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博士学位論文

On stability of spatial patterns for mass-conserved reaction-diffusion systems
(保存量をもつ反応拡散系における安定な空間パターンについて)

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Contents

| | | |
|-----------|--|-----------|
| 1 | Introduction. | 2 |
| | | |
| I | Shape of stable steady-state solutions in mass-conserved linear reaction-diffusion systems | 7 |
| 2 | Introduction. | 7 |
| 3 | Preliminaries. | 8 |
| 4 | Problem setting. | 10 |
| 5 | Main results. | 11 |
| 6 | Numerical simulation. | 14 |
| 7 | Summary and Discussion. | 15 |
| | | |
| II | Stability of 2-mode stationary solutions in mass-conserved reaction-diffusion compartment model | 18 |
| 8 | Introduction. | 18 |
| 9 | Problem setting. | 22 |
| 9.1 | Basic assumptions | 22 |
| 9.2 | Linearized eigenvalue problem for 2-mode stationary solution . . | 23 |
| 10 | Main results. | 24 |
| 11 | Summary and discussion. | 28 |
| | | |
| A | Appendix | 31 |
| A.1 | An example of Assumption 3, 4. | 31 |
| A.2 | Proof. | 32 |

1 Introduction.

Reaction-diffusion equations are used as model equations for various pattern formation phenomena in physics, chemistry, and biology. The existence and stability of solutions corresponding to characteristic patterns, such as stationary patterns and traveling waves in actual phenomena are important to understand the phenomena from the mathematical viewpoint. Recently, mass-conserved reaction-diffusion systems have been used as mathematical models for various phenomena such as cell polarity, and phase separation between solid and liquid phases [5], [21], [26], [13], [10], [27], [16]. This study's main objective is the mathematical analysis of mass-conserved reaction-diffusion system for the cell polarity model.

Cell polarity refers to the spatial localization of some chemical substances within a cell. For example, in a phenomenon called asymmetric cell division, it is known that a mother cell localizes a specific protein during cell division to produce a daughter cell that differs from the mother cell. Cell polarity is also known to be observed in chemotaxis, in which cells migrate in response to a concentration gradient of a chemical substance. For these reasons, cell polarity is considered to be important for cell differentiation and for cells to acquire anisotropic functions. Various model equations have been introduced to understand cell polarity from a mathematical point of view [10], [21].

Since cell polarity is an intracellular phenomenon, it is difficult to model and rigorously analyze all the elements involved in the phenomenon. For example, cells have a complex shape. In addition, many proteins interact with each other in a complex manner in the cell polarity, and it is difficult to analyze all of them. Many previous studies have modeled the cell shape in simple forms, such as a circle, or examined the models with a reduction for the number of components under various assumptions [21], [10], [26].

Although we can't expect that such a conceptual model and the original phenomenon will be in perfect quantitative agreement, the introduction and analysis of a simple model that reproduces the qualitative properties of cell polarity can be expected to identify essential elements of the cell polarity phenomenon or to provide some insight into the phenomenon. For example, previous study [21] introduced a 6-component reaction-diffusion system under one-dimensional periodic boundary conditions and a 2-component reaction-diffusion system that simplifies the 6-component system. These model equations reproduce various features of cell polarity by numerical simulation. In the view of analysis, the 2-component equations provide various suggestions for the stability of steady-state solutions and the dynamics of solutions.

The 2-component model is expressed as

$$(*) \begin{cases} \frac{\partial u}{\partial t} = D_u \frac{\partial^2 u}{\partial x^2} - f(u, v) \\ \frac{\partial v}{\partial t} = D_v \frac{\partial^2 v}{\partial x^2} + f(u, v) \end{cases} \quad x \in (0, K),$$

where u and v are the concentrations of proteins U and V in the plasma membrane and cytoplasm, respectively. Although a cell is a three-dimensional object, the cell membrane and cytoplasm are modeled as intervals $(0, K)$, where periodic boundary conditions are imposed. The parameter K is a positive constant corresponding to the cell size. D_u and D_v are diffusion coefficients of U and

V . The reaction term f represents the interconversion between U and V . That is, $f > 0$ represents the conversion from U to V , and $f < 0$ represents the conversion from V to U . In particular, it can be seen that only the sign of the reaction term differs in the U and V equations. This means that in the above model, only the conversion between proteins U and V is considered, ignoring the effects of synthesis and degradation of proteins. Such an assumption is reasonable because cell polarity phenomena occur on a time scale faster than the time required for protein synthesis and degradation [5]. From the nature of this reaction term and the periodic boundary conditions, the total mass of U and V , $\int(u+v)dx$ is shown to be conserved in the system (*). Due to this property, equation (*) is called a mass-conserved reaction-diffusion system.

While the model equation above is 2-component reaction-diffusion system with periodic boundary condition, various other models have been introduced as equations with conserved quantities. For example, a cell polarity model with homogeneous Neumann boundary conditions has been introduced, in which the mass conservation law holds also. In particular, the dynamics of a front-like pattern called wave-pinning has been analyzed [13], [14]. A cell polarity model defined on regions resembling the actual cell shape is called a bulk-surface model. In the bulk-surface model, the cytoplasm is a region in 2D or 3D space, such as a unit sphere, and the cell membrane is its boundary. The bulk-surface model has been the subject of many previous studies, including mathematical analyses such as the stability of the stationary solutions [23], [24], [3], [17], [18].

We can extend the 2-component model to more multi-component cases. Let $N \geq 3$ be an integer and consider the following N -component equation.

$$\begin{aligned} \frac{\partial u_i}{\partial t} &= D_i \frac{\partial^2 u_i}{\partial x^2} + f_i(u_1, \dots, u_N) \quad (i = 1, \dots, N) \\ \sum_{i=1}^N f_i &= 0 \end{aligned}$$

where u_i and D_i are the concentrations of i -th chemical substance and diffusion coefficients of these, respectively. f_i represents the interaction between the substances. For the above equations, for example, if periodic boundary conditions are imposed, the total amount of substance $\int(u_1 + \dots + u_N)dx$ is a conserved quantity. This model equation is derived as a cell polarity model that incorporates more chemicals into the model than the 2-component model [21], [10], [19], [26].

As mentioned above, many kinds of equations have been introduced as mathematical models of cell polarity. But in general, the more complex the model equations are, the more complex the mathematical analysis becomes. On the other hand, the knowledge obtained from the analysis of simple model equations may be helpful for the analysis of more complex model equations. Based on these motivations, we limit the study in this thesis to 2-component mass-conserved reaction-diffusion equations defined on a 1-dimensional interval. Although the equation is simpler than other model equations, it is known that the model qualitatively reproduces cell polarity phenomena [5], [21], [13], [10]. Various mathematical and numerical analyses have been performed on the equations, including bifurcation analysis, stationary problems, stability of stationary solutions, and dynamics of solutions [16], [14], [15], [6], [7], [25], [12], [2], [8], [9], [4].

One of the crucial issues in mass-conserved reaction-diffusion systems is the shape of the stable steady-state solutions. Mathematically, the non-constant stationary solution in (*) corresponds to the polarity pattern. In particular, many cell polarity phenomena require that a chemical substance is localized at only one location in the cell. This situation mathematically corresponds to a stationary solution with a shape that has only one peak. Therefore, the question of what shape of the steady-state solution is stable is not only mathematically but also biologically important [21].

This thesis considers the following equation: a mathematical generalization of the model equation (*).

$$(**) \begin{cases} \partial_t u = d_1 \partial_x^2 u + k_1 g(x, u, v) \\ \partial_t v = d_2 \partial_x^2 v - k_2 g(x, u, v) \end{cases} \quad x \in (0, K),$$

where $u = u(t, x)$ and $v = v(t, x)$ are unknown functions. The function g is a real-valued function continuous on \bar{I} for x and of class C^2 for u and v . d_1, d_2, k_1, k_2 are positive constants. The reaction term depends on the spatial variable. Such a reaction term can be used, for example, in a model where chemicals U and V are affected by some other chemical substances in the cell, or extracellular signals [26], [21], [8]. In particular, if $k_1 = k_2 = 1$ and $g(x, u, v) = -f(u, v)$, equation (**) is consistent with (*). For equation (**), $\int_I (k_2 u + k_1 v) dx$ is conserved when periodic or homogeneous Neumann boundary conditions are imposed. In the cell polarity model, u and v represent the concentrations of chemicals, and $\int_I (u + v) dx$ is conserved if $k_1 = k_2$. This corresponds to the conservation of mass in the cell. Therefore, when $k_1 \neq k_2$, model equation (**) does not correspond to the cell polarity model. On the other hand, the model equation (**) becomes equivalent to the Fix-Cagnalp model describing solid-liquid phase separation and each other by choosing the reaction term g appropriately and applying linear transforming to the unknown functions [16]. In this context, k_1, k_2 become constants determined from the parameters of the original Fix-Cagnalp model, and the analysis for the case $k_1 \neq k_2$ also makes sense.

Against this background, we consider the cell polarity model (*) as one of the generalized equations (**) and perform mathematical analysis on (**). This problem setting helps to understand mass-conserved reaction-diffusion systems in a model-independent systematic manner, and provide a perspective for applying the results obtained in this study to other models than the cell polarity model.

By transforming the variables in equation (**) as $t \rightarrow k_1 t, x \rightarrow \sqrt{k_2/d_2} x$, equation (**) is expressed as

$$\begin{cases} \partial_t u = d \partial_x^2 u + g(x, u, v) & (t > 0, x \in I), \\ \tau \partial_t v = \partial_x^2 v - g(x, u, v) & (t > 0, x \in I), \\ u(0, x) = u_0(x), v(0, x) = v_0(x) & (x \in I), \end{cases} \quad (1)$$

where $\tau := k_1/k_2, d := (d_1 k_2)/(d_2 k_1)$, and $g(x/\sqrt{k_v/d_v}, u, v)$ and $K/\sqrt{k_v/d_v}$ are replaced by $g(x, u, v)$ and K , respectively. u_0, v_0 are real-valued smooth functions.

This study considers the following homogeneous Neumann or periodic bound-

any conditions for (1).

$$\begin{aligned} (N.B.C) \quad & \partial_x u = \partial_x v = 0 \quad (t > 0, x = 0, K). \\ (P.B.C) \quad & \begin{cases} u(t, 0) = u(t, K), \quad \partial_x u(t, 0) = \partial_x u(t, K) & (t > 0), \\ v(t, 0) = v(t, K), \quad \partial_x v(t, 0) = \partial_x v(t, K) & (t > 0). \end{cases} \end{aligned}$$

Here, the following conserved quantity exists for a classical solution (u, v) in (1) with $(N.B.C)$ or $(P.B.C)$.

$$s := \frac{1}{K} \int_I (u(t, x) + \tau v(t, x)) dx \equiv \frac{1}{K} \int_I (u_0(x) + \tau v_0(x)) dx.$$

In fact, due to the boundary conditions and exchanging integrals and derivatives, it follows

$$\begin{aligned} \frac{d}{dt} \int_I (u(t, x) + \tau v(t, x)) dx &= \int_I (\partial_t u(t, x) + \tau \partial_t v(t, x)) dx = \int_I (d \partial_x^2 u(t, x) + \partial_x^2 v(t, x)) dx \\ &= [d \partial_x u(t, x) + \partial_x v(t, x)]_{x=0}^{x=K} = 0 \end{aligned}$$

Therefore, s is constant in the range of t for which (u, v) exists. In this study, we call equation (1) with $(N.B.C)$ or $(P.B.C)$ mass-conserved reaction-diffusion system.

We consider the shape of the stable steady-state for a mass-conserved reaction-diffusion system. This study treats the following two cases for g .

$$g(x, u, v) = -p(x)u + q(x)v, \quad (2)$$

$$g(x, u, v) = f(u, v), \quad (3)$$

where $p, q \in C(\bar{I})$ and $f \in C^2(\mathbb{R}^2)$. The first case is that the reaction terms are linear for u and v . Note that the coefficients of $p(x)$ and $q(x)$ are taken as above only for the convenience of later calculations, and it is not essential in mathematical analysis. We call a mass-conserved reaction-diffusion system with reaction term (2) mass-conserved linear reaction-diffusion system.

The authors of the previous study [26] treated a mass-conserved linear reaction-diffusion system for mathematical analysis of cell polarity models. The author of this thesis analyzed the existence, uniqueness and shape of the stable stationary solutions for a mass-conserved linear reaction-diffusion system under several conditions on the coefficient functions p and q . The conditions on p and q are derived from the model's background and are explained in detail in the first part of this thesis. The stable stationary solutions qualitatively reproduce the polarity patterns.

The reaction term (3) corresponds to the case where the reaction term does not depend on spatial variables. In the second part of this thesis, the shape of the stable stationary solution, in this case, is discussed.

There are many previous studies on stable steady-state solutions of (1) with (3). Significantly, the reaction term $f(u, v) = -f_0(u + \gamma v) + v(\gamma \geq 0)$ has been used in models of cell polarity and phase separation [21], [5], [27], and it is known that, when we choose the parameters appropriately, the stable stationary solution is spatially monotone [15], [6], [9]. In these previous studies, the results of stability are proved by comparing eigenvalues of a linearized eigenvalue problem in (1) and the ones in a scalar non-local equation which is related to (1).

Mathematical techniques in the previous studies are not applicable to general reaction terms. Also, previous studies have obtained results for eigenvalues of linearized eigenvalue problems but not for eigenfunctions. In mass-conserved reaction-diffusion systems, numerical calculations show dynamics in which multiple stripe patterns converge to spatially monotonic patterns [5]. To understand these dynamics, analysis of linearized eigenvalue problems around spatially non-monotonic stationary solutions is essential, and especially, eigenfunctions are important for understanding the dynamics of solutions near stationary solutions. Therefore, this study aims to analyze not only eigenvalues but also eigenfunctions.

