

TRAVELING WAVE FOR A COUPLED INCOMPRESSIBLE DARCY'S FREE BOUNDARY MODEL WITH UNDERCOOLING EFFECT AND SURFACE TENSION

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Abstract. We present a two-dimensional free-boundary Hele-Shaw model to describe certain aspects of eukaryotic cell motility on substrates. The key ingredients of this model are Darcy's law for the overdamping motion of the cytoplasm as a confined viscous droplet, with a particular boundary condition for the Young–Laplace equation. This particular condition describes the active force induced by the cytoskeleton, which can be generated in cells either by actin polymerization against the membrane or by actomyosin contraction of cortical filaments, which adhere to the membrane. In addition, in this model we take into account the friction exerted by the membrane on the substrate. First, we study the linear stability of the steady state and prove that above a threshold, the disk is linearly unstable. This analysis highlights the stabilizing effect of undercooling. Then, using a bifurcation argument, we prove the existence of traveling waves that describe a persistent motion in cell migration and justify the relevance of the model. We emphasize in particular that the friction exerted by the membrane on the substrate has a stabilizing effect on cell dynamics.

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1. INTRODUCTION

1.1. Biological context and modeling

Cell motility is a biological process involved in numerous biological phenomena such as immune response, wound healing, embryonic development, and cancer propagation. Although different types of cell migration exist, they are all governed by the same mechanisms and rely on a cell's ability to polarize. This means that the cell is able to break its internal symmetry and possesses a defined front and rear [16, 36]. Once the cell is polarized, cell migration can occur. This relies on cytoskeletal activity via the polymerization of actin filaments at the front of the cell, and the contraction of acto-myosin fibers that push the cytoskeleton from rear to front [1].

The cell is enclosed by the plasma membrane, which protects and separates the contents of the cell from the external environment. It also enables communication with the external environment. The plasma membrane

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contributes to the mechanical properties of cell movement via membrane tension. Membrane tension induces an opposite force to membrane extension. It results from the inextensible nature of the membrane, which creates in-plane tension, and from the energy derived from adhesion between the cytoskeleton and the membrane. As the cell is deformed, membrane tension changes rapidly, causing the cell surface tension to vary. Membrane tension also regulates polarization between the front and rear of the cell [40].

In this paper, we propose and study a model describing this phenomenon, taking into account the action of the membrane on cell motility. The proposed model is a free-boundary model given by:

$$\begin{cases} \mathbf{u} + \nabla P = 0 & \text{in } \Omega(t), & (1.1a) \\ \operatorname{div}(\mathbf{u}) = 0 & \text{in } \Omega(t), & (1.1b) \\ V_n = \mathbf{u} \cdot \mathbf{n} & \text{on } \partial\Omega(t), & (1.1c) \\ P = \gamma\kappa + \chi_c f_{\text{act}}(c) + \chi_u f_{\text{und}}(V_n) & \text{on } \partial\Omega(t), & (1.1d) \\ \partial_t c = \operatorname{div}(\nabla c - (1-a)\mathbf{u}c) & \text{in } \Omega(t), & (1.1e) \\ (\nabla c + a\mathbf{u}c) \cdot \mathbf{n} = 0 & \text{on } \partial\Omega(t), & (1.1f) \\ c(0, \mathbf{x}) = c^{\text{in}}(\mathbf{x}) & \text{in } \Omega^{\text{in}}, & (1.1g) \\ \Omega(0) = \Omega^{\text{in}}. & & (1.1h) \end{cases}$$

This free-boundary model is in continuity with the model proposed by [25]. The cell is modeled by a droplet of incompressible fluid confined between two parallel plates and containing polarity markers of concentration c . $\mathbf{u}$ denotes the gap-averaged planar flow and P the pressure of the fluid. Thin-film lubrication and Hele-Shaw approximations yield velocity $\mathbf{u}$ and pressure P satisfying Darcy's law (1.1a). The kinematic condition (1.1c) indicates that the normal velocity of the sharp interface is given by the normal velocity of the fluid.

Initially, the fluid is contained in $\Omega^{\text{in}} \subset \mathbb{R}^2$ a simply connected bounded open. c^{in} is a given smooth non-negative function defined on Ω^{in} , which represents the concentration of a solute at time $t = 0$. In (1.1), we seek a family of open sets $\Omega(t)$ of $\mathbb{R}^2$ with boundary $\partial\Omega(t)$, whose curvature (positive for a circle) is κ , and a concentration function $c(t, \mathbf{x})$ defined on $\Omega(t)$.

The cell membrane is modeled by the boundary $\partial\Omega(t)$. The action of the membrane on the cell is modeled by the force $-\chi_u f_{\text{und}}(V_n)$ where $\chi_u > 0$ and V_n is the normal velocity of the boundary. In a different context, this type of expression is found in kinetic undercooling issues in the context of liquid undercooling [3, 15, 18]. We assume that f_{und} satisfies:

$$f_{\text{und}} \in C^1(\mathbb{R}), \quad (1.2a)$$

$$f_{\text{und}} \text{ is an odd and increasing function,} \quad (1.2b)$$

$$f'_{\text{und}}(0) > 0. \quad (1.2c)$$

The case $\chi_u = 0$ means neglecting the action of the cell membrane and considering that it behaves in the same way as the rest of the cell. In this case, we find the model of [25] which is studied in [2].

In the same way as in [25], we assume that polarity markers are rear markers, meaning that the rear part of the cell is defined by the area with the highest concentration of markers. These markers induce an active force at the edge of the cell given by $-\chi_c f_{\text{act}}(c)$ with $\chi_c > 0$ and f_{act} satisfying:

$$f_{\text{act}} \in C^1(\mathbb{R}^+), \quad (1.3a)$$

$$f_{\text{act}} \text{ is an increasing function,} \quad (1.3b)$$

$$f_{\text{act}}(0) = 0, \quad (1.3c)$$

$$\lim_{x \rightarrow +\infty} f_{\text{act}}(x) = L_c < +\infty. \quad (1.3d)$$

This force is used to model the action of the cytoskeleton on the cell.

The boundary condition (1.1d) is obtained as the balance of the forces acting on the membrane and can be seen as a perturbation of the Young–Laplace equation. γ designates the effective surface tension and is given, κ designates the curvature.

To close the system, the internal solute transport problem is formulated in (1.1e) and (1.1f). In the bulk $\Omega(t)$, fast adsorption on the top and bottom plates (or onto an adhered cortex) is assumed. With rapid on and off rates, the quasi-2D transport dynamics are given by (1.1e) and (1.1f) where $a \in [0, 1]$ is the steady fraction of adsorbed molecules not convected by the average flow and the effective diffusion coefficient is assumed to be 1.

In (1.1f), a zero solute flux on the moving boundary $\partial\Omega(t)$ is imposed. Simply put, the solute is effectively convected at a slower velocity than that of the fluid. Hence, its concentration decreases (increases) towards an advancing (retracting) front.

The solute can be any cytoplasmic protein controlling the active force-generation or adhesion machinery. In this work, it is assumed that the concentration c either induces an inwards pulling force or inhibits an outwards pushing force.

Formally, the boundary condition (1.1f) induces the conservation of molecular content over time, that is, for all time t it holds that:

$$M := \int_{\Omega(t)} c(t, x, y) \, dx \, dy = \int_{\Omega^{\text{in}}} c^{\text{in}}(x, y) \, dx \, dy. \quad (1.4)$$

From the incompressibility constraint (1.1b) it follows that the cell domain area $|\Omega^{\text{in}}|$ is constant over time.

Let us briefly comment on the existing literature concerning (1.1). Moving interface problems have raised many interesting and challenging mathematical issues. A well-known example is the Stefan problem, which describes the dynamics of the boundary between ice and water. In the biophysical community, we find a large number of free boundary models to describe tumor and tissue growth, cell motility, and other phenomena. We refer to [39, 41] for a review.

Most of them are formulated through a fluid approach with surface tension. Some tumor growth models (*e.g.* [19–21]) resemble our model (1.1). However, there is an important difference: tumor growth naturally involves expanding domain while we consider here incompressible solutions. In the context of the motility of eukaryotic cells on substrates, various free boundary problems have been derived and studied, see [5–8, 29, 30, 37]. The existence of traveling wave solutions for these models is proved in [5, 6, 8, 37].

In the 1D setting, the Keller–Segel system with free boundaries as a model for contraction driven motility was introduced and studied in [32–35].

In the context of sharp interface limit, some models for cell motility were studied in [13, 14]. These models differ from our approach in that no polarity markers are involved. However, they are similar to our model in that they take into account an overcooling force at the edge of the cell (the sign is opposite to that of an undercooling force). We note that traveling wave solutions for a moving boundary problem of Hele–Shaw type have been studied in the case with kinetic undercooling regularization in [22]. This model, which models the motion of a bubble in an exterior Hele–Shaw flow, differs from our model in its point of view and in the absence of polarity markers and coupling with them.

1.2. Comparing with [5, 6, 8, 37] and [2, 24]

In the model presented here, area conservation is inherent due to the incompressibility of the flow. In contrast, the model presented in [5, 6, 8, 37] does not enforce $\text{div } u = 0$, and the pressure adheres to a specific constitutive law. To address area conservation, a phenomenological ‘restoring force’ p_e is introduced in the dynamic condition. The dependence of p_e on volume makes this problem explicitly non-local. If in [5, 6, 8, 37] were to impose $\text{div } u = 0$, this model would become equivalent to the passive Hele–Shaw drop, with no traveling waves.

Our c density is analogous to the m in [5, 6, 8, 37] but with two key distinctions:

- In our model, c governs a normal boundary force in the dynamic condition, while the m in [5, 6, 8, 37] induces a negative pressure (isotropic contractility) in the bulk. This implies different interpretations of pressure: ours

is the pressure of an incompressible cytoplasmic fluid that is pushed on the boundary, whereas in [5, 6, 8, 37] it describes the pressure of an active gel.

- The transport equation differs. In [5, 6, 8, 37], m follows advection-diffusion transport with an advection speed equal to u . This results in a no-flux boundary condition. In our case, assuming advection-diffusion-absorption dynamics for c , we obtain a non-standard no-flux condition. In simpler terms, an advancing boundary induces a decreasing gradient (depletion) of c , while a retracting boundary induces an increasing gradient (accumulation) of c . For us, gradients in c can only be induced through the boundary condition because $\operatorname{div} u = 0$.

Moreover, in this work, we seek to understand the impact of membrane friction on the substrate on cell migration. Membrane friction is reflected in the additional term $\chi_u f_{\text{und}}(V_n)$ that was not present in [2]. From a mathematical point of view, this new term modifies the nature of the boundary conditions, as they become Robin conditions. From a modeling point of view, this new term describes the forces that exerted of the membrane, a physical phenomenon widely described in the literature, see [38] *e.g.*, and which had been omitted until now in [2, 24].

