

Nonlinear stability in a free boundary model of active locomotion

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Abstract

The simplest model of contraction-driven self-propulsion of keratocytes reduces to a one dimensional Keller-Segel system with free boundaries. This “active” model involving both dissipation and anti-dissipation features stationary and traveling wave solutions representing static and moving cells, respectively. The goal of this paper is to provide the first rigorous proof of the asymptotic nonlinear stability of both of such solutions. In the case of stationary solutions, the linear stability is established using the spectral theorem for compact, self-adjoint operators, and thus linear stability is determined solely by eigenvalues. For traveling waves the picture is more complex because the linearized problem is non-self-adjoint, opening the possibility of a “dark” area in the phase space which is not “visible” in the purely eigenvalue/eigenvector approach. To establish linear stability in this case we employ spectral methods together with the Gearhart-Pruss-Greiner Theorem, which requires a uniform bound on the resolvent of the linear operator. For both stationary and traveling wave solutions, nonlinear stability is then proved by showing how the nonlinear part of the problem may be controlled by the linear part and then employing a Grönwall inequality argument. The developed methodology can prove useful also in other problems involving non-Hermitian and non-reciprocal operators which are ubiquitous in the description of active matter.

1 Introduction

The ability of cells to self-propel is fundamental for many aspects of development, homeostasis and disease. For example, stem cells need to move to form tissues and organs but cell migration is equally critical during tissue repair [26, 73, 75, 81]. The active machinery behind self-propulsion resides in the cytoskeleton—a meshwork of actin filaments that is cross-linked by myosin motors. The main active processes in the cytoskeleton are the polymerization of actin fibers and the relative sliding of actin fibers induced by myosin motors [2, 40]. The molecular and biochemical basis of these processes is basically known, however the corresponding mathematical theory is still under development and a variety of multiscale simulation approaches targeting various cell motility mechanisms can be found in the literature [8, 17, 18, 38, 54, 61, 80, 85].

Aiming at the development of a rigorous mathematical approach, we focus here on the simplest phenomenon of self-propulsion in keratocytes. They move by advancing the front through active polymerization with a simultaneous formation of adhesion clusters. After the adhesion of the protruding part of the cell is secured, the cytoskeleton contracts due to activity of myosin motors. This active contraction leads to detachment at the rear and depolymerization of the actin network. All three components of the motility mechanism (polymerization, contraction, and adhesion) depend upon continuous ATP hydrolysis and require intricate regulation by complex signaling pathways involving chemical and mechanical feedback loops [10, 77].

Contractile force generation is of fundamental importance for cell migration. Using actin fibers as a substrate, myosin motors generate forces which are ultimately responsible for both motility initiation and the steady locomotion of keratocytes [1, 20, 35, 79]. In view of such a central role in cell motility played by active contraction and to achieve relative analytical transparency of the mathematical analysis, we consider in this paper a prototypical model of cell motility which emphasizes contraction as the main driving mechanism while accounting for polymerization and adhesion only in a schematic manner.

Our stylized model of cell motility is based on a one-dimensional projection of the complex intracellular dynamics onto the direction of locomotion. Specifically, we assume that the motor part of a cell can be viewed

as a one-dimensional continuum layer bounded by the two free boundaries representing the front and the rear of the moving cell. We make a simplifying physical assumption that actin polymerization and de-polymerization can take place only on these boundaries and that these phenomena can be modeled as an influx of mass at the front boundary and its disappearance at the rear boundary. While adhesion is treated for simplicity as passive spatially inhomogeneous viscous friction, the actomyosin contraction is represented by active spatially inhomogeneous prestress [47].

We begin by writing the force balance in the form $\sigma' = \xi v$, where σ is axial stress, ξ the coefficient of viscous friction and prime denotes the spatial derivative. To decouple the force balance equation from the mass transport equation we assume infinite compressibility of our solid gel by writing $\sigma = \eta v' + km$, where η is the bulk viscosity, $m(x, t)$ is the mass density of myosin motors and $k > 0$ is a constant representing contractile pre-stress per unit motor mass. The density of motors is modeled by an advection-diffusion equation where the advection is due to the flow of actin: $\partial_t m + (mv)' - Dm'' = 0$. Behind this assumption is the idea that myosin motors, actively cross-linking the actin network, are advected by the network flow and can also diffuse due to thermal fluctuations [15, 39, 82]. To ensure that the moving cell maintains its size, we introduce a phenomenological cortex/osmolarity mediated quasi-elastic interaction between the front and the back of the self-propelling fragment [9, 30, 51, 64]. This assumption suggests that the boundaries of our moving active segment are linked through an effective linear spring which regulates the value of the stress on the free boundaries $l_-(t)$ and $l_+(t)$: $\sigma_0^\pm = -k_e(L(t) - L_0)/L_0$, where $L(t) = l_+(t) - l_-(t)$ is the length of the moving segment, k_e is the effective elastic stiffness and L_0 is the reference length of the spring. Finally, we assume the free boundaries move with the internal flow: $\partial_t l_\pm = v(l_\pm)$. We imply here that the addition and deletion of F-actin particles inserted at the front and taken away at the rear does not contribute to fronts propulsion. We also impose a zero flux condition for the active component $m'(l_\pm(t), t) = 0$ ensuring that the average concentration of motors $m_0 = \frac{1}{L_0} \int_{l_-(t)}^{l_+(t)} m(x, t) dx$ is preserved. To complete the setting of the ensuing (statically determinate) mechanical problem we impose the initial conditions $l_\pm(0) = l_\pm^0$ and $m(x, 0) = m^0(x)$.

The resulting one-dimensional model reduces to a dynamical system of a Keller–Segel-type with free boundaries as it was first established in [62]. However, in contrast to its chemotactic analog, the nonlocality in this mechanical system is due to mechanical rather than chemical feedback [63]

To emphasize the universality of the emerging problem, we now present a physically different but mathematically equivalent presentation of the model which was introduced in [68, 69] and which we use in what follows. We also switch to a more formal mathematical description as appropriate for the subsequent rigorous analysis.

The cell, which is now fluid, is again modeled in time-dependent interval centered at a point $c(t)$ and with width $L(t)$: $\Omega(t) = (c(t) - L(t)/2, c(t) + L(t)/2) \subset \mathbb{R}$. For each $t \geq 0$, the velocity of fluid in the cell is $u(x, t) \in \mathbb{R}$ for $x \in \Omega(t)$. Since the cell is thin in the dorsal direction, most of the fluid within the cell lies close to the cell membrane. Therefore, we may assume the flow of incompressible fluid is dominated by friction and follows Darcy’s law:

$$p' = \zeta u,$$

where $p(\cdot, t) : \Omega(t) \rightarrow \mathbb{R}$ is fluid pressure within the cell, $\zeta > 0$ is the constant adhesion coefficient and the prime denotes spatial derivative. As in [62, 69], the constitutive equation within the cell is

$$p = \mu u' + km,$$

where $m(\cdot, t) : \Omega(t) \rightarrow \mathbb{R}_+$ is the density of myosin within the cell, $\mu > 0$ is the viscosity coefficient, and $k > 0$ is the contractility of myosin. Myosin density evolves in time according to the advection-diffusion equation, which, after applying Darcy’s law is

$$\partial_t m = Dm'' - (m\phi)'. \quad (1)$$

To ensure that the total myosin mass is conserved in time, the myosin density satisfies no-flux boundary conditions: $m' = 0$.

For a boundary condition for pressure, we consider pressure induced by the elastic restoring force due to the cell membrane cortex tension. This pressure is then described by

$$p = -k_e \frac{L(t) - L_0}{L_0}, \quad (2)$$

where L_0 is the length of the cell in a “reference configuration” in which the cell membrane is relaxed, and $k_e > 0$ is the *inverse compressibility coefficient*, which measures the “stiffness” of the cell. It is convenient to use the quantity $\phi = p/\zeta$ rather than p itself, and we will employ ϕ going forward. Then for instance, the variable ϕ at the boundary satisfies the Dirichlet condition:

$$\zeta \phi = -k_e \frac{L(t) - L_0}{L_0}. \quad (3)$$

Finally, we assume that the interval $\Omega(t)$ evolves via a kinematic Hele-Shaw type velocity-matching boundary condition:

$$\partial_t L(t) = \phi'(c(t) + L(t)/2, t) - \phi'(c(t) - L(t)/2, t) \quad (4)$$

$$\partial_t c(t) = \frac{1}{2} (\phi'(c(t) + L(t)/2, t) + \phi'(c(t) - L(t)/2, t)). \quad (5)$$

A relative analytical transparency of the problem is achieved due to the fact that the variable ϕ satisfies a linear elliptic equation :

$$-\mu\phi'' + \zeta\phi = km, \quad (6)$$

The resulting nonlocal model of the moving cell, described by two coupled equations (1), (6), represents a direct analog of the Keller-Segel system in its Hele-Shaw version. While, as we have already mentioned, the *infinitely compressible* solid gel version of this model was first introduced in its one dimensional form in [62, 63], the same model was re-interpreted in its *incompressible fluid* form in [68, 69] where the Hele-Shaw formulation opened the way towards two dimensional analysis capturing an important new effect: the evolution of the cell shape.

In the present paper we revisit the one dimensional Keller-Segel system with free boundaries which captures the key biological effects while being amenable to formal mathematical analysis. Our rigorous study of nonlinear stability in this problem complements numerous direct numerical simulations which have been conducted in similar free boundary problems [44, 55, 56, 65, 71]. In this respect it is important to mention that physically different free-boundary-type models of cell motility, emphasizing various other parts of the self-propulsion machinery employed by motile cells, have been studied using rigorous mathematical analysis, see for instance, [23, 24]. Our paper differs from this mathematical work fundamentally as we have to deal with non-standard non-local boundary condition.

Last but not least, we mention that phase field models of cell motility, representing a mathematical alternative to our free boundary formulation (front capturing rather than front tracking), have been the subject of extensive research efforts [12, 13, 14, 84, 86]. In particular, closely related free boundary models of tumor growth were studied in [25, 36, 37]. While the corresponding numerical models allow for very efficient numerical studies, they are not as readily amenable for rigorous stability analysis as free boundary models.

The free boundary model based on the (1), (6), representing the main subject of the present study, is known to have a family of traveling wave solutions, which describe steady cell motion. They bifurcate from a family stationary solutions, representing non-moving cells at a threshold measuring the level of internal activity. In [62, 63], the stable stationary solutions were identified analytically and the nature of the corresponding bifurcation around the threshold value of parameter was investigated using weakly nonlinear analysis of the bifurcating traveling wave solutions. Significant numerical evidence that traveling waves bifurcating from homogeneous stationary states have finite reserve of stability was also given. In [68, 69], the bifurcation between stationary and traveling wave solutions was studied more formally in two dimensions, and the corresponding complex shapes of the traveling waves were found analytically near the bifurcation point and numerically away from it. Additionally, linear stability was investigated for both stationary and traveling wave solutions, with certain eigenvalues being explicitly calculated analytically. This previous work suggested stability of stationary solutions up to the bifurcation point and also hinted towards nonlinear stability of the bifurcated traveling waves.

In the present paper, we build on this previous work. First of all, we present a rigorous study of the bifurcation from stationary solutions to traveling waves. The analogous proof in two dimensions has been already obtained in [68] however it required a complicated change of variables to account for rotational symmetry. In the one dimensional problem the analysis is shown to be much more transparent. Then we prove that all eigenvalues of traveling wave solutions have negative real part. In [68, 69], a candidate for the leading eigenvalue was identified and was shown numerically to have negative real part. In this respect the analysis in this paper is much more exhaustive. Our main result is the proof of asymptotic stability of both stationary states and traveling waves for appropriate parameter values. The complexity of the traveling wave case is in the non-self-adjoint (NSA) nature of the linearized operator. Despite this we proved the nonlinear stability of such waves with respect to arbitrary smooth perturbations, which complements the previous study [63] dealing the perturbations of the traveling wave type only. In particular, we proved that there exist multiple families of stationary solutions and traveling waves, but the only solutions which may be stable are a family of homogeneous stationary solutions and the traveling waves bifurcating from them. Moreover, it was shown analytically that, for appropriate parameter values, homogeneous stationary solutions are stable with respect to perturbations in the class of traveling waves.

To complement this short summary we first reiterate that our key mathematical objective is establishing nonlinear stability in a prototypical model of cell motility. Mathematically, it amounts to proving stability of the stationary and traveling wave solutions with respect to arbitrary perturbations. The main mathematical challenge is due to the non self-adjoint (non-Hermitian, or non-reciprocal) nature of the linearized operator in this problem which is an important general feature of PDE models of active matter [5, 27, 31, 74, 83].

It is known, for instance, that for NSA operators, eigenvectors do not necessarily span the entire domain of the operator (see, e.g., [41] for a simple example of this phenomenon in one dimension). Therefore, common stability analysis based only on eigenvalues and eigenvectors may not be sufficient [78].

Indeed, a typical approach in the cases when the linearized problem is self-adjoint, see for instance [3, 57], would be to divide the eigenmodes of the linearized system into stable modes (with negative real part eigenvalues) and finitely many center eigenmodes (with zero real part eigenvalues). Then, already in the nonlinear setting, solutions in the stable manifold are shown to be controlled (bounded) by solutions in the center manifold. Finally, a nonlinear ODE is derived for solutions in the center manifold, from which it can be easily shown that all center manifold solutions asymptotically approach the equilibrium, and thus all other solutions also approach it. However, the key underlying assumption in this approach is that eigenvectors of the linearized operator span the entire domain of the operator, which may not be the case for NSA operators which may exhibit a “dark” area in the phase space which is not “visible” in the purely eigenvalue/eigenvector approach.

In those cases comprehensive analysis may require considering the entire spectrum rather than only eigenvalues. To this end we establish linear stability by applying the Gearhart-Pruss-Greiner Theorem [33], which instead of eigenvalues, operates with bounds on the resolvent of the linear operator. Therefore, in the case when eigenvectors do not span the domain of the operator A , the Gearhart-Pruss-Greiner Theorem indeed allows one to establish stability in the “dark” part of the domain which invisible to eigenvectors. Specifically, we use the fact that instability can be controlled via the *resolvent operator*

$$R_\mu = (\mu I - A)^{-1}$$

for μ with positive real part. The crucial idea is to bound μ away from any point of the entire spectrum, not just the eigenvalues. Moreover, in infinite dimensions, such a bound rules out the case that a sequence of eigenvalues has negative real parts converging to zero. It should be noted that while our techniques are sufficient to establish stability without need to prove that the eigenvectors of the linearization span its domain, it is shown in [48] that, at least in some NSA problems, eigenvectors span the domain anyway, and in these cases, negative eigenvalues may be sufficient for stability.