In the second part of this thesis, the reaction-diffusion compartment model is introduced to understand the stability of nonmonotonic stationary solutions in mass-conserved reaction-diffusion systems and the dynamics of solutions in the vicinity of the stationary solutions. The reaction-diffusion compartment model is a system in which the domain of the original reaction-diffusion system is divided into multiple regions, and diffusion coupling is imposed between the regions. Analysis of the linearized eigenvalue problem in the reaction-diffusion compartment model may provide helpful information about the stability of non-monotonic stationary solutions in the original equations. These details will be discussed again in Part II.

Part I

Shape of stable steady-state solutions in mass-conserved linear reaction-diffusion systems

2 Introduction.

In this part, we consider the shape of stable steady-state solutions in mass-conserved linear reaction-diffusion systems. First, we explain the background of the problem.

Let us consider the following 4-component reaction-diffusion system.

$$\begin{cases} \partial_t u = d_1 \partial_x^2 u + f(u, v) & (t > 0, x \in I), \\ \partial_t v = d_2 \partial_x^2 v - f(u, v) & (t > 0, x \in I), \\ \partial_t w_s = d_s \partial_x^2 w_s - \tilde{p}(u)w_s + \tilde{q}(u)w_f & (t > 0, x \in I), \\ \partial_t w_f = d_f \partial_x^2 w_f + \tilde{p}(u)w_s - \tilde{q}(u)w_f & (t > 0, x \in I), \\ (P.B.C). \end{cases} \quad (4)$$

(4) was introduced in [26] as a mathematical model of cell polarity. u, v, w_s and w_f are the concentrations of proteins U, V, W_s and W_f . U, V are upstream proteins and W_s, W_f are downstream proteins in intracellular signaling. d_1, d_2, d_s, d_f are the diffusion coefficients for each substance and supposed $0 < d_1 < d_2, 0 < d_s \leq d_f$. Also, $(P.B.C)$ here means that periodic boundary conditions are imposed on all unknown functions. Hereafter, we will use $(P.B.C)$, or $(N.B.C)$ in the same sense when there is no risk of misunderstanding.

In the above equations, $\tilde{p}(u), \tilde{q}(u)$ represent the effect of the upstream protein U on the downstream proteins W_s, W_f . For example, if \tilde{p} is strictly increasing, the higher the concentration of U is, the stronger the conversion from W_s to W_f becomes. On the contrary, if \tilde{p} is strictly decreasing, the higher the concentration of U is, the weaker the conversion from W_s to W_f becomes.

Let us consider the situation that U, V form polarity patterns. This situation corresponds mathematically to that $u(t, x), v(t, x)$ converge to a nonconstant stationary solution $u^*(x), v^*(x)$. In this case, the time evolution of w_s and w_f can be expressed by the following 2-component system.

$$\begin{cases} \partial_t w_s = d_s \partial_x^2 w_s - p^*(x)w_s + q^*(x)w_f & (t > 0, x \in I), \\ \partial_t w_f = d_f \partial_x^2 w_f + p^*(x)w_s - q^*(x)w_f & (t > 0, x \in I), \\ (P.B.C). \end{cases} \quad (5)$$

$$p^*(x) := \tilde{p}(u^*(x)), \quad q^*(x) := \tilde{q}(u^*(x)).$$

The total mass $\int_I (w_s + w_f) dx$ is conserved in the above equation.

The questions addressed in [26] are when U and V localize, do W_s, W_f also localize and in which direction do W_s and W_f localize with respect to the direction in which U localizes. Here, the direction of localization means the

point of highest concentration. Mathematically, the questions can be rephrased as follows: if (u, v) is the nonconstant stationary solution, does (w_s, w_f) also converge to a nonconstant stationary solution and at which point does the stationary solution reach its maximum with respect to the maximum point of u ?

From the above background, we treat a mass-conserved linear reaction-diffusion system.

$$\begin{cases} \partial_t w = d\partial_x^2 w - p(x)w + q(x)z & (t > 0, x \in I), \\ \tau\partial_t z = \partial_x^2 z + p(x)w - q(x)z & (t > 0, x \in I), \\ (P.B.C), \end{cases} \quad (6)$$

where $p, q \in C(\bar{I})$, and d, τ are positive constants. We note that unknown functions and coefficient functions in (5) are replaced as w, z, p, q in (6). In (6), $\int_I (w + \tau z) dx$ is conserved quantity, which can be regarded as a generalization of the conserved quantity in (5). The case $\tau = 1$ corresponds to mass conservation.

In this thesis, we consider the existence, uniqueness, and shapes of stationary solutions to (6). We suppose that $p(x) > 0, q(x) > 0$ ($x \in \bar{I}$). This condition is derived from the fact that $\tilde{p}(u)w_s, \tilde{q}(u)w_f$ represent the reaction between U and W_s, W_f in the original model equation (4).

For such linear partial differential equations, the strong comparison principle holds [22], and (6) is one of the equations called an order-preserving system. In particular, in the case of equation (6), the existence of stationary solutions, which is uniquely determined with respect to the conserved quantities and their stability have been shown by using the theory of order-conserving dynamical systems [20]. Therefore, the unique existence of a stable stationary solution to (6) is not a new result in this study. However, the shape of the stationary solution has yet to be analyzed in previous studies. Therefore, in this thesis, we show the existence and uniqueness of the stationary solutions and, as a new result, the shape of the stationary solutions, using a different method than in the previous study [20], although the results overlap with those of the previous research. The main methods of proof are the theory of boundary value problems for second-order linear differential equations and Sherman-Morrison formula for linear integro-differential equations.

The contents of this part are described below. Section 3 provides the mathematical tools used in this study. In this study, we use results on boundary value problems for second-order linear differential equations. Section 4 presents mathematical assumptions and problem settings in this study. In section 5, we introduce the main result of this study, namely, the unique existence of stationary solutions and their shape, and give its proof. In particular, the shape of the stationary solution corresponds to the polarity pattern observed in actual cell polarity phenomena. In section 6, we show a numerical simulation that corresponds to the main result.

3 Preliminaries.

The following section describes the mathematical tools used in this study. The primary tool is the theory of boundary value problems in second-order linear ordinary differential equations.

This study often deals with the following equations

$$u''(x) + b(x)u(x) = c(x) \quad (x \in J := (0, l)), \quad (7)$$

where l is positive constant, $' := \frac{d}{dx}$ and $b, c \in C(\bar{J})$. Let us consider the following boundary conditions.

$$\begin{aligned} \cos \alpha u(0) - \sin \alpha u'(0) &= 0 \quad (0 \leq \alpha < \pi), \\ \cos \beta u(l) - \sin \beta u'(l) &= 0 \quad (0 < \beta \leq \pi). \end{aligned} \quad (8)$$

The equation (7) with (8) is called a non-homogeneous boundary value problem. For example, the case $\alpha = 0, \beta = \pi$ corresponds to the homogeneous Dirichlet boundary condition, and the case $\alpha = \beta = \frac{\pi}{2}$ corresponds to the homogenous Neumann boundary condition.

The solution to the non-homogeneous boundary value problem can be constructed as follows. Initially, let us consider the following equation.

$$u''(x) + b(x)u(x) = 0 \quad (x \in J), \quad (9)$$

Let u_1, u_2 be the solutions of (9) satisfying $(u_1(0), u_1'(0)) = (\sin \alpha, \cos \alpha), (u_2(l), u_2'(l)) = (\sin \beta, \cos \beta)$. If u_1, u_2 are linearly independent, there exists unique solution $u(x)$ in (7) represented by

$$u(x) = \int_0^l G(x, y)c(y)dy,$$

G is the green function represented as follows.

$$G(x, y) := \begin{cases} \frac{1}{k}u_1(x)u_2(y) & (0 \leq x \leq y), \\ \frac{1}{k}u_1(y)u_2(x) & (y \leq x \leq l), \end{cases} \quad (10)$$

where $k := u_1(x)u_2'(x) - u_1'(x)u_2(x) \equiv u_1(0)u_2'(0) - u_1'(0)u_2(0)$. Note that if u_1, u_2 are linearly independent, $k \neq 0$.

When u_1, u_2 are not linearly independent, a solution for a non-homogeneous boundary problem may not exist. The fact that they are not linearly independent means that there exists a solution to (9) that simultaneously satisfies the boundary conditions (8). Except in the case of all coefficient functions being constants or certain coefficient functions, a method has yet to be found to solve the problem explicitly. It is generally difficult to verify linear independence. However, if $b(x) > 0 (x \in J)$, it is satisfied.

Proption 3.1. *Suppose that $b(x) > 0 (x \in J)$, and $\alpha = \beta = \pi/2$. Then u_1, u_2 are linearly independent.*

Proof. Suppose u_1, u_2 are linearly dependent. This means there exist a constant r such that $u_1(x) = ru_2(x)$, hence $u_1'(0) = u_1'(l) = 0$. Since u_1 is solution of (9),

$$u_1''(x) - b(x)u_1(x) = 0 \quad (x \in J).$$

Multiplying both sides by u_1 and integrating on I ,

$$\begin{aligned} \int_I (u_1'' - bu_1)u_1 dx &= \int_I u_1''u_1 dx - \int_I bu_1^2 dx \\ &= - \int_I \frac{1}{2}(u_1')^2 dx - \int_I bu_1^2 dx \\ &= 0. \end{aligned}$$

Therefore, $u_1 \equiv 0$, because $b(x) > 0$. This contradicts to $u_1(0) = 1$. \square

From the above proposition, we obtain the next corollary.

Corollary 3.1. *Suppose $b(x) > 0$ ($x \in J$), then there exists a unique solution in the following problem.*

$$\begin{cases} u''(x) + b(x)u(x) = c(x) & (x \in I), \\ u'(0) = u'(l) = 0. \end{cases}$$

4 Problem setting.

In this section, we prepare the problem settings for this study. The main interest of this study is the shape of the stationary solution in (4). The coefficient functions p, q represent the influence from the upstream protein U in the original model equations. Hence, an important question is how the shape of the steady-state solution is affected by p and q .

The equation for the stationary solution of (4) is represented as follows.

$$\begin{cases} dw'' - p(x)w + q(x)z = 0 & (x \in I), \\ v'' + p(x)w - q(x)z = 0 & (x \in I), \\ \langle w \rangle + \tau \langle z \rangle = s, \\ (P.B.C). \end{cases} \quad (11)$$

where $\langle \phi \rangle := (1/K) \int_I \phi(x) dx$. We regard s as a parameter of stationary solutions $(w(x; s), z(x; s))$. Since all term in (11) is linear about w, z , solutions are represented by $(w(x; s), z(x; s)) = s(w(x; 1), z(x; 1))$. Therefore, we consider the case $s = 1$ hereafter.

We assume the following for (4).

Assumption 1. $p, q \in C(\bar{I})$, and p, q satisfy the following conditions.

- (i) p, q are periodic functions with period K , and $p(x) > 0, q(x) > 0$ ($x \in \bar{I}$).
- (ii) $p(x) = p(K - x)$, $q(x) = q(K - x)$ ($x \in I$).

The second condition in the above assumption implies that the graphs of p and q are symmetric about the axis $x = K/2$. This assumption implies that the upstream protein U forms a polarity in the direction $x = K/2$. Specifically, u^* takes its maximum value at $x = K/2$ and is symmetric about the axis $x = K/2$. Note that to suppose $K/2$ is the maximum point of u^* is not essential, since (P.B.C) is imposed on (11).

Furthermore, let us define function $\tilde{\rho}(x) := \frac{p(x)}{d^{-1}p(x) + q(x)}$, and assume the following.

Assumption 2. $\tilde{\rho}$ is strictly increasing on $(0, K/2)$.

This assumption is a mathematical generalization of the problem settings in [26]. Previous study [26] treats, for example, the case p, q are strictly increasing and decreasing functions on $(0, K/2)$, respectively. Assumption 2 is satisfied in this case. In addition, Assumption 2 holds if p is strictly increasing and q

is a positive constant function. The main result presented in this thesis is a generalization of the result of [26] in this sense.

The stationary problem (11) is equivalent to a linear integro-differential equation. Taking the sum of two equations in (11),

$$dw'' + z'' = 0 \quad (x \in I).$$

From the periodic boundary conditions, it follows that there exists a constant c such that

$$dw(x; 1) + z(x; 1) = c \quad (x \in I). \quad (12)$$

Taking a spatial average of both sides of (12), it follows

$$\begin{aligned} c &= d\langle w \rangle + \langle z \rangle \\ &= d(1 - \tau\langle z \rangle) + \langle z \rangle \\ &= d + (1 - d\tau)\langle z \rangle. \end{aligned}$$

We used the relation $\langle w \rangle + \tau\langle z \rangle = 1$ above. Substituting c to (12), we obtain the following.

$$w(x; 1) = 1 + \frac{1 - d\tau}{d}\langle z \rangle - \frac{1}{d}z(x; 1).$$

Finally, substituting $w(x; 1)$ to (11), it follows that

$$\begin{cases} z'' - \rho(x)z + \frac{1 - d\tau}{d}\langle z \rangle p(x) = -p(x) & (x \in I), \\ w(x; 1) = 1 + \frac{1 - d\tau}{d}\langle z \rangle - \frac{1}{d}z(x; 1) & (x \in I), \\ (P.B.C), \end{cases} \quad (13)$$

where $\rho(x) := d^{-1}p(x) + q(x)$. z satisfies the linear integral differential equation. If we find the solution z , we obtain w also. Conversely, if (w, z) is a solution of (13), then it is a solution of (11). In the proof of the main result presented in the next section, we treat the stationary problem (13).

5 Main results.

In this study, we obtain the following main result about the shape of the solution for (11).

Theorem 5.1. *Suppose that Assumption 1 and Assumption 2 hold. Then there exists unique solution $(w^*(x), z^*(x))$ to (11). Moreover, it satisfies*

- (i) $w^*(x) > 0, z^*(x) > 0 \quad (x \in I)$.
- (ii) $w^*(x) = w^*(K - x), z^*(x) = z^*(K - x) \quad (x \in I)$.
- (iii) w^*, z^* are strictly decreasing and increasing function on $(0, K/2)$ respectively.

Moreover, when we let $\tilde{\rho}$ in Assumption 2 be strictly decreasing function on $(0, K/2)$, then w^*, z^* are strictly increasing and decreasing function on $(0, K/2)$ respectively.