Note also that a simpler model based on rigid geometry was used in [10, 11] to describe communication between cells and also certain trajectory aspects of cell migration in [17, 27, 28] and that a Cahn–Hilliard Model for Cell Motility was studied in [13]. However, in these different models, the emphasis is placed on internal dynamics rather than on the influence of cell shape, which is the distinctive feature of the work we are presenting here.

1.3. On traveling waves

A remarkable feature of cell motility is the appearance of sustained movement in a given direction without an external cue, see [4, 23, 41]. This phenomenon, known as spontaneous polarization, see [9, 17, 31] *e.g.*, is mathematically described by the existence of traveling wave solutions and is the main subject of this article.

A traveling wave is characterized by a domain with a fixed shape $\tilde{\Omega}$ moving at a constant velocity $V \in \mathbb{R}$ in a fixed direction $\mathbf{w} \in \mathbb{R}^2$. We then have:

$$\Omega(t) = \tilde{\Omega} + tV\mathbf{w}.$$

Without loss of generality, assume that $V \geq 0$ and $\mathbf{w} = (1, 0)$. In this case, the normal velocity at the boundary of the cell satisfies $V_n = Vn_x$.

Using the traveling wave ansatz:

$$c = c(x - Vt, y), \quad P = P(x - Vt, y), \quad \Omega(t) = \tilde{\Omega} + (Vt, 0),$$

we obtain that a solution of model (1.1), which is a traveling wave for this model, is defined as follows in Definition 1.1.

Definition 1.1. A traveling wave solution of the model (1.1) is given by a domain $\tilde{\Omega} \subset \mathbb{R}^2$, $V \geq 0$ a scalar velocity and two functions P and c satisfying:

$$\begin{cases} -\Delta P = 0 & \text{in } \tilde{\Omega}, & (1.5a) \\ P = \gamma\kappa + \chi_c f_{\text{act}}(c) + \chi_u f_{\text{und}}(Vn_x) & \text{on } \partial\tilde{\Omega}, & (1.5b) \\ -\nabla P \cdot \mathbf{n} = Vn_x & \text{on } \partial\tilde{\Omega}, & (1.5c) \\ \operatorname{div}((V, 0)c + \nabla c + (1 - a)\nabla Pc) = 0 & \text{in } \tilde{\Omega}, & (1.5d) \\ (\nabla c + a(V, 0)c) \cdot \mathbf{n} = 0 & \text{on } \partial\tilde{\Omega}. & (1.5e) \end{cases}$$

Proposition 1.2. Let $V \geq 0$ be given. If c and P are solutions of (1.5) associated with V then c and P are of the form:

$$\begin{aligned} P(x, y) &= p_1 - Vx & \text{with } p_1 \in \mathbb{R}, \\ c(x, y) &= \frac{M}{\int_{\tilde{\Omega}} e^{-aVx'} dx' dy'} e^{-aVx}, \end{aligned}$$

where $(x, y) \in \tilde{\Omega}$ and $M \geq 0$ is the total quantity of markers.

Furthermore, $\partial\tilde{\Omega}$ is characterized by the curvature equation, given for all $(x, y) \in \partial\tilde{\Omega}$:

$$\gamma\kappa(x, y) = p_1 - Vx - \chi_c f_{\text{act}}\left(\frac{Me^{-aVx}}{\int_{\tilde{\Omega}} e^{-aVx'} dx' dy'}\right) - \chi_u f_{\text{und}}(Vn_x). \quad (1.6)$$

Remark 1.3. We say that a traveling wave $(\tilde{\Omega}, V)$ of (1.1) is non-trivial if the velocity is not zero. When it is non-trivial, we call it a traveling wave, while when it is trivial, we call it a steady state.

By taking $V = 0$ in Proposition 1.2, it follows that the model admits a unique steady state, which is radially symmetrical.

Proposition 1.4. *The model (1.1) admits an unique steady state given by:*

$$\begin{cases} c^0(\mathbf{x}) = \frac{M}{|\Omega^0|} & \mathbf{x} \in \Omega^0, \\ P^0(\mathbf{x}) = \frac{\gamma}{R_0} + \chi_c f_{\text{act}}(c^0(\mathbf{x})) & \mathbf{x} \in \Omega^0, \\ \mathbf{u}^0(\mathbf{x}) = 0 & \mathbf{x} \in \Omega^0, \\ \Omega^0 = B(0, R_0), \end{cases} \quad \begin{matrix} (1.7a) \\ (1.7b) \\ (1.7c) \\ (1.7d) \end{matrix}$$

where $R_0 = \sqrt{\frac{|\Omega^{\text{in}}|}{\pi}}$. This steady state is radially symmetric.

1.4. Main results

First, we study the steady state given by (1.7) by performing a linear stability analysis around this steady state. The model depends on the parameters $a, \chi_c, \chi_u, M, R_0$ and the functions f_{act} and f_{und} . We have chosen to consider χ_c as the bifurcation parameter, but we could also have considered $M, R_0, a, f'_{\text{act}}(c^0)$ or $f'_{\text{und}}(0)$. So in the following, to perform a stability analysis and obtain a bifurcation result, we should vary the value of the parameter χ_c . We set:

$$\chi_c^* = \frac{R_0 + \chi_u f'_{\text{und}}(0)}{R_0 a c^0 f'_{\text{act}}(c^0)}. \quad (1.8)$$

We then have the following stability result.

Theorem 1.5 (Stability of the steady state). *If $\chi_c < \chi_c^*$ then the steady state (1.7) is linearly stable. On the opposite, if $\chi_c > \chi_c^*$, then the steady state (1.7) is linearly unstable.*

In order to validate the model's relevance to cell motility, we then investigate the existence of traveling waves. This is the aim of this paper. To do so, we propose an implicit approach based on a bifurcation argument. This approach allows us to clearly identify what happens to a cell with a fixed volume as χ_c increases. Using χ_c as a bifurcation parameter allows us to compare our result with previous ones and to conclude on the impact of membrane friction on the stability of the steady state.

Theorem 1.6 (Existence of traveling waves). *Assume that f_{act} satisfies assumptions (1.3). For all $a \in (0, 1]$, $\gamma > 0$, $R_0 > 0$, and $\chi_u > 0$ there exists a one parameter family of traveling wave solutions $(\tilde{\Omega}_{\chi_c}, V_{\chi_c})$ of (1.1), parameterized by $\chi_c \in (\chi_c^*, +\infty)$ such that $|\tilde{\Omega}_{\chi_c}| = \pi R_0^2$.*

Plan of the paper

This work is organized as follows. First, in Section 2 we prove the characterization of the traveling waves given by Proposition 1.2 from which follows the characterization of the unique radially symmetric steady state (Prop. 1.4). Then in Section 3, we study the linear stability of the system and we prove Theorem 1.5. Section 4 contains the proof of the existence of traveling waves by implicit construction (Thm. 1.6). Finally, we give some conclusions.

2. CHARACTERIZATION OF TRAVELING WAVES

In this section, we prove the Proposition 1.2 in order to characterize the traveling waves of the model. The proof is based on the Definition 1.1, which defines traveling waves of the model. The Proposition 1.4 follows from the result by taking $V = 0$.

Proof of Proposition 1.2. We set $\tilde{\mathbf{u}} = -\nabla P - \mathbf{u}_{\text{cm}}$ where $\mathbf{u}_{\text{cm}}$ is the velocity of the cell center of mass. From the total force balance on the cell, we have that for all $t \geq 0$:

$$\mathbf{u}_{\text{cm}}(t) = -\frac{1}{|\Omega^{\text{in}}|} \int_{\partial\Omega(t)} (\chi_c f_{\text{act}}(c) + \chi_u f_{\text{und}}(V_n)) \mathbf{n} \, d\sigma.$$

The traveling wave assumption implies that $\mathbf{u}_{\text{cm}} = (V, 0)$. Thus, setting $\phi = -P - Vx$ we have:

$$\tilde{\mathbf{u}} = \nabla\phi.$$

Moreover, from (1.5a), we deduce that ϕ satisfies $-\Delta\phi = 0$ in $\tilde{\Omega}$ and from (1.5c) we deduce that ϕ also satisfies $\nabla\phi \cdot \mathbf{n} = 0$ on $\partial\tilde{\Omega}$. On the one hand, we have that:

$$\int_{\tilde{\Omega}} |\nabla\phi|^2 \, d\mathbf{x} = - \int_{\tilde{\Omega}} \phi \Delta\phi \, d\mathbf{x} + \int_{\partial\tilde{\Omega}} \phi \nabla\phi \cdot \mathbf{n} \, d\sigma = 0.$$

On the other hand, we have that:

$$\int_{\tilde{\Omega}} |\nabla\phi|^2 \, d\mathbf{x} = \int_{\tilde{\Omega}} |\tilde{\mathbf{u}}|^2 \, d\mathbf{x}.$$

Thus we have that $\tilde{\mathbf{u}} = 0$ on $\tilde{\Omega}$. It follows that for all $(x, y) \in \tilde{\Omega}$:

$$P(x, y) = p_1 - Vx,$$

with $p_1 \in \mathbb{R}$.

By substituting $\nabla P = -(V, 0)$ in (1.5d) and (1.5e), the concentration of markers satisfies the following problem:

$$\begin{cases} \operatorname{div}(\nabla c + a(V, 0)c) = 0 & \text{in } \tilde{\Omega}, \end{cases} \quad (2.1a)$$

$$\begin{cases} (\nabla c + a(V, 0)c) \cdot \mathbf{n} = 0 & \text{on } \partial\tilde{\Omega}. \end{cases} \quad (2.1b)$$

The non-negative solutions of (2.1) are given by:

$$c(x, y) = c_1 e^{-aVx}, \quad (2.2)$$

with $c_1 > 0$ and $(x, y) \in \tilde{\Omega}$. Indeed, we can see that functions of the form (2.2) are solutions of (2.1). If we assume that $c(x, y) = c_1(x, y)e^{-aVx}$ is a solution of (2.1), then we have that:

$$\begin{aligned} 0 &= \int_{\tilde{\Omega}} c_1(x, y) \operatorname{div}(\nabla c(x, y) + a(V, 0)c(x, y)) \, dx \, dy \\ &= \int_{\tilde{\Omega}} \nabla c_1(x, y) \cdot (\nabla c(x, y) + a(V, 0)c(x, y)) \, dx \, dy \\ &= \int_{\tilde{\Omega}} |\nabla c_1(x, y)|^2 e^{-aVx} \, dx \, dy, \end{aligned}$$

from which we deduce that $|\nabla c_1| = 0$ on $\tilde{\Omega}$. Finally, remember that the total number of markers M is constant, so c_1 must be such that $\int_{\tilde{\Omega}} c_1 e^{-aVx} dx dy = M$. This leads to

$$c_1 = \frac{M}{\int_{\tilde{\Omega}} c_1 e^{-aVx'} dx' dy'}.$$

To find the curvature equation (1.6), we inject the expressions found for P and c into equation (1.5b). $\square$

3. STUDY OF THE STEADY STATE

In this section, we prove Theorem 1.5 about the stability of steady state. Inspired by [2], we first linearize the problem (1.1) around the steady state (1.7) (see Lem. 3.1). We derive an eigenvalue problem from this linearized problem and study its spectrum. To this end, we prove that, using Fourier analysis, we can decompose the study of the spectrum into the study of the spectrum of simpler problems (see Lem. 3.2). Next, we demonstrate that when $\chi_c < \chi_c^*$ then the eigenvalues are all negative real parts (see Lem. 3.4 and Rem. 3.6). Finally, from the decomposition of the spectrum study, we derive an explicit condition on the eigenvalues (see Lem. 3.8). Thus, when $\chi_c > \chi_c^*$, we can exhibit a positive real part eigenvalue. This proves the Theorem 1.5.