We prove our main *nonlinear stability* result in two steps. First, we prove the *linear stability* for the NSA operator using the analysis of the resolvent as described above. Then the question becomes whether linear stability implies nonlinear stability. In finite dimensions a natural second step would be to use the Hartman-Grobman Theorem [4] which is a well known tool for concluding nonlinear stability from linear stability. However, even in finite dimensions this theorem requires the absence of eigenvalues with zero real part. Our problem has a zero eigenvalue (a slow manifold) which appears in the linearized operator due to translational symmetry and requires the use of the notion of “stability up to shifts”. Moreover, our problem is infinite dimensional.

Therefore, our second step is the proof of the appropriate analog of the Hartman-Grobman Theorem specifically tailored for our model. While there are several extensions of the Hartman-Grobman Theorem to infinite dimensions, e.g. [6], most of these results apply to a smooth nonlinear operators mapping a Banach space to itself whereas in our parabolic PDE problem, the operator maps a Sobolev space H^2 to L^2 . Even though there are some Hartman-Grobman type results for parabolic equations [52], they are not directly applicable to our problem.

We deal with the problem by establishing subtle bounds on the derivatives of the solution in the neighborhood of a pitchfork bifurcation which allow the linear part of the nonlinear operator to dominate its nonlinear part. The ensuing proof is then equivalent to establishing the existence of a Lyapunov function (or Lyapunov functionals in the infinite dimensional setting) for traveling wave solutions, see [11, 53, 72] for related results. It is important to emphasize that our methods are readily generalizable to other similar situations when the task is to prove asymptotic stability of solutions in a PDE model in the vicinity of a bifurcation point.

Our methods for establishing stability in this paper are similar some of the methods described in the comprehensive texts on stability of traveling waves [43, 59, 70]. Several studies, e.g. [49, 50, 60], prove *spectral stability* of traveling wave solutions, meaning they show that the spectrum of the operator is shown to consist only of points with negative real part. Most of these studies use the *Evans function* to compute the spectrum. The Evans function is a tool for finding eigenvalues (or more generally, the spectrum) of linearizations about traveling wave solutions [7, 19, 34]. The Evans function is particularly well suited to traveling wave problems because, unlike other methods for calculating eigenvalues, it can easily separate the eigenvalues from the continuous spectrum which arises for operators on unbounded domains—the usual case for traveling wave operators. We do not use the Evans function for two reasons. First, our traveling waves are not on an unbounded domain because, being a free boundary problem, the domain is bounded at all times and moves with the wave; we show that there is no continuous spectrum for our problem. Second, we may use the results of Crandall and Rabinowitz in [22] (complimenting their more well-known bifurcation result [21]) to calculate the small velocity asymptotic value of the leading eigenvalue without reference to the Evans function.

Beyond spectral stability, other studies use techniques similar to ours to prove linear and nonlinear stability, e.g., [19, 42, 45]. In each case, this is done by using spectral theory to place bounds on the semigroup generated by the linearization, thus establishing linear stability, and then showing that the linear part of the nonlinear problem dominates, thereby proving nonlinear stability. We follow this strategy, with the main spectral theoretic tool being the Gearhart-Pruss-Greiner Theorem.

2 Infinite rigidity limit

Below we distinguish between two versions of our model of cell motion. The first one to which we refer as “Model A” assumes, as in the original derivation, that the size of the cell is controlled by an elastic spring, whose elastic modulus will be our “stiffness” parameter. By considering an asymptotic limit when such stiffness tends to infinity, we will derive a “stiff limit” of the original model to which we refer in what follows as “Model B.” In this limiting model, which is analytically much more transparent, the cell has a fixed size.

As we have shown in the Introduction, in our model A, the myosin density m , pressure ϕ , length L , and center c satisfy the PDE system:

$$\begin{cases} -\mu\phi'' + \zeta\phi = km & x \in \Omega(t) \end{cases} \quad (7)$$

$$\begin{cases} m_t = Dm'' - (m\phi')' & x \in \Omega(t) \end{cases} \quad (8)$$

$$\begin{cases} \zeta\phi = -k_e \frac{L(t) - L_0}{L_0} & x \in \partial\Omega(t) \end{cases} \quad (9)$$

$$\begin{cases} m' = 0 & x \in \partial\Omega(t) \end{cases} \quad (10)$$

$$\begin{cases} \partial_t L(t) = \phi'(c(t) + L(t)/2, t) - \phi'(c(t) - L(t)/2, t) \end{cases} \quad (11)$$

$$\begin{cases} \partial_t c(t) = \frac{1}{2} (\phi'(c(t) + L(t)/2, t) + \phi'(c(t) - L(t)/2, t)) \end{cases} \quad (12)$$

An important feature of this model is that total myosin mass is conserved in time:

$$\frac{d}{dt} \int_{c(t)-L(t)/2}^{c(t)+L(t)/2} m(x, t) dx = 0. \quad (13)$$

To nondimensionalize this model, we make several rescalings. We rescale x by $x \rightarrow x/L_0$. Since L and c are measures of distance, they are rescaled in the same way: $L \rightarrow L/L_0$, $c \rightarrow c/L_0$. We also rescale time by $t \rightarrow tD/L_0^2$, pressure by $\phi \rightarrow \phi\pi\zeta/k_e$ and myosin density by $m \rightarrow mL_0^2/M$ where M is the total myosin mass.

After such normalization, the variables x , t , m , ϕ , L , and c are all dimensionless quantities and the PDE system (7)-(12) can be re-written in the form

$$\begin{cases} -Z\phi'' + \phi = Pm & c - L/2 < x < c + L/2 \end{cases} \quad (14)$$

$$\begin{cases} m_t = m'' - K(m\phi')' & c - L/2 < x < c + L/2 \end{cases} \quad (15)$$

$$\begin{cases} \phi = 1 - L & x = c \pm L/2 \end{cases} \quad (16)$$

$$\begin{cases} m_x = 0 & x = c \pm L/2 \end{cases} \quad (17)$$

$$\begin{cases} L_t = K(\phi'(c + L/2) - \phi'(c - L/2)) \end{cases} \quad (18)$$

$$\begin{cases} c_t = K \frac{\phi'(c + L/2) + \phi'(c - L/2)}{2} \end{cases} \quad (19)$$

where

$$Z = \frac{\mu}{\zeta L_0^2} \quad P = \frac{kM}{k_e L_0} \quad K = \frac{k_e}{D\zeta}, \quad (20)$$

are the main non-dimensional parameters of the model. Furthermore, in these rescaled coordinates, the total myosin mass is

$$\int_{c(t)-L(t)/2}^{c(t)+L(t)/2} m(x, t) dx = 1. \quad (21)$$

The simpler and analytically much more transparent can be obtained if we consider is the limit of model A as the “stiffness” coefficient k_e tends to infinity. To this end, suppose $k_e = k_e^*/\varepsilon$ where ε is a small, positive constant. Each of the coefficients P , K in (20) depend on k_e . Therefore, we denote them $P_\varepsilon = \varepsilon P_1$, and $K_\varepsilon = K_{-1}/\varepsilon$ respectively where

$$P_1 = \frac{kM}{k_e^* L_0}, \quad K_{-1} = \frac{k_e^*}{D\zeta}. \quad (22)$$

To derive the limiting behavior of solutions to (14), we turn to asymptotic analysis. For each $\varepsilon > 0$, let ϕ_ε , m_ε , L_ε , and c_ε solve (14)-(19) with coefficients P_ε , and K_ε for $0 \leq t < T$ with initial conditions $m_\varepsilon(0, x) = \bar{m}(x)$, $L_\varepsilon(0) = \bar{L}$, and $c_\varepsilon(0) = \bar{c}$. We expand each of ϕ_ε , m_ε , L_ε , and c_ε in small ε :

$$\phi_\varepsilon = \phi_0 + \varepsilon\phi_1 + O(\varepsilon^2) \quad m_\varepsilon = m_0 + \varepsilon m_1 + O(\varepsilon^2) \quad (23)$$

$$L_\varepsilon = L_0 + \varepsilon L_1 + O(\varepsilon^2) \quad c_\varepsilon = c_0 + \varepsilon c_1 + O(\varepsilon^2). \quad (24)$$

Now we substitute these expansions along with the expansions for P_ε and K_ε and compare terms of like power of ε . Note that the free boundary requires that the boundary conditions be expanded not only in ε , but also x so that all boundary conditions are evaluated at $x = c_0 \pm L_0/2$.

In zero order, (14) becomes $-Z_0\phi_{0,xx} + \phi_0 = 0$ with boundary condition $\phi_0 = 1 - L_0$. We explicitly calculate

$$\phi_0 = (1 - L_0) \frac{\cosh\left(\frac{c_0 - x}{\sqrt{Z_0}}\right)}{\cosh\left(\frac{L_0}{2\sqrt{Z_0}}\right)} \quad (25)$$

In order -1 , (15) has only one nontrivial term:

$$K_{-1}(m_0\phi_{0,x})_x = 0. \quad (26)$$

We conclude that $m_0\phi_{0,x}$ is constant in x . Since the initial condition \bar{m} is arbitrary in $H^2(-L_0/2, L_0/2)$, and since ϕ_0 given by (25) does not depend on m_0 , this can only be accomplished if $\phi_{0,x} = 0$. This, in turn, implies $\phi_0 = 0$ and $L_0 = 1$.

Since $\phi_0 = 0$, in zero order, (15) becomes

$$m_{0,t} = m_{0,xx} - K_{-1}(m_0\phi_{1,x})_x. \quad (27)$$

Where ϕ_1 satisfies the first order expansions of (14) and its boundary condition (16):

$$\begin{cases} -Z\phi_{1,xx} + \phi_1 = P_1 m_0 & c_0 - L_0/2 < x < c_0 + L_0/2 \\ \phi_1 = -L_1 & x = c_0 \pm L_0/2 \end{cases} \quad (28)$$

In zero order, (18) becomes

$$L_{0,t} = K_{-1}(\phi_{1,x}(c_0 + L_0/2) - \phi_{1,x}(c_0 - L_0/2)). \quad (29)$$

On the other hand, we know that $L_0 \equiv 1$, so $L_{0,t} = 0$. Therefore, ϕ_1 has to satisfy three boundary conditions:

$$\phi_1(c_0 - L_0/2) = -L_1, \quad \phi_1(c_0 + L_0/2) = -L_1, \quad \phi_{1,x}(c_0 - L_0/2) = \phi_{1,x}(c_0 + L_0/2). \quad (30)$$

We conclude that L_1 is determined by these three conditions. That is, L_1 is chosen so that ϕ_1 meets periodic boundary conditions.

Since ϕ_1 satisfies periodic boundary conditions, we may determine c_0 by the zero order expansion of (19):

$$c_{0,t} = K_{-1}\phi_{1,x}(c_0 + L_0/2). \quad (31)$$

To complete the stiff limit model, we omit the subscript indices so we write $m = m_0$, $L = L_0 = 1$, $c = c_0$. It is also convenient to denote $\phi = K_{-1}\phi_1$ and $P = P_1 K_{-1}$. Therefore, we write the stiff limit PDE model as:

$$\begin{cases} -Z\phi_{xx} + \phi = Pm & c(t) - 1/2 < x < c(t) + 1/2 \end{cases} \quad (32)$$

$$\begin{cases} m_t = m_{xx} - (m\phi_x)_x & c(t) - 1/2 < x < c(t) + 1/2 \end{cases} \quad (33)$$

$$\begin{cases} m_x = 0 & x = c(t) \pm 1/2 \end{cases} \quad (34)$$

$$\begin{cases} \phi(c - 1/2) = \phi(c + 1/2) \end{cases} \quad (35)$$

$$\begin{cases} \phi_x(c - 1/2) = \phi_x(c + 1/2) \end{cases} \quad (36)$$

$$\begin{cases} c_t = \phi_x(c + 1/2). \end{cases} \quad (37)$$

Once again, the total myosin mass is conserved and its value is 1. As we have already mentioned, in the rest of the ensuing paper ‘‘Model B’’ will be the main focus of our study. Note first that Model B has stationary solution $m = 1$ and $\phi = P$. As we are going to see, for P sufficiently small, such solution is asymptotically stable, but for large P , it becomes unstable and bifurcate into traveling wave solution. In the linearization of Model B about traveling waves, the invariance of traveling waves to translation manifests itself through a zero eigenvalue. By factorizing the shifts, the corresponding eigenvector is identified with 0, and in this way the

zero eigenvalue is effectively removed. This is accomplished by changing coordinates via the transformation $x \rightarrow x - c(t)$. In these coordinates, (32)-(37) become

$$\begin{cases} -Z\phi_{xx} + \phi = Pm & -1/2 < x < 1/2 \end{cases} \quad (38)$$

$$\begin{cases} m_t = m_{xx} + \phi_x(1/2)m_x - (m\phi_x)_x & -1/2 < x < 1/2 \end{cases} \quad (39)$$

$$\begin{cases} m_x = 0 & x = \pm 1/2 \end{cases} \quad (40)$$

$$\begin{cases} \phi(-1/2) = \phi(1/2) \end{cases} \quad (41)$$

$$\begin{cases} \phi_x(-1/2) = \phi_x(1/2) \end{cases} \quad (42)$$

$$\begin{cases} c_t = \phi_x(1/2). \end{cases} \quad (43)$$

In the new coordinates, we observe that the center coordinate c is partial decoupled from m . Therefore, we can drop the c coordinate, effectively identifying all solutions that are the same up to the center coordinate. Thus, for instance, a stationary solution to (38)-(42) becomes identified with an equivalence class of traveling wave solutions to (32)-(37). Furthermore, if a stationary solution to (38)-(43) is asymptotically stable, then the corresponding traveling wave solutions to (32)-(37) are asymptotically stable *up to shifts* in the sense that a solution whose initial condition is a perturbation of a traveling wave solution converges to a different traveling wave solution with the same velocity, but a different ("shifted") center coordinate.

In what follows we refer to the result of transforming coordinates in "Model B" and dropping the c component as "Model C," which we formulate more succinctly as

$$\partial_t m = F_C(m) = m_{xx} + \phi_x(1/2)m_x - (m\phi_x)_x, \quad \begin{cases} -Z\phi'' + \phi = Pm & -1/2 < x < 1/2 \\ \phi(1/2) = \phi(-1/2) \\ \phi_x(-1/2) = \phi_x(1/2). \end{cases} \quad (44)$$

The domain of F_C is $X_C^2 := \left\{ m \in H^2(-1/2, 1/2) : m_x(\pm 1/2) = 0, \int_{-1/2}^{1/2} m \, dx = 1 \right\}$.