Remark 5.1. When $s > 0$, Theorem 5.1 holds for solutions $(w(x; s), z(x; s))$ in (11).

The stationary solution presented by Theorem 5.1 corresponds to the polarity pattern of W_s , W_f in the original model equation (4). (i) is a natural consequence that comes from the fact that the unknown functions in (4) represent the concentrations of chemical substances. (ii) and (iii) correspond to the shape of the polarity pattern, which means that W_s forms the polarity in the direction of $x = 0$, i.e., opposite to U , and W_f forms the polarity in the same $x = K/2$ direction as U . On the other hand, when we reverse the monotonicity of $\tilde{\rho}$ in Assumption 2, the directions of polarities of W_s and W_f are also reversed. We show the proof only in the case $\tilde{\rho}$ is strictly increasing on $(0, K/2)$ since the method of proof is almost the same in both cases.

Let us show the outline of the proof of Theorem 5.1. Using a linear operator, we reformulate the first equation of (13).

$$(\mathcal{H} + \mathcal{P})z = -p(x),$$

$$\mathcal{H}\phi := \frac{d^2\phi}{dx^2} - \rho(x)\phi, \quad \mathcal{P}\phi := \frac{1-d\tau}{d}\langle\phi\rangle p(x).$$

If inverse operator $(\mathcal{H} + \mathcal{P})^{-1}$ exists, we can express the solution as $z(x) = (\mathcal{H} + \mathcal{P})^{-1}(-p(x))$. From Sherman-Morrison formula, $(\mathcal{H} + \mathcal{P})^{-1}$ exists, if \mathcal{H}^{-1} exists and constant $c^* := 1 + \frac{1-d\tau}{d}\langle\mathcal{H}^{-1}p\rangle \neq 0$, and the solution z^* of (13) is represented as following.

$$z^*(x) = (\mathcal{H} + \mathcal{P})^{-1}(-p(x)) = \left(\mathcal{H}^{-1} - \frac{1}{c^*}\mathcal{H}^{-1}\mathcal{P}\mathcal{H}^{-1}\right)(-p(x)).$$

We can check the properties of z^* from the expression above. We can obtain the results for w^* from the second equation in (13).

Let us consider the next auxiliary problem.

$$\begin{cases} k'' - \rho(x)k = -p(x) & (x \in I), \\ (P.B.C). \end{cases} \quad (14)$$

We can regard this boundary value problem as (11) without the term of the spatial average. The following lemma holds.

Lemma 5.1. A unique solution to (14) exists, and the solution is evenly symmetric to $K/2$.

Proof. (Uniqueness and symmetry) Suppose that k_1 and k_2 are solutions of (14). Substituting each of k_1 and k_2 to (14), and taking the difference between each equation, we obtain

$$\tilde{k}'' - \rho(x)\tilde{k} = 0,$$

where $\tilde{k} := k_1 - k_2$. Multiplying both side of above equation by \tilde{k} , and integrating it for the interval I , we obtain

$$\begin{aligned} \int_I (\tilde{k}'' - \rho(x)\tilde{k}) \tilde{k} dx &= \left[\tilde{k}'\tilde{k}\right]_{x=0}^{x=K} - \int_I \left\{(\tilde{k}')^2 + \rho(x)\tilde{k}^2\right\} dx \\ &= - \int_I \left\{(\tilde{k}')^2 + \rho(x)\tilde{k}^2\right\} dx = 0, \end{aligned}$$

accordingly, $\tilde{k} \equiv 0$, then $k_1 = k_2$. This means the uniqueness of solutions. Moreover, if k is a solution to (14), $k(K-x)$ is also a solution to (14) since p and ρ are evenly symmetric for $K/2$. By the uniqueness of solutions, $k(x) = k(K-x)$. Therefore, $k(x)$ is evenly symmetric for $K/2$.

(Existence of solution) If the solution k exists, k is evenly symmetric with respect to $K/2$ and periodic function with period K . Hence $k'(0) = k'(K/2) = k'(K) = 0$. Therefore, we only have to prove the existence of the solution of an equation as follows.

$$\begin{cases} k'' - \rho(x)k = -p(x) & x \in (0, K/2), \\ k'(0) = k'(K/2) = 0. \end{cases} \quad (15)$$

From Corollary 2.1, there exists unique solution k_N to (15). Let function k_P as following

$$k_P(x) := \begin{cases} k_N(x) & (0 \leq x \leq K/2) \\ k_N(K-x) & (K/2 < x \leq K) \end{cases}$$

k_P satisfies (14). This means the existence of the solution. \square

Lemma 5.2. *Let k^* be the solution to (14). k^* satisfies*

(i) k^* is strictly increasing on $(0, K/2)$.

(ii) $0 < k^*(x) < d \quad (x \in I)$.

Proof. (Proof of (i)) First, we prove $\frac{dk^*}{dx}(x) \geq 0 \quad (x \in (0, K/2))$. Suppose k^* doesn't satisfy this condition, and we will show a contradiction. From Lemma 5.1, the derivative of k^* takes 0 at $x = 0, K/2$. Hence, there exist $x_1 \in (0 < K/2)$ and positive constant $\delta_1 = \delta_1(x_1)$, such that

$$\begin{aligned} \frac{dk^*}{dx}(x_1) < 0, \quad \frac{d^2k^*}{dx^2}(x_1) &= 0, \\ \frac{dk^*}{dx}(x) < 0, \quad \frac{d^2k^*}{dx^2}(x) > 0, \quad (x \in I_{\delta_1} \subset (0, K/2)), \end{aligned} \quad (16)$$

where $I_\delta := (x_1, x_1 + \delta)$ for $\delta > 0$. In the view of (15),

$$\begin{aligned} \frac{d^2k^*}{dx^2}(x) > 0 &\Leftrightarrow \rho(x)k^*(x) - p(x) > 0, \\ &\Leftrightarrow k^*(x) > \frac{p(x)}{\rho(x)} = \tilde{\rho}(x), \end{aligned} \quad (17)$$

therefore, $k^*(x) > \tilde{\rho}(x) \quad (x \in I_{\delta_1})$. Due to Assumption 2, $\tilde{\rho}$ is strictly increasing function in $(0, K/2)$, then $k^*(x) > \tilde{\rho}(x_1) \quad (x \in I_{\delta_1})$. However, due to (16), there exists a constant $\delta_2 = \delta_2(x_1) > 0$, such that

$$k^*(x_1) = \tilde{\rho}(x_1) \quad k^*(x) < \tilde{\rho}(x_1) \quad (x \in I_{\delta_2} \subset (0, K/2)).$$

Let $\delta_3 := \min\{\delta_1, \delta_2\}$, then $k^*(x) < \tilde{\rho}(x_1)$ and $k^*(x) > \tilde{\rho}(x_1) \quad (x \in I_{\delta_3})$. This is contradiction, then $\frac{dk^*}{dx}(x) \geq 0 \quad (x \in (0, K/2))$. This means k^* is increasing function in $(0, K/2)$.

Next, we prove k^* is strictly increasing on I_1 . Suppose k^* doesn't satisfy it, then there exists open interval $(a, b) \subset (0, K/2)$, such that $\frac{dk^*}{dx}(x) = 0$ for $x \in (a, b)$. Therefore k^* is constant in (a, b) , then $\frac{d^2k^*}{dx^2}(x) = 0$. In view of (17), $k^*(x) = \tilde{\rho}(x)$ ($x \in (a, b)$), then $\tilde{\rho}(x)$ is constant in (a, b) . This is a contradiction. (Proof of (ii)) Due to Lemma 5.1, k^* is symmetric with respect to $x = K/2$ and strictly increasing in $(0, K/2)$. Hence we only have to prove that $k^*(0) > 0$, $k^*(K/2) < d$. Because k^* takes minimum at $x = 0$, $\frac{d^2k^*}{dx^2}(0) \geq 0$ and $k^*(0) \geq \tilde{\rho}(0) > 0$, due to (17). It is proved that $k^*(K/2) < d$ by same manners. \square

Proof of Theorem 5.1 By Lemma 5.1 and Lemma 5.2, $k^* = \mathcal{H}^{-1}(-p^*)$, $0 < \langle k^* \rangle < d$. From this inequality, we can estimate the constant c^* as follows.

$$c^* = 1 - \frac{1 - d\tau}{d} \langle k^* \rangle = \frac{d - \langle k^* \rangle + d\tau \langle k^* \rangle}{d} > 0.$$

Then, $c^* \neq 0$. It concludes that we can apply the Sherman-Morrison formula. The solution is represented as follows.

$$\begin{aligned} z^*(x) &= \left(1 + \frac{1 - d\tau}{c^*d} \langle k^* \rangle \right) k^*(x) = \frac{d k^*(x)}{d - (1 - d\tau) \langle k^* \rangle} \\ w^*(x) &= 1 + \frac{1 - d\tau}{d} \langle z^* \rangle - \frac{1}{d} z^*(x) = \frac{d - k^*(x)}{d - (1 - d\tau) \langle k^* \rangle}. \end{aligned}$$

From Lemma 5.2, k^* is positive and strictly increasing function on $(0, K/2)$. Moreover, by the inequality $0 < \langle k^* \rangle < d$, we can calculate $d - (1 - d\tau) \langle k^* \rangle = d - \langle k^* \rangle + d\tau \langle k^* \rangle > 0$. Hence, w^* and z^* satisfy (i)~(iii). \square

Remark 5.2. In the previous study [26], we obtained results similar to Theorem 5.1 in the case $\tau = 1$. This study generalizes the results to the case $\tau > 0$.

6 Numerical simulation.

In this section, we show the numerical simulation corresponding to Theorem 5.1. We refer to the previous study [26] for the setting of the numerical simulation as follows.

$$\begin{cases} \partial_t u = d_1 \partial_x^2 u - \left(\alpha + \frac{\beta_2}{1 + \beta_1 u^2} \right) u + \gamma v & (t > 0, x \in I), \\ \partial_t v = d_2 \partial_x^2 v + \left(\alpha + \frac{\beta_2}{1 + \beta_1 u^2} \right) u - \gamma v & (t > 0, x \in I), \\ \partial_t w_s = d_s \partial_x^2 w_s - \mu_1 u w_s + \mu_2 \frac{\delta_2}{1 + \delta_1 u^2} w_f & (t > 0, x \in I), \\ \partial_t w_f = d_f \partial_x^2 w_f + \mu_1 u w_s - \mu_2 \frac{\delta_2}{1 + \delta_1 u^2} w_f & (t > 0, x \in I), \\ (P.B.C), \end{cases} \quad (18)$$

where $\alpha, \beta_1, \beta_2, \gamma, \delta_1, \delta_2, \mu_1$ and μ_2 are positive constants. The equation (18) is the same as the model equation (4) with the following terms.

$$f(u, v) = - \left(\alpha + \frac{\beta_2}{1 + \beta_1 u^2} \right) u + \gamma v,$$

$$\tilde{p}(u) = \mu_1 u, \quad \tilde{q}(u) = \mu_2 \frac{\delta_2}{1 + \delta_1 u^2}.$$

We note that \tilde{p} and \tilde{q} are strictly increasing and decreasing functions, respectively.

First, we perform a numerical simulation for the first and second equations in (18) with the following parameters

$$d_1 = 2.40 \times 10^{-5}, d_2 = 1.44 \times 10^{-3}, \alpha = 0.06, \beta_1 = 4.50, \beta_2 = 4.00, \gamma = 0.20, K = 1.00,$$

and the initial condition

$$u(0, x) = \begin{cases} u_0 (\Delta x)^{-1} & (x = K/2), \\ 0.0 & (x \neq K/2). \end{cases}$$

$$v(0, x) = v_0 \quad (0 \leq x \leq K),$$

where Δx is the spatial step width, where we choose $\Delta x = 0.02$. u_0 is a positive constant and we choose $u_0 = 0.26$ in the following simulation. v_0 corresponds to the spatially homogeneous equilibrium for u_0 , namely

$$v_0 = \gamma^{-1} \left(\alpha + \frac{\beta_2}{1 + \beta_1 u_0^2} \right) u_0.$$

As a result of the simulation, we obtain a stationary unimodal pattern with a peak at $x = 0.5$ (Fig. 1). Let us denote the pattern as $(u^*(x), v^*(x))$. This unimodal pattern corresponds to the cell polarity pattern in the direction of the axis $x = 0.5$. For $u^*(x)$, we perform the numerical simulation on the following equation.

$$\begin{cases} \partial_t w_s = d_s \partial_x^2 w_s - \mu_1 u^*(x) w_s + \mu_2 \frac{\delta_2}{1 + \delta_1 (u^*(x))^2} w_f & (t > 0, x \in I), \\ \partial_t w_f = d_f \partial_x^2 w_f + \mu_1 u^*(x) w_s - \mu_2 \frac{\delta_2}{1 + \delta_1 (u^*(x))^2} w_f & (t > 0, x \in I), \\ (P.B.C), \end{cases} \quad (19)$$

where we choose the following parameters and initial condition.

$$d_s = 1.28 \times 10^{-4}, d_f = 3.20 \times 10^{-3}, \delta_1 = 0.5, \delta_2 = 10.0, \mu_1 = 1.0, \mu_2 = 0.2, K = 1.0.$$

$$w_s(0, x) = w_f(0, x) = 1.00 \quad (0 \leq x \leq K).$$

We obtain the stationary pattern $w_s^*(x), w_f^*(x)$ by the numerical simulation for (19). w_s^* and w_f^* have the peaks on $x = 0$ and $x = K/2$, respectively (Fig. 2).