Lemma 3.1. *The linearized problem associated to (1.1) around the steady state (1.7) is given by:*

$$\begin{cases} -\Delta \tilde{P} = 0 & \text{in } \Omega^0, \\ \partial_t \tilde{\rho} = -\partial_r \tilde{P} & \text{on } \partial\Omega^0, \\ \tilde{P} = -\frac{\gamma}{R_0^2} (\partial_{\theta\theta}^2 \tilde{\rho} + \tilde{\rho}) + \chi_c \tilde{c} f'_{\text{act}}(c^0) - \chi_u \partial_r \tilde{P} f'_{\text{und}}(0) & \text{on } \partial\Omega^0, \\ \partial_t \tilde{c} = \Delta \tilde{c} & \text{in } \Omega^0, \\ \left(\nabla \tilde{c} - a \nabla \tilde{P} c^0 \right) \cdot \mathbf{n} = 0 & \text{on } \partial\Omega^0. \end{cases} \quad \begin{array}{l} (3.1a) \\ (3.1b) \\ (3.1c) \\ (3.1d) \\ (3.1e) \end{array}$$

Proof. We perform a formal expansion of the solution $(c, \mathbf{u})$ near the steady state $(c^0, \mathbf{u}^0)$. Let $\varepsilon > 0$ small. For all $t \geq 0$ we set:

$$\Omega(t) = \{(x, y) = (r \cos \theta, r \sin \theta) \text{ s.t. } 0 \leq r < R_0 + \varepsilon \tilde{\rho}(t, \theta) \text{ and } \theta \in (-\pi, \pi]\}, \quad (3.2)$$

and for all $\mathbf{x} \in \Omega(t)$:

$$\begin{aligned} c(t, \mathbf{x}) &= c^0 + \varepsilon \tilde{c}(t, \mathbf{x}) + \mathcal{O}(\varepsilon^2), \\ P(t, \mathbf{x}) &= P^0 + \varepsilon \tilde{P}(t, \mathbf{x}) + \mathcal{O}(\varepsilon^2), \end{aligned}$$

Using the fact that P^0 satisfies (1.7b) and P satisfies (1.1a) and (1.1b), we deduce that:

$$-\Delta \tilde{P} = 0, \quad \text{in } \Omega^0.$$

The equation (3.2) induces that the boundary of the domain Ω can be parameterized and thus we obtain that for all $\theta \in (-\pi, \pi]$ we have:

$$\mathbf{n}(t, \theta) = \begin{pmatrix} \cos \theta \\ \sin \theta \end{pmatrix} - \varepsilon \frac{\partial_{\theta} \tilde{\rho}(t, \theta)}{R_0} \begin{pmatrix} -\sin \theta \\ \cos \theta \end{pmatrix} + \mathcal{O}(\varepsilon^2).$$

Thus, on $\partial\Omega(t)$, we have:

$$\nabla P \cdot \mathbf{n} = \nabla P^0 \cdot \mathbf{n} - \varepsilon \partial_r \tilde{P} + \mathcal{O}(\varepsilon^2)$$

and also:

$$V_n = \varepsilon \partial_t \tilde{\rho}(t, \theta) + \mathcal{O}(\varepsilon^2).$$

Using (1.1c), we can therefore deduce that, for all $\theta \in (-\pi, \pi]$ and $t \geq 0$, we have:

$$\partial_t \tilde{\rho}(t, \theta) = -\partial_r \tilde{P}(t, R_0, \theta)$$

The linearisation of the curvature is given for all $\theta \in (-\pi, \pi]$ and $t \geq 0$ by:

$$\kappa(t, \theta) = \frac{1}{R_0} - \frac{\varepsilon}{R_0^2} (\partial_{\theta\theta}^2 \tilde{\rho}(t, \theta) + \tilde{\rho}(t, \theta)) + \mathcal{O}(\varepsilon^2).$$

Since

$$f_{\text{act}}(c) = f_{\text{act}}(c^0) + \varepsilon \tilde{c} f'_{\text{act}}(c^0) + \mathcal{O}(\varepsilon^2)$$

and

$$f_{\text{und}}(V_n) = \varepsilon \partial_t \rho(t, \theta) f'_{\text{und}}(0) + \mathcal{O}(\varepsilon^2),$$

we have that (1.1d) leads to that on $\partial\Omega^0$ we have:

$$\tilde{P} = -\frac{\gamma}{R_0^2} (\partial_{\theta\theta}^2 \tilde{\rho} + \tilde{\rho}) + \chi_c \tilde{c} f'_{\text{act}}(c^0) + \chi_u \partial_t \rho f'_{\text{und}}(0).$$

Moreover, using the fact that c^0 satisfies (1.7a) and c satisfies (1.1e) and (1.1f), we deduce that in Ω^0 :

$$\partial_t \tilde{c} = \Delta \tilde{c}.$$

The boundary condition (1.1f) leads to:

$$\left(\nabla \tilde{c} - a \nabla \tilde{P} c^0 \right) \cdot \mathbf{n} = 0 \quad \text{on } \partial\Omega^0.$$

□

The eigenvalue problem associated with the linearized problem (3.1) is given by:

$$\begin{cases} -\Delta \tilde{P} = 0 & \text{in } \Omega^0, \\ \lambda \tilde{\rho} = -\partial_r \tilde{P} & \text{on } \partial\Omega^0, \\ \tilde{P} = -\frac{\gamma}{R_0^2} (\partial_{\theta\theta}^2 \tilde{\rho} + \tilde{\rho}) + \chi_c \tilde{c} f'_{\text{act}}(c^0) - \chi_u \partial_r \tilde{P} f'_{\text{und}}(0) & \text{on } \partial\Omega^0, \\ \lambda \tilde{c} = \Delta \tilde{c} & \text{in } \Omega^0, \\ \left(\nabla \tilde{c} - a \nabla \tilde{P} c^0 \right) \cdot \mathbf{n} = 0 & \text{on } \partial\Omega^0, \end{cases} \quad \begin{array}{l} (3.3a) \\ (3.3b) \\ (3.3c) \\ (3.3d) \\ (3.3e) \end{array}$$

where $\lambda \in \mathbb{C}$, since the problem (3.3) is not self-adjoint.

As the problem (3.3) is radially symmetric, the spectral analysis can be performed using Fourier analysis. We establish the following lemma on the properties of the complex Fourier coefficients of eigenfunctions.

Lemma 3.2. *Let $\lambda \in \mathbb{C}$. The eigenfunctions, satisfying (3.3) associated with the eigenvalue λ are of the form:*

$$\begin{aligned} \rho(\theta) &= \sum_{m \in \mathbb{N}} \rho_{\text{cm}} \cos(m\theta) + \sum_{m \in \mathbb{N}} \rho_{\text{sm}} \sin(m\theta), \\ c(r, \theta) &= \sum_{m \in \mathbb{N}} c_{\text{cm}}(r) \cos(m\theta) + \sum_{m \in \mathbb{N}} c_{\text{sm}}(r) \sin(m\theta), \\ P(r, \theta) &= \sum_{m \in \mathbb{N}} P_{\text{cm}}(r) \cos(m\theta) + \sum_{m \in \mathbb{N}} P_{\text{sm}}(r) \sin(m\theta), \end{aligned}$$

with for all $m \in \mathbb{N}$ and $r \in [0, R_0]$ $(\rho_{\text{cm}}, c_{\text{cm}}(r), P_{\text{cm}}(r)) \in \mathbb{C}^3$ and $(\rho_{\text{sm}}, c_{\text{sm}}(r), P_{\text{sm}}(r)) \in \mathbb{C}^3$.

Moreover for all $m \in \mathbb{N}$, $(\rho_{\text{cm}}, c_{\text{cm}}, P_{\text{cm}})$ (resp. $(\rho_{\text{sm}}, c_{\text{sm}}, P_{\text{sm}})$) satisfies:

$$\begin{cases} -\left(\partial_{rr}^2 + \frac{1}{r}\partial_r - \frac{m^2}{r^2}\right)P_{\text{cm}} = 0 & r \in (0, R_0), \end{cases} \quad (3.4a)$$

$$\lambda \rho_{\text{cm}} = -\partial_r P_{\text{cm}}(R_0), \quad (3.4b)$$

$$\begin{cases} P_{\text{cm}}(R_0) = \frac{\gamma}{R_0^2}(m^2 - 1)\rho_{\text{cm}} + \chi_c c_{\text{cm}}(R_0)f'_{\text{act}}(c^0) - \chi_u \partial_r P_{\text{cm}}(R_0)f'_{\text{und}}(0), \end{cases} \quad (3.4c)$$

$$\begin{cases} \lambda c_{\text{cm}} = \left(\partial_{rr}^2 + \frac{1}{r}\partial_r - \frac{m^2}{r^2}\right)c_{\text{cm}} & r \in (0, R_0), \end{cases} \quad (3.4d)$$

$$\partial_r c_{\text{cm}}(R_0) - a \partial_r P_{\text{cm}}(R_0) c^0 = 0. \quad (3.4e)$$

Proof. The result follows from the linearity of (3.3), the independence of the cosine and sine modes, and the fact that for all $m \in \mathbb{N}$:

$$\partial_{\theta\theta}^2 \rho_{\text{cm}} = -m^2 \rho_{\text{cm}}.$$

□

Remark 3.3. We deduce from Lemma 3.2 and the independence of the cosine and sine perturbations that studying the eigenvalues of (3.3) is equivalent to the study, for all $m \in \mathbb{N}$, of those of (3.4). Indeed, for $m \in \mathbb{N}$, if $\lambda_m \in \mathbb{C}$ is an eigenvalue of (3.4) associated with the eigenfunctions $(\rho_{\lambda_m}, c_{\lambda_m}, P_{\lambda_m})$ then λ_m is an eigenvalue of (3.3) associated with the eigenfunctions:

$$\begin{aligned} \rho(\theta) &= \rho_{\lambda_m} \cos(m\theta), \\ c(r, \theta) &= c_{\lambda_m}(r) \cos(m\theta), \\ P(r, \theta) &= P_{\lambda_m}(r) \cos(m\theta). \end{aligned}$$

In the sequel, for all $m \in \mathbb{N}$, we denote by λ_m the eigenvalue associated to the mode m .