3 Stationary Solutions

We can now address the stability (up to shifts) of homogeneous stationary solutions $m = 1$ and $\phi = P$ of model B, by analyzing the $m = 1$ solution to model C. Its asymptotic stability will be proved in the form of the following:

Theorem 3.1. *If $P/Z < \pi^2$, then there exists $\varepsilon > 0$ such that if $m_0 \in H^1(-1/2, 1/2)$ with $\|m_0 - 1\|_{H^1} < \varepsilon$, then if $m(x, t)$ solves $\partial_t m = F_C(m)$ with $m(0, x) = m_0(x)$, then*

$$\lim_{t \rightarrow \infty} \|m(\cdot, t) - m_0\|_{L^2} = 0. \quad (45)$$

A key step in proving Theorem 3.1 is the analysis of stability of the corresponding linear problem. The linearized operator S_C is defined by

$$S_C u = DF_C(1)u = u'' - \phi'', \quad (46)$$

where ϕ is defined as in (44) (with $m = u$) and $u \in \tilde{X}_C^2 := \left\{ u \in H^2(-1/2, 1/2) : u_x(\pm 1/2) = 0, \int_{-1/2}^{1/2} u \, dx = 0 \right\}$.

We first prove the following theorem establishing the linear stability of stationary states:

Theorem 3.2. *If $P/Z < \pi^2$, then there exists $\omega > 0$ such that if $m(x, t)$ solves $\partial_t u = S_C u$ in \tilde{X}_2 with $u(0, x) = u_0(x)$, then*

$$\|u(\cdot, t)\|_{L^2} < \|u_0\|_{L^2} e^{-\omega t}. \quad (47)$$

The main tool in proving Theorem 3.2 is expectedly the Spectral Theorem for compact self-adjoint operators [46], which states that a compact, self-adjoint operator has a basis of eigenvectors. The operator S_C is not compact, but we will show that its inverse is, and S_C shares the eigenvectors of its inverse. Therefore, we may reduce the problem of linear stability to the problem of stability of individual eigenstates, with the exponential decay in Theorem 3.2 given by a uniform negativity of the corresponding eigenvalues. To complete this proof, we must only show (via three Lemmas below) that (i) S_C is self-adjoint, (ii) all eigenvalues of S_C are negative and bounded away from zero, and (iii) S_C has compact inverse.

First we prove self-adjointness. Let X be a Hilbert space and let $D(A) \subset X$ be a dense subspace of X which is the domain of an operator $A : D(A) \rightarrow X$. Recall that the adjoint of A is an operator A^* such that $\langle u, A^*v \rangle = \langle Au, v \rangle$ for all $u, v \in D(A)$. The operator A is self-adjoint if $A = A^*$. Therefore, we introduce the following bilinear form to determine whether or not an operator is self-adjoint:

Definition 3.3. Let X be an inner product space, and let $A : X \rightarrow X$. The *adjoint commutator* of A is $H : X \times X \rightarrow \mathbb{R}$ defined by

$$H(u, v) = \langle Au, v \rangle - \langle u, Av \rangle. \quad (48)$$

If the adjoint commutator is identically zero, then A is self-adjoint. Otherwise, A is non-self-adjoint.

Lemma 3.4. *The linearization S_C of F_C about the stationary solution $m = 1$ is self-adjoint with respect to the L^2 inner product.*

Proof. Let $H : \tilde{X}_2 \times \tilde{X}_2 \rightarrow \mathbb{R}$ be the adjoint commutator of S_C . Let $u_1, u_2 \in \tilde{X}_2$. Let ϕ_i solve $-Z\phi_i'' + \phi_i = Pu_i$ with periodic boundary conditions. Then

$$H(u_1, u_2) = \int_{-1/2}^{1/2} u_2(u_1'' - \phi_1'') dx - \int_{-1/2}^{1/2} u_1(u_2'' - \phi_2'') dx \quad (49)$$

$$= \int_{-1/2}^{1/2} (u_1' u_2' - u_2' u_1') dx + \int_{-1/2}^{1/2} \left[u_1 \frac{\phi_2 - Pu_2}{Z} - u_2 \frac{\phi_1 - Pu_1}{Z} \right] dx \quad (50)$$

$$= \frac{1}{PZ} \int_{-1/2}^{1/2} [(-Z\phi_1'' + \phi_1)\phi_2 - (-Z\phi_2'' + \phi_2)\phi_1] dx \quad (51)$$

$$= \frac{1}{P} \int_{-1/2}^{1/2} (\phi_1' \phi_2' - \phi_2' \phi_1') dx \quad (52)$$

$$= 0. \quad (53)$$

□

Now we show the negativity of the eigenvalues of S_C .

Proposition 3.5. *If $P/Z < \pi^2$, then all eigenvalues of S_C are negative and bounded away from 0.*

Proof. Assume $P/Z < \pi^2$. Let u be an eigenvector of S_C and let λ be its eigenvalue. Since S_C is self adjoint, λ real and u is real-valued. Without loss of generality, we may assume $\|u\|_{L^2} = 1$. Let ϕ solve $-Z\phi'' + \phi = Pu$ with periodic boundary conditions on $(-1/2, 1/2)$. Then u and λ satisfy $u'' - \phi'' = \lambda u$. Multiplying by u and integrating we find

$$\begin{aligned} \lambda &= \int_{-1/2}^{1/2} u'' u - \phi'' u \\ &= - \int_{-1/2}^{1/2} u'^2 dx - \frac{1}{Z} \int_{-1/2}^{1/2} (\phi - Pu)u dx \\ &= - \int_{-1/2}^{1/2} u'^2 dx + \frac{P}{Z} \int_{-1/2}^{1/2} u^2 dx - \frac{1}{PZ} \int_{-1/2}^{1/2} \phi(-Z\phi'' + \phi) dx \\ &= - \int_{-1/2}^{1/2} u'^2 dx + \frac{P}{Z} - \frac{1}{P} \int_{-1/2}^{1/2} \phi'^2 dx - \frac{1}{PZ} \int_{-1/2}^{1/2} \phi^2 dx \\ &\leq - \int_{-1/2}^{1/2} u'^2 dx + \frac{P}{Z}. \end{aligned}$$

It is well known that the optimal constant in the Poincaré inequality in an interval of length 1 is $1/\pi$ [58]. The Poincaré inequality applies to u since $\int_{-1/2}^{1/2} u(x) dx = 0$. Therefore, we conclude that

$$\lambda \leq \frac{P}{Z} - \pi^2 < 0. \quad (54)$$

Therefore all eigenvalues of S_C are negative and bounded away from 0. □

Finally, we show that the inverse of the linearization is compact.

Lemma 3.6. *If $P/Z < \pi^2$, then S_C is invertible and $S_C^{-1} : X \rightarrow X$ is compact.*

Proof. Assume $P/Z < \pi^2$. By proposition 3.5, 0 is not an eigenvalue of S_C . That S_C is invertible follows from the Lax-Milgram Theorem (see Proposition 5.3 for details).

First we show that S_C^{-1} is bounded. Suppose, to the contrary that it is unbounded. Then there exist sequences $(v_k) \subset \tilde{X}_C^2$ and $(w_k) \subset L^2(-1/2, 1/2)$ such that

$$S_C v_k = w_k, \quad \|v_k\|_{L^2} = 1, \quad \|w_k\|_{L^2} \leq 1/k. \quad (55)$$

Let ϕ_k satisfy $-Z\phi_k'' + \phi_k = Pv_k$ with periodic boundary conditions. Then the following sequence is bounded:

$$\langle w_k, v_k \rangle_{L^2} = \langle S_C v_k, v_k \rangle_{L^2} = -\|v_k'\|_{L^2}^2 + \langle \phi_k'', v_k \rangle_{L^2}. \quad (56)$$

The sequence $\langle \phi_k'', v_k \rangle_{L^2}$ is bounded in k due to Proposition 6.1 in Appendix A. Since the (56) as a whole is bounded, we conclude that $\|v_k'\|_{L^2}$ is bounded in k as well.

Since $\|v_k\|_{L^2}$ and $\|v_k'\|_{L^2}$ are both bounded, we conclude that (v_k) is bounded with respect to the H^1 norm. By the Banach-Alaoglu Theorem [66], there is a subsequence also called v_k which converges weakly in $H^1(-1/2, 1/2)$ and thus also in L^2 . By Morrey's inequality [29] and the Arzela-Ascoli theorem [16], $H^1(-1/2, 1/2) \subset\subset L^2(-1/2, 1/2)$, so we may assume that (v_k) converges strongly to some $v \in L^2$. Since $\|w_k\|_{L^2} \leq 1/k$, $w_k \rightarrow 0$ in $L^2(-1/2, 1/2)$. Therefore, v is a weak solution to $S_C v = 0$. Since $\lambda I - S_C$ is invertible, we conclude that $v = 0$. But since $\|v_k\|_{L^2} = 1$, we also have $\|v\|_{L^2} = 1$, a contradiction. Therefore, S_C^{-1} is a bounded operator.

Now we show that $S_C^{-1} : L^2(-1/2, 1/2) \rightarrow L^2(-1/2, 1/2)$ is compact. To that end, suppose that $(v_k) \subset \tilde{X}_C^2$ and $(w_k) \subset L^2(-1/2, 1/2)$ such that

$$S_C v_k = w_k \quad \text{and} \quad \|w_k\|_{L^2} \leq 1. \quad (57)$$

We need to show that there (v_k) has a convergent subsequence. But this follows from the same logic as the above step. Since S_C^{-1} is a bounded operator, (v_k) is a bounded sequence in $L^2(-1/2, 1/2)$. Therefore, once again each term in (56) is bounded, so (v_k) has a weakly convergent subsequence in X^1 and a strongly convergent subsequence in X^0 . Therefore, S_C^{-1} is compact. \square

We can now prove the linear stability of stationary states.

Proof of Theorem 3.2. Assume $P/Z < \pi^2$. Then by Proposition 3.5, there exists $\omega > 0$ so that all for all eigenvalues λ of S_C , $\lambda \leq -\omega$ (in fact, we may choose $\omega = \pi^2 - P/Z$). By Lemma 3.6, S_C has compact inverse. By Lemma 3.4, S_C is self-adjoint, and therefore S_C^{-1} is also self-adjoint. By the spectral theorem [46], the eigenvectors of S_C^{-1} form an orthonormal set that spans a dense subset of \tilde{X}_2 . Denote these eigenvectors (v_n) for $n \in \mathbb{N}$ (since \tilde{X}_C^2 has countable dimension, we can enumerate the eigenvectors in this way). The eigenvectors of S_C^{-1} are also eigenvectors of S_C . For each $n \in \mathbb{N}$, let λ_n be the eigenvalue of λ_n corresponding to v_n .

Suppose $u(x, t)$ solves $\partial_t u = S_C u$ in \tilde{X}_2 with $u(0, x) = u_0(x) \in \tilde{X}_C^2$. Since the span of (v_n) is dense in \tilde{X}_C^2 , we may write any $u(x, t)$ as an infinite linear combination of these eigenvectors:

$$u(x, t) = \sum_{n=1}^{\infty} c_n(t) v_n(x), \quad (58)$$

for coefficients $c_n : [0, \infty) \rightarrow \mathbb{R}$. Substituting this expansion into the linear evolution equation, we obtain

$$\sum_{n=1}^{\infty} c_n'(t) v_n(x) = \sum_{n=1}^{\infty} c_n(t) S_C v_n(x) = \sum_{n=1}^{\infty} \lambda_n c_n(t) v_n(x). \quad (59)$$

By the orthogonality of the eigenvectors, we conclude that the sums must agree term-by-term, so for each n , $c_n' = \lambda_n c_n$, so

$$c_n(t) = c_n(0) e^{\lambda_n t}. \quad (60)$$

Thus,

$$\|u(\cdot, t)\|_{L^2} = \sqrt{\langle u, u \rangle_{L^2}} = \sqrt{\sum_{n=1}^{\infty} c_n^2(t)} = \sqrt{\sum_{n=1}^{\infty} c_n^2(0) e^{2\lambda_n t}} = e^{-\omega t} \sqrt{\sum_{n=1}^{\infty} c_n^2(0)} = e^{-\omega t} \|u(0, \cdot)\|_{L^2}.$$

Thus, the desired result holds. \square

It remains to show that the full, nonlinear stability result of Theorem 3.1 holds. To this end, we consider the *nonlinear part* Ψ of F_C defined for $u \in \tilde{X}_C^2$ by

$$\Psi(u) = F_C(1 + u) - S_C u = \phi'(1/2)u' - (u\phi')', \quad (61)$$

where ϕ solves $-Z\phi'' + \phi = Pu$ with periodic boundary conditions in $(-1/2, 1/2)$. The key to our proof of nonlinear stability is showing that the nonlinear part Ψ dominates the linear part S_C . We begin with a Lemma which gives a bound on $\Psi(u)$ in terms of u .

Lemma 3.7. *Let $\Psi : H^2([-1/2, 1/2]) \rightarrow H^1([-1/2, 1/2])$ be defined as in (61). Then there exists $C > 0$ independent of u , P , and Z such that*

$$\|\Psi(u)\|_{L^2} \leq \frac{CP}{Z} \|u\|_{L^2} \|u\|_{H^1}. \quad (62)$$

Proof. We make a direct calculation using estimates from Proposition 6.1 in Appendix A:

$$\|\Psi(u)\|_{L^2}^2 = \int_{-1/2}^{1/2} [(\phi'(1/2) - \phi'(x))u'(x) - u(x)\phi''(x)]^2 dx \quad (63)$$

$$\leq 2 \int_{-1/2}^{1/2} (\phi'(1/2) - \phi'(x))^2 (u'(x))^2 dx + 2 \int_{-1/2}^{1/2} (\phi''(x))^2 (u(x))^2 dx \quad (64)$$

$$\leq 4|\phi'(1/2)|^2 \|u'\|_{L^2}^2 + 4\|\phi'^2 u'^2\|_{L^1} + 2\|\phi''^2 u^2\|_{L^1} \quad (65)$$

$$\leq \frac{P^2}{Z^2} \|u\|_{L^1}^2 \|u'\|_{L^2}^2 + 4\|\phi'\|_{L^\infty}^2 \|u'\|_{L^2}^2 + 2\|\phi''\|_{L^4}^2 \|u\|_{L^4}^2 \quad (66)$$

$$\leq \frac{2P^2}{Z^2} \|u\|_{L^1}^2 \|u\|_{H^1}^2 + \frac{8P^2}{Z^2} \|u\|_{L^4}^4 \quad (67)$$

By Hölder's inequality, $\|u\|_{L^1} \leq \|u\|_{L^2}$. From the Gagliardo-Nirenberg inequality, there exists $C_1 > 0$ independent of u such that

$$\|u\|_{L^4} \leq C_1 \|u\|_{H^1}^{1/2} \|u\|_{L^1}^{1/2}. \quad (68)$$

Substituting (68) into (67) and letting $C^2 = 2 + 8C_1$, we obtain

$$\|\Psi(u)\|_{L^2} \leq C \frac{P}{Z} \|u\|_{L^2} \|u\|_{H^1}. \quad (69)$$

□

Our next goal is to show that if $\|u\|_{L^2}$ is small, then so is $\|\Psi(u)\|_{L^2}$. However, Lemma 3.7 is not sufficient to accomplish this because even if $\|u\|_{L^2}$ is small, $\|u\|_{H^1}$ may be large. Therefore, the following Lemma shows that if $\|u(\cdot, t)\|_{L^2}$ is small for all t , then $\|u'(\cdot, t)\|_{L^2}$ does not exceed $\|u'(\cdot, 0)\|_{L^2}$.