7 Summary and Discussion.

Against the background of the mathematical analysis for the cell polarity model (4), we analyzed the shape of the stationary solution for (6). The coefficient

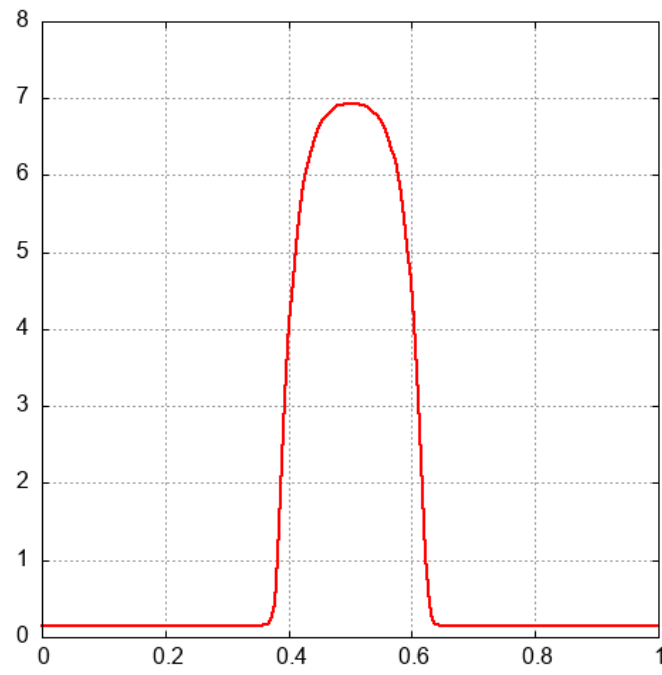


Figure 1: The numerical simulation for (18). The horizontal axis corresponds to x and the red line corresponds to $u^*(x)$. The above figure shows only u component.

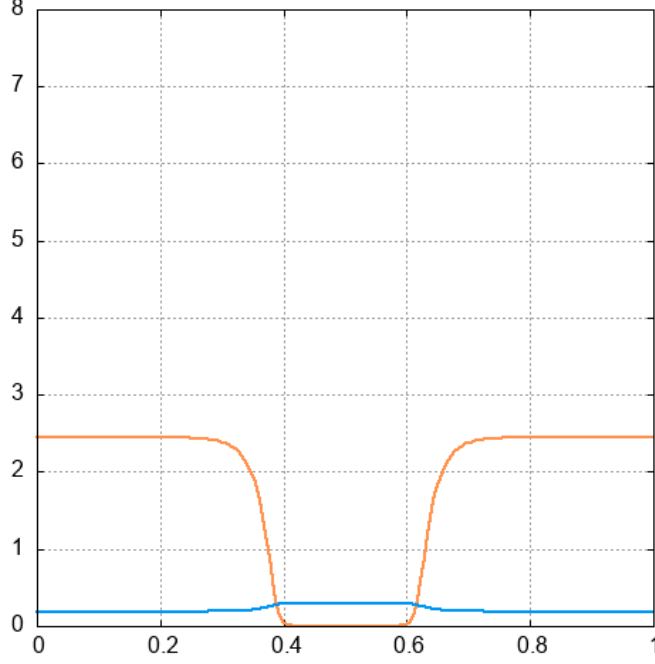


Figure 2: The numerical simulation for (19). The horizontal axis corresponds to x . The orange and blue lines correspond to $w_s^*(x)$ and $w_f^*(x)$, respectively.

functions p, q are positive-valued, evenly symmetric with respect to the axis $x = K/2$ and satisfy $\tilde{\rho} = p(x)/\{(1/d)p(x) + q(x)\}$ become strictly monotone on $(0, K/2)$ in connection with the cell polarity model. The results show that if $\tilde{\rho}$ strictly increasing on $(0, K/2)$, for stationary solution (w^*, z^*) , w^* is strictly decreasing on $(0, K/2)$, and z^* is strictly increasing on $(0, K/2)$. This means that in the original model equation (4), W_s forms a polarity in the direction $x = 0$, and W_f forms a polarity in the direction $x = K/2$. In addition, if the monotonicity of $\tilde{\rho}$ is reversed, the direction of polarity is also reversed. These results mathematically show that the stationary pattern appearing in model equation (4) qualitatively reproduces the polarity pattern observed in the cell polarity phenomenon.

Compared to the previous study [26], this thesis also makes two mathematical generalizations. First, the monotonicity assumption for the coefficient functions p and q is generalized to the assumption for the monotonicity of $\tilde{\rho}$. This makes the results of this study applicable to more general model equations. Second, for the constant τ , we extend our results to the arbitrary positive number τ , not only to the case $\tau = 1$ as in the previous study [26]. In the case, $\tau \neq 1$, the conserved quantity differs from the mass conservation law in the cell polarity model. On the other hand, a mass-conserved reaction-diffusion system is equivalent to a model equation for phase separation [16], in which conserved quantity appears for $\tau \neq 1$. This result is important for applying our method and results to mathematical analysis for other model equations.

Part II

Stability of 2-mode stationary solutions in mass-conserved reaction-diffusion compartment model

8 Introduction.

In this part, we consider the equation (1) with the reaction term (3).

$$\begin{cases} \partial_t u = d\partial_x^2 u + f(u, v) & (t > 0, x \in I), \\ \tau \partial_t v = \partial_x^2 v - f(u, v) & (t > 0, x \in I). \end{cases} \quad (20)$$

As introduced in section 1, this equation was introduced as a conceptual model of cell polarity and is known as a model that qualitatively reproduces cell polarity phenomena [5], [21].

In the previous study [5], $(P.B.C)$ is imposed on (20) with $\tau = 1$, $f(u, v) = -au/(u^2 + b)$ ($a, b > 0$). For this case, certain constant stationary solutions, which are stable in the absence of diffusion terms, become unstable with diffusion terms. This property is similar to Turing instability [28]. The numerical simulation with the initial condition, the constant stationary solution with a small perturbation, shows that a stripe pattern appears and converges to a unimodal pattern over time. In this simulation, the height of some peaks in the stripe pattern decreases while one of the other peaks increase over time. These dynamics continue until there is finally only one peak (fig. 3).

To understand the transient dynamics, we consider a linearized eigenvalue problem. Let (u, v) be a stationary solution of (20) with $(N.B.C)$ or $(P.B.C)$, then there exists a constant c such that

$$du + v \equiv c \quad (x \in I). \quad (21)$$

Hence, u satisfies the following scalar equation.

$$du'' + f(u, c - du) = 0.$$

Therefore, u is constant, or N -symmetric solution. In the case of $(N.B.C)$, u is N -symmetric, if u is strictly increasing or decreasing on $(0, K/N)$. In other words, we can construct the graph of u on I by extending the one on $(0, K/N)$ repeatedly. Additionally, if u is N -symmetric, v is also N -symmetric due to (35). Therefore, stationary solutions for (20) can be classified by using N -mode stationary solution defined below.

Definition 1. Let N be a natural number. If (u, v) is stationary solution of (20) with $(N.B.C)$ and u has exactly $(N - 1)$ critical points on I , (u, v) is called N -mode stationary solution. If (u, v) is stationary solution of (20) with $(P.B.C)$ and u has exactly $(2N - 1)$ critical points on I and satisfies $u'(0) = u'(K) = 0$, (u, v) is called N -mode stationary solution.

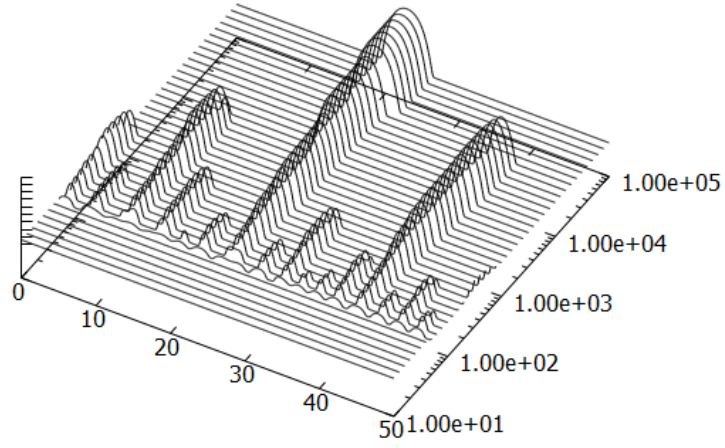


Figure 3: The numerical simulation for (20). $f(u, v) = -au/(u^2 + b) + v$, $a = 1.0$, $b = 0.1$, $d = 0.02$, $\tau = 1.0$, $K = 50.0$, $s = 2.0$. The initial condition for the above simulation is the constant stationary solution with a small perturbation

Note that when (u, v) is 1-mode stationary solution under $(N.B.C)$, u and v are strictly monotone functions on I . If (u, v) is 1-mode stationary solution under $(P.B.C)$, u and v are even symmetric functions for the axis $x = K/2$, and the shapes of the functions are unimodal.

The previous study [5] considers the linearized eigenvalue problem for N -mode stationary solutions for $N \geq 2$ and derive the following instability condition for N -mode stationary solution by performing formal asymptotic analysis on the eigenvalue problem. Let (u^*, v^*) be N -mode stationary solution of (20) under $(P.B.C)$. We regard conserved quantity $s = (1/K) \int_I (u^* + \tau v^*) dx$ as the parameter of the stationary solution $P(x; s) = (u^*(x; s), v^*(x; s))$. We also assume that c in (35) is function of s defined on an appropriate interval. According to [5], it is indicated that N -mode stationary solution $P(x; s)$ is unstable, if $\frac{dc}{ds}(s) < 0$.

This study aims to understand the transient dynamics by introducing reaction-diffusion compartment model. The reaction-diffusion compartment model is the following coupled reaction-diffusion system.

$$\begin{cases} \partial_t u_j = d \partial_x^2 u_j + f(u_j, v_j), & t > 0, x \in I_j, \\ \tau \partial_t v_j = \partial_x^2 v_j - f(u_j, v_j), & \end{cases} \quad (22)$$

where $j \in \{1, 2\}$, $I_1 := (0, K/2)$ and $I_2 := (K/2, K)$. (u_j, v_j) are unknown functions defined on I_j . In this study, we call (22) the reaction-diffusion compartment model, or simply compartment model. The system (22) corresponds to the situation that the original system (20) is divided into multiple regions, which we call compartments, and a reaction-diffusion system is considered in each compartment. For the case of (22), a new boundary $x = K/2$ appears. We impose the following boundary conditions on (22).

$$\begin{cases} \partial_x u_1 = \partial_x v_1 = 0 & (t > 0, x = 0), \\ d \partial_x u_1 = \varepsilon \alpha (u_2 - u_1) = d \partial_x u_2 & (t > 0, x = K/2), \\ \partial_x v_1 = \varepsilon (v_2 - v_1) = \partial_x v_2 & (t > 0, x = K/2), \\ \partial_s u_2 = \partial_x v_2 = 0 & (x = K), \end{cases} \quad (23)$$

where $\alpha > 0, \varepsilon \geq 0$. In the perspective of physics, the above boundary condition corresponds to the situation where a semipermeable membrane separates the original interval I at $x = K/2$, and the substances diffuse through the semipermeable membrane [1]. ε and α represent the strength and ratio of the diffusive coupling, respectively.

We introduce the relationship between the compartment model and mass-conserved reaction-diffusion systems. Let $\varepsilon = 0$ on the boundary condition (23), then (22) turn to the following.

$$\begin{cases} \partial_t u_1 = d \partial_x^2 u_1 + f(u_1, v_1) & (t > 0, x \in I_1), \\ \tau \partial_t v_1 = \partial_x^2 v_1 - f(u_1, v_1) & (t > 0, x \in I_1), \\ \partial_x u_1 = \partial_x v_1 = 0 & (t > 0, x = 0, K/2). \end{cases} \quad (24)$$

$$\begin{cases} \partial_t u_2 = d \partial_x^2 u_2 + f(u_2, v_2) & (t > 0, x \in I_2), \\ \tau \partial_t v_2 = \partial_x^2 v_2 - f(u_2, v_2) & (t > 0, x \in I_2), \\ \partial_x u_2 = \partial_x v_2 = 0 & (t > 0, x = K/2, K). \end{cases} \quad (25)$$

There is no diffusive coupling between I_1 and I_2 . Each of (24) and (25) is a mass-conserved reaction-diffusion system with the interval length $K/2$.

On the other hand, let us consider the case $\varepsilon \rightarrow \infty$. Suppose that derivatives of u_j, v_j at $x = K/2$ are bounded regardless of ε , then

$$u_1(t, 0) - u_2(t, 0), v_1(t, 0) - v_2(t, 0) \rightarrow 0 \quad (\varepsilon \rightarrow \infty).$$

Hence the differences of the values and derivatives of (u_1, v_1) and (u_2, v_2) at $x = K/2$ converge to 0 when ε tends to infinity. Formally, we can regard (22) with (23) turn to be single mass-conserved reaction-diffusion system defined on I with (N.B.C) when $\varepsilon \rightarrow \infty$.

From the above discussion, (22) is equal to (24) when $\varepsilon = 0$, and is formally the original mass-conserved reaction-diffusion system when $\varepsilon \rightarrow +\infty$. Therefore, we can expect that the analysis of the dynamics of the solution in the compartment model (22) will lead to the understanding of the dynamics of the solution in the mass-conserved reaction-diffusion system (20). In particular, we analyze the linearized eigenvalue problem in the compartmental model to understand the dynamics of the stripe pattern in (20).

The compartment model with the boundary condition (23) imposed has properties similar to a mass-conserved reaction-diffusion system. The following conservation law holds in (20) with (23).

$$\int_{I_1} \{u_1(t, x) + \tau v_1(t, x)\} dx + \int_{I_2} \{u_2(t, x) + \tau v_2(t, x)\} dx \equiv \text{Const.}$$

Note that in (22), the conservation laws do not hold in each compartment. We introduce the following symbols.

$$s_j(t) := \frac{2}{K} \int_{I_j} (u_j + \tau v_j) dx =: \langle u_j \rangle_j + \tau \langle v_j \rangle_j \quad (j = 1, 2).$$

where $\langle \cdot \rangle_j$ denotes the spatial average on the interval I_j and $\langle u \rangle_j := \frac{2}{K} \int_{I_j} u(x) dx$. The conserved quantity for the system eqrefeq:2-2 is defined as follows.

$$s := \frac{1}{K} \left[\int_{I_1} (u_1(t, x) + \tau v_1(t, x)) dx + \int_{I_2} (u_2(t, x) + \tau v_2(t, x)) dx \right] = \frac{1}{2} (s_1(t) + s_2(t))$$

where s is the constant determined by the initial value of the system (22). Note that $(s_1 + s_2)$ becomes constant independent of time, but each s_j itself is not necessarily constant.