Lemma 3.4. If $m \geq 1$ and $0 \leq \chi_c \leq \frac{1}{ac^0 f'_{\text{act}}(c^0)}$, then all the eigenvalues of (3.4) have non-positive real parts.

Remark 3.5. The result also holds true for the case $m = 0$. This case is dealt with in more detail in the proof of Proposition 3.9.

Proof. Let $m \geq 1$. Let $\lambda_m \in \mathbb{C}$ be an eigenvalue of (3.4) associated with ρ_m, c_m and P_m . For all $r \in (0, R_0)$ and $\theta \in (-\pi, \pi]$, we set:

$$\begin{aligned} \rho(\theta) &= \rho_m \cos(m\theta), \\ c(r, \theta) &= c_m(r) \cos(m\theta), \\ P(r, \theta) &= P_m(r) \cos(m\theta). \end{aligned}$$

We also set $Q = c - ac^0 P$. Thus, Q follows the following problem:

$$\begin{cases} -\Delta Q = \Delta c & \text{in } \Omega^0, \end{cases} \quad (3.5a)$$

$$\begin{cases} (1 - a\chi_c c^0 f'_{\text{act}}(c^0))P = \frac{\gamma}{R_0^2}(m^2 - 1)\rho + \chi_c f'_{\text{act}}(c^0)Q + \lambda_m \chi_u f'_{\text{und}}(0)\rho & \text{on } \partial\Omega^0, \end{cases} \quad (3.5b)$$

$$\begin{cases} \nabla Q \cdot \mathbf{n} = 0 & \text{on } \partial\Omega^0. \end{cases} \quad (3.5c)$$

Thus using (3.4) and (3.5) we compute:

$$\begin{aligned}\lambda_m \int_{\Omega^0} |c|^2 d\mathbf{x} &= \int_{\Omega^0} \bar{c} \Delta c d\mathbf{x} = \int_{\Omega^0} (\bar{Q} + ac^0 \bar{P}) \Delta Q d\mathbf{x} \\ &= - \int_{\Omega^0} |\nabla Q|^2 d\mathbf{x} - ac^0 \int_{\Omega^0} \nabla \bar{P} \cdot \nabla Q d\mathbf{x} \\ &= - \int_{\Omega^0} |\nabla Q|^2 d\mathbf{x} - ac^0 \int_{\partial\Omega^0} Q \nabla \bar{P} \cdot \mathbf{n} d\sigma.\end{aligned}$$

Since

$$\begin{aligned}\int_{\partial\Omega^0} Q \nabla \bar{P} \cdot \mathbf{n} d\sigma &= \frac{1}{\chi_c f'_{\text{act}}(c^0)} \left[\int_{\partial\Omega^0} (1 - ac^0 \chi_c f'_{\text{act}}(c^0)) P \nabla \bar{P} \cdot \mathbf{n} d\sigma \right. \\ &\quad \left. - \left(\frac{\gamma}{R_0^2} (m^2 - 1) + \lambda_m \chi_u f'_{\text{und}}(0) \right) \int_{\partial\Omega^0} \rho \nabla \bar{P} \cdot \mathbf{n} d\sigma \right] \\ &= \frac{1}{\chi_c f'_{\text{act}}(c^0)} \left[(1 - ac^0 \chi_c f'_{\text{act}}(c^0)) \int_{\Omega^0} |\nabla P|^2 d\mathbf{x} \right. \\ &\quad \left. + \overline{\lambda_m} \frac{\gamma}{R_0^2} (m^2 - 1) \int_{\partial\Omega^0} |\rho|^2 d\sigma + \chi_u f'_{\text{und}}(0) \int_{\partial\Omega^0} |\nabla P \cdot \mathbf{n}|^2 d\sigma \right].\end{aligned}$$

We deduce that for all $\lambda_m \in \mathbb{C}$ eigenvalue of (3.4) we have:

$$\begin{aligned}\lambda_m \int_{\Omega^0} |c|^2 d\mathbf{x} + \frac{\overline{\lambda_m}}{\chi_c f'_{\text{act}}(\bar{c})} \frac{\gamma}{R_0^2} (m^2 - 1) \int_{\partial\Omega^0} |\rho|^2 d\sigma \\ = - \int_{\Omega^0} |\nabla Q|^2 d\mathbf{x} - a\bar{c} \frac{1 - ac^0 \chi_c f'_{\text{act}}(c^0)}{\chi_c f'_{\text{act}}(c^0)} \int_{\Omega^0} |\nabla P|^2 d\mathbf{x} - \frac{\chi_u f'_{\text{und}}(0)}{\chi_c f'_{\text{act}}(c^0)} \int_{\partial\Omega^0} |\nabla P \cdot \mathbf{n}|^2 d\sigma.\end{aligned}$$

The result follows from this equality. $\square$

Remark 3.6. It seems that the result holds for all $\chi_c > 0$ as long as $\chi_c < \chi_c^*$. We do not prove this here. However, the study of traveling waves in Section 4 suggests that the result may indeed extend to all χ_c such that $\chi_c < \chi_c^*$.

Lemma 3.7. *Let $m \in \mathbb{N}$. The eigenfunctions of (3.4) associated with the eigenvalue $\lambda_m \in \mathbb{C}$ are given by:*

$$\begin{pmatrix} \rho \\ c(r) \\ P(r) \end{pmatrix} = \begin{pmatrix} \hat{\rho}_{m\lambda} \\ \hat{c}_{m\lambda} I_m(-r\lambda_m^{\frac{1}{2}}) \\ \hat{P}_{m\lambda} r^m \end{pmatrix},$$

where $0 \leq r < R_0$ and, $(\hat{\rho}_{m\lambda}, \hat{c}_{m\lambda}, \hat{P}_{m\lambda}) \in \mathbb{C}^3$ solution of:

$$\begin{cases} \lambda_m \hat{\rho}_{m\lambda} = -m R_0^{m-1} \hat{P}_{m\lambda}, \end{cases} \quad (3.6a)$$

$$\begin{cases} R_0^m \hat{P}_{m\lambda} = \left(\frac{\gamma}{R_0^2} (m^2 - 1) + \lambda_m \chi_u f'_{\text{und}}(0) \right) \hat{\rho}_{m\lambda} + \chi_c f'_{\text{act}}(c^0) I_m(-R_0 \lambda_m^{\frac{1}{2}}) \hat{c}_{m\lambda}, \end{cases} \quad (3.6b)$$

$$\begin{cases} \lambda_m^{\frac{1}{2}} I'_m(-R_0 \lambda_m^{\frac{1}{2}}) \hat{c}_{m\lambda} = \lambda_m a c^0 \hat{\rho}_{m\lambda}. \end{cases} \quad (3.6c)$$

I_m denotes the modified Bessel function of the first kind of order m .

We recall that for $m \in \mathbb{N}$, the modified Bessel function of the first kind of order m is defined for all $z \in \mathbb{C}$ by

$$I_m(z) = \sum_{k=0}^{+\infty} \frac{1}{k!(k+m)!} \left(\frac{z}{2} \right)^{2k+m}.$$

Proof. From Lemma 3.2, we deduce that for all $0 \leq r < R_0$ that:

$$\rho = \hat{\rho}_{m\lambda} \in \mathbb{C}$$

and since P satisfies (3.4a), the Laplace equation:

$$P(r) = \hat{P}_{m\lambda} r^m,$$

with $\hat{P}_{m\lambda} \in \mathbb{C}$. Moreover, as c satisfies (3.4d) and thus, by the definition of Bessel functions, we have:

$$c(r) = \hat{c}_{m\lambda} I_m\left(-r\lambda_m^{\frac{1}{2}}\right),$$

where $0 \leq r < R_0$, $\hat{c}_{m\lambda} \in \mathbb{C}$ and I_m is the modified Bessel function of the first kind of order m .

As ρ and P satisfy (3.4b), it follows that:

$$\lambda_m \hat{\rho}_{m\lambda} = -m \hat{P}_{m\lambda} R_0^{m-1}.$$

Likewise, since ρ , c and P satisfy (3.4c), we have that:

$$\hat{P}_{m\lambda} R_0^m = \frac{\gamma}{R_0^2} (m^2 - 1) \hat{\rho}_{m\lambda} + \chi_c f'_{\text{act}}(c^0) \hat{c}_{m\lambda} I_m\left(-R_0 \lambda_m^{\frac{1}{2}}\right) - m \chi_u f'_{\text{und}}(0) R_0^{m-1} \hat{P}_{m\lambda}.$$

Combining this with the previous equality, we obtain that:

$$R_0^m \hat{P}_{m\lambda} = \left(\frac{\gamma}{R_0^2} (m^2 - 1) + \lambda_m \chi_u f'_{\text{und}}(0) \right) \hat{\rho}_{m\lambda} + \chi_c f'_{\text{act}}(c^0) I_m\left(-R_0 \lambda_m^{\frac{1}{2}}\right) \hat{c}_{m\lambda}.$$

Finally as ρ , c and P satisfy (3.4e) and (3.4b), we have:

$$-\lambda_m^{\frac{1}{2}} I'_m\left(-R_0 \lambda_m^{\frac{1}{2}}\right) \hat{c}_{m\lambda} + \lambda_m a c^0 \hat{\rho}_{m\lambda} = 0.$$

□

Lemma 3.8. Let $m \in \mathbb{N}$. Let $\lambda_m \in \mathbb{C}$ be an eigenvalue of (3.4), then λ_m is such that

$$H_m(\lambda_m) = 0,$$

with if $m \geq 1$, H_m defined for all $z \in \mathbb{C}$ by:

$$\begin{aligned} H_m(z) = & z m \frac{a \chi_c c^0 f'_{\text{act}}}{R_0} I_m\left(-R_0 z^{\frac{1}{2}}\right) + \frac{z^{\frac{1}{2}}}{2} \left[z \left(1 + \frac{m}{R_0} \chi_u f'_{\text{und}}(0) \right) + \frac{\gamma}{R_0^3} m (m^2 - 1) \right] \\ & \times \left[I_{m-1}\left(-R_0 z^{\frac{1}{2}}\right) + I_{m+1}\left(-R_0 z^{\frac{1}{2}}\right) \right], \end{aligned}$$

and if $m = 0$, H_0 defined for all $z \in \mathbb{C}$ by:

$$H_0(z) = z^{\frac{3}{2}} I_1\left(-R_0 z^{\frac{1}{2}}\right).$$

Proof. Using the recurrence relations on Bessel functions: $2I'_m = I_{m+1} + I_{m-1}$ if $m \geq 1$ and $I'_0 = I_1$, the result follows from Lemma 3.7. □