Lemma 3.8. *Suppose $P/Z < \pi^2$. Let $T, \varepsilon > 0$ and let u be a solution to $\partial_t u = S_C u + \Psi(u)$ in $C^1([0, T]; \tilde{X}_C^2)$. There exists $U^* > 0$ such that if $\|u'(\cdot, 0)\|_{L^2} < \varepsilon$ and $\|u(\cdot, t)\|_{L^2} < U^*$ for all $0 \leq t \leq T$, then*

$$\|u'(\cdot, t)\|_{L^2} \leq \varepsilon \quad \text{for all } 0 \leq t \leq T. \quad (70)$$

Proof. Write the evolution equation for u as

$$\partial_t u - u'' = -\phi'' + \Psi(u). \quad (71)$$

Square both sides and integrate to obtain

$$\|-\phi'' + \Psi(u)\|_{L^2}^2 = \int_{-1/2}^{1/2} (\partial_t u)^2 - 2(\partial_t u)u'' + (u'')^2 dx \quad (72)$$

$$= \|\partial_t u\|_{L^2}^2 + 2 \int_{-1/2}^{1/2} (\partial_t u')u' dx + \|u''\|_{L^2}^2 \quad (73)$$

$$= \|\partial_t u\|_{L^2}^2 + \frac{d}{dt} \|u'\|_{L^2}^2 + \|u''\|_{L^2}^2. \quad (74)$$

Thus,

$$\frac{d}{dt} \|u'\|_{L^2}^2 \leq \|-\phi'' + \Psi(u)\|_{L^2}^2 - \|u''\|_{L^2}^2 \quad (75)$$

$$\leq 2\|\phi''\|_{L^2}^2 + 2\|\Psi(u)\|_{L^2}^2 - \|u''\|_{L^2}^2. \quad (76)$$

From Lemma 3.7, there exists C_1 independent of u such that $\|\Psi(u)\|_{L^2} \leq C_1 \|u\|_{L^2} \|u\|_{H^1}$. Moreover, by Proposition 6.1 in Appendix A, $\|\phi''\|_{L^2} \leq 2P/Z \|u\|_{L^2}$. Since $\int_{-1/2}^{1/2} u dx = 0$ and $u'(\pm 1/2, t) = 0$, we may apply the Poincaré inequality to both u and u' with the optimal Poincaré constant $1/\pi$:

$$\|u\|_{L^2} \leq \frac{1}{\pi} \|u'\|_{L^2} \quad \text{and} \quad \|u'\|_{L^2} \leq \frac{1}{\pi} \|u''\|_{L^2}. \quad (77)$$

Thus,

$$\frac{d}{dt} \|u'\|_{L^2}^2 \leq 8 \frac{P^2}{Z^2} \|u\|_{L^2}^2 + 2C_1^2 \|u\|_{L^2}^2 \|u\|_{H^1}^2 - \pi^2 \|u'\|_{L^2}^2 \quad (78)$$

$$\leq 8 \frac{P^2}{Z^2} \|u\|_{L^2}^2 + 2C_1^2 \|u\|_{L^2}^2 (\|u\|_{L^2} + \|u'\|_{L^2})^2 - \pi^2 \|u'\|_{L^2}^2 \quad (79)$$

$$\leq -(\pi^2 - 4C_1^2 \|u\|_{L^2}^2) \|u'\|_{L^2}^2 + 8 \frac{P^2}{Z^2} \|u\|_{L^2}^2. \quad (80)$$

Let $U^* < \pi/(4C_1)$. Then if $\|u\|_{L^2} \leq U^*$ for all $0 < t < T$,

$$\frac{d}{dt} \|u'\|_{L^2}^2 \leq -R_1 \|u'\|_{L^2}^2 + R_2 \quad (81)$$

where

$$R_1 = \pi^2 - 4C_1^2(U^*)^2 > \frac{\pi^2}{2} \quad \text{and} \quad R_2 = 8 \frac{P^2}{Z^2}(U^*)^2. \quad (82)$$

Let $q(t) = \|u'(\cdot, t)\|_{L^2}^2 - R_2/R_1$. Then q satisfies $q' \leq -R_1 q$. By the Grönwall's inequality, $q(t) \leq q(0)e^{-R_1 t}$. We conclude that if $q(0) < 0$, then $q(t) < 0$ for all $t > 0$. Thus, if $\|u\|_{L^2} \leq U^*$, and if

$$\|u'(\cdot, 0)\|_{L^2} < \sqrt{\frac{R_2}{R_1}}, \quad \text{then} \quad \|u'(\cdot, t)\|_{L^2} < \sqrt{\frac{R_2}{R_1}} \quad (83)$$

for all $t > 0$. Letting $U^* < \varepsilon/(4\pi)$, we have

$$\sqrt{\frac{R_2}{R_1}} < 4\pi U^* < \varepsilon, \quad (84)$$

so the desired result holds. \square

Proof of Theorem 3.1. Let $u = m - 1$. Then u solves

$$\begin{cases} \partial_t u = S_C u + \Psi(u) & -1/2 < x < 1/2, \ t > 0 \\ u' = 0 & x = \pm 1/2, \ t > 0 \\ u(\cdot, 0) = m_0 - 1 := u_0 & t = 0. \end{cases} \quad (85)$$

Let $S(t)$ be the semigroup generated by S_C . By Theorem 3.2, there exists $\omega > 0$ such that $\|S(t)\|_{L^2} \leq e^{-\omega t}$. We observe that

$$\int_0^t S(t-\tau) \Psi(u(\tau, \cdot)) d\tau = \int_0^t S(t-\tau) (u'(\tau) - S_C u(\tau, \cdot)) d\tau \quad (86)$$

$$= \int_0^t \frac{d}{d\tau} (S(t-\tau) u(\tau, \cdot)) d\tau \quad (87)$$

$$= S(t-\tau) u(\tau, \cdot) \Big|_0^t \quad (88)$$

$$= u(\cdot, t) - S(t) u(0, \cdot) \quad (89)$$

$$= u(\cdot, t) - S(t) u_0. \quad (90)$$

Thus we may write

$$u(\cdot, t) = S(t) u_0 + \int_0^t S(t-\tau) \Psi(u(\tau, \cdot)) d\tau. \quad (91)$$

Taking the L^2 norm of both sides, we find that

$$\|u(\cdot, t)\|_{L^2} \leq e^{-\omega t} \|u_0\|_{L^2} + \int_0^t e^{\omega(\tau-t)} \|\Psi(u(\tau, \cdot))\|_{L^2} d\tau. \quad (92)$$

Lemma 3.7 provides an estimate for Ψ in terms of a constant C , leading to

$$\|u(\cdot, t)\|_{L^2} \leq e^{-\omega t} \|u_0\|_{L^2} + C \int_0^t e^{\omega(\tau-t)} \|u(\tau, \cdot)\|_{L^2} \|u(\tau, \cdot)\|_{H^1} d\tau. \quad (93)$$

Let $\varepsilon = \omega\pi/(2C(1+\pi))$, and let U^* be as in Lemma 3.8. Suppose that $\|u'(0, \cdot)\|_{L^2} < \varepsilon$ and $\|u(0, \cdot)\|_{L^2} < U^*$. Let

$$W = \{t \geq 0 : \|u(\tau, \cdot)\|_{L^2} \leq U^* \text{ for all } 0 \leq \tau \leq t\}. \quad (94)$$

By continuity, W is a closed interval and $0 \in W$. Thus, either $W = [0, \infty)$ or W has a positive maximum. Let $T \in W$. Then, after applying the Poincaré inequality and Lemma 3.8, for any $0 \leq t \leq T$,

$$\begin{aligned} \|u(\cdot, t)\|_{L^2} &\leq e^{-\omega t} \|u_0\|_{L^2} + C \int_0^t e^{\omega(\tau-t)} \|u(\tau, \cdot)\|_{L^2} \left(1 + \frac{1}{\pi}\right) \|u'(\tau, \cdot)\|_{L^2} d\tau \\ &\leq e^{-\omega t} \|u_0\|_{L^2} + C \int_0^t e^{\omega(\tau-t)} \|u(\tau, \cdot)\|_{L^2} \left(1 + \frac{1}{\pi}\right) \varepsilon d\tau \\ &\leq e^{-\omega t} \|u_0\|_{L^2} + \frac{\omega}{2} \int_0^t e^{\omega(\tau-t)} \|u(\tau, \cdot)\|_{L^2} d\tau. \end{aligned} \quad (95)$$

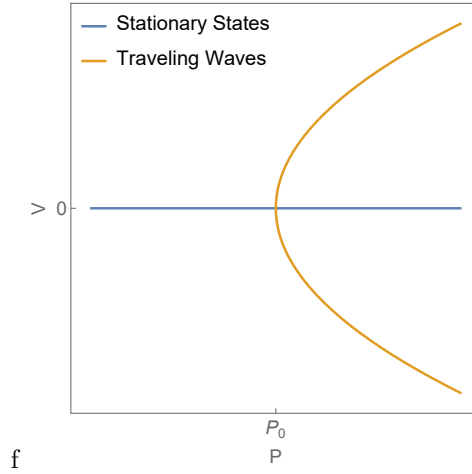


Figure 1: This diagram shows the pitchfork bifurcation from stationary states to traveling waves which is structurally the same in our all three models.

Therefore, by Grönwall's inequality,

$$\|u(\cdot, t)\|_{L^2} \leq \|u_0\|_{L^2} e^{-\omega t/2} \quad (96)$$

for all $0 \leq t \leq T$. Therefore, $\|u(\cdot, T)\|_{L^2} < U^*$ and so by continuity, $T \neq \max W$. Since $T \in W$ is arbitrary, we conclude that W does not have a maximum so $W = [0, \infty)$ and $\|u(\cdot, t)\|_{L^2} \leq U^*$ for all $t > 0$. That is, (96) holds for all $t \geq 0$ provided $\|u(0, \cdot)\|_{L^2} < U^*$ and $\|u'(0, \cdot)\|_{L^2} < \varepsilon$. Note that from the proof of Lemma 3.8, $U^* < \varepsilon$. Therefore, the desired result holds. \square

4 Traveling Waves

By now we have seen that provided $P/Z < \pi^2$, the stationary solution $m = 1$ to model B is asymptotically stable (up to shifts). A key step in the proof of this stability result was Proposition 3.5, which shows that for $P/Z < \pi^2$, all eigenvalues of S_C are negative.

We observe that $u(x) = \cos(2\pi x)$ is an eigenvector of S_C (since it is also an eigenvector of $-Z\phi'' + \phi$ with periodic boundary conditions on $(-1/2, 1/2)$). Its eigenvalue is $-4\pi^2 + \frac{P}{Z} \frac{1}{1 + \frac{1}{4\pi^2 Z}}$. If, for fixed $Z > 0$, the parameter P is large enough, this eigenvalue is positive. This observation hints that for some critical value $P_0 > \pi^2 Z$ of P , the largest eigenvalue of S_C will reach zero, and for $P > P_0$, the stationary solution $m = 1$ will become unstable.

In this section, we show that for any $Z > 0$, there exists a number $V^* > 0$ and a smooth function $P_T : (-V^*, V^*) \rightarrow \mathbb{R}$ such that if $P = P_T(V)$, then there exists a traveling wave solution to the model B with velocity V and center $c = Vt$. This family of traveling wave solutions parameterized by V bifurcates from the family of stationary states at $V = 0$ and $P = P_T(0) = P_0$. This bifurcation will be shown to be of the type illustrated in Figure 1.

Remark 4.1. We note that the implied traveling wave solutions and the associated bifurcation structure for both model A and model B were first computed in [62, 63]. Here, in the framework of model B, we provide a rigorous proof of the existence of these traveling wave solutions and present the formal global analysis of the corresponding bifurcation.

Observe first that $m(x, t)$ is a traveling wave solution with velocity V in model B if $m(x, t) = m_T(x - Vt)$ where m_T satisfies

$$\begin{cases} m_T'' + Vm_T' - (m_T\phi_T')' = 0 & -1/2 < x < 1/2 \\ m_T'(\pm 1/2) = 0 \end{cases} \quad \text{with} \quad \begin{cases} -Z\phi_T'' + \phi_T' = P(V)m_T & -1/2 < x < 1/2 \\ \phi_T(1/2) = \phi_T(-1/2) \\ \phi_T'(1/2) = \phi_T'(-1/2) = V. \end{cases} \quad (97)$$

We further observe that a solution to this equation is $m_T = \Lambda e^{\phi_T - Vx}$ for any $\Lambda \in \mathbb{R}$. The value of $\Lambda = \Lambda(V)$

can be determined by the provision that $\int_{-1/2}^{1/2} m dx = 1$, and the value of ϕ_T therefore satisfies

$$\begin{cases} -Z\phi_T'' + \phi_T = P(V)\Lambda(V)e^{\phi_T(x)-Vx} & -1/2 < x < 1/2 \\ \phi_T(-1/2) = \phi_T(1/2) \\ \phi_T'(-1/2) = \phi_T'(1/2) = V. \end{cases} \quad (98)$$

Note that (98) has three boundary conditions: not only must ϕ_T satisfy periodic boundary conditions, but also $\phi_T'(\pm 1/2) = V$. Thus, $P(V)$ is selected so that ϕ_T can satisfy this extra condition.