Similar to (20), we can consider 2-mode stationary solutions in the compartmental model (22). Let $P(x; s) = (u^*(x; s), v^*(x; s))$ be a 1-mode stationary solution satisfying $\langle u^* \rangle_1 + \tau \langle v^* \rangle_1 = s$ in (24). The 2-mode stationary solution in the compartment model refers to the function P^2 such that

$$P^2(x; s) := \begin{cases} P(x; s) & (x \in I_1), \\ P(K - x; s) & (x \in I_2). \end{cases}$$

For any α, ε , P^2 is a stationary solution of (22). Since the stationary solution under the Neumann boundary condition is evenly extended, it is clear that P^2

satisfies the Neumann boundary conditions for $x = 0, K$, and we can confirm that P^2 enjoys the boundary condition at $x = K/2$.

Let us consider the stability of P^2 . When $\varepsilon = 0$, the stability of P^2 in (22) is essentially the same as the stability of P in the reaction-diffusion system (24). In particular, if P is a stable (unstable) stationary solution in (24), then P^2 is a stable (unstable) stationary solution in (22). Next, when $\varepsilon > 0$, if P is unstable, then P^2 is also unstable. On the other hand, it needs to be clarified whether P^2 is also stable if P is stable.

In this study, we assume that there exists a stable stationary solution P of (24), and consider a linearized eigenvalue problem for the stationary solution P^2 in the case $\varepsilon > 0$.

9 Problem setting.

9.1 Basic assumptions

First, we assume the existence of 1-mode stationary solutions in (24). The stationary problem in (24) is represented as follows.

$$\begin{cases} d\partial_x^2 u + f(u, v) = 0 & (x \in I_1), \\ \partial_x^2 v - f(u, v) = 0 & (x \in I_1), \\ \partial_x u = \partial_x v = 0 & (x = 0, K/2), \\ \langle u \rangle_1 + \tau \langle v \rangle_1 = s. \end{cases} \quad (26)$$

The last equation of (26) corresponds to the conserved quantity.

Assumption 3. There exist constant $\bar{s} \in \mathbb{R}$ and positive number η such that (26) has a family of solutions $P(\cdot; s) = (u^*(\cdot; s), v^*(\cdot; s)) \in \{C^2(\bar{I}_1)\}^2$ ($s \in (\bar{s} - \eta, \bar{s} + \eta)$), and the following holds.

(i) $P(\cdot; \bar{s})$ is 1-mode stationary solution.

(ii) u^*, v^* are continuously differentiable about s on $(\bar{s} - \eta, \bar{s} + \eta)$.

From (ii) above, we can define a function $c(s) := du^*(\cdot; s) + dv^*(\cdot; s)$ ($s \in (\bar{s} - \eta, \bar{s} + \eta)$) and $c(s)$ is continuously differentiable.

Next, we assume that $P(\cdot; \bar{s})$ is spectrally stable. In the following, let \mathcal{L}_1 be the linearized operator at $P(\cdot; \bar{s})$, and let $\mathcal{D}(\mathcal{L}_1), \sigma(\mathcal{L}_1)$ be the domain and spectrum of \mathcal{L}_1 .

$$\begin{aligned} \mathcal{L}_1 : X_1 &\rightarrow X_1, \quad X_1 := (L^2(I_1))^2, \\ \mathcal{L}_1 \Phi &= \mathcal{L}_1 \begin{pmatrix} \phi \\ \psi \end{pmatrix} = \begin{pmatrix} d\partial_x^2 \phi + f_u^*(x)\phi + f_v^*(x)\psi \\ \tau^{-1} \{ \partial_x^2 \psi - f_u^*(x)\phi - f_v^*(x)\psi \} \end{pmatrix} \quad (x \in I_1), \\ \mathcal{D}(\mathcal{L}_1) &= \{ \Phi \in (H^2(I_1))^2 \mid \partial_x \Phi = 0 \ (x = 0, K/2) \}, \end{aligned}$$

where $f_u^*(x) := f_u(u^*(x; \bar{s}), v^*(x; \bar{s}))$, $f_v^*(x) := f_v(u^*(x; \bar{s}), v^*(x; \bar{s}))$. We define the inner product $\langle \mathbf{u}, \mathbf{v} \rangle_{X_1} := \langle u_1, v_1 \rangle_{L^2(I_1)} + \langle u_2, v_2 \rangle_{L^2(I_1)}$ for any $\mathbf{u} = (u_1, u_2), \mathbf{v} = (v_1, v_2) \in X_1$. Note that X_1 is Hilbert space induced by $\langle \cdot, \cdot \rangle_{X_1}$.

Assumption 4. There exists positive real number γ_1 , such that $\sigma(\mathcal{L}_1) = \{0\} \cup \Sigma_1$, $\Sigma_1 \subset \{\lambda \in \mathbb{C}; \operatorname{Re} \lambda < -\gamma_1\}$. Moreover, 0 is simple eigenvalue with corresponding eigenfunction $\partial_s P(\cdot; \bar{s})$.

Let \mathcal{L}_1^* be the conjugate operator of \mathcal{L}_1 .

$$\mathcal{L}_1^* \Phi = \begin{pmatrix} d\partial_x^2 \phi + f_u^*(x)\phi - \tau^{-1} f_u^*(x)\psi \\ \tau^{-1} \partial_x^2 \psi + f_v^*(x)\phi - \tau^{-1} f_v^*(x)\psi \end{pmatrix} \quad (x \in I_1).$$

Since \mathcal{L}_1 has a simple eigenvalue 0, \mathcal{L}_1^* also has a simple eigenvalue 0, and the constant function $\mathbf{a} := \frac{2}{K} \begin{pmatrix} 1 \\ \tau \end{pmatrix}$ is an eigenfunction corresponding to 0. In this case $\langle \partial_s P(\cdot; \bar{s}), \mathbf{a} \rangle_{X_1} = 1$. In fact, since $\langle P(\cdot; s), \mathbf{a} \rangle_{X_1} = s$ from the definition of conserved quantities, we can obtain the above relation by differentiating both sides of this relation by s .

There is an example satisfying the above Assumption 3, 4 with the reaction term $f(u, v) = u(1 - u^2) + \tau v$. In this case, we can construct a stationary solution concretely by using Jacobi's elliptic functions and we can analyze the spectrum of the corresponding linearized operator in detail. We explain this example in Appendix A.1.

9.2 Linearized eigenvalue problem for 2-mode stationary solution

The linearized eigenvalue problem for 2-mode stationary solution P^2 is expressed as follows.

$$\begin{cases} \lambda \Phi_j = \mathcal{L} \Phi_j & (x \in I_j), \\ \partial_x \Phi_1 = \mathbf{0} & (x = 0), \\ \partial_x \Phi_1 = \varepsilon A(\Phi_2 - \Phi_1) = \partial_x \Phi_2 & (x = K/2), \\ \partial_x \Phi_2 = \mathbf{0} & (x = K), \end{cases} \quad (27)$$

where $\Phi_j(x) := (\phi_j(x), \psi_j(x)) \in (H^2(I_j))^2$, $A := \operatorname{diag} \left\{ \frac{\alpha}{d}, 1 \right\}$, and

$$\mathcal{L} \Phi_j = \begin{pmatrix} d\partial_x^2 \phi_j + f_u(P^2(x; \bar{s}))\phi_j + f_v(P^2(x; \bar{s}))\psi_j \\ \tau^{-1} \{ \partial_x^2 \psi_j - f_u(P^2(x; \bar{s}))\phi_j - f_v(P^2(x; \bar{s}))\psi_j \} \end{pmatrix} \quad (x \in I_j)$$

Next, we introduce the following functions.

$$\Phi(x) := \begin{cases} \Phi_1(x) & (x \in I_1), \\ \Phi_2(x) & (x \in I_2). \end{cases}$$

$$\Phi_e := \frac{\Phi(x) + \Phi(K-x)}{2}, \quad \Phi_o := \frac{\Phi(x) - \Phi(K-x)}{2} \quad (x \in I_1 \cup I_2).$$

Φ_e and Φ_o are even and odd symmetric functions with respect to $x = K/2$, respectively. In other words, the following holds.

$$\Phi_e(x) = \Phi_e(K-x), \quad \Phi_o(x) = -\Phi_o(K-x) \quad (x \in I_1 \cup I_2).$$

Hence, eigenfunctions of (27) can be decomposed as $\Phi(x) = \Phi_e(x) + \Phi_o(x)$. In this sense, we denote Φ_e and Φ_o as even and odd parts of Φ , respectively. By

decomposing both sides of the eigenvalue problem (27) into even and odd parts, we can derive the following two equations for Φ_e, Φ_o .

$$\begin{cases} \lambda \Phi_e = \mathcal{L}\Phi_e & (x \in I_1), \\ \partial_x \Phi_e = 0 & (x = 0, K/2). \end{cases} \quad (28)$$

$$\begin{cases} \lambda \Phi_o = \mathcal{L}\Phi_o & (x \in I_1), \\ \partial_x \Phi_o = 0 & (x = 0), \\ \partial_x \Phi_o = -2\varepsilon A\Phi_o & (x = K/2). \end{cases} \quad (29)$$

(28) is eigenvalue problem with $(N.B.C)$ imposed on I_1 , and (29) is eigenvalue problem with Neumann boundary condition at $x = 0$ and Robin boundary condition at $x = K/2$. Note that (28) and (29) are independent of each other.

Suppose that Φ_e, Φ_o satisfy (28), (29) for certain $\lambda \in \mathbb{C}$. Also, suppose that $\Phi_e \not\equiv 0$ or $\Phi_o \not\equiv 0$ holds. In this case, $\Phi = \Phi_e + \Phi_o$ is eigenfunction corresponding to eigenvalue λ in (27). Conversely, when we find an eigenpair $\{\lambda, \Phi\}$ in (27), the even and odd parts of Φ are eigenfunctions in (28) and (29) for λ , respectively. Therefore, the two eigenproblems (28) and (29) are equivalent to the eigenvalue problem (27).

(28) is the same as the linearized eigenvalue problem of P in (24). Thus, for some $\Phi_e \not\equiv 0$, if $\{\lambda, \Phi_e, \Phi_o\}$ satisfies (28) and (29), $\lambda \in \sigma(\mathcal{L}_1)$ holds. From Assumption 4, this eigenvalue does not affect the stability of P^2 . Therefore, in the following, we consider the case $\Phi_e \equiv 0$ and treat (29) only.

In the eigenvalue problem (29), if $\varepsilon = 0$, this is also equivalent to the linearized eigenvalue problem for P in (24). In particular, from Assumption 4, when $\varepsilon = 0$, $\{0, \partial_s P\}$ satisfies (29). Let us regard ε as a parameter of the eigenpair $\{\lambda, \Phi_o\}$, and consider the variation of eigenpair in a neighborhood of $\{0, \partial_s P\}$ with respect to ε .

10 Main results.

In this section, we show the main results of this study. The following result gives sufficient conditions for the 2-mode stationary solution P^2 to become unstable.

Theorem 10.1. *Suppose Assumption 3 and Assumption 4 hold. Then there exists a positive constant η , function $\lambda(\cdot) \in C^1((-\eta, \eta); \mathbb{R})$, and map $\Phi(\cdot) \in C^1((-\eta, \eta); (H^2(I_1))^2)$ such that*

$$\begin{cases} \lambda(\varepsilon)\Phi(\varepsilon) = \mathcal{L}\Phi(\varepsilon) & (x \in I_1), \\ \partial_x \Phi(\varepsilon) = \mathbf{0} & (x = 0), \\ \partial_x \Phi(\varepsilon) = -2\varepsilon A\Phi(\varepsilon) & (x = K/2), \end{cases}$$

for $\varepsilon \in (-\eta, \eta)$. $\lambda(\varepsilon), \Phi(\varepsilon)$ satisfy that $\lambda(0) = 0, \Phi(0)(x) = \Phi(x; 0) = \partial_s P(x; \bar{s})$. Moreover,

$$\begin{aligned} \lambda(\varepsilon) &= \varepsilon \lambda_1 + O(\varepsilon^2) & (\varepsilon \rightarrow 0), \quad \lambda_1 &= -\frac{4}{K} \{ \alpha \partial_s u^*(K/2; \bar{s}) + \partial_s v^*(K/2; \bar{s}) \} \\ \Phi(\varepsilon) &= \partial_s P(\cdot; \bar{s}) + O(\varepsilon) & (\varepsilon \rightarrow 0). \end{aligned}$$

The relation $\lambda(\varepsilon) = \varepsilon\lambda_1 + O(\varepsilon^2)$ in the above theorem represents the asymptotic expansion for ε in the neighborhood of simple eigenvalue 0. The λ_1 is the coefficient of the principal term of this asymptotic expansion. If λ_1 is positive, there exists a positive real eigenvalue when $0 < \varepsilon \ll 1$. That is, $\{\alpha\partial_s u^*(K/2; \bar{s}) + \partial_s v^*(K/2; \bar{s})\} < 0$ is a sufficient condition for P^2 to be unstable.

In particular, when $\alpha = d$, λ_1 is represented more simply.

$$\lambda_1 = -\frac{4}{K} \frac{d}{ds} c(\bar{s}).$$

In this case, the sufficient condition for the instability is expressed as $\frac{d}{ds} c(\bar{s}) < 0$.

Theorem 10.1 also shows the dynamics of solutions in a neighborhood of P^2 . The $\Phi(\varepsilon)$ in Theorem 10.1 represents odd part of eigenfunction in (27). Let us denote $\Phi(x; \varepsilon)$ as the eigenfunction corresponding to $\lambda(\varepsilon)$ in the eigenvalue problem (27).

$$\Phi(x; \varepsilon) = \begin{cases} \partial_s P(x; \bar{s}) + O(\varepsilon) & (x \in I_1) \\ -\partial_s P(K - x; \bar{s}) + O(\varepsilon) & (x \in I_2) \end{cases}$$

In other words, the eigenfunction is approximated by odd symmetric extension of $\partial_s P$ with respect to $x = K/2$. $\partial_s P$ represents the variation of the stationary solution as the conserved quantity s increases, and in particular, $\partial_s P$ is considered to represent the direction in which the stationary pattern grows [5]. From this, the above eigenfunctions correspond to the dynamics where one pattern decays and the other grows, as observed by numerical calculations.