Proposition 3.9. *If $0 \leq \frac{\chi_c}{\chi_c^*} < 1$, then (3.3) admits $\lambda = 0$ as an eigenvalue of multiplicity three and all its other eigenvalues have a negative real part.*

If $\frac{\chi_c}{\chi_c^} > 1$, then (3.3) admits a positive eigenvalue.*

Proof. When $m = 0$, for all $z \in \mathbb{C}$, we have:

$$H_0(z) = z^{\frac{3}{2}} I_1(-R_0 z^{\frac{1}{2}}).$$

$z = 0$ is a solution of $H_0(z) = 0$. This eigenvalue is associated with the eigenfunctions defined for all $r \in [0, R_0]$ by:

$$\begin{pmatrix} \hat{\rho}_{00}^1 \\ \hat{c}_{00}^1(r) \\ \hat{P}_{00}^1(r) \end{pmatrix} = \begin{pmatrix} 1 \\ 0 \\ -\frac{\gamma}{R_0^2} \end{pmatrix} \quad \text{and} \quad \begin{pmatrix} \hat{\rho}_{00}^2 \\ \hat{c}_{00}^2(r) \\ \hat{P}_{00}^2(r) \end{pmatrix} = \begin{pmatrix} 0 \\ 1 \\ \chi_c f'_{\text{act}}(c^0) \end{pmatrix}.$$

The function I_1 is linked to J_1 the Bessel function of the first kind of order 1. We recall that for all $z \in \mathbb{C}$ and $m \in \mathbb{N}$, we have $I_m(z) = i^{-m} J_m(iz)$ with $J_m(z) = \sum_{k=0}^{\infty} \frac{(-1)^k}{k!(k+m)!} \left(\frac{z}{2}\right)^{2k+m}$. Thus the other roots of H_0 are given by $\lambda_{0k} = -\frac{x_{1k}^2}{R_0^2}$ where $x_{1k} \in \mathbb{R}$ is the k^{th} root of J_1 . We have that the eigenvalue $\lambda_{0k} < 0$ is associated with the eigenfunction defined for all $r \in [0, R_0]$ by:

$$\begin{pmatrix} \hat{\rho}_{0k} \\ \hat{c}_{0k}(r) \\ \hat{P}_{0k}(r) \end{pmatrix} = \begin{pmatrix} 0 \\ J_0\left(\frac{x_{1k}}{R_0} r\right) \\ \chi_c f'_{\text{act}}(c^0) J_0(x_{1k}) \end{pmatrix}.$$

When $m = 1$, for all $z \in \mathbb{C}$ we have:

$$H_1(z) = \frac{z^{\frac{3}{2}}}{2} \left(1 + \frac{1}{R_0} \chi_u f'_{\text{und}}(0)\right) \left[I_0(-R_0 z^{\frac{1}{2}}) + I_2(-R_0 z^{\frac{1}{2}})\right] + z \frac{a \chi_c c^0 f'_{\text{act}}}{R_0} I_1(-R_0 z^{\frac{1}{2}}).$$

Thus $z = 0$ is a solution of $H_1(z) = 0$. This eigenvalue is associated with the eigenfunction defined for all $r \in [0, R_0]$ by:

$$\begin{pmatrix} \hat{\rho}_{10} \\ \hat{c}_{10}(r) \\ \hat{P}_{10}(r) \end{pmatrix} = \begin{pmatrix} 1 \\ 0 \\ 0 \end{pmatrix}.$$

If $m \geq 2$ then $z = 0$ is solution of $H_m(z) = 0$. Nevertheless, since $\gamma > 0$, from (3.6) and $I_m(0) = 0$, we deduce that $\lambda = 0$ is associate to the zero eigenfunction defined for all $r \in [0, R_0]$ by:

$$\begin{pmatrix} \hat{\rho}_{m0} \\ \hat{c}_{m0}(r) \\ \hat{P}_{m0}(r) \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \\ 0 \end{pmatrix}$$

and $\lambda = 0$ is not an eigenvalue of (3.4) when $m \geq 2$. We can therefore conclude the first point using Remark 3.6.

In order to exhibit a positive eigenvalue, we expand H_1 around 0. For all z close to 0, we have:

$$\begin{aligned} H_1(z) &= \frac{z^{\frac{3}{2}}}{2} \left(1 + \frac{\chi_u f'_{\text{und}}(0)}{R_0} - a c^0 \chi_c f'_{\text{act}}(c^0) + \frac{R_0^2 z}{8} \left(3 + \frac{3 \chi_u f'_{\text{und}}(0)}{R_0} - a c^0 \chi_c f'_{\text{act}}(c^0)\right)\right) \\ &\quad + \mathcal{O}\left(|z|^{\frac{7}{2}}\right). \end{aligned}$$

The function $z \mapsto 1 + \frac{\chi_u f'_{\text{und}}(0)}{R_0} - ac^0 \chi_c f'_{\text{act}}(c^0) + \frac{R_0^2 z}{8} \left(3 + \frac{3\chi_u f'_{\text{und}}(0)}{R_0} - ac^0 \chi_c f'_{\text{act}}(c^0) \right)$ admits z_1 as root, with z_1 defined by:

$$z_1 = \frac{8 \left(ac^0 \chi_c f'_{\text{act}}(c^0) - 1 - \frac{\chi_u f'_{\text{und}}(0)}{R_0} \right)}{R_0^2 \left(3 \left(1 + \frac{\chi_u f'_{\text{und}}(0)}{R_0} \right) - ac^0 \chi_c f'_{\text{act}}(c^0) \right)}.$$

$z_1 \in \mathbb{R}$ changes sign and becomes positive when χ_c exceeds $\frac{R_0 + \chi_u f'_{\text{und}}(0)}{R_0 ac^0 f'_{\text{act}}(c^0)} = \chi_c^*$. Furthermore, z_1 approaches a true root λ_1 of H_1 . Indeed, when $ac^0 \chi_c f'_{\text{act}}(c^0)$ is close to $1 + \frac{\chi_u f'_{\text{und}}(0)}{R_0}$, performing a Taylor expansion of order 1 of the function $x \mapsto \frac{8x}{R_0^2 \left(2 \left(1 + \frac{\chi_u f'_{\text{und}}(0)}{R_0} \right) - x \right)}$ around 0, we have:

$$\begin{aligned} \lambda_1 &= \frac{4}{R_0^2 + \chi_u f'_{\text{und}}(0) R_0} \left(ac^0 \chi_c f'_{\text{act}}(c^0) - \left(1 + \frac{\chi_u f'_{\text{und}}(0)}{R_0} \right) \right) \\ &\quad + o \left(\left| ac^0 \chi_c f'_{\text{act}}(c^0) - \left(1 + \frac{\chi_u f'_{\text{und}}(0)}{R_0} \right) \right| \right) \end{aligned}$$

associated with the eigenfunction defined for all $r \in [0, R_0]$ by:

$$\begin{pmatrix} \hat{\rho}_{1\lambda_1} \\ \hat{c}_{1\lambda_1}(r) \\ \hat{P}_{1\lambda_1}(r) \end{pmatrix} = \begin{pmatrix} \frac{-\chi_c f'_{\text{act}} I_1 \left(-R_0 \lambda_1^{\frac{1}{2}} \right)}{R_0 + \chi_u f'_{\text{und}}(0)} \\ \lambda_1 I_1 \left(-r \lambda_1^{\frac{1}{2}} \right) \\ \frac{\chi_c f'_{\text{act}} I_1 \left(-R_0 \lambda_1^{\frac{1}{2}} \right) \lambda_1}{R_0 + \chi_u f'_{\text{und}}(0)} r \end{pmatrix}.$$

Thus when $\chi_c > \chi_c^*$, (3.3) admits λ_1 as positive eigenvalue. $\square$

4. EXISTENCE OF TRAVELING WAVES

In this section, we prove Theorem 1.6 using a bifurcation argument. The arguments of the proof are inspired by those used in [2] in the case where $\chi_u = 0$. In order to prove the theorem, we define a functional $\mathcal{F}$ to which we can apply the Crandall–Rabinowitz bifurcation theorem [12] at the point $\chi_c = \chi_c^*$.

Since the disk of radius R_0 with $V = 0$ is a solution of (1.5), we seek other solutions of (1.5) such that the domain $\tilde{\Omega}$ is a perturbation of the disk. We therefore look for $\tilde{\Omega}$ such that:

$$\tilde{\Omega} = \{(r \cos(\theta), r \sin(\theta)) \text{ s.t. } 0 \leq r \leq R_0 + \rho(\theta) \text{ and } \theta \in (-\pi, \pi]\}$$

with $\rho : \mathbb{R} \rightarrow (-R_0, +\infty)$ a 2π -periodic function satisfying:

$$\int_{-\pi}^{\pi} (R_0 + \rho(\theta))^2 - R_0^2 d\theta = 0.$$

This latter condition ensures that $|\tilde{\Omega}| = \pi R_0^2$. The boundary of domain $\tilde{\Omega}$ is parameterized by:

$$\{(R_0 + \rho(\theta)) \cos \theta, (R_0 + \rho(\theta)) \sin \theta\} \quad \text{for } \theta \in (-\pi, \pi].$$

For all $\theta \in (-\pi, \pi]$, the outward normal vector to $\partial\tilde{\Omega}$ is given by:

$$\mathbf{n}(\theta) = \begin{pmatrix} n_1(\theta) \\ n_2(\theta) \end{pmatrix} = \frac{1}{\left((R_0 + \rho(\theta))^2 + \rho'(\theta)^2\right)^{\frac{1}{2}}} \begin{pmatrix} (R_0 + \rho(\theta)) \cos \theta + \rho'(\theta) \sin \theta \\ (R_0 + \rho(\theta)) \sin \theta - \rho'(\theta) \cos \theta \end{pmatrix}$$

and the mean curvature by:

$$\kappa(\theta) = \frac{(R_0 + \rho(\theta))^2 + 2\rho'(\theta)^2 - (R_0 + \rho(\theta))\rho''(\theta)}{\left((R_0 + \rho(\theta))^2 + \rho'(\theta)^2\right)^{\frac{3}{2}}}. \quad (4.1)$$

The condition on the boundary domain (1.6) can be expressed as:

$$\gamma\kappa(\theta) + V(R_0 + \rho(\theta)) \cos \theta + \chi_c f_{\text{act}}\left(c_1(V, \rho)e^{-aV(R_0 + \rho(\theta)) \cos \theta}\right) + \chi_u f_{\text{und}}(Vn_1(\theta)) = p_1, \quad (4.2)$$

where $\theta \in (-\pi, \pi]$ and $c_1(V, \rho) = \frac{M}{\int_{-\pi}^{\pi} \int_0^{R_0 + \rho(\theta)} e^{-aVr \cos \theta} r \, dr \, d\theta}$.