Solutions to (98) may be approximated asymptotically in small V as shown in the following Lemma:

Lemma 4.2. *Let $Z > 0$. Suppose that m_T , ϕ_T and $P(V)$ solve (97). In small V , $P(V)$ and m_T have the asymptotic forms*

$$P(V) = P_0 + V^2 P_2 + O(V^4) \quad (99)$$

$$m_T(x) = 1 + V m_1(x) + V^2 m_2(x) + O(V^3), \quad (100)$$

where

- P_0 solves

$$\tanh\left(\frac{\sqrt{1-P_0}}{2\sqrt{Z}}\right) = P_0 \frac{\sqrt{1-P_0}}{2\sqrt{Z}} \quad \text{or equivalently} \quad \tan\left(\frac{\sqrt{P_0-1}}{2\sqrt{Z}}\right) = P_0 \frac{\sqrt{P_0-1}}{2\sqrt{Z}}. \quad (101)$$

- P_2 is given by

$$P_2 = \frac{P_0(6P_0^6 - 15P_0^5 - 3P_0^4(56Z - 5) + P_0^3(514Z - 6) - 1044P_0^2Z + 72P_0Z(55Z - 1) + 5280Z^2)}{288(P_0 - 1)^4(P_0^2 - 12Z)}. \quad (102)$$

- m_1 is given by

$$m_1(x) = \frac{x}{P_0 - 1} - \frac{P_0 \sqrt{\frac{P_0^3 - P_0^2 + 4Z}{(P_0 - 1)P_0^2}} \sin\left(\frac{\sqrt{P_0 - 1}x}{\sqrt{Z}}\right)}{2P_0 - 2} \quad (103)$$

- m_2 is given by

$$m_2(x) = A + Bx^2 + (C + Dx^2) \cos\left(\frac{\sqrt{P_0 - 1}}{\sqrt{Z}}x\right) + Ex \sin\left(\frac{\sqrt{P_0 - 1}}{\sqrt{Z}}x\right) + F \cos\left(\frac{2\sqrt{P_0 - 1}}{\sqrt{Z}}x\right) \quad (104)$$

with

$$A = \frac{-6P_0Z + P_0 + 24Z - 1}{24(P_0 - 1)^4} \quad (105)$$

$$B = \frac{12 - 12P_0}{24(P_0 - 1)^4} \quad (106)$$

$$C = \frac{(P_0(28Z - 3) + 3P_0^2 - 60Z) \sqrt{\frac{P_0^3 - P_0^2 + 4Z}{Z}}}{96(P_0 - 1)^4} \quad (107)$$

$$D = -\frac{P_0 \sqrt{\frac{P_0^3 - P_0^2 + 4Z}{Z}}}{8(P_0 - 1)^3} \quad (108)$$

$$E = \frac{(4 - 3P_0) \sqrt{Z} \sqrt{\frac{P_0^3 - P_0^2 + 4Z}{Z}}}{8(P_0 - 1)^{7/2}} \quad (109)$$

$$F = \frac{(3 - 4P_0)(P_0^3 - P_0^2 + 4Z)}{48(P_0 - 1)^4}. \quad (110)$$

Proof. We first introduce expansions for $\Lambda(V)$ and ϕ_T :

$$\Lambda(V) = \Lambda_0 + V^2 \Lambda_2 + O(V^4), \quad (111)$$

$$\phi_T(x) = \phi_0(x) + V \phi_1(x) + V^2 \phi_2(x) + V^3 \phi_3(x) + O(V^4). \quad (112)$$

Observe that neither the expansion for P (99) nor the expansion for Λ (111) have terms that are of odd order in V . This is because we expect symmetry in traveling wave solutions with respect to the sign of V . Therefore,

$P(V)$ and $\Lambda(V)$ are even functions of V and for $m_T(x)$ and $\phi_T(x)$, the transformation $V \mapsto -V$ is equivalent to $x \mapsto -x$.

Since $m_T(x) = \Lambda(V)e^{\phi_T(x)-Vx}$, we have may expand the exponential to obtain $1 = \Lambda_0 e^{\phi_0}$, $m_1(x) = \Lambda_0 e^{\phi_0}(\phi_1 - x)$ and

$$m_2(x) = \Lambda_2 e^{\phi_0} + \frac{1}{2} \Lambda_0 e^{\phi_0} (x^2 - 2x\phi_1 + \phi_1^2 + 2\phi_2). \quad (113)$$

We conclude that ϕ_0 is constant and $\Lambda_0 = e^{-\phi_0}$. Substituting the expansion (112) into (98) and comparing terms of like order in V , we obtain $\phi_0 = P_0$ in zero order and the following differential equations in first through third order:

$$\begin{cases} -Z\phi_1'' + (1 - P_0)\phi_1 = -P_0x & -1/2 < x < 1/2 \\ \phi_1(1/2) = \phi_1(-1/2) \\ \phi_1'(1/2) = \phi_1'(-1/2) = 1 \end{cases} \quad (114)$$

$$\begin{cases} -Z\phi_2'' + (1 - P_0)\phi_2 = P_2 + P_0 e^{P_0} \Lambda_2 + \frac{P_0}{2}(\phi_1 - x)^2 & -1/2 < x < 1/2 \\ \phi_2(1/2) = \phi_2(-1/2) \\ \phi_2'(1/2) = \phi_2'(-1/2) = 0 \end{cases} \quad (115)$$

$$\begin{cases} -Z\phi_3'' + (1 - P_0)\phi_3 = (\phi_1 - x)(P_0(\Lambda_2 e^{P_0} + \phi_2) + P_2) + \frac{1}{6}P_0(\phi_1 - x)^3 & -1/2 < x < 1/2 \\ \phi_3(1/2) = \phi_3(-1/2) \\ \phi_3'(1/2) = \phi_3'(-1/2) = 0. \end{cases} \quad (116)$$

The solution to (114) is

$$\phi_1(x) = \frac{P_0 x}{P_0 - 1} - \frac{1}{2} \frac{P_0}{P_0 - 1} \csc\left(\frac{\sqrt{P_0 - 1}}{2\sqrt{Z}}\right) \sin\left(\frac{\sqrt{P_0 - 1}}{2\sqrt{Z}}x\right). \quad (117)$$

In order to satisfy the additional condition $\phi_1'(\pm 1/2) = 1$, P_0 must solve (101). Therefore, (103) is obtained as $m_1(x) = \phi_1(x) - x$.

In (115), Λ_2 is determined by the condition that

$$\frac{d^2}{dV^2} \int_{-1/2}^{1/2} m_T(x) dx = \frac{d^2}{dV^2} \int_{-1/2}^{1/2} \Lambda(V) e^{\phi_T - Vx} dx = 0. \quad (118)$$

The value of Λ_2 is

$$\Lambda_2 = -e^{-P_0} P_2 - \frac{e^{-P_0} (3P_0^2 - 60Z + 2)}{48(P_0 - 1)^2}. \quad (119)$$

The solution to (115) can be found using elementary methods and has the form

$$\phi_2(x) = P_2 + a_0 + a_2 x^2 + (b_0 + b_2 x^2) \cos\left(\frac{\sqrt{P_0 - 1}}{\sqrt{Z}}x\right) + c_1 x \sin\left(\frac{\sqrt{P_0 - 1}}{\sqrt{Z}}x\right) + d_0 \cos\left(\frac{2\sqrt{P_0 - 1}}{\sqrt{Z}}x\right) \quad (120)$$

where

$$a_0 = \frac{P_0^2(1 - 30Z) + P_0(48Z - 1)}{24(P_0 - 1)^4} \quad (121)$$

$$a_2 = -\frac{P_0}{2(P_0 - 1)^3} \quad (122)$$

$$b_0 = \frac{(P_0(28Z - 3) + 3P_0^2 - 60Z) \sqrt{P_0^3 - P_0^2 + 4Z}}{96(P_0 - 1)^4 \sqrt{Z}} \quad (123)$$

$$b_2 = -\frac{P_0 \sqrt{P_0^3 - P_0^2 + 4Z}}{8(P_0 - 1)^3 \sqrt{Z}} \quad (124)$$

$$c_1 = \frac{P_0 \sqrt{P_0^3 - P_0^2 + 4Z}}{8(P_0 - 1)^{7/2}} \quad (125)$$

$$d_0 = \frac{-4P_0 Z - P_0^4 + P_0^3}{48(P_0 - 1)^4}. \quad (126)$$

Note that the only dependence on P_2 in ϕ_2 is the leading term—none of the other coefficients depend on P_2 . Therefore, we write $\phi_2 = P_2 + \tilde{\phi}_2$, where $\tilde{\phi}_2$ is independent of P_2 . We similarly write $\Lambda_2 = -e^{-P_0} P_2 + \tilde{\Lambda}_2$.

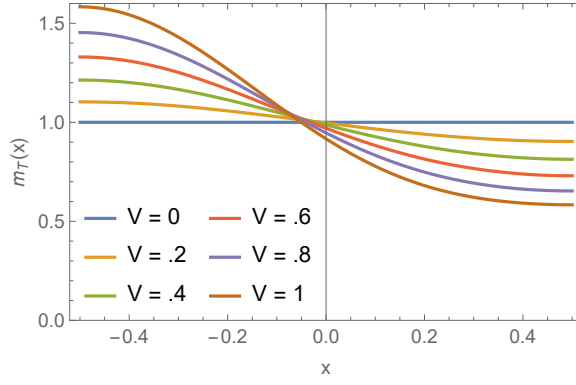


Figure 2: Traveling waves with low velocity have nearly constant myosin density ($m_T \approx 1$), but traveling waves with higher velocity are increasingly asymmetric.

In third order, we do not need to find an explicit solution ϕ_3 . Instead, we divide the right hand side of the differential equation in (116) to separate terms that explicitly depend on P_2 from those that do not:

$$-Z\phi_3'' + (1 - P_0)\phi_3 = P_2f(x) + g(x), \quad (127)$$

where $f(x) = \phi_1 - x$ and $g(x) = P_0(\phi_1 - x)(e^{P_0}\tilde{\Lambda}_2 + \tilde{\phi}_2) + \frac{1}{6}P_0(\phi_1 - x)^3$. The three boundary conditions that ϕ_3 must satisfy (periodic boundary conditions with $\phi_3'(\pm 1/2) = 0$) determine P_2 , which we show as follows. Let $U(x) = \sin(x\sqrt{P_0 - 1}/\sqrt{Z})$. Then

$$\int_{-1/2}^{1/2} (P_2f(x) + g(x))U(x) dx = \int_{-1/2}^{1/2} (-Z\phi_3'' + (1 - P_0)\phi_3)U(x) dx \quad (128)$$

$$= -Z\phi_3'U(x)|_{-1/2}^{1/2} + Z\phi_3U'|_{-1/2}^{1/2} + \int_{-1/2}^{1/2} \phi_3(-ZU'' + (1 - P_0)U) dx \quad (129)$$

$$= 0. \quad (130)$$

Therefore, we may explicitly calculate

$$\begin{aligned} P_2 &= -\frac{\int_{-1/2}^{1/2} g(x)U(x) dx}{\int_{-1/2}^{1/2} f(x)U(x) dx} \\ &= \frac{P_0(6P_0^6 - 15P_0^5 - 3P_0^4(56Z - 5) + P_0^3(514Z - 6) - 1044P_0^2Z + 72P_0Z(55Z - 1) + 5280Z^2)}{288(P_0 - 1)^4(P_0^2 - 12Z)}. \end{aligned} \quad (131)$$

Therefore, substituting (131) into (120), and then into (113), we obtain (104). \square

Remark 4.3. The existence of this bifurcation is demonstrated for the 1D in [62, 63] and in 2D in [68] (see also [69]). The value of P_2 in (102) is identical to the result given in [63] (see Appendix D).

Remark 4.4. Lemma 4.2 gives the asymptotic form of traveling wave solutions if they exist, but it does not prove that such solutions exist. To prove existence, we have Theorem 4.5 below.

A plot of the asymptotic approximation of $m_T(x)$ given by Lemma 4.2 for several values of V is given in Figure 2.

We can now prove the following result (see also [63]):

Theorem 4.5. *Let $Z > 0$ and suppose P_0 satisfies*

$$\tanh\left(\frac{\sqrt{1 - P_0}}{2\sqrt{Z}}\right) = P_0 \frac{\sqrt{1 - P_0}}{2\sqrt{Z}}. \quad (132)$$

and $\frac{1 - P_0}{Z} \neq -n^2\pi^2$ for any integer n . Then there exists $V^* > 0$ and a continuous function $P_T : (-V^*, V^*) \rightarrow \mathbb{R}$ such that for each $V \in (-V^*, V^*)$, there exists a family traveling wave solutions $(m_T, \phi_T, Vt + c_0)$ of velocity V to (32)-(37) with $P = P_T(V)$ and $c_0 \in \mathbb{R}$. Moreover, $P_T(0) = P_0$.

The parameter V^* in Theorem 4.5 is the (not explicitly known) largest velocity for which traveling waves must exist. That is, the bifurcation of stationary solutions to traveling waves is a strictly local result in a neighborhood of $(m, V) = (1, 0)$. The main tool to prove this theorem will be the Crandall-Rabinowitz Theorem [21], which we quote in Appendix B. Essentially, the Crandall-Rabinowitz Theorem gives conditions under which an equation of the form $\mathcal{F}(x, t) = 0$ has two families of solutions: a *trivial branch* where $x = 0$ and t parameterizes the family, and a *nontrivial branch* where x and t are both parameterized by a new parameter s , and the two families meet at $(x, t) = (0, 0)$. In Theorem 4.5, the trivial branch corresponds to the stationary homogeneous solution $m = 1$ for any value of P . The nontrivial branch corresponds to the traveling wave solutions parameterized by their velocity and with activity parameter $P = P_T(V)$. The two families of solutions meet at $P = P_T(0) = P_0$ satisfying (132).

Proof of Theorem 4.5. Given $Z > 0$, let $P = P_0$ be such that (132) holds. Let

$$X = \left\{ \mu \in H^2(-1/2, 1/2) : \mu'(-1/2) = \mu'(1/2) = 0, \int_{-1/2}^{1/2} \mu(x) dx = 0 \right\} \quad (133)$$

and

$$Y = \{m \in L^2(-1/2, 1/2) \times \mathbb{R}\}. \quad (134)$$

Define $\mathcal{F} : X \times \mathbb{R} \rightarrow Y$ by

$$\mathcal{F}(\mu, \tau) = \mu'' + \phi'(1/2)\mu' - ((\mu + 1)\phi')'. \quad (135)$$

where ϕ satisfies $-Z\phi'' + \phi = (P_0 + \tau)(1 + \mu)$ with periodic boundary conditions in $(-1/2, 1/2)$. Observe that

$$m(x, t) = \mu(x - \phi'(1/2)t, t) + 1 \quad (136)$$

is a traveling wave solution to (15) if and only if $\mathcal{F}(\mu, \tau) = 0$. If $\phi'(1/2) = 0$, then m is a stationary solution, i.e., a traveling wave with velocity 0.

We will show that \mathcal{F} satisfies the hypotheses of the Crandall-Rabinowitz Theorem.

- It is clear that $\mathcal{F}(0, \tau) = 0$ for all τ .
- It is also clear that \mathcal{F} is twice continuously differentiable.
- The linearization of \mathcal{F} in μ at $(\mu, \tau) = (0, 0)$ is

$$0 = D_\mu \mathcal{F}(0, 0)u = u'' - \psi'' \quad (137)$$

where ψ satisfies $-Z\psi'' + \psi = P_0 u$ with periodic boundary conditions on $(-1/2, 1/2)$. Note that this is the operator S_C in (46). To show that the third hypothesis of the Crandall-Rabinowitz Theorem is satisfied, we need to show two things:

- There exists a unique (up to multiplicative constant) nonzero solution $u_0 \in X$ to $D_\mu \mathcal{F}(0, 0)u_0 = 0$, and
- there exists a co-dimension one subspace X' of X such that if $w \in X'$, then there exists a solution $u \in X$ to $D_\mu \mathcal{F}(0, 0)u = w$.