Remark 10.1. *The sufficient condition $\frac{d}{ds} c(\bar{s}) < 0$ for instability at $\alpha = d$ is the same as the condition for instability of the stripe stationary solution, which was predicted in the previous study [5].*

The basic idea of the proof for Theorem 10.1 is to apply the implicit function theorem to the eigenvalue problem (29). As we have already seen, when $\varepsilon = 0$, (29) is an eigenvalue problem with (N.B.C). Due to Assumption 4, the eigenpair $\{0, \partial_s P(\cdot; \bar{s})\}$ satisfies (29). When $\varepsilon > 0$, $\partial_s P(\cdot; \bar{s})$ is not an eigenfunction since it does not satisfy the Robin boundary conditions. However, when ε is sufficiently small, (29) can be considered as a problem under almost (N.B.C), and we can expect that there exist eigenpairs close to $\{0, \partial_s P(\cdot; \bar{s})\}$. In this case, we regard $\{0, \partial_s P(\cdot; \bar{s})\}$ as the zero point of a map on an appropriate Banach space and apply the implicit function theorem to construct eigenvalues and eigenfunctions that depend on the parameter ε .

However, since the boundary condition of (29) changes if the parameter ε changes, we can't apply the implicit function theorem directly to (29). This is because the implicit function theorem requires that the domain of the map does not change depending on the parameter.

We transform the above equation to apply the implicit function theorem to (29). Let the function g satisfies $g \in C^2(\bar{I}_1)$, $g'(0) = 0$, and $g'(K/2) = 2$. We note that a typical example of g is $g(x) = \frac{2}{K}x^2$. Using this g , we define $\tilde{\Phi}(x) := e^{\varepsilon g(x)A} \Phi(x)$. $\tilde{\Phi}$ satisfies the following equation.

$$\begin{cases} \lambda \tilde{\Phi} = \mathcal{L}_1 \tilde{\Phi} + B(\varepsilon) \tilde{\Phi} & x \in I_1, \\ \partial_x \tilde{\Phi} = 0 & x = 0, K/2, \end{cases} \quad (30)$$

where, $B(\cdot)$ is operator-valued function.

$$\begin{aligned}
B : \mathbb{R} &\rightarrow \mathbb{B}((H^2(I_1))^2, X_1), \\
B(\varepsilon) &= M(\varepsilon) + \varepsilon B_1 + \varepsilon^2 B_2, \\
M(\varepsilon)\Phi &:= \begin{pmatrix} 0 & f_v^*(x)(e^{\varepsilon(\gamma-1)g(x)} - 1) \\ -\tau^{-1}f_u^*(x)(e^{\varepsilon(1-\gamma)g(x)} - 1) & 0 \end{pmatrix} \begin{pmatrix} \phi \\ \psi \end{pmatrix}, \\
B_1\Phi &:= \begin{pmatrix} -d\gamma(g''(x) + 2g'(x)\partial_x) & 0 \\ 0 & -\tau^{-1}(g''(x) + 2g'(x)\partial_x) \end{pmatrix} \begin{pmatrix} \phi \\ \psi \end{pmatrix}, \\
B_2\Phi &:= \begin{pmatrix} d(\gamma g'(x))^2 & 0 \\ 0 & \tau^{-1}(g'(x))^2 \end{pmatrix} \begin{pmatrix} \phi \\ \psi \end{pmatrix},
\end{aligned}$$

where $\gamma := \alpha/d$. Note that B is C^1 map on \mathbb{R} and satisfies $B(0) = 0$, $\|B(\varepsilon)\|_{\mathbb{B}((H^2(I_1))^2, X_1)} = O(\varepsilon)$ ($\varepsilon \rightarrow 0$). Since the boundary conditions of equation (30) do not depend on ε , the implicit function theorem is applicable to this equation.

Let us define the map \mathcal{T} as follows.

$$\begin{aligned}
\mathcal{T} : \mathbb{R} \times \mathbb{R} \times \mathcal{D}(\mathcal{L}_1) &\rightarrow \mathbb{R} \times X_1 \\
\mathcal{T}(\varepsilon, \lambda, \Phi) &:= \begin{pmatrix} \langle \Phi, \mathbf{a} \rangle_{X_1} - 1 \\ \lambda \Phi - \mathcal{L}_1 \Phi - B(\varepsilon)\Phi \end{pmatrix}
\end{aligned}$$

To reduce the degree of freedom for eigenfunctions, we define the first component of the value of \mathcal{T} as above. \mathcal{T} is C^1 map and satisfies $\mathcal{T}(0, 0, \partial_s P(\cdot; \bar{s})) = 0$ from Assumption 3.

Due to the definition of \mathcal{T} , the partial derivatives of \mathcal{T} at $(0, 0, \partial_s P)$ are represented as follows.

$$\begin{aligned}
\partial_\varepsilon \mathcal{T}(0, 0, \partial_s P)[\varepsilon] &= \begin{pmatrix} 0 \\ -\varepsilon B'(0)\partial_s P \end{pmatrix}, \\
\partial_{(\lambda, \Phi)} \mathcal{T}(0, 0, \partial_s P)[\lambda, \Phi] &= \begin{pmatrix} \langle \Phi, \mathbf{a} \rangle \\ \lambda \partial_s P - \mathcal{L}\Phi \end{pmatrix},
\end{aligned}$$

where $\partial_\varepsilon \mathcal{T}$ and $\partial_{(\lambda, \Phi)} \mathcal{T}$ represent partial derivatives with respect to $\varepsilon \in \mathbb{R}$ and $(\lambda, \Phi) \in \mathbb{R} \times \mathcal{D}(\mathcal{L}_1)$, respectively. Let us define $\mathcal{A} := \partial_{(\lambda, \Phi)} \mathcal{T}(0, 0, \partial_s P) \in \mathbb{B}(\mathbb{R} \times \mathcal{D}(\mathcal{L}_1), \mathbb{R} \times X_1)$. We obtain the following lemma.

Lemma 10.1. *There exists the inverse $\mathcal{A}^{-1} \in \mathbb{B}(\mathbb{R} \times X_1, \mathbb{R} \times \mathcal{D}(\mathcal{L}_1))$ such that*

$$\mathcal{A}^{-1}[\mu, \Psi] = \begin{pmatrix} \langle \Psi, \mathbf{a} \rangle_{X_1} \\ (\mu - \langle \Phi_1, \mathbf{a} \rangle_{X_1})\partial_s P + \Phi_1 \end{pmatrix} \quad (\mu \in \mathbb{R}, \Psi \in X_1), \quad (31)$$

where Φ_1 is a particular solution for the equation $\mathcal{L}_1 \Phi = \langle \Psi, \mathbf{a} \rangle_{X_1} \partial_s P - \Psi$ ($\Phi \in \mathcal{D}(\mathcal{L}_1)$).

Proof. Since \mathcal{A} is closed operator, it is enough to show that \mathcal{A} is bijection due to the closed graph theorem. Suppose $\mathcal{A}[\lambda, \Phi] = 0$.

$$\begin{pmatrix} \langle \Phi, \mathbf{a} \rangle \\ \lambda \partial_s P - \mathcal{L}_1 \Phi \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \end{pmatrix}. \quad (32)$$

\mathcal{L}_1 has simple eigenvalue 0, then it satisfies that $\langle \lambda \partial_s P, \mathbf{a} \rangle_{X_1} = 0$ due to Fredholm alternative. Hence, $\lambda = 0$. This means Φ is an eigenfunction corresponding

to simple eigenvalue 0. Therefore, $\Phi = r\partial_s P$ for certain constant r . Substituting Φ to the first equation of (32), it follows that

$$\langle r\partial_s P, \mathbf{a} \rangle_{X_1} = r\langle \partial_s P, \mathbf{a} \rangle_{X_1} = r = 0.$$

Then, \mathcal{A} is injection.

Next, take any $(\mu, \Psi) \in \mathbb{R} \times X_1$ and show that there exists (λ, Φ) such that $\mathcal{A}[\lambda, \Phi] = (\mu, \Psi)$. Let us consider the following equation.

$$\begin{cases} \langle \Phi, \mathbf{a} \rangle_{X_1} = \mu, \\ \lambda \partial_s P - \mathcal{L}_1 \Phi = \Psi. \end{cases} \quad (33)$$

The relation $\langle \Psi - \lambda \partial_s P, \mathbf{a} \rangle_{X_1} = 0$ is a necessary and sufficient condition for the existence of a solution to the second equation above. Therefore, if $\lambda = \langle \Psi, \mathbf{a} \rangle_{X_1}$, the general solution of the second equation of (33) is expressed as $\Phi = r\partial_s P + \Phi_1$, where r is an arbitrary constant and Φ_1 is a particular solution of the equation $\mathcal{L}_1 \Phi = \langle \Psi, \mathbf{a} \rangle_{X_1} \partial_s P - \Psi$. Substituting Φ into the left-hand side of the first equation of (33), we obtain

$$\langle \Phi, \mathbf{a} \rangle_{X_1} = \langle r\partial_s P + \Phi_1, \mathbf{a} \rangle_{X_1} = r\langle \partial_s P, \mathbf{a} \rangle_{X_1} + \langle \Phi_1, \mathbf{a} \rangle_{X_1} = r + \langle \Phi_1, \mathbf{a} \rangle_{X_1}$$

Therefore, if $r = \mu - \langle \Phi_1, \mathbf{a} \rangle_{X_1}$, Φ satisfies the first equation. Thus, the solution of (33) is represented as follows.

$$(\lambda, \Phi) = (\langle \Psi, \mathbf{a} \rangle_{X_1}, (\mu - \langle \Phi_1, \mathbf{a} \rangle_{X_1})\partial_s P + \Phi_1)$$

This concludes that \mathcal{A} is surjective. Therefore \mathcal{A}^{-1} exists and be represented by (31). \square

The implicit function theorem is applicable since Lemma 10.1 holds, and \mathcal{T} is C^1 map.

Proof of Theorem 10.1

Applying the implicit function theorem to $\mathcal{T}(0, 0, \partial_s P) = 0$, there exists some positive number ε_0 and a C^1 function $\lambda(\varepsilon)$ and C^1 map $\Phi(\varepsilon)$ taking values in $(H^2(I_1))^2$ defined on $(-\varepsilon_0, \varepsilon_0)$ such that $\mathcal{T}(\varepsilon, \lambda(\varepsilon), \Phi(\varepsilon)) = 0$ ($-\varepsilon_0 < \varepsilon < \varepsilon_0$), $\lambda(0) = 0$, $\Phi(0) = \partial_s P$, and these satisfy

$$\begin{pmatrix} \lambda'(0) \\ \Phi'(0) \end{pmatrix} = -\mathcal{A}^{-1} \partial_\varepsilon \mathcal{T}(0, 0, \partial_s P) = \begin{pmatrix} \langle B'(0) \partial_s P, \mathbf{a} \rangle_{X_1} \\ -\langle \Phi_1, \mathbf{a} \rangle_{X_1} \partial_s P + \Phi_1 \end{pmatrix}_1$$

where Φ_1 is a particular solution of the equation $\mathcal{L}_1 \Phi = B'(0) \partial_s P + \langle B'(0) \partial_s P, \mathbf{a} \rangle_{X_1} \partial_s P$.

Since $B'(0) = M'(0) + B_1$,

$$\lambda'(0) = \langle B'(0) \partial_s P, \mathbf{a} \rangle_{X_1} = \langle M'(0) \partial_s P, \mathbf{a} \rangle_{X_1} + \langle B_1 \partial_s P, \mathbf{a} \rangle_{X_1}$$

$$\begin{aligned} \langle M'(0) \partial_s P, \mathbf{a} \rangle_{X_1} &= \left\langle \begin{pmatrix} 0 & (\gamma-1)gf_v^* \\ \frac{\gamma-1}{\tau}gf_u^* & 0 \end{pmatrix} \begin{pmatrix} \partial_s u^* \\ \partial_s v^* \end{pmatrix}, \frac{2}{K} \begin{pmatrix} 1 \\ \tau \end{pmatrix} \right\rangle_{X_1} \\ &= \frac{2}{K} \left\langle \begin{pmatrix} (\gamma-1)gf_v^* \partial_s v^* \\ \frac{\gamma-1}{\tau}gf_u^* \partial_s u^* \end{pmatrix}, \begin{pmatrix} 1 \\ \tau \end{pmatrix} \right\rangle_{X_1} \\ &= \frac{2(\gamma-1)}{K} \int_{I_1} g(x) \{f_u^*(x) \partial_s u^*(x; \bar{s}) + f_v^*(x) \partial_s v^*(x; \bar{s})\} dx \end{aligned}$$

$\partial_s P(x; \bar{s})$ is the eigenfunction corresponding to 0 in \mathcal{L}_1 , then it holds that

$$f_u^*(x) \partial_s u^*(x; \bar{s}) + f_v^*(x) \partial_s v^*(x; \bar{s}) = -d \partial_x^2 u^*(x; \bar{s}) = \partial_x^2 v_s^*(x; \bar{s}).$$

From above, it follows that

$$\begin{aligned} \langle M'(0) \partial_s P, \mathbf{a} \rangle_{X_1} &= -\frac{2}{K} \int_{I_1} g(x) \{ \gamma d \partial_x^2 u^*(x; \bar{s}) + \partial_x^2 v_s^*(x; \bar{s}) \} dx \\ &= -\frac{2}{K} \int_{I_1} g(x) \partial_x^2 \{ \alpha u^*(x; \bar{s}) + v_s^*(x; \bar{s}) \} dx \\ &= -\frac{2}{K} [g(x) \partial_x \{ \alpha \partial_s u^*(x; \bar{s}) + \partial_s v^*(x; \bar{s}) \}]_{x=0}^{x=K/2} \quad (34) \\ &\quad + \frac{2}{K} \int_{I_1} g'(x) \partial_x \{ \alpha \partial_s u^*(x; \bar{s}) + \partial_s v^*(x; \bar{s}) \} dx \\ &= \frac{2}{K} \int_{I_1} g'(x) \partial_x \{ \alpha \partial_s u^*(x; \bar{s}) + \partial_s v^*(x; \bar{s}) \} dx. \quad (35) \end{aligned}$$