As we are looking for traveling waves in the x -direction, we restrict ourselves to domains $\tilde{\Omega}$ symmetrical about the x -axis. We then introduce the functional spaces:

$$\begin{aligned} X &= \{\rho \in \mathcal{C}_{\text{per}}^{2,\alpha}(-\pi, \pi) : \rho(\theta) = \rho(-\theta), \forall \theta \in (-\pi, \pi)\}, \\ Y &= \{\rho \in \mathcal{C}_{\text{per}}^{0,\alpha}(-\pi, \pi) : \rho(\theta) = \rho(-\theta), \forall \theta \in (-\pi, \pi)\}. \end{aligned}$$

Therefore, the existence of a boundary $\partial\tilde{\Omega}$ solving (1.6) is equivalent to the existence of a function $\rho \in X$ solving (4.2).

The existence of a branch of traveling waves, and therefore the proof of the Theorem 1.6, follows from the following result, which characterizes the nature of the bifurcation: pitchfork.

Theorem 4.1. *Assume that f_{act} satisfies assumptions (1.3). For all $a \in (0, 1]$, $\gamma > 0$, $R_0 > 0$, and $\chi_u > 0$, there exists an interval $I = (-\varepsilon, \varepsilon)$ and four functions $\rho : I \times (-\pi, \pi] \rightarrow X$, $\chi_c : I \rightarrow \mathbb{R}$, $V : I \rightarrow \mathbb{R}$, and $p_1 : I \rightarrow \mathbb{R}$ such that for all $s \in I$:*

- (1) *the function $\theta \mapsto \rho(s, \theta)$ is a solution of (4.2) with $\chi_c = \chi_c(s)$, $V = V(s)$, and $p_1 = p_1(s)$,*
- (2) *$\chi_c(s) = \chi_c^* + \eta s^2 + o(s^2)$, with $\eta \in \mathbb{R}$, $\eta \neq 0$,*
- (3) *$V(s) = s + o(s)$,*
- (4) *$p_1(s) = o(s)$.*

The proof of the theorem relies on the definition of a functional $\mathcal{F}$ related to the problem. We will prove that this functional satisfies the properties required to apply the Crandall–Rabinowitz theorem [12], the theorem is recalled in Appendix A, Theorem A.1, and derive the conditions giving the expressions for χ_c , V , and p_1 .

Let $\mathcal{F} : \mathbb{R} \times X \times \mathbb{R} \times \mathbb{R} \rightarrow \mathbb{R}$ the functional defined for all $(\chi_c, \rho, V, p_1) \in \mathbb{R} \times X \times \mathbb{R} \times \mathbb{R}$ by:

$$\begin{aligned} \mathcal{F}(\chi_c, \rho, V, p_1) &= \left(\gamma\kappa(\theta) + \chi_c f_{\text{act}}\left(c_1(V, \rho)e^{-aV(R_0 + \rho(\theta)) \cos \theta}\right) \right. \\ &\quad \left. + \chi_u f_{\text{und}}(Vn_1(\theta)) + V(R_0 + \rho(\theta)) \cos \theta - p_1 - \frac{\gamma}{R_0} \right) \\ &\quad \int_{-\pi}^{\pi} (R_0 + \rho(\theta))^2 - R_0^2 \, d\theta; \int_{-\pi}^{\pi} \rho(\theta) \cos \theta \, d\theta. \end{aligned} \quad (4.3)$$

Lemma 4.2. *The functional $\mathcal{F}$ defined by (4.3) satisfies the following properties:*

- (1) $\mathcal{F}(\chi_c, 0, 0, 0) = 0$ for all $\chi_c \in \mathbb{R}$.
- (2) $\text{Ker } \partial_{(\rho, V, p_1)} \mathcal{F}(\chi_c^*, 0, 0, 0)$ is a one dimensional subspace of $X \times \mathbb{R} \times \mathbb{R}$ spanned by $(0, 1, 0)$.
- (3) $\text{Range } \partial_{(\rho, V, p_1)} \mathcal{F}(\chi_c^*, 0, 0, 0)$ is a closed subspace of $Y \times \mathbb{R} \times \mathbb{R}$ of codimension 1.
- (4) $\partial_{\chi_c} \partial_{(\rho, V, p_1)} \mathcal{F}(\chi_c^*, 0, 0, 0)[0, 1, 0] \notin \text{Range } \partial_{(\rho, V, p_1)} \mathcal{F}(\chi_c^*, 0, 0, 0)$.

Proof. Item (1). When $\rho = 0$, using the expression of the mean curvature (4.1), we have for all $\theta \in (-\pi, \pi]$, $\kappa(\theta) = \frac{1}{R_0}$. Thus for all $\chi_c \in \mathbb{R}$, we have $\mathcal{F}(\chi_c, 0, 0, 0) = 0$.

Item (2). Let $\chi_c \in \mathbb{R}$. Let $\mathcal{L}_{\chi_c}$ be the linear operator defined by:

$$\begin{aligned} \mathcal{L}_{\chi_c} : X \times \mathbb{R} \times \mathbb{R} &\rightarrow Y \times \mathbb{R} \times \mathbb{R} \\ (\rho, V, p_1) &\mapsto \mathcal{F}_\rho(\chi_c, 0, 0, 0)[\rho] + \mathcal{F}_V(\chi_c, 0, 0, 0)[V] + \mathcal{F}_{p_1}(\chi_c, 0, 0, 0)[p_1]. \end{aligned}$$

For all $(\rho, V, p_1) \in X \times \mathbb{R} \times \mathbb{R}$ we have:

$$\begin{aligned} \mathcal{L}_{\chi_c}(\rho, V, p_1) = &\left(-\gamma \frac{\rho + \rho''}{R_0^2} - \frac{\chi_c c^0 f'_{\text{act}}(c^0)}{R_0} \int_{-\pi}^{\pi} \rho(\theta) d\theta - ac^0 \chi_c f'_{\text{act}}(c^0) R_0 V \cos \theta \right. \\ &+ R_0 V \cos \theta - p_1 + \chi_u f'_{\text{und}}(0) V \cos \theta ; \\ &\left. 2R_0 \int_{-\pi}^{\pi} \rho(\theta) d\theta ; \int_{-\pi}^{\pi} \rho(\theta) \cos \theta d\theta \right) \end{aligned}$$

and thus in particular for $\chi_c = \chi_c^*$ we have:

$$\mathcal{L}_{\chi_c^*}(\rho, V, p_1) = \left(-\gamma \frac{\rho + \rho''}{R_0^2} - \frac{R_0 + \chi_u f'_{\text{und}}(0)}{a R_0^2} \int_{-\pi}^{\pi} \rho(\theta) d\theta - p_1 ; 2R_0 \int_{-\pi}^{\pi} \rho(\theta) d\theta ; \int_{-\pi}^{\pi} \rho(\theta) \cos \theta d\theta \right).$$

The elements (ρ, V, p_1) of $\text{Ker } \partial_{(\rho, V, p_1)} \mathcal{F}(\chi_c^*, 0, 0, 0)$ are therefore such that

$$\rho'' + \rho = -\frac{R_0^2}{\gamma} p_1, \tag{4.4}$$

with the conditions

$$\begin{cases} \int_{-\pi}^{\pi} \rho(\theta) d\theta = 0, \\ \int_{-\pi}^{\pi} \rho(\theta) \cos \theta d\theta = 0, \\ \rho \text{ even function.} \end{cases}$$

As ρ even, necessarily the condition $\int_{-\pi}^{\pi} \rho(\theta) \sin \theta d\theta = 0$ holds. The solutions to the differential equation (4.4) are given, for all $\theta \in (-\pi, \pi]$, by

$$\rho(\theta) = A \cos \theta + B \sin \theta - \frac{R_0^2}{\gamma} p_1$$

where $A, B \in \mathbb{R}$.

We have:

$$\int_{-\pi}^{\pi} \rho(\theta) d\theta = -2\pi \frac{R_0^2}{\gamma} p_1$$

and thus necessarily $p_1 = 0$. This leads to:

$$\begin{aligned} \int_{-\pi}^{\pi} \rho(\theta) \cos \theta d\theta &= A\pi, \\ \int_{-\pi}^{\pi} \rho(\theta) \sin \theta d\theta &= B\pi \end{aligned}$$

which implies $A = 0$ and $B = 0$. We then have $\rho = 0$ and

$$\text{Ker } \partial_{(\rho, V, p_1)} \mathcal{F}(\chi_c^*, 0, 0, 0) = \text{Span}\{(0, 1, 0)\}.$$

Item (3). To prove this property, we demonstrate that:

$$\text{Range } \partial_{(\rho, V, p_1)} \mathcal{F}(\chi_c^*, 0, 0, 0) = \left\{ (h, C_1, C_2) \in Y \times \mathbb{R} \times \mathbb{R} \text{ s.t. } \int_{-\pi}^{\pi} h(\theta) \cos \theta \, d\theta = 0 \right\}.$$

Let $(h, C_1, C_2) \in \text{Range } \partial_{(\rho, V, p_1)} \mathcal{F}(\chi_c^*, 0, 0, 0)$. Thus there exists $\rho \in X$ and $p_1 \in \mathbb{R}$ such that:

$$-\gamma \frac{\rho + \rho''}{R_0^2} - \frac{R_0 + \chi_u f'_{\text{und}}(0)}{a R_0^2} \int_{-\pi}^{\pi} \rho(\theta) \, d\theta - p_1 = h. \quad (4.5)$$

By multiplying it by $\cos \theta$ and integrating it over $[-\pi, \pi]$ we obtain that necessarily h is such that:

$$\int_{-\pi}^{\pi} h(\theta) \cos \theta \, d\theta = 0.$$

Reciprocally, let $h \in \mathcal{C}_{\text{per}}^{0, \alpha}(-\pi, \pi)$ and $p_1 \in \mathbb{R}$. The (4.5) admits a solution in $\mathcal{C}_{\text{per}}^{2, \alpha}(-\pi, \pi)$ if and only if $\int_{-\pi}^{\pi} h(\theta) \cos \theta \, d\theta = \int_{-\pi}^{\pi} h(\theta) \sin \theta \, d\theta = 0$. The general solutions are of the form:

$$\rho(\theta) = \bar{\rho}(\theta) + k_1 \cos(\theta) + k_2 \sin(\theta),$$

where $\bar{\rho}$ is an even particular solution.