First we show (i). Consider the function

$$u_0(x) = \frac{\sqrt{Z} \operatorname{sech}\left(\frac{\sqrt{1-P_0}}{2\sqrt{Z}}\right) \sinh\left(\frac{\sqrt{1-P_0}x}{\sqrt{Z}}\right)}{(1-P_0)^{3/2}} + \frac{x}{P_0-1}. \quad (138)$$

Observe that $u'_0(\pm 1/2) = 0$ and $\int_{-1/2}^{1/2} u_0(x) dx = 0$, so $u_0 \in X$. Moreover, one may check that provided P_0 satisfies (132), then $D_\mu \mathcal{F}(0, 0)u_0 = 0$. Now suppose that u_1 and u_2 are both nonzero solutions to (137). Let ψ_i solve $-Z\psi_i'' + \psi_i = P_0 u_i$ with periodic boundary conditions on $(-1/2, 1/2)$ for $i = 1, 2$. Observe that for each i , since the second derivatives of u_i and ψ_i are equal, we have

$$u_i - \psi_i = \alpha_i x - \beta_i \quad (139)$$

We also observe that

$$\int_{-1/2}^{1/2} \psi_i dx = P_0 \int_{-1/2}^{1/2} u_i dx + Z \int_{-1/2}^{1/2} \psi_i'' dx = 0. \quad (140)$$

Therefore, $\beta_1 = \beta_2 = 0$. Now, suppose for some i , $\psi'_i(\pm 1/2) = 0$. Then $\alpha_i = 0$ and $u_i = \psi_i$. Thus, u_i satisfies $-Zu_i'' + u_i = P_0 u_i$ with periodic boundary conditions. Thus, u_i is an eigenvector of the second derivative operator with eigenvalue $(1 - P_0)/Z$. The eigenvalues of the second derivative operator on X are $-n^2\pi^2$ for positive integers n . By assumption, $(1 - P_0)/Z \neq -n^2\pi^2$, so this is a contradiction.

Therefore, $\psi'_i(\pm 1/2) \neq 0$, and we may assume without loss of generality that the u_i are scaled such that $\psi'_i(\pm 1/2) = 1$ for $i = 1, 2$, so $\alpha_i = -1$. Then $u_i = \psi_i - x$. Let $w = u_1 - u_2$. Then

$$w = (\psi_1 - x) - (\psi_2 - x) = \psi_1 - \psi_2. \quad (141)$$

Thus, w satisfies $-Zw'' + w = P_0 w$ with periodic boundary conditions on $(-1/2, 1/2)$. Once again, since $(1 - P_0)/Z \neq -n^2\pi^2$, the only solution is $w = 0$. We conclude that $u_1 = u_2$ and u_0 is unique up to a multiplicative constant.

Now we show (ii). Observe that since ψ satisfies $\psi'' = (P_0 u - \psi)/Z$, we may write

$$D_m \mathcal{F}(0, 0)u = u'' - \frac{P_0}{Z}u + \frac{1}{Z}\psi. \quad (142)$$

We may abstract this operator as $D_m \mathcal{F}(0, 0) = B + K$ where $Bu = u'' - (P_0/Z)u$ and $K : u \mapsto \psi$. We make two observations. First, K is a bounded operator. This follows from standard elliptic estimates and is proved in Proposition 6.1 in Appendix A. Second, the operator B is invertible on X and its inverse B^{-1} is compact. Therefore, we may write

$$I - B^{-1}D_m \mathcal{F}(0, 0) = I - B^{-1}(B + K) = -B^{-1}K \quad (143)$$

and

$$I - D_\mu \mathcal{F}(0, 0)B^{-1} = I - (B + K)B^{-1} = -KB^{-1}. \quad (144)$$

Since B^{-1} is compact, so are $B^{-1}K$ and KB^{-1} . We conclude that $D_\mu \mathcal{F}(0, 0)$ is a Fredholm operator. We recall that the index of a Fredholm operator is the difference between the dimension of its kernel and the codimension of its range. We also recall that the index of a self-adjoint operator is zero. Since B and K are both self-adjoint over $L^2([-1/2, 1/2])$, so is $D_\mu \mathcal{F}(0, 0)$. Therefore, the codimension of the range of $D_\mu \mathcal{F}(0, 0)$ is equal to the dimension of the kernel, which we have just proved is 1.

- Finally, we must show that $D_{\mu s} \mathcal{F}(0, 0)u_0$ is not in the range of the operator $D_\mu \mathcal{F}(0, 0)$. Observe that since $D_\mu \mathcal{F}(0, 0)$ is self-adjoint, its image is orthogonal to its kernel. That is, for any $u \in X$, $\langle D_\mu \mathcal{F}(0, 0)u, u_0 \rangle_{L^2} = 0$. It is therefore sufficient to show that $\langle D_{\mu s} \mathcal{F}(0, 0)u_0, u_0 \rangle_{L^2} \neq 0$. The mixed second derivative is

$$D_{\mu s} \mathcal{F}(0, 0)u = u'' - \tilde{\psi}'' \quad (145)$$

where $\tilde{\psi}$ satisfies $-Z\tilde{\psi}'' + \tilde{\psi} = u$. Therefore, $\tilde{\psi} = \psi/P_0$. We conclude that

$$\langle D_{\mu s} \mathcal{F}(0, 0)u_0, u_0 \rangle_{L^2} = \int_{-1/2}^{1/2} \left(u_0'' - \frac{\psi_0''}{P_0} \right) u_0 dx = \int_{-1/2}^{1/2} \left(1 - \frac{1}{P_0} \right) u_0 u_0'' dx = \int_{-1/2}^{1/2} \left(1 - \frac{1}{P_0} \right) (u_0')^2 dx.$$

Since $P_0 \neq 1$, $\langle D_{\mu s} \mathcal{F}(0, 0)u_0, u_0 \rangle_{L^2} \neq 0$.

Since all the hypotheses of the Crandall-Rabinowitz Theorem hold, in a neighborhood of $(\mu, \tau) = (0, 0)$, the only solutions to $\mathcal{F}(\mu, \tau) = 0$ are $\mu = 0$ and a smooth family of solutions $(\mu(s), \tau(s))$ parameterized by s in some small interval $(-s^*, s^*)$ with $\mu(s) \not\equiv 0$, and these two families of solutions meet at $(0, 0)$. Let $m_T(s) = 1 + \mu(s)$ and $P_T(s) = P_0 + \tau(s)$. Since all solutions to $\mathcal{F} = 0$ are traveling waves with some velocity (or stationary solutions if the velocity is zero), it only remains to show that $m_T(s)$ and $P_T(s)$ may be reparameterized (at least locally near $s = 0$) by velocity. Let $V(s)$ be the velocity of $m_T(s)$. It is sufficient to show that $V'(0) \neq 0$. Let $\phi_T(s)$ satisfy $-Z\phi_T'' + \phi_T = P_T(s)m_T(s)$ with periodic boundary conditions on $(-1/2, 1/2)$. Then $V(s) = \partial_x \phi_T(s)|_{x=1/2}$. Therefore, $V'(0)$ is $\psi'(1/2)$ where ψ solves

$$-Z\psi'' + \psi = \frac{\partial}{\partial s} P_T(s)m_T(s) \Big|_{s=0} = \frac{\partial P_T}{\partial s}(0)m_T(0) + P_T(0) \frac{\partial m_T}{\partial s}(0) = \frac{\partial P_T}{\partial s}(0) + P_0 \frac{\partial \mu}{\partial s}(0), \quad (146)$$

with periodic boundary conditions. Since \mathcal{F} is twice differentiable, $\mu(s)$ is also continuously differentiable and $\mu'(0)$ spans the null space of $\mathcal{F}_\mu(0, 0)$. Without loss of generality, we may assume that $\mu(s)$ is parameterized such that

$$\frac{d\mu}{ds}(0) = \mu_0. \quad (147)$$

Let ψ_0 solve $-Z\psi_0'' + \psi_0 = P_0\mu_0$ with periodic boundary conditions on $(-1/2, 1/2)$. Then ψ_0 and ψ differ by a constant, so $V'(0) = \psi_0'(1/2)$. We may explicitly calculate $\psi_0'(1/2) = 1$, so $V'(0) \neq 0$. Therefore, we may reparameterize m_T and P_T by V for V in some small interval $(-V^*, V^*)$. \square

Remark 4.6. All the analysis in the proof of Theorem 4.5 can be done if X is replaced with a more restrictive domain, such as a set of C^r functions. Therefore, we conclude that the traveling wave solutions m_T , ϕ_T are infinitely differentiable and depend smoothly on V in the C^r -norm for any r .

Given $Z > 0$, the condition (132) satisfied by P_0 has (potentially) infinitely many solutions. Therefore, Theorem 4.5 proves the existence of not just one, but infinitely many families of traveling wave solutions, each bifurcating from the stationary solution for a different solution P to (132). In Section 3, we observed that for $P/Z < \pi^2$, the eigenvalues of the linearization S_C of model C about the stationary solution are all negative. In the proof of Theorem 4.5, we observe that if P satisfies (132), S_C has a zero eigenvalue. We conclude that as P/Z increases from π^2 , each solution of (132) corresponds to one of the eigenvalues of S_C becoming positive. Therefore, we conjecture that for all families of traveling waves except those bifurcating from the smallest solution of (132), the linearization of model C about these traveling waves has some positive eigenvalues, and therefore these traveling waves are unstable. The only traveling wave solutions that may be stable are those bifurcating from the smallest solution to (132). Therefore, when using the notation P_0 , we refer to this value. The following Lemma shows the existence of this smallest solution and provides the illuminating estimate that, for large Z , $P_0/Z \geq \pi^2$ with equality in the limit $Z \rightarrow \infty$.

Lemma 4.7. *Suppose that $P_0 = P_0(Z)$ is the smallest positive solution to*

$$\tanh\left(\frac{\sqrt{1-P_0}}{2\sqrt{Z}}\right) = \frac{P_0\sqrt{1-P_0}}{2\sqrt{Z}} \quad (148)$$

besides $P_0 = 1$ whenever such a solution exists. Then $P_0(Z)$ exists for all $Z > 0$ except $Z = 1/12$ and in large Z , $P_0(Z)$ expands as

$$P_0(Z) = \pi^2 Z + 1 - \frac{8}{\pi^2} + O(1/Z). \quad (149)$$

Proof. First suppose $0 < Z < 1/12$. Let $v = \sqrt{1-P_0}/(2\sqrt{Z})$. Then v and Z satisfy

$$k_1(z) := \frac{v - \tanh(v)}{4v^3} = Z. \quad (150)$$

It is easy to show that k_1 is continuous on $(0, \infty)$, $\lim_{v \rightarrow 0^+} k_1(v) = 1/12$, $\lim_{v \rightarrow \infty} k_1(v) = 0$, and k_1 is monotonically decreasing. Thus, for any $Z \in (0, 1/12)$, there exists a unique $v \in (0, \infty)$ satisfying (150). Therefore, $P_0(Z) = \tanh(v)/v \in (0, 1)$ is uniquely determined.

Now suppose $Z > 1/12$. Write (148) as

$$\tan\left(\frac{\sqrt{P_0-1}}{2\sqrt{Z}}\right) = \frac{P_0\sqrt{P_0-1}}{2\sqrt{Z}} \quad (151)$$

and let $w = \sqrt{P_0-1}/(2\sqrt{Z})$. Then w and Z satisfy

$$k_2(w) = \frac{\tan(w) - w}{4w^3} = Z. \quad (152)$$

Similarly to k_1 , it is easy to show that k_2 is continuous on $(0, \pi/2)$, $\lim_{w \rightarrow 0^+} k_2(w) = 1/12$, $\lim_{w \rightarrow \pi/2^-} k_2(w) = \infty$, and k_2 is monotonically increasing on $(0, \pi/2)$. Thus, for any $Z \in (1/12, \infty)$, there exists a unique $w \in (0, \pi/2)$ satisfying (152). Therefore, $P_0(Z) = \tan(w)/w \in (1, \infty)$. Thus, for all positive Z other than $Z = 1/12$, (148) has a smallest positive solution other than 1. It should be noted that using a similar line of reasoning, we may show that (152) has a unique solution in each interval of the form $(n\pi/2, (n+2)\pi/2)$ for $n > 0$ odd. These correspond to the other (larger than P_0) solutions to (132) referenced above.

As $Z \rightarrow \infty$ the corresponding solution w to $k_2(w) = Z$ approaches $\pi/2$. Therefore, we expand w in large Z as $w(Z) = \pi/2 + w_1/Z + w_2/Z^2 + O(1/Z^3)$. We expand (152) in large Z and compare terms of like order in Z to obtain $w = \pi/2 - 2/(Z\pi^3) + O(1/Z^2)$. Finally, using $P_0 = 1 + 4Zw^2$, we have

$$P_0 = \pi^2 Z + \left(1 - \frac{8}{\pi^2}\right) + O(1/Z). \quad (153)$$

□

5 Stability of Traveling Waves

In this section we study the nonlinear stability of traveling wave solutions to Model B. As shown in Theorem 4.5, traveling wave solutions of velocity V sufficiently small exist provided P has the prescribed value $P_T(V)$. Such a traveling wave solution has the form $m(x, t) = m_T(x - Vt)$ with $c = c_0 + Vt$ where m_T is a stationary solution to model C . For ease of analysis we will study the stability of these solutions to model C which, as described in Section 3, implies *stability up to shifts* of traveling wave solutions to model B.

As in Section 3, we describe model C by the dynamical system $\partial_t m = F_C(m)$ with F_C given by (44). The linearization about m_T about traveling waves is:

$$T_C u := DF_C(m_T) = u'' + \phi'(1/2)m_T' + Vu' - (m_T\phi')' - (u\phi_T)', \quad (154)$$

where ϕ and ϕ_T satisfy respectively

$$\begin{cases} -Z\phi'' + \phi = Pu & -1/2 < x < 1/2 \\ \phi(1/2) = \phi(-1/2) \\ \phi_x(-1/2) = \phi_x(1/2) \end{cases} \quad \text{and} \quad \begin{cases} -Z\phi_T'' + \phi_T = Pm_T & -1/2 < x < 1/2 \\ \phi_T(1/2) = \phi_T(-1/2) \\ \phi_{T,x}(-1/2) = \phi_{T,x}(1/2), \end{cases} \quad (155)$$

and $u \in \tilde{X}_C^2 := \left\{ m \in H^2(-1/2, 1/2) : m_x(\pm 1/2) = 0, \int_{-1/2}^{1/2} u \, dx = 0 \right\}$. The coefficient V appears because the velocity of the traveling wave is $V = \phi_T'(1/2)$.

