \bar{T}_{1,\sigma} \\ \bar{T}_{2,\xi} & \bar{T}_{2,\xi} & \bar{T}_{2,\xi} \\ 0 & 0 & 0 \end{pmatrix} , \ \bar{A}_3 = \begin{pmatrix} \bar{T}_{1,\sigma} & \bar{T}_{1,\sigma} & \bar{T}_{1,\sigma} \\ 0 & 0 & 0 \\ 0 & 0 & 0 \end{pmatrix} .$$

Using the transition rates (5.33), (5.37) we obtain the following linearized coefficients at the homogeneous states

$$\begin{split} T_{1,\sigma} &= \bar{T}_{1,\sigma} = T_{1,\sigma}^{0} \ , \ T_{1,u} = \bar{T}_{1,u} = 0 \\ T_{2,u} &= \bar{T}_{2,u} = \frac{\lambda_{2} \left(\frac{\alpha\sigma}{2}\right)}{\lambda_{2} \left(\frac{\sigma}{2}\right)} T_{2,u}^{0} \ , \ T_{2,\xi} = \bar{T}_{2,\xi} = \frac{\lambda'_{2} \left(\frac{\alpha\sigma}{2}\right)}{\lambda'_{2} \left(\frac{\sigma}{2}\right)} \frac{\lambda_{2} \left(\frac{\sigma}{2}\right)}{\lambda_{2} \left(\frac{\alpha\sigma}{2}\right)} T_{2,\xi}^{0} \\ T_{3,u} &= \bar{T}_{3,u} = T_{3,u}^{0} \ . \end{split}$$

The transition between the choice of coefficients yielding oscillatory patterns and the ones that does not produce such patterns is characterized by the reversal of the first inequality in (5.36). To obtain such a switch we choose

$$\frac{\lambda_2\left(\frac{\alpha\sigma}{2}\right)}{\lambda_2\left(\frac{\sigma}{2}\right)} = \phi\left(\alpha\right) \text{ where } \phi\left(\alpha\right) = e^{\alpha^2 - 1}.$$

The superexponential growth of the function ϕ seems to be crucial to obtain the desired bifurcation with this scheme. This type of superexponential growth is known in chemical reactions and can result from a threshold activation energy that is able to produce exponential dependences. With this functional choices we have

$$\begin{split} T_{1,\sigma} &= \bar{T}_{1,\sigma} = T_{1,\sigma}^0 \;,\; T_{1,u} = \bar{T}_{1,u} = 0 \\ T_{2,u} &= \bar{T}_{2,u} = e^{\alpha^2 - 1} T_{2,u}^0 \;,\; T_{2,\xi} = \bar{T}_{2,\xi} = \frac{\alpha e^{\alpha^2 - 1}}{e^{\alpha^2 - 1}} T_{2,\xi}^0 = \alpha T_{2,\xi}^0 \\ T_{3,u} &= \bar{T}_{3,u} = T_{3,u}^0 \;. \end{split}$$

We choose the coefficients for "small" mutant concentrations as in (5.34).

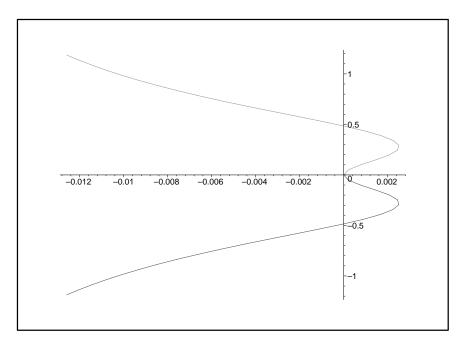


Figure 6: $\alpha = 1.0$

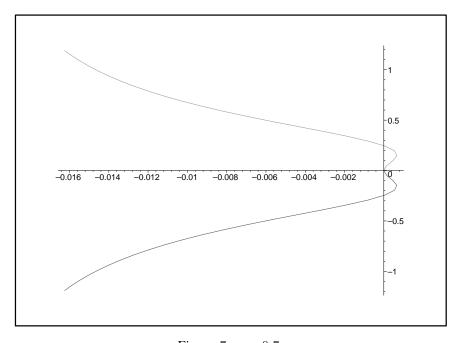


Figure 7: $\alpha = 0.7$

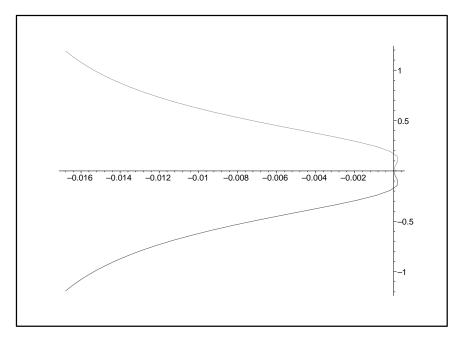


Figure 8: $\alpha = 0.65$

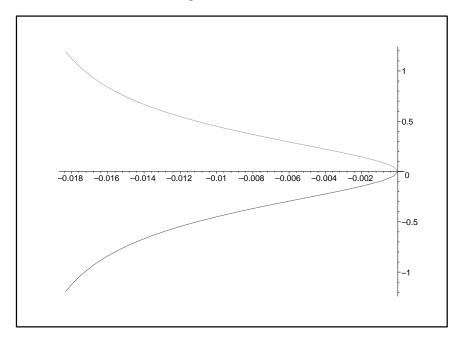


Figure 9: $\alpha = 0.5$

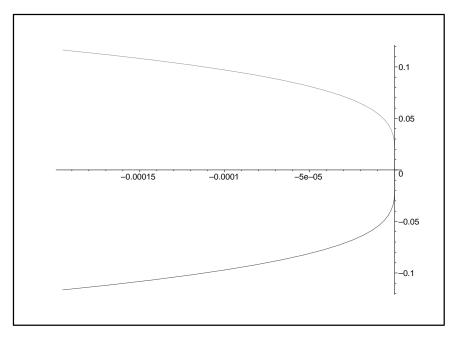


Figure 10: Here the scale is magnified in comparison with previous figures. $\alpha=0.6$

The following figures show the branch with the root with the largest real part for the dispersion relation corresponding to (5.38) for different values of α . For arbitrary α it contains a "neutral" bifurcation branch given by the values

$$z=\pm ik\ ,\ k\in\mathbb{R}\ .$$

Calculating the dispersion relation reduces to solving a polynomial equation of degree ten. Figures 6, ..., 11 show the form of the most unstable branch for $\alpha = 1, 0.7, 0.65, 0.5$ and for a magnified scale near the bifurcation value for $\alpha = 0.6, 0.61$.

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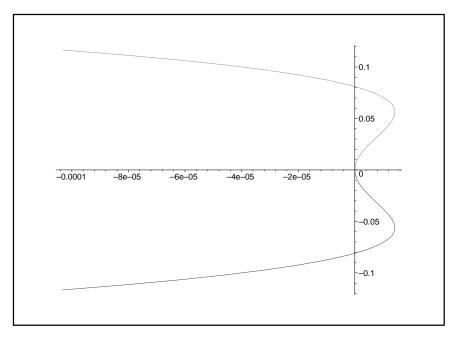


Figure 11: Here the scale is magnified in comparison with previous figures. $\alpha=0.61$

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