Let $(h, C_1, C_2) \in \text{Range } \partial_{(\rho, V, p_1)} \mathcal{F}(\chi_c^*, 0, 0, 0)$. As $h \in Y$ and is even, necessarily we have that $\int_{-\pi}^{\pi} h(\theta) \sin \theta \, d\theta = 0$. Assume that $\int_{-\pi}^{\pi} h(\theta) \cos \theta \, d\theta = 0$. There exists $\rho \in X$ solution of (4.5). Taking the even part of the general solutions, we obtain that:

$$\rho(\theta) = \frac{1}{2} [\bar{\rho}(\theta) + \bar{\rho}(-\theta)] + k_1 \cos(\theta).$$

We choose k_1 such that $\int_{-\pi}^{\pi} \rho(\theta) \cos \theta \, d\theta = C_2$.

Integrating (4.5) with respect to θ yields to:

$$\left(-\frac{\gamma}{R_0^2} - \frac{2\pi(R_0 + \chi_u f'_{\text{und}}(0))}{a R_0^2} \right) \int_{-\pi}^{\pi} \rho(\theta) \, d\theta - 2\pi p_1 = \int_{-\pi}^{\pi} h(\theta) \, d\theta.$$

We thus choose p_1 such that $\int_{-\pi}^{\pi} \rho(\theta) \, d\theta = C_1$.

Item (4). For all $(\chi_c, \rho, V, p_1) \in \mathbb{R} \times X \times \mathbb{R} \times \mathbb{R}$ we have:

$$\partial_{\chi_c} \mathcal{L}_{\chi_c}(\rho, V, p_1) = \left(-\frac{c^0 f'_{\text{act}}(c^0)}{R_0} \int_{-\pi}^{\pi} \rho(\theta) \, d\theta - a c^0 f'_{\text{act}}(c^0) R_0 V \cos \theta; 0; 0; 0 \right).$$

In particular, we have for $\chi_c = \chi_c^*$ and $(\rho, V, p_1) = (0, 1, 0)$:

$$\partial_{\chi_c} \mathcal{L}_{\chi_c^*}(0, 1, 0) = (-a c^0 f'_{\text{act}}(c^0) R_0 \cos \theta; 0; 0; 0).$$

By contradiction, assume that

$$\partial_{\chi_c} \partial_{(\rho, V, p_1)} \mathcal{F}(\chi_c^*, 0, 0, 0)[0, 1, 0] \in \text{Range } \partial_{(\rho, V, p_1)} \mathcal{F}(\chi_c^*, 0, 0, 0).$$

Then there exists $(\rho, V, p_1) \in X \times \mathbb{R} \times \mathbb{R}$ such that:

$$\begin{cases} \gamma \frac{\rho + \rho''}{R_0^2} + \frac{R_0 + \chi_u f'_{\text{und}}(0)}{a R_0^2} \int_{-\pi}^{\pi} \rho(\theta) d\theta + p_1 = a c^0 f'_{\text{act}}(c^0) R_0 \cos \theta \\ \int_{-\pi}^{\pi} \rho(\theta) d\theta = \int_{-\pi}^{\pi} \rho(\theta) \cos \theta d\theta = \int_{-\pi}^{\pi} \rho(\theta) \sin \theta d\theta = 0. \end{cases}$$

By multiplying by $\cos(\theta)$ and integrating the first line over $[-\pi, \pi]$, we obtain:

$$\begin{aligned} & \gamma \int_{-\pi}^{\pi} \rho(\theta) \cos \theta d\theta + \gamma \int_{-\pi}^{\pi} \rho''(\theta) \cos \theta d\theta \\ & + \left(\frac{R_0 + \chi_u f'_{\text{und}}(0)}{a} \int_{-\pi}^{\pi} \rho(\theta) d\theta + p_1 \right) \int_{-\pi}^{\pi} \cos \theta d\theta = a c^0 f'_{\text{act}}(c^0) R_0^3 \int_{-\pi}^{\pi} \cos^2 \theta d\theta. \end{aligned}$$

Since $\rho \in X$, ρ is 2π -periodic and thus $\int_{-\pi}^{\pi} \rho''(\theta) \cos \theta d\theta = \int_{-\pi}^{\pi} \rho(\theta) \cos \theta d\theta$. Then we have:

$$a c^0 f'_{\text{act}}(c^0) R_0^3 \pi = 0,$$

which is a contradiction as $a > 0$, $f'_{\text{act}}(c^0) > 0$, $c^0 > 0$ and $R_0 > 0$. $\square$

Proof of Theorem 4.1. We apply the Crandall–Rabinowitz bifurcation theorem [12] to the functional $\mathcal{F}$ around the bifurcation point $(\chi_c^*, 0, 0, 0)$. Then for any complement $Z = Z_1 \times Z_2 \times Z_3$ of $\text{Ker } \mathcal{F}(\chi_c^*, 0, 0, 0)$ in $X \times \mathbb{R} \times \mathbb{R}$, there exists a neighborhood N of $(\chi_c^*, 0, 0, 0)$ in $\mathbb{R} \times X \times \mathbb{R} \times \mathbb{R}$, an interval $I = (-\varepsilon, \varepsilon)$ for some $\varepsilon > 0$ and four continuous functions $\varphi : I \rightarrow \mathbb{R}$, $\psi_1 : I \rightarrow Z_1$, $\psi_2 : I \rightarrow Z_2$ and $\psi_3 : I \rightarrow Z_3$ such that for all $s \in I$:

$$\mathcal{F}(\varphi(s), \psi_1(s), \psi_2(s), \psi_3(s)) = (0, 0, 0)$$

and

$$\varphi(0) = \chi_c^*, \quad \psi_1(0) = 0, \quad \psi_2(0) = 0, \quad \psi_3(0) = 0.$$

We can note that for all $s \in (-\varepsilon, \varepsilon)$, $\psi_1(s)$ denotes a function.

In particular, the Crandall–Rabinowitz bifurcation theorem implies that:

$$\mathcal{F}^{-1}(0, 0, 0) \cap N = \{(\varphi(s), s(0, 1, 0) + s(\psi_1(s), \psi_2(s), \psi_3(s))) : s \in I\} \cup \{(\chi_c, 0, 0, 0) : (\chi_c, 0, 0, 0) \in N\}$$

and thus the solutions (χ_c, ρ, V, p_1) of the equation $\mathcal{F}(\chi_c, \rho, V, p_1) = (0, 0, 0)$ are of the form:

$$\begin{cases} \chi_c(s) = \varphi(s), \end{cases} \quad (4.6)$$

$$\begin{cases} \rho(s, \theta) = s\psi_1(s)(\theta), \end{cases} \quad (4.7)$$

$$\begin{cases} V(s) = s + s\psi_2(s), \end{cases} \quad (4.8)$$

$$\begin{cases} p_1(s) = s\psi_3(s), \end{cases} \quad (4.9)$$

where $s \in I$ and $\theta \in (-\pi, \pi]$. In addition, they satisfy for all $\theta \in (-\pi, \pi]$:

$$\begin{aligned} \chi_c(0) &= \chi_c^*, \\ \rho(0, \theta) &= 0 \quad \text{and} \quad \partial_s \rho(0, \theta) = 0, \\ V(0) &= 0 \quad \text{and} \quad V'(0) = 1, \\ p_1(0) &= 0 \quad \text{and} \quad p'_1(0) = 0. \end{aligned}$$

Thus we have for all $s \in I$:

$$V(s) = s + o(s) \quad \text{and} \quad p_1(s) = o(s).$$

The proof of item (4.1) on the expression of χ_c follows from Lemmas 4.3 and 4.4. The proofs of these lemmas use the fact that the functions $\theta \mapsto \rho(0, \theta)$ and $\theta \mapsto \partial_s \rho(0, \theta)$ and their derivatives with respect to θ vanish. Moreover as (χ_c, ρ, V, p_1) is solution of the equation $\mathcal{F}(\chi_c, \rho, V, p_1) = (0, 0, 0)$, we have for all $s \in I$:

$$\int_{-\pi}^{\pi} \rho(s, \theta) \cos \theta \, d\theta = 0 \quad \text{and} \quad \int_{-\pi}^{\pi} (R_0 + \rho(s, \theta))^2 - R_0^2 \, d\theta = 0.$$

Thus we deduce that for all $n \in \mathbb{N}$ we have:

$$\int_{-\pi}^{\pi} \partial_s^n \rho(0, \theta) \cos \theta \, d\theta = 0, \quad \text{and} \quad \int_{-\pi}^{\pi} \partial_s^2 \rho(0, \theta) \, d\theta = 0.$$

□

Lemma 4.3. *Assume*

$$\partial_\theta^n \rho(0, \theta) = \partial_\theta^n \partial_s \rho(0, \theta) = 0, \quad \forall n \in \mathbb{N}, \forall \theta \in (-\pi, \pi].$$

Then, we have $\chi'_c(0) = 0$.

Proof. For all $s \in I$ and $\theta \in (-\pi, \pi]$, we set

$$z(s, \theta) = c_1(V(s), \rho(s, \theta)) e^{-aV(s)(R_0 + \rho(s, \theta)) \cos \theta}.$$

We thus have:

$$z(0, \theta) = c_1(V(0), \rho(0, \theta)) e^{-aV(0)(R_0 + \rho(0, \theta)) \cos \theta} = c^0.$$

We differentiate with respect to s the first component of $\mathcal{F}$ and we have for all $s \in I$ and $\theta \in (-\pi, \pi]$:

$$\begin{aligned} 0 &= \gamma \partial_s \kappa(s, \theta) + \chi'_c(s) f_{\text{act}}(z(s, \theta)) + \chi_c(s) f'_{\text{act}}(z(s, \theta)) \partial_s z(s, \theta) \\ &\quad + \chi_u f'_{\text{und}}(V(s) n_1(s, \theta)) (V'(s) n_1(s, \theta) + V(s) \partial_s n_1(s, \theta)) \\ &\quad + V'(s) (R_0 + \rho(s, \theta)) \cos \theta + V(s) \partial_s \rho(s, \theta) \cos \theta - p'_1(s). \end{aligned} \tag{4.10}$$

Evaluating it at $s = 0$, it leads to:

$$0 = \gamma \partial_s \kappa(0, \theta) + \chi'_c(0) f_{\text{act}}(c^0) + \chi_c^* f'_{\text{act}}(c^0) \partial_s z(0, \theta) + \chi_u f'_{\text{und}}(0) n_1(0, \theta) + R_0 \cos \theta.$$

As $\partial_\theta \rho(s, \theta) = s \partial_\theta \psi_1(s, \theta)$, we have $\partial_\theta \rho(0, \theta) = 0$. We then have:

$$n_1(0, \theta) = \frac{1}{R_0} (R_0 \cos \theta + \partial_\theta \rho(0, \theta) \sin \theta) = \cos \theta.$$