Also of interest is the nonlinear part of F_C near $m = m_T$. However, due to the quadratic nature of the nonlinearities in F_C , this nonlinear part has the exact same form as the nonlinear part of F_C about $m = 1$:

$$\Psi(u) = F_C(m_T + u) - T_C u = \phi'(1/2)u' - (u\phi')', \quad (156)$$

with ϕ given in (155). Using the nonlinear part Ψ , and letting $u = m - m_T$, we may rewrite the evolution equation (44) as

$$\partial_t u = T_C u + \Psi(u). \quad (157)$$

Similar to Section 3, our analysis in this section is focused on proving two key results:

1. 0 is an asymptotically stable equilibrium of the linearized problem $u_t = T_C u$, and
2. m_T is an asymptotically stable equilibrium of the nonlinear problem $m_t = F_C(m)$.

In this section however, a new challenge arises: the operator T_C is non self-adjoint, meaning that the spectral theorem used in the proof of linear stability in Theorem 3.2 no longer applies.

Indeed, while, as we have already mentioned in the Introduction, a self-adjoint operator with compact inverse has a basis of eigenvectors, no such basis is guaranteed if the operator is non self-adjoint operator, meaning that there may be a portion of the domain of the operator that is “dark,” hidden from the eigenvectors. Since the action of the operator on this “dark” space cannot be determined from the eigenvectors, it is not sufficient merely to show that all the eigenvalues of the operator have negative real part. Instead, we rely on the Gearhart-Prüss-Greiner Theorem [33], which we quote in Appendix C.

The Gearhart-Prüss-Greiner Theorem overcomes the problem of a possible “dark” part of the domain by considering not just eigenvalues, but the entire *spectrum* of the operator. The spectrum of a linear operator L is the set of all $\lambda \in \mathbb{C}$ so that the operator $\lambda I - L$ does not have a bounded inverse. Note that if $\lambda I - L$ is not invertible because it is not injective (one-to-one), then λ is an eigenvalue of L . If L is a finite dimensional linear operator (a matrix), then the rank-nullity theorem applies and $\lambda I - L$ is invertible if and only if it is injective. In the infinite dimensional case, however, a linear operator may be injective but not surjective, and thus not invertible. Even if $\lambda I - L$ is invertible, the inverse may not be bounded. Thus, the spectrum of L may consist of more than just eigenvalues. If $\lambda I - L$ does have a bounded inverse, $(\lambda I - L)^{-1}$ is called a *resolvent* operator of L , and the set of λ such that the resolvent exists (that is the complement of the spectrum) is called the *resolvent set*. The solution $x(t)$ to the linear system $x_t = Lx$ can be written in terms of the resolvent via a line integral in the complex plane as an inverse Fourier Transform:

$$x(t) = \lim_{s \rightarrow \infty} \frac{1}{2\pi i} \int_{w-is}^{w+is} e^{\lambda t} (\lambda I - L)^{-1} x(0) \, d\lambda \quad (158)$$

for $w \in \mathbb{R}$ sufficiently large [33]. If $x(0)$ can be written $x(0) = \sum_{n=1}^{\infty} c_n x_n$ for eigenvectors x_n of L with eigenvalues λ_n , then if $w > \sup_n \operatorname{Re} \lambda_n$,

$$x(t) = \lim_{s \rightarrow \infty} \frac{1}{2\pi i} \int_{w-is}^{w+is} e^{\lambda t} (\lambda I - L)^{-1} \sum_{n=1}^{\infty} c_n x_n \, d\lambda \quad (159)$$

$$= \sum_{n=1}^{\infty} c_n x_n \lim_{s \rightarrow \infty} \frac{1}{2\pi i} \int_{w-is}^{w+is} \frac{e^{\lambda t}}{\lambda - \lambda_n} \, d\lambda \quad (160)$$

$$= \sum_{n=1}^{\infty} c_n x_n \frac{e^{wt}}{2\pi} \int_{-\infty}^{\infty} \frac{e^{ist}}{w + is - \lambda_n} \, ds \quad (161)$$

$$= \sum_{n=1}^{\infty} c_n x_n \frac{e^{wt}}{2\pi} \left(2\pi e^{(\lambda_n - w)t} \right) \quad (162)$$

$$= \sum_{n=1}^{\infty} c_n e^{\lambda_n t} x_n, \quad (163)$$

as expected. However, (158) holds even if $x(0)$ cannot be written as a sum of eigenvectors (i.e., if the eigenvectors of L do not span the domain of L) provided the resolvent $((w + is)I - L)^{-1}$ exists for all $s \in \mathbb{R}$ and w is sufficiently large. The Gearhart-Prüss-Greiner Theorem provides conditions on the resolvent and spectrum of L such that, via (158), all solutions $x(t)$ converge to 0 exponentially fast.

Since the solutions to the linearized problem $u_t = T_C u$ are $u(t) = S(t)u(0)$, if the conclusions of the Gearhart-Prüss-Greiner Theorem hold, then $\lim_{t \rightarrow \infty} \|u(t)\| \leq \lim_{t \rightarrow \infty} e^{-\sigma t} \|u(0)\| = 0$, so 0 is asymptotically stable in the linearized system. Therefore, to establish linear stability, we must prove that each of the three hypotheses of the Gearhart-Prüss-Greiner Theorem hold for the operator T_C . We will begin with condition (ii), then condition (i), and finally condition (iii), see Appendix C. Before proceeding with these steps, however, we show that T_C is non self-adjoint.

Theorem 5.1. *There exists $Z^*, V^* > 0$ such that if $Z > Z^*$ and $0 < |V| < V^*$, the operator T_C is non self-adjoint.*

Proof. As in the proof of Lemma 3.4, we will use the adjoint commutator. We will show that there exists $V^* > 0$ and $u_1, u_2 \in \tilde{X}_C^2$ so that if $0 < |V| < V^*$, then the adjoint commutator H for the operator $T_C = T_C(V)$ evaluated at u_1, u_2 is nonzero. This shows that $T_C(V)$ is non self-adjoint.

Let $u_1(x) = \sin(\pi x)$ and $u_2(x) = \cos(2\pi x)$. Both u_1 and u_2 are in \tilde{X}_C^2 . For $i = 1, 2$ let ψ_i satisfy $-Z\psi_i'' + \psi_i = P_T(V)u_i$ with periodic boundary conditions in $(-1/2, 1/2)$. Then

$$\begin{aligned} H(u_1, u_2) &= \int_{-1/2}^{1/2} u_1 u_2'' - u_2 u_1'' dx + \int_{-1/2}^{1/2} m'_T(u_1 \psi_2'(1/2) - u_2 \psi_1'(1/2)) dx + V \int_{-1/2}^{1/2} u_1 u_2' - u_2 u_1' dx \\ &\quad - \int_{-1/2}^{1/2} u_1 (m_T \psi_2')' - u_2 (m_T \psi_1')' dx - \int_{-1/2}^{1/2} u_1 (u_2 \phi_T')' - u_2 (u_1 \phi_T')' dx. \end{aligned} \quad (164)$$

The function ψ_1, ψ_2 depend on V through $P_T(V)$, but from Lemma 4.2, $P'_T(0) = 0$, so $\partial_V \psi_i|_{V=0} = 0$. Also from Proposition 4.2, the traveling wave solution satisfy $\partial_V m_T|_{V=0} = m_1$ given by (103) and $\partial_V \phi_T|_{V=0} = m_1(x) + x$. Therefore,

$$\begin{aligned} \partial_V H(u_1, u_2)|_{V=0} &= \int_{-1/2}^{1/2} u_1 u_2'' - u_2 u_1'' dx + \int_{-1/2}^{1/2} m'_1(u_1 \psi_2'(1/2) - u_2 \psi_1'(1/2)) dx + \int_{-1/2}^{1/2} u_1 u_2' - u_2 u_1' dx \\ &\quad - \int_{-1/2}^{1/2} u_1 (m_1 \psi_2')' - u_2 (m_1 \psi_1')' dx - \int_{-1/2}^{1/2} u_1 (u_2 \phi_1')' - u_2 (u_1 \phi_1')' dx. \end{aligned} \quad (165)$$

Since each of the functions $m_1, \phi_1, u_1, u_2, \psi_1$, and ψ_2 are explicitly known, and using $P_0 = \pi^2 Z + O(1)$ from Lemma 4.7, we may explicitly calculate the integrals in (165) and find the asymptotic expansion of the result in large Z :

$$\partial_V H(u_1, u_2)|_{V=0} = -3 + O(1/Z). \quad (166)$$

Therefore, for sufficiently large Z^* , if $Z > Z^*$, then $\partial_V H(u_1, u_2)|_{V=0} \neq 0$. Thus, there exists V^* so that if $0 < |V| < V^*$, $H(u_1, u_2) \neq 0$. We conclude that for $Z > Z^*$ and $0 < |V| < V^*$, $A_T(V)$ is non self-adjoint. \square

Condition (ii): the resolvent set of T_C contains the right half-plane, see appendix C.

To establish that condition (ii) holds, we prove a sequence of four results. First, we show that the resolvent of T_C , if it exists, is compact. Then we show that for some $\lambda_0 > 0$, there exists a unique weak solution to $(\lambda_0 - T_C)u = w$ for each w , which implies that the resolvent $(\lambda_0 I - T_C)^{-1}$ exists. Next, we use the first two results to show that the spectrum of T_C consists only of its eigenvalues. Finally, we show that all the eigenvalues of T_C have negative real part. Thus, the resolvent set contains all complex numbers with positive real part, and condition (ii) is satisfied.

Proposition 5.2. *Suppose $\lambda \in C$ such that $\lambda I - T_C$ is invertible. Then $(\lambda I - T_C)^{-1} : L^2(-1/2, 1/2) \rightarrow L^2(-1/2, 1/2)$ is a compact operator.*

Proof. To be compact, $(\lambda I - T_C)^{-1}$ must be bounded. Suppose, to the contrary that it is unbounded. Then there exist sequences $(v_k) \subset \tilde{X}_C^2$ and $(w_k) \subset L^2(-1/2, 1/2)$ such that

$$(\lambda I - T_C)v_k = w_k, \quad \|v_k\|_{L^2} = 1, \quad \|w_k\|_{L^2} \leq 1/k. \quad (167)$$

Let ϕ_k satisfy $-Z\phi_k'' + \phi_k = P v_k$ with periodic boundary conditions. Then the following sequence is bounded:

$$\begin{aligned} \langle w_k, v_k \rangle_{L^2} &= \langle (\lambda I - T_C)v_k, v_k \rangle_{L^2} \\ &= \lambda \|v_k\|_{L^2}^2 + \|v_k'\|_{L^2}^2 + \langle (V - \phi_k')v_k', v_k \rangle_{L^2} + \langle (\phi_k'(1/2) - \phi_k')m_T', v_k \rangle_{L^2} \\ &\quad - \langle \phi_k'' v_k, v_k \rangle_{L^2} - \langle \phi_k'' m_T, v_k \rangle_{L^2}. \end{aligned} \quad (168)$$

Every term in this sequence is individually bounded due to Proposition 6.1 in Appendix A except possibly $\|v'_k\|_{L^2}^2$ and $\langle (V - \phi'_T)v'_k, v_k \rangle_{L^2}$. However, the sum of these terms must be bounded. While the former is quadratic in $\|v'_k\|_{L^2}$, the latter is at most linear. Therefore, they must both be independently bounded as well.

Since $\|v_k\|_{L^2}$ and $\|v'_k\|_{L^2}$ are both bounded, we conclude that (v_k) is bounded with respect to the H^1 norm. The remaining arguments giving rise to a contradiction and proving that $(\lambda I - T_C)^{-1}$ is bounded and, moreover, compact, are identical to those in the proof of Lemma 3.6. \square

Proposition 5.3. *There exists $V^* > 0$ and $\lambda_0 \geq 0$ such that for each $w \in X^0$, there exists a unique weak solution $u \in X^1$ to $T_C u = w$.*

Proof. Define the bilinear form $B : X^1 \times X^1 \rightarrow \mathbb{R}$ by

$$B[u, v] = \langle u', v' \rangle_{L^2} - \langle (\phi'(1/2) - \phi')m'_T + (V - \phi'_T)u' - m_T\phi'' - u\phi''_T, v \rangle_{L^2}. \quad (169)$$

Then $u \in X^1$ is a weak solution to $T_C u = w$ if and only if $B[u, v] = \langle w, v \rangle_{L^2}$ for all $v \in X^1$. We claim that there exist $a, b, V^* > 0$ and $\lambda_0 \geq 0$ such that

- $|B[u, v]| \leq a\|u\|_{H^1}\|v\|_{H^1}$
- $b\|v\|_{H^1}^2 \leq B[v, v] + \lambda_0\|v\|_{L^2}^2$.

The proof of these facts follows from the Poincaré inequality and the fact that $\|\phi'_T\|_{L^2} = O(V)$. Therefore, by the Lax-Milgram Theorem, there exists a unique weak solution to $(\lambda_0 I - T_C)u = w$. \square

Proposition 5.4. *The spectrum of T_C consists only of its eigenvalues.*

Proof. This proof is essentially showing that the Fredholm alternative applies to T_C . Let $\lambda \in \mathbb{C}$, and let λ_0 be defined as in 5.3. Define $\hat{T}_C = \lambda_0 I - T_C$ and let $\lambda' = \lambda_0 - \lambda$. Then $\lambda I - T_C = \hat{T}_C - \lambda' I$. By Proposition 5.3, \hat{T}_C is invertible, and by Proposition 5.2, \hat{T}_C^{-1} is compact. Therefore, we may apply the Fredholm alternative for compact operators [28] to see that exactly one of the following holds:

- $(I - \lambda'\hat{T}_C^{-1})v = \hat{T}_C^{-1}w$ has a unique solution for each $w \in X^0$,
- $(I - \lambda'\hat{T}_C^{-1})v = 0$ has a nontrivial solution.

In either case, we may multiply by \hat{T}_C to see that either $(\lambda I - T_C)v = w$ has a unique solution for all $w \in X^0$ or $(\lambda I - T_C)v = 0$. Therefore, either $\lambda I - T_C$ is invertible (with bounded inverse per Proposition 5.2) and therefore λ is not in the spectrum, or λ is an eigenvalue of T_C . Therefore, the spectrum of T_C consists only of its eigenvalues. \square

The following lemma show that all eigenvalues of T_C have negative real part except possibly one. The following Theorem concerns this remaining eigenvalue showing that it too has negative real part, thus proving the desired result.