On the other hand,

$$\begin{aligned} \langle B_1 \partial_s P, \mathbf{a} \rangle_{X_1} &= \left\langle \begin{pmatrix} -d\gamma(g'' \partial_s u^*) + 2g' \partial_x \partial_s u^* \\ -\tau^{-1}(g'' \partial_s v^* + 2g' \partial_x \partial_s v^*) \end{pmatrix}, \frac{2}{K} \begin{pmatrix} 1 \\ \tau \end{pmatrix} \right\rangle_{X_1} \\ &= -\frac{2}{K} \int_{I_1} \{ d\gamma(g''(x) \partial_s u^*(x; \bar{s}) + 2g'(x) \partial_x \partial_s u^*(x; \bar{s})) \\ &\quad + g''(x) \partial_s v^*(x; \bar{s}) + 2g'(x) \partial_x \partial_s v^*(x; \bar{s}) \} dx \\ &= -\frac{2}{K} \int_{I_1} \{ d\gamma(g''(x) \partial_s u^*(x; \bar{s}) + 2g'(x) \partial_x \partial_s u^*(x; \bar{s})) \\ &\quad + g''(x) \partial_s v^*(x; \bar{s}) + 2g'(x) \partial_x \partial_s v^*(x; \bar{s}) \} dx \\ &= -\frac{2}{K} \int_{I_1} \{ g''(x) (\alpha \partial_s u^*(x; \bar{s}) + \partial_s v^*(x; \bar{s}) + 2g'(x) \partial_x (\partial_s u^*(x; \bar{s}) + \partial_s v^*(x; \bar{s}))) \} dx \\ &= -\frac{2}{K} \int_{I_1} \{ g''(x) (\alpha \partial_s u^*(x; \bar{s}) + \partial_s v^*(x; \bar{s})) \} dx \\ &\quad - \frac{4}{K} \int_{I_1} \{ g'(x) \partial_x (\partial_s u^*(x; \bar{s}) + \partial_s v^*(x; \bar{s})) \} dx \\ &= -\frac{2}{K} [g'(x) (\alpha \partial_s u^* + \partial_s v^*)]_{x=0}^{x=K/2} + \frac{2}{K} \int_{I_1} \{ g'(x) \partial_x (\alpha \partial_s u^*(x; \bar{s}) + \partial_s v^*(x; \bar{s})) \} dx \\ &\quad - \frac{4}{K} \int_{I_1} \{ g'(x) \partial_x (\partial_s u^*(x; \bar{s}) + \partial_s v^*(x; \bar{s})) \} dx \\ &= -\frac{2}{K} g'(K/2) (\alpha \partial_s u^* + \partial_s v^*)|_{x=K/2} - \frac{2}{K} \int_{I_1} \{ g'(x) \partial_x (\partial_s u^*(x; \bar{s}) + \partial_s v^*(x; \bar{s})) \} dx \\ &= -\frac{4\varepsilon}{K} (\alpha \partial_s u^* + \partial_s v^*)|_{x=K/2} - \langle M'(0) \partial_s P, \mathbf{a} \rangle_{X_1}. \quad (36) \end{aligned}$$

(35) and (36) lead to the desired assertion. \square

11 Summary and discussion.

We have considered the stability of the 2-mode stationary solution $P^2(x; \bar{s})$ in the mass-conserved reaction-diffusion compartment model. The reaction-

diffusion compartment model becomes formally original mass-conserved reaction-diffusion system (20) when the parameter ε in the boundary condition (23) tends to infinity. Therefore, we expect the stability of the stationary solution in the compartmental model leads to the one of (20).

In this study, we analyze the linearized eigenvalue problem (27) around 2-mode stationary solution P^2 under Assumption 3 and 4. We construct P^2 by even expansion of the stable 1-mode stationary solution P in the mass-conserved reaction-diffusion system (24).

The linearized eigenvalue problem (27) can be decomposed into even and odd parts of eigenfunctions. The even and odd parts are eigenfunctions for the eigenvalue problem with $(N.B.C)$ on I_1 and for the eigenvalue problem with Neumann and Robin boundary conditions, respectively. From Assumption 4, the eigenvalues in (28) do not affect the stability of the stationary solution, so we only need to consider (29). The boundary condition of (29) includes the parameter ε , which corresponds to the strength of the diffusive coupling. From Assumption 4, when $\varepsilon = 0$, $\{0, \partial_s P\}$ is eigenpair in (29). By using the implicit function theorem, we construct eigenvalues and eigenfunctions $\{\lambda(\varepsilon), \Phi(\varepsilon)\}$ in the neighborhood of $\{0, \partial_s P\}$ when ε is small enough, and obtain the Theorem 10.1. From this result, we obtain the sufficient condition of instability of P^2 in the case $0 < \varepsilon \ll 1$. We also proved rigorously that $\Phi(\varepsilon)$ is approximated by $\partial_s P$ if ε is sufficiently small. These eigenfunctions correspond to the pattern dynamics observed in mass-conserved reaction-diffusion systems.

The present framework can be generalized to N -mode stationary solutions corresponding to more complex patterns. Dividing the original interval $I = (0, K)$ into N compartments, where every compartment has equal length, the following expression is given.

$$\begin{cases} \partial_t u_j = d\partial_x^2 u_j + f(u_j, v_j) & (t > 0, x \in I_j), \\ \tau \partial_t v_j = \partial_x^2 v_j - f(u_j, v_j) & (t > 0, x \in I_j), \\ \partial_x u_1 = \partial_x v_1 = 0 & (t > 0, x = 0), \\ d\partial_x u_j = \varepsilon \alpha(u_2 - u_1) = d\partial_x u_2 & (t > 0, x = jK/N, j = 1, \dots, N-1), \\ \partial_x v_j = \varepsilon(v_2 - v_1) = \partial_x v_2, & (t > 0, x = jK/N, j = 1, \dots, N-1), \\ \partial_s u_N = \partial_x v_N = 0 & (t > 0, x = K), \end{cases} \quad (37)$$

where $I_j := ((j-1)K/N, jK/N)$. Let (u_j, v_j) be defined on I_j . For the above equations, like the case of 2-mode stationary solutions, we can construct N -mode stationary solutions by expanding the 1-mode stationary solutions on I_1 . However, when N is 3 or more, the decomposition of even and odd parts, as in the linearized eigenvalue problem for 2-mode stationary solutions, is not applicable. The generalization to N -mode stationary solutions is left to future work.

In this study, we consider the linearized eigenvalue problem in the compartmental model, aiming at the stability analysis of the 2-mode stationary solution in (20). Therefore, it is the essential question whether the analysis of the eigenvalue problem (27) leads to the stability of the stationary solution in the original equation (20). To study this question, let us consider the odd part equation (29) again. In the view of the boundary conditions of (29), we can expect that if $\varepsilon \rightarrow \infty$, the Robin boundary condition turns to Dirichlet boundary condition, namely $\Phi(K/2) = 0$. Therefore, if eigenvalues and eigenfunctions $\{\lambda(\varepsilon), \Phi(\varepsilon)\}$

constructed in the present study converges to certain eigenpair $\{\lambda^\infty, \Phi^\infty\}$ when $\varepsilon \rightarrow \infty$, these satisfy the following.

$$\begin{cases} \lambda^\infty \Phi^\infty = \mathcal{L}\Phi^\infty & (x \in I_1), \\ \partial_x \Phi^\infty = 0 & (x = 0), \\ \Phi^\infty = 0 & (x = K/2). \end{cases} \quad (38)$$

The odd extension of Φ^∞ is an eigenfunction corresponds to λ^∞ for linearized eigenvalue problem about the 2-mode stationary solution of the original mass-conserved reaction-diffusion system (20). If the real part of λ^∞ is positive, the 2-mode stationary solution is unstable. Thus, the stability analysis in the compartment model is expected to lead to the stability analysis in the original model equation. However, the above discussion is still a formal one. Mathematically rigorous analysis for the existence of $\{\lambda^\infty, \Phi^\infty\}$ and the sign of λ^∞ are left to the future work.

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A Appendix

A.1 An example of Assumption 3, 4.

This Appendix introduces an example satisfying Assumption 3, 4. We consider the following equations.

$$\begin{cases} \partial_t u = d\partial_x^2 u + u(1 - u^2) + v & (x \in (-l/2, l/2)), \\ \partial_t v = \partial_x^2 v - u(1 - u^2) - v & (x \in (-l/2, l/2)), \\ (N.B.C), \end{cases} \quad (39)$$

where $0 < d < 1$. This equation is a mass-conserved reaction-diffusion system with the reaction term $f(u, v) = u(1 - u^2) + v$ and $\tau = 1$. l is a positive constant, and the interval is rewritten as $(-l/2, l/2)$ for convenience. We rewrite the interval as $I = (-l/2, l/2)$.

The stationary problem in (39) is expressed as follows.

$$\begin{cases} d\partial_x^2 u + u(1 - u^2) + v = 0 & (x \in I), \\ \partial_x^2 v - u(1 - u^2) - v = 0 & (x \in I), \\ \frac{1}{l} \int_I (u + v) dx = s, \\ (N.B.C). \end{cases} \quad (40)$$

Let (u, v) be a solution of (40). There exists a certain constant c such that $du + v \equiv c$. This c can be computed from the conservation law.

$$c = s - \frac{1-d}{l} \int_I u(x) dx.$$

Therefore, the above stationary problem can be expressed as follows.

$$\begin{cases} d\partial_x^2 u + u(1 - d - u^2) + \left(s - \frac{1-d}{l} \int_I u(x) dx\right) = 0 & (x \in I), \\ (N.B.C). \end{cases} \quad (41)$$

Transforming the variables in (41) as $x \rightarrow \frac{2}{l}x$, $u \rightarrow \frac{u}{\sqrt{1-d}}$, equation (41) is expressed as follows.

$$\begin{cases} \tilde{d}\partial_x^2 u + u(1 - u^2) + \frac{s}{(1-d)^{\frac{3}{2}}} - \langle u \rangle = 0 & (x \in (-1, 1)), \\ (N.B.C), \end{cases} \quad (42)$$

where $\tilde{d} := \frac{d}{1-d} \frac{4}{l^2}$, and $\langle u \rangle = \frac{1}{2} \int_{-1}^1 u(x) dx$ in the following.

Considering the case $s = \langle u \rangle = 0$ in the above stationary problem,

$$\begin{cases} \tilde{d}\partial_x^2 u + u(1 - u^2) = 0 & (x \in (-1, 1)), \\ (N.B.C). \end{cases} \quad (43)$$

This problem is the same as the stationary problem for the Allen-Cahn equation.

When $0 < \tilde{d} < \frac{4}{\pi^2}$, there exists a nonconstant solution to (43). In particular, it is known that Jacobi's elliptic function can specifically express the solution. Therefore, in the following, suppose $d < \frac{l^2}{l^2 + \pi^2}$.

Let $\text{sn}(x, k)$ be a Jacobi elliptic function with $-1 < k < 1$, where k is the parameter of the elliptic function. $\text{sn}(x, k)$ is the inverse function of the following elliptic integral.

$$\text{sn}^{-1}(y, k) := \int_0^y \frac{dt}{\sqrt{1-t^2}\sqrt{1-k^2t^2}} \quad (-1 < y < 1).$$

Let us denote $K(k)$ and $E(k)$ as the complete elliptic integrals of the first and second kinds.

$$K(k) = \int_0^1 \frac{dt}{\sqrt{1-t^2}\sqrt{1-k^2t^2}}, \quad E(k) = \int_0^1 \frac{\sqrt{1-k^2t^2}}{\sqrt{1-t^2}} dt$$

We consider the case $0 < k < 1$ in the following part. Let us define $\alpha \in (0, 1)$ as unique solution of the relation $k = \sqrt{\frac{\alpha^2}{2-\alpha^2}}$. The exact solution of (43) can be expressed as follows.

$$u^*(x; \tilde{d}(k)) = \frac{\sqrt{2}k}{1+k^2} \text{sn}(K(k)x, k) \quad (x \in (-1, 1)), \quad \tilde{d}(k) := \frac{1}{(1+k^2)\{K(k)\}^2}$$

We note that it follows that $0 < \tilde{d}(k) < \frac{4}{\pi^2}$ in the case $0 < k < 1$, u^* is odd function on $(-1, 1)$, and $u^*(x; \tilde{d}(-k)) = -u^*(x; \tilde{d}(k))$ ($k \in (0, 1)$).

Let us omit to show the parameter and write $u^*(x)$ in place of $u^*(x; \tilde{d}(k))$. Let us put $v^*(x) := -\tilde{d}u^*(x)$, then $S(x) := \sqrt{1-\tilde{d}}(u^*((l/2)x), v^*((l/2)x))$ is the stationary solution of the equation (40).

A.2 Proof.

In the following, we show that S satisfies Assumption 3, 4. First, prepare the following symbols.

$$\begin{aligned} C_N^2[-1, 1] &:= \{u \in C^2[-1, 1] | u' = 0 \text{ } (x = \pm 1)\}, \\ H_N^2(-1, 1) &:= \{u \in H^2(-1, 1) | \partial_x u = 0 \text{ } (x = \pm 1)\}, \\ G : H_N^2(-1, 1) \times \mathbb{R} &\rightarrow L^2(-1, -1) \\ G(u, s) &:= \tilde{d}\partial_x^2 u + u(1-u^2) + \frac{s}{(1-d)^{\frac{3}{2}}} - \langle u \rangle \end{aligned}$$

Note that G is a C^1 map and satisfies $G(u^*, 0) = 0$.