Moreover, as for all $s \in I$ and $\theta \in (-\pi, \pi]$ we have:

$$\begin{aligned} \partial_s z(s, \theta) &= (\partial_1 c_1(V(s), \rho(s, \theta)) V'(s) + \partial_2 c_1(V(s), \rho(s, \theta)) \partial_s \rho(s, \theta)) e^{-aV(s)(R_0 + \rho(s, \theta)) \cos \theta} \\ &\quad - a(V'(s)(R_0 + \rho(s, \theta)) + V(s) \partial_s \rho(s, \theta)) \cos \theta c_1(V(s), \rho(s, \theta)) e^{-aV(s)(R_0 + \rho(s, \theta)) \cos \theta}. \end{aligned}$$

As $\partial_1 c_1(0, 0) = 0$, it follows that:

$$\partial_s z(0, \theta) = -a R_0 \cos \theta c^0.$$

Finally, using the definition of χ_c^* (cf (1.8)), we have for all $\theta \in (-\pi, \pi]$:

$$\begin{aligned} 0 &= \gamma \partial_s \kappa(0, \theta) + \chi'_c(0) f_{\text{act}}(c^0) + (\chi_u f'_{\text{und}}(0) + R_0 - \chi_c^* a R_0 c^0 f'_{\text{act}}(c^0)) \cos \theta \\ &= \gamma \partial_s \kappa(0, \theta) + \chi'_c(0) f_{\text{act}}(c^0). \end{aligned}$$

As for all $\theta \in (-\pi, \pi]$ we have $\partial_s \kappa(0, \theta) = 0$, it follows that necessarily $\chi'_c(0) = 0$. □

Lemma 4.4. *Assume*

$$\partial_\theta^n \rho(0, \theta) = \partial_\theta^n \partial_s \rho(0, \theta) = \partial_\theta^n \partial_s^2 \rho(0, \theta) = 0, \quad \forall n \in \mathbb{N}, \forall \theta \in (-\pi, \pi].$$

Then, we have

$$\chi_c''(0) = -\frac{(R_0 + \chi_u f_{\text{und}}'(0))aR_0}{2(f_{\text{act}}'(c^0))^2} \left(f_{\text{act}}''(c^0) + \frac{M}{2\pi R_0^2} f_{\text{act}}'''(c^0) \right) + \frac{\chi_u f_{\text{und}}'''(0)}{3ac^0 R_0 f_{\text{act}}'(c^0)}.$$

Proof. Differentiating twice with respect to s (4.10) and using the fact that for all $\theta \in (-\pi, \pi]$ we have $\partial_s z(0, \theta) = -ac^0 R_0 \cos \theta$ and the result of the previous lemma, it follows that, for all $\theta \in (-\pi, \pi]$:

$$\begin{aligned} 0 &= \gamma \partial_{\text{sss}}^3 \kappa(0, \theta) + \chi_c'''(0) f_{\text{act}}'(c^0) - 3ac^0 R_0 \chi_c''(0) f_{\text{act}}'(c^0) \cos \theta \\ &\quad - 3\chi_c^* ac^0 R_0 \cos \theta \partial_{\text{ss}}^2 z(0, \theta) f_{\text{act}}''(c^0) \\ &\quad - \chi_c^* f_{\text{act}}'''(c^0) (ac^0 R_0 \cos \theta)^3 + \chi_c^* f_{\text{act}}'(c^0) \partial_{\text{sss}}^3 z(0, \theta) + \chi_u f_{\text{und}}'''(0) \cos^3 \theta \\ &\quad + 3\chi_u f_{\text{und}}''(0) \cos^2 \theta V'''(0) + \chi_u f_{\text{und}}'(0) (V'''(0) \cos \theta + 3\partial_{\text{ss}}^2 n_1(0, \theta)) \\ &\quad + V'''(0) R_0 \cos \theta + 3\partial_{\text{ss}}^2 \rho(0, \theta) \cos \theta - p_1'''(0). \end{aligned}$$

We multiply the previous equality by $\cos \theta$ and integrate in θ over $(-\pi, \pi)$, we thus have:

$$\begin{aligned} 0 &= \gamma \int_{-\pi}^{\pi} \partial_{\text{sss}}^3 \kappa(0, \theta) \cos \theta \, d\theta - 3\pi ac^0 R_0 \chi_c''(0) f_{\text{act}}'(c^0) \\ &\quad - 3\chi_c^* ac^0 R_0 f_{\text{act}}''(c^0) \int_{-\pi}^{\pi} \partial_{\text{ss}}^2 z(0, \theta) \cos^2 \theta \, d\theta \\ &\quad - \frac{3}{4} \chi_c^* f_{\text{act}}'''(c^0) \pi (ac^0 R_0)^3 + \chi_c^* f_{\text{act}}'(c^0) \int_{-\pi}^{\pi} \partial_{\text{sss}}^3 z(0, \theta) \cos \theta \, d\theta \\ &\quad + \frac{3}{4} \chi_u f_{\text{und}}'''(0) \pi + \chi_u f_{\text{und}}'(0) V'''(0) \pi + V'''(0) R_0 \pi. \end{aligned}$$

From [2] (Appendix C), we have for all $\theta \in (-\pi, \pi]$:

$$\begin{aligned} \int_{-\pi}^{\pi} \partial_{\text{ss}}^2 z(0, \theta) \cos^2 \theta \, d\theta &= \frac{a^2 M}{2}, \\ \int_{-\pi}^{\pi} \partial_{\text{sss}}^3 z(0, \theta) \cos \theta \, d\theta &= -\frac{aM}{R_0} V'''(0) - \frac{2M}{\pi R_0^3} \int_{-\pi}^{\pi} \partial_{\text{sss}}^3 \rho(0, \theta) \cos \theta \, d\theta, \end{aligned}$$

and

$$\int_{-\pi}^{\pi} \partial_{\text{sss}}^3 \kappa(0, \theta) \cos \theta \, d\theta = 0.$$

It follows that:

$$\begin{aligned} 0 &= -3\pi ac^0 R_0 \chi_c''(0) f_{\text{act}}'(c^0) - \frac{3}{2} \chi_c^* a^3 c^0 R_0 f_{\text{act}}''(c^0) M \\ &\quad - \frac{1}{R_0} aM \chi_c^* f_{\text{act}}'(c^0) V'''(0) - \frac{3}{4} \pi \chi_c^* f_{\text{act}}'''(c^0) (ac^0 R_0)^3 \\ &\quad + \chi_u f_{\text{und}}'''(0) \pi + \chi_u f_{\text{und}}'(0) V'''(0) \pi + V'''(0) R_0 \pi, \\ &= -3\pi ac^0 R_0 f_{\text{act}}'(c^0) \chi_c''(0) - \frac{3\chi_c^* a^3 M^2}{2\pi R_0} \left(f_{\text{act}}''(c^0) + \frac{M}{2\pi R_0^2} f_{\text{act}}'''(c^0) \right) + \frac{3}{4} \pi \chi_u f_{\text{und}}'''(0). \end{aligned}$$

It leads to:

$$\chi_c''(0) = \frac{-\chi_c^* a^2 M}{2\pi f_{\text{act}}'(c^0)} \left(f_{\text{act}}''(c^0) + \frac{M}{2\pi R_0^2} f_{\text{act}}'''(c^0) \right) + \frac{\chi_u f_{\text{und}}'''(0)}{4ac^0 R_0 f_{\text{act}}'(c^0)}.$$

We conclude using the expressions of χ_c^* and of c^0 . □

5. CONCLUSION AND PERSPECTIVES

We have proved that, despite simplifying the principles governing cell motility, the model remains relevant for its representation. It captures the phenomena of cell migration and polarization depending on the parameters. We observe that the cell membrane has an impact on the shape of the traveling wave domain through its action on the curvature (see Eq. (1.6)).

Furthermore, our study highlights the stabilizing effect of membrane undercooling on the cell. We can compare the steady state stability threshold obtained without taking into account the undercooling effect, $\chi_u = 0$ see [2], with the one obtained when this effect is taken into account. Indeed, the threshold under which the stationary state is stable is greater than in the case where the membrane effect is neglected.

In future work extending [26], we plan to investigate different approaches to discretize the model with implicit temporal discretization of curvature and the undercooling effect. Finite element methods are used for the spatial discretizations. The term added by the undercooling effect requires precautions to be taken regarding the functional spaces chosen to discretize the model. The velocity trace on the domain boundary must always be well defined.

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APPENDIX A. A THEOREM OF CRANDALL–RABINOWITZ

We recall here the classical Bifurcation Theorem of Crandall–Rabinowitz [12] that we used to prove Theorem 4.1.

Given U, V two real Banach spaces and a continuous map $\mathcal{F} : \mathbb{R} \times U \rightarrow V$, the goal is to analyze the structure of the solution set

$$\mathcal{F}[\lambda, u] = 0, \quad (\lambda, u) \in \mathbb{R} \times U.$$

Theorem A.1 (Local bifurcation [12]). *Let U, V be Banach spaces, W a neighborhood of $(\lambda_0, 0)$ in $\mathbb{R} \times U$, and $\mathcal{F} : W \rightarrow V$. Suppose that the following properties are satisfied*

- (1) $\mathcal{F}(\lambda, 0) = 0$ for all λ in a neighborhood of λ_0 ;
- (2) the Fréchet partial derivatives $\partial_u \mathcal{F}, \partial_\lambda \mathcal{F}, \partial_{\lambda u} \mathcal{F}$ exist and are continuous;
- (3) $\text{Ker } \partial_u \mathcal{F}(\lambda_0, 0)$ is a one dimensional subspace of U spanned by a nonzero vector $u_0 \in U$;
- (4) $\text{Range } \partial_u \mathcal{F}(\lambda_0, 0)$ is a closed subspace of V of codimension 1;
- (5) $\partial_{\lambda u} \mathcal{F}(\lambda_0, 0)[u_0] \notin \text{Range } \partial_u \mathcal{F}(\lambda_0, 0)$.

Then, for any complement Z of $\text{Ker } \partial_u \mathcal{F}(\lambda_0, 0)$ in U , there exist a neighborhood N of $(\lambda_0, 0)$ in $\mathbb{R} \times U$, an interval $I = (-\varepsilon, \varepsilon)$ for some $\varepsilon > 0$ and two continuous functions

$$\varphi : (-\varepsilon, \varepsilon) \rightarrow \mathbb{R}, \quad \psi : (-\varepsilon, \varepsilon) \rightarrow Z,$$

such that $\varphi(0) = \lambda_0$, $\psi(0) = 0$ and

$$\mathcal{F}^{-1}[0] \cap U = \{(\varphi(s), su_0 + s\psi(s)) : |s| < \varepsilon\} \cup \{(\lambda, 0) : (\lambda, 0) \in N\}.$$

Furthermore, if $\partial_{uu} \mathcal{F}$ is continuous then the functions φ and ψ are once continuously differentiable.