We consider the following linearized eigenvalue problem for $u^*(x)$ to (42).

$$\begin{aligned} L : L^2(-1, 1) &\rightarrow L^2(-1, 1) \\ L\phi &:= \tilde{d}\partial_x^2 \phi + \{1 - 3(u^*)^2\}\phi - \langle \phi \rangle = \mu\phi \\ \mathcal{D}(L) &:= H_N^2(-1, 1), \end{aligned}$$

where, μ is eigenvalue of L , $L_0\phi := \tilde{d}\partial_x^2 \phi + \{1 - 3(u^*)^2\}\phi$, and $A\phi := -\langle \phi \rangle$.

Note that all eigenvalue of L is a real number since L is a self-adjoint operator. The following lemma holds.

Lemma A.1 Suppose all eigenvalues of L are negative, then S satisfies Assumption 3, 4.

Proof. Since 0 is not eigenvalue of L , L^{-1} exists. From the implicit function theorem, there exists a C^1 -curve $\varphi(\cdot; s) \in \mathcal{D}(L)$ for s in a neighborhood of $s = 0$, and $\varphi(\cdot; s)$ satisfy

$$\tilde{d}\partial_x^2\varphi + \varphi(1 - \varphi^2) + \frac{s}{(1 - d)^{\frac{3}{2}}} - \langle \varphi \rangle = 0.$$

By applying the Sobolev embedding theorem, we can choose $\varphi(\cdot; s)$ as C^1 -curve in C_N^2 . Therefore, Assumption 3 holds. For the proof about Assumption 4, we note that the eigenvalues for the linearized eigenvalue problem for $u^*(x)$ to (42) are the same as the ones for $\sqrt{1 - d}u^*((2/l)x)$ to (41). From this fact, Theorem 1.3 of [16] is applicable, which lead to show Assumption 4 holds for S \square

We prove all eigenvalue of L is negative in the following part. Let $\{\kappa_n\}_{n=0}^\infty$ be eigenvalues of L_0 satisfying $\kappa_0 > \kappa_1 > \kappa_2 > \dots$. We note that κ_0, κ_1 and κ_2 are represented as following [29].

$$\kappa_0 = -1 + \sqrt{1 + 3(1 - \alpha^2)^2} > 0, \kappa_1 = -\frac{3}{2}\alpha^2 < 0, \kappa_2 = -1 - \sqrt{1 + 3(1 - \alpha^2)^2} < 0$$

Especially, L_0 has only one positive eigenvalue.

By Sherman-Morrison formula, when $\lambda \notin \sigma(L_0)$, necessary and sufficient condition of $\lambda \in \sigma(L)$ is $\langle (L_0 - \lambda)^{-1}[1] \rangle = 1$. Let us define $H(k, \lambda) := \langle (L_0 - \lambda)^{-1}[1] \rangle$, then

$$H(k, \lambda) = \frac{6(1 + k^2) \left(1 - \frac{E(k)}{K(k)}\right) - (\lambda + 3)(1 + k^2)^2}{(k^2 + 1)^2(\lambda^2 + 2\lambda) - 3(k^2 - 1)^2} \quad (44)$$

This fomula is derived by calculating $(L_0 - \lambda)(c_1(u^*)^2 + c_2) = 1$ and comparing the coefficients c_1, c_2 on both sides [11] with using the following fomula.

$$\langle (u^*)^2 \rangle = \frac{2}{1 + k^2} \left(1 - \frac{E(k)}{K(k)}\right)$$

In the following, we will show how $\lambda \notin \sigma(L)$ when $\lambda \geq 0$.

(Case.1 $0 \leq \lambda < \kappa_0$): First, we consider the case $\lambda = 0$.

$$H(k, 0) = \frac{1 + k^2}{(1 - k^2)^2} \left\{ 1 + k^2 - 2 \left(1 - \frac{E(k)}{K(k)}\right) \right\}.$$

Due to the fact $E(k) > K(k)(1 - k^2)$ ($0 < k < 1$),

$$H(k, 0) > \frac{1 + k^2}{1 - k^2} > 1 \quad (0 < k < 1). \quad (45)$$

Thus, for $0 < k < 1$, $\lambda = 0$ is not eigenvalue of L . This means that L has a bounded inverse.

Next, we consider the case $0 < \lambda < \kappa_0$. From $k = \sqrt{\frac{\alpha^2}{2-\alpha^2}}$, dividing the denominator and numerator of (44) by $(k^2 + 1)^2$,

$$H(\alpha, \lambda) = \frac{3(2 - \alpha^2) \left(1 - \frac{E}{K}\right) - (\lambda + 3)}{(\lambda^2 + 2\lambda) - 3(1 - \alpha^2)^2}.$$

Hence

$$H_\lambda = \frac{3(1 - \alpha^2)^2 + (\lambda^2 + 6\lambda + 6) - 6(\lambda + 1)(2 - \alpha^2)(1 - E/K)}{\{(\lambda^2 + 2\lambda) - 3(1 - \alpha^2)^2\}^2}$$

Since $E(k) > K(k)(1 - k^2)$ ($0 < k < 1$), it holds that $1 - E/K < k^2 = \frac{\alpha^2}{2-\alpha^2}$. Therefore,

$$H_\lambda > \frac{3(1 - \alpha^2)^2 + (\lambda^2 + 6\lambda + 6) - 6(\lambda + 1)\alpha^2}{\{(\lambda^2 + 2\lambda) - 3(1 - \alpha^2)^2\}^2} = \frac{3(1 - \alpha^2)^2 + \lambda^2 + 6(\lambda + 1)(1 - \alpha^2)}{\{(\lambda^2 + 2\lambda) - 3(1 - \alpha^2)^2\}^2}.$$

Thus $H_\lambda > 0$ when $\lambda \geq 0$. This inequality and (45) conclude that $H(k, \lambda) > 1$ ($0 < k < 1$). Therefore, when $0 < \lambda < \kappa_0$, $\lambda \notin \sigma(L)$.

(Case.2 $\kappa_0 < \lambda$): When $0 < k < 1$, $H(k, \lambda) < 0$. Then, $H(k, \lambda) \neq 1$. This implies $\lambda \notin \sigma(L)$.

(Case. 3 $\lambda = \kappa_0$): Suppose $\kappa_0 \in \sigma(L)$ and we will show a contradiction. Let $\psi(x)$ be the corresponding eigenfunction. Hence

$$\begin{aligned} (L - \kappa_0)\psi &= (L_0 + A - \kappa_0)\psi = 0 \\ (L_0 - \kappa_0)\psi &= -A\psi \end{aligned}$$

Let $h(x) := -A\psi$ and consider the next problem.

$$(L_0 - \kappa_0)\phi = h(x)$$

Since κ_0 is the eigenvalue of L_0 , the necessary and sufficient condition for the existence of a solution to the above equation is

$$\langle \eta_0, h \rangle = 0,$$

where $\langle \cdot, \cdot \rangle$ denotes inner product on $L^2(-1, 1)$. Hence

$$\langle \eta_0, h \rangle = -\langle \eta_0, A\psi \rangle = \langle \psi \rangle \langle \eta_0, 1 \rangle = 0$$

Note that κ_0 is a simple eigenvalue, and η_0 is not sign-changing on $(-1, 1)$ from Sturm-Liouville theory. Then $\langle \eta_0, 1 \rangle \neq 0$. It concludes $\langle \psi \rangle = 0$.

From above, $A\psi = 0$. Therefore, ψ is an eigenfunction corresponding to the eigenvalue κ_0 of L_0 . From the simplicity of κ_0 , $\psi = r\eta_0$ for certain constant r . On the other hand, since $\langle \psi \rangle = 0$, $r = 0$. This is inconsistent with the assumption that ψ is an eigenfunction. Therefore $\kappa_0 \notin \sigma(L)$.

References

- [1] D. M BURLEY. Mathematical model of a kidney machine. *Mathematical Spectrum*, 8(3):69–75, 1975.

- [2] Jann-Long Chern, Yoshihisa Morita, and Tien-Tsan Shieh. Asymptotic behavior of equilibrium states of reaction–diffusion systems with mass conservation. *Journal of Differential Equations*, 264(2):550–574, 2018.
- [3] Rocky Diegmiller, Hadrien Montanelli, Cyrill B Muratov, and Stanislav Y Shvartsman. Spherical caps in cell polarization. *Biophysical journal*, 115(1):26–30, 2018.
- [4] Shin-Ichiro Ei and Shyuh-Yaur Tzeng. Spike solutions for a mass conservation reaction-diffusion system. *Discrete and Continuous Dynamical Systems*, 40(6):3357–3374, 2020.
- [5] Shuji Ishihara, Mikiya Otsuji, and Atsushi Mochizuki. Transient and steady state of mass-conserved reaction-diffusion systems. *Physical Review E*, 75(1):015203, 2007.
- [6] Shuichi Jimbo and Yoshihisa Morita. Lyapunov function and spectrum comparison for a reaction–diffusion system with mass conservation. *Journal of Differential Equations*, 255(7):1657–1683, 2013.
- [7] Kousuke Kuto and Tohru Tsujikawa. Bifurcation structure of steady-states for bistable equations with nonlocal constraint. In *Conference Publications*, volume 2013, pages 467–476. Conference Publications, 2013.
- [8] Masataka Kuwamura, Sungrim Seirin-Lee, and Shin-ichiro Ei. Dynamics of localized unimodal patterns in reaction-diffusion systems for cell polarization by extracellular signaling. *SIAM Journal on Applied Mathematics*, 78(6):3238–3257, 2018.
- [9] Evangelos Latos, Yoshihisa Morita, and Takashi Suzuki. Stability and spectral comparison of a reaction-diffusion system with mass conservation. *Journal of Dynamics and Differential Equations*, 30(2):823–844, 2018.
- [10] Sungrim Seirin Lee and Tatsuo Shibata. Self-organization and advective transport in the cell polarity formation for asymmetric cell division. *Journal of theoretical biology*, 382:1–14, 2015.
- [11] Yasuhito Miyamoto, Tatsuki Mori, Tohru Tsujikawa, and Shoji Yotsutani. Stability for stationary solutions of a nonlocal allen-cahn equation. *Journal of Differential Equations*, 275:581–597, 2021.
- [12] Tatsuki Mori, Kousuke Kuto, Masaharu Nagayama, Tohru Tsujikawa, and Shoji Yotsutani. Global bifurcation sheet and diagrams of wave-pinning in a reaction-diffusion model for cell polarization. In *Conference Publications*, volume 2015, pages 861–877. Conference Publications, 2015.
- [13] Yoichiro Mori, Alexandra Jilkine, and Leah Edelstein-Keshet. Wave-pinning and cell polarity from a bistable reaction-diffusion system. *Biophysical journal*, 94(9):3684–3697, 2008.
- [14] Yoichiro Mori, Alexandra Jilkine, and Leah Edelstein-Keshet. Asymptotic and bifurcation analysis of wave-pinning in a reaction-diffusion model for cell polarization. *SIAM journal on applied mathematics*, 71(4):1401–1427, 2011.

- [15] Yoshihisa Morita. Spectrum comparison for a conserved reaction-diffusion system with a variational property. *J. Appl. Anal. Comput.*, 2:57–71, 2012.
- [16] Yoshihisa Morita and Toshiyuki Ogawa. Stability and bifurcation of non-constant solutions to a reaction–diffusion system with conservation of mass. *Nonlinearity*, 23(6):1387–1411, 2010.
- [17] Yoshihisa Morita and Kunimochi Sakamoto. Turing type instability in a diffusion model with mass transport on the boundary. *Discrete and Continuous Dynamical Systems*, 40(6):3813–3836, 2020.
- [18] Yoshihisa Morita and Sungrim Seirin-Lee. Long time behavior and stable patterns in high-dimensional polarity models of asymmetric cell division. *Journal of Mathematical Biology*, 82:1–38, 2021.
- [19] Seán M Murray and Victor Sourjik. Self-organization and positioning of bacterial protein clusters. *Nature Physics*, 13(10):1006–1013, 2017.
- [20] Toshiko Ogiwara, Danielle Hilhorst, and Hiroshi Matano. Convergence and structure theorems for order-preserving dynamical systems with mass conservation. *Discrete and Continuous Dynamical Systems*, 40(6):3883–3907, 2020.
- [21] Mikiya Otsuji, Shuji Ishihara, Carl Co, Kozo Kaibuchi, Atsushi Mochizuki, and Shinya Kuroda. A mass conserved reaction–diffusion system captures properties of cell polarity. *PLoS computational biology*, 3(6):e108, 2007.
- [22] M. H. Protter and H. F. Weinberger. *Maximum Principles in Differential Equations*. Springer, New York, 1984.
- [23] Andreas Rätz and Matthias Röger. Turing instabilities in a mathematical model for signaling networks. *Journal of mathematical biology*, 65:1215–1244, 2012.
- [24] Andreas Rätz and Matthias Röger. Symmetry breaking in a bulk–surface reaction–diffusion model for signalling networks. *Nonlinearity*, 27(8):1805, 2014.
- [25] Takashi Okuda Sakamoto. Hopf bifurcation in a reaction–diffusion system with conservation of mass. *Nonlinearity*, 26(7):2027, 2013.
- [26] Sungrim Seirin-Lee, Tsubasa Sukekawa, Tomohiro Nakahara, Hiroshi Ishii, and Shin-Ichiro Ei. Transitions to slow or fast diffusions provide a general property for in-phase or anti-phase polarity in a cell. *Journal of Mathematical Biology*, 80(6):1885–1917, 2020.
- [27] Takashi Suzuki and Souhei Tasaki. Stationary fix-caginalp equation with non-local term. *Nonlinear Analysis: Theory, Methods Applications*, 71(3-4):1329–1349, 2009.
- [28] Alan Mathison Turing. The chemical basis of morphogenesis. *Bulletin of mathematical biology*, 52(1-2):153–197, 1990.
- [29] Tohru Wakasa. Exact eigenvalues and eigenfunctions associated with linearization for chafee-infante problem. *Funkcialaj Ekvacioj*, 49(2):321–336, 2006.