Lemma 5.5. *For V sufficiently small the eigenvalues of $T_C = T_C(V)$ all have negative real part bounded away from 0 except possibly one. Moreover, when $V = 0$, all the eigenvalues of $T_V(0)$ are negative (and real) except for a zero eigenvalue with multiplicity 1.*

Proof. The domain of $T_C(V)$ is \tilde{X}_C^2 , which has the (Schauder) basis $\mathcal{B} = \{v_1, v_2, v_3, \dots\}$ where $v_n(x) = \sin(n\pi x)$ for n odd, and $v_n(x) = \cos(n\pi x)$ for n even. For each $n, m \in \mathbb{N}$, define

$$a_{mn} = \langle v_m, T_C(V)v_n \rangle_{L^2} \quad (170)$$

Treating $A = (a_{mn})$ as an “infinite matrix” operator on ℓ^2 , we see that λ is an eigenvalue of $T_C(V)$ if and only if $\lambda/2$ is an eigenvalue of A . In particular, the eigenvalues of A and $T_C(V)$ have the same sign.

Many of the terms in $T_C(V)$ vanish as $V \rightarrow 0$. In particular, the traveling waves m_T and ϕ_T and their derivatives depend smoothly on V in L^2 . Moreover, when $V = 0$, m_T and ϕ_T are both constant in x (they are stationary states). Therefore, writing $m_T = 1 + \tilde{m}_T$, there exists $C_1, V^* > 0$ so that if $|V| < V^*$, then

$$\|m'_T\|_{L^1}, \|\phi'_T\|_{L^1}, \|\phi''_T\|_{L^1}, \|\tilde{m}_T\|_{L^1} \leq C_1|V|. \quad (171)$$

For each m , let ϕ_m solve $-Z\phi''_m + \phi_m = P_T(V)v_m$ with periodic boundary conditions in $(-1/2, 1/2)$. For each n, m , define

$$d_{mn} = \langle v_m, \phi'_n(1/2)m'_T + Vv'_n - \tilde{m}_T\phi''_n - m'_T\phi'_n - v'_n\phi'_T - v_n\phi''_T \rangle_{L^2}. \quad (172)$$

From (171) and Lemma 5.7, there exists $C > 0$ independent of m such that

$$\sum_{n=1}^{\infty} |d_{mn}| \leq C|V| \quad \text{and} \quad \sum_{m=1}^{\infty} |d_{mn}| \leq C|V|. \quad (173)$$

Then we may write for each n, m :

$$a_{mn} = \langle v_m, T_C(0)v_n \rangle_{L^2} + d_{mn}. \quad (174)$$

The operator $T_C(0)$ (which is equal to $S_C(P_0)$) is defined by $T_C(0)u = u'' - \phi''$ where ϕ solves $-Z\phi'' + \phi = P_0u$ with periodic boundary conditions in $(-1/2, 1/2)$. Thus, letting $c_{mn} = \langle v_n, T_C(0)v_m \rangle_{L^2}$, we have $a_{mn} = c_{mn} + d_{mn}$. We can explicitly calculate c_{mn} :

$$c_{mn} = \begin{cases} -n^2\pi^2 + \frac{P_0}{Z} \frac{1}{1 + \frac{1}{\pi^2 n^2 Z}} & n = m \text{ even} \\ -n^2\pi^2 + \frac{P_0}{Z} \frac{1}{1 + \frac{1}{\pi^2 n^2 Z}} - \frac{4P_0 \coth\left(\frac{1}{2\sqrt{Z}}\right)}{\sqrt{Z}(1 + n^2\pi^2 Z)^2} & n = m \text{ odd} \\ 0 & n \neq m \text{ either } m \text{ or } n \text{ even} \\ -\frac{4P_0(-1)^{\frac{m+1}{2} + \frac{n+1}{2}} \coth\left(\frac{1}{2\sqrt{Z}}\right)}{\sqrt{Z}(\pi^2 m^2 Z + 1)(\pi^2 n^2 Z + 1)} & n \neq m \text{ both odd.} \end{cases} \quad (175)$$

To show that all the eigenvalues of A are negative except possibly one of them we will use Theorem 3 of [76], which gives a Gershgorin-type result showing that all eigenvalues of an infinite matrix have negative real part. While possibly not all eigenvalues of A have negative real part, we will see using Theorem 3 of [76] that all eigenvalues of $D = B - I$ do have negative real part, and that all but one of these eigenvalues has real part less than -1 , thus proving the desired result.

The specific result of Theorem 3 of [76] is that there are countably many eigenvalues $\hat{\lambda}_n$ of $B = (b_{mn})$ and for each n ,

$$|\hat{\lambda}_n - b_{nn}| < Q_n := \sum_{\substack{m=1 \\ m \neq n}}^{\infty} |b_{mn}|, \quad (176)$$

provided the following conditions are met:

1. $b_{nn} \neq 0$ for any n and $\lim_{n \rightarrow \infty} |b_{nn}| = \infty$.
2. There exists $0 < \rho < 1$ so that for each odd n ,

$$\frac{Q_n}{|b_{nn}|} < \rho. \quad (177)$$

3. For each odd n, m with $n \neq m$, $|b_{nn} - b_{mm}| \geq Q_n + Q_m$
4. For each m , $\sup\{|b_{mn}| : n \in \mathbb{N}\} < \infty$.

We will show that B satisfies each of these conditions for small enough $V < V^*$ and large enough Z .

1. Observe that

$$b_{nn} < -n^2\pi^2 + \frac{P_0}{Z} \frac{1}{\frac{1}{n^2\pi^2 Z} + 1} + C|V| - 1. \quad (178)$$

Let $0 < \varepsilon < 1/(2 + 2\pi^2)$. Using Lemma 4.7, there exists Z^* large enough that for all $Z > Z^*$, $P_0/Z < \pi^2 + \varepsilon/2$. There also exists $V^* > 0$ so that if $|V| < V^*$, $C|V| < \varepsilon/2$. Therefore, for large enough Z , $b_{nn} < -\pi^2(n^2 - 1) - 1 + \varepsilon < 0$. It is clear that $\lim_{n \rightarrow \infty} |b_{nn}| = \infty$.

2. We have

$$Q_n = \sum_{\substack{m=1 \\ m \neq n}}^{\infty} |b_{mn}| \leq \sum_{\substack{m=1 \\ m \neq n}}^{\infty} |c_{mn}| + \sum_{\substack{m=1 \\ m \neq n}}^{\infty} |d_{mn}| \quad (179)$$

If n is even, $Q_n \leq \sum_{n=1}^{\infty} |d_{mn}| < C|V| < \varepsilon/2$. If n is odd, we can explicitly calculate a convenient upper bound for Q_n :

$$Q_n < Q_n + \frac{4P_0 \coth\left(\frac{1}{2\sqrt{Z}}\right)}{\sqrt{Z}(\pi^2 n^2 Z + 1)^2} \quad (180)$$

$$\leq \sum_{\substack{m=1 \\ m \text{ odd}}}^{\infty} \frac{4P_0 \coth\left(\frac{1}{2\sqrt{Z}}\right)}{\sqrt{Z}(\pi^2 m^2 Z + 1)(\pi^2 n^2 Z + 1)} + \sum_{m=1}^{\infty} |d_{mn}| \quad (181)$$

$$\leq \frac{P_0}{Z} \frac{1}{1 + n^2\pi^2 Z} + C|V| \quad (182)$$

$$< \frac{\pi^2 + \varepsilon/2}{1 + \pi^2} + \frac{\varepsilon}{2} \quad \text{assuming } Z^* \geq 1. \quad (183)$$

We conclude that whether n is even or odd, (183) is an upper bound for Q_n . We have already seen that for $Z > Z^*$, $b_{nn} < -1 + \varepsilon$. Thus, for any n ,

$$\frac{Q_n}{|b_{nn}|} < \frac{\pi^2 + \varepsilon/2}{(1 + \pi^2)(1 - \varepsilon)} + \frac{\varepsilon/2}{1 - \varepsilon} < \frac{\pi^2 + \frac{1}{4+4\pi^2}}{(1 + \pi^2)\left(1 - \frac{1}{2+2\pi^2}\right)} + \frac{1}{(4 + 4\pi^2)\left(1 - \frac{1}{2+2\pi^2}\right)} = \frac{2 + 5\pi^2 + 4\pi^4}{2 + 6\pi^2 + 4\pi^4} < 1. \quad (184)$$

Therefore, letting $\rho = \frac{2+5\pi^2+4\pi^4}{2+6\pi^2+4\pi^4}$, the second condition is satisfied.

3. Let $n, m \in \mathbb{N}$ be odd with $n \neq m$. One can verify that for any $Z > 0$,

$$0 < \frac{4\sqrt{Z} \coth\left(\frac{1}{2\sqrt{Z}}\right)}{(1 + \pi^2 Z)^2} < 1. \quad (185)$$

Then if $Z > Z^*$ and $Z > Z^*$,

$$|b_{nn} - b_{mm}| \geq \pi^2 |n^2 - m^2| - \frac{P_0}{Z} \left| \frac{1}{\frac{1}{n^2 \pi^2 Z} + 1} - \frac{1}{\frac{1}{m^2 \pi^2 Z} + 1} \right| \quad (186)$$

$$- \left| \frac{4P_0 \coth\left(\frac{1}{2\sqrt{Z}}\right)}{\sqrt{Z}(1 + n^2 \pi^2 Z)^2} - \frac{4P_0 \coth\left(\frac{1}{2\sqrt{Z}}\right)}{\sqrt{Z}(1 + m^2 \pi^2 Z)^2} \right| - 2C|V| \quad (187)$$

$$\geq \pi^2 |n^2 - m^2| - 2\frac{P_0}{Z} - \varepsilon \quad (188)$$

$$> 3\pi^2 - 2(\pi^2 - \varepsilon/2) - \varepsilon \quad (189)$$

$$> \pi^2 - 2\varepsilon. \quad (190)$$

On the other hand, we have seen that for each n , if $Z > Z^*$ and $|V| < V^*$, then $Q_n < 1$, so $Q_n + Q_m < 2 < \pi^2 - 2\varepsilon$. Thus condition 3 is satisfied.

4. This is clear.

Thus, the eigenvalues of B are enumerated $\hat{\lambda}_1, \hat{\lambda}_2, \hat{\lambda}_3, \dots$, and for each n , $|b_{nn} - \hat{\lambda}_n| < Q_n$. Thus, for $n \geq 2$,

$$\operatorname{Re} \hat{\lambda}_n < b_{nn} + Q_n < -4\pi^2 + \frac{P_0}{V_0} + C|V| < -3\pi^2 + \varepsilon < -1. \quad (191)$$

Since the eigenvalues of A are $\lambda_n = \hat{\lambda}_n + 1$, we conclude that all λ_n have negative real part bounded away from 0 except for possibly λ_1 . The eigenvalues of $T_C(V)$ are $2\lambda_n$ for $n = 1, 2, 3, \dots$, so the desired result holds.

In the case $V = 0$, the operator $T_C(0)$ is exactly the operator shown to have exactly one zero eigenvalue in the proof of Theorem 4.5. Therefore, $T_C(0)$ has all negative eigenvalues (real because the operator is self-adjoint) except for one zero eigenvalue. \square

Theorem 5.6. *There exists $V^*, Z^* > 0$ such that if $0 < |V| < V^*$ and $Z > Z^*$, then resolvent set of T_C contains $\{z \in \mathbb{C} : \operatorname{Re} z \geq 0\}$.*

Proof. Due to Proposition 5.4, we need only show that all eigenvalues of T_C have negative real part. Lemma 5.5 gives V^* and Z^* so that if $|V| < V^*$ and $Z > Z^*$, then all but possibly one of the eigenvalues of $T_C(V)$ has negative real part. We also know that when $V = 0$, this one eigenvalue is zero. Therefore, we only need to show that for $0 < |V| < V^*$, this eigenvalue has negative real part.

Since T_C depends on V , both explicitly, and through m_T and ϕ_T , we write $T_C = T_C(V)$. For the operator $T_C(V)$, the parameter $P = P_T(V)$ is given by Theorem 4.5. We also consider the linearization $S_C(P)$ of F about $m = 1$ with arbitrary $P > 0$. We will make use of Corollary 1.13 and Theorem 1.16 in [22] which from which we conclude the following:

- There exists neighborhoods $U_1, U_2 \subset \mathbb{R}$ of 0 and $P_0 \in \mathbb{R}$ respectively and smooth functions $\lambda : U_1 \rightarrow \mathbb{R}$ and $\mu : U_2 \rightarrow \mathbb{R}$ such that $\lambda(V)$ is an eigenvalue of $T_C(V)$ and $\mu(P)$ is an eigenvalue of $T_C(P)$, and $\lambda(0) = \mu(P_0) = 0$.
- λ and μ satisfy:

$$-\mu'(P_0) \lim_{V \rightarrow 0} \frac{VP'_T(V)}{\lambda(V)} = 1. \quad (192)$$

By Lemma 5.5, $\lambda(0) = 0$ is the largest eigenvalue of $T_C(0)$. Since T_C depends smoothly on V , so does $\lambda(V)$. Therefore, for small V , $\lambda(V)$ is the eigenvalue of $T_C(V)$ with the largest real part. Moreover, for small V , $\lambda(V)$ has the same sign as $-VP'(V)\mu'(P_0)$. From Proposition 4.7, $P'_T(0) = 0$. For similar reasons, $\lambda'(0) = 0$. So after two applications of L'Hôpital's rule on (192), we obtain $\lambda(V) = \frac{1}{2}\lambda''(0)V^2 + O(V^3)$ and

$$\lambda''(0) = -2P''_T(0)\mu'(P_0). \quad (193)$$

Therefore, if $P''_T(0)\mu'(P_0) > 0$, then there exists $V^* > 0$ such that if $0 < |V| < V^*$, then $\lambda(V) < 0$. We will show that for sufficiently large Z , both $P''_T(0)$ and $\mu'(P_0)$ are positive, thus proving the desired result.

First we show that $\mu'(P_0)$ is positive. The eigenvalue equation satisfied by $\mu(P)$ is

$$u'' - \phi'' = \mu(P)u, \quad -Z\phi'' + \phi = Pu, \quad (194)$$

where $m(\pm 1/2) = 0$ and ϕ satisfies periodic boundary conditions. We write $P = P_0 + \varepsilon$ for some small ε , and expand m , ϕ , and μ in ε :

$$u = u_0 + \varepsilon u_1 + O(\varepsilon^2) \quad (195)$$

$$\phi = \phi_0 + \varepsilon \phi_1 + O(\varepsilon^2) \quad (196)$$

$$\mu = \mu_1 \varepsilon + O(\varepsilon^2). \quad (197)$$

Observe that $\mu_1 = \mu'(P_0)$. Solving the zero order in ε equation, we find u_0 and ϕ_0 up to a multiplicative constant:

$$u_0 = \frac{x}{P_0 - 1} - \frac{1}{2} \frac{P_0}{P_0 - 1} \csc\left(\frac{\sqrt{P_0 - 1}}{\sqrt{Z}}\right) \sin\left(\frac{\sqrt{P_0 - 1}x}{\sqrt{Z}}\right), \quad \phi_0 = u_0 + x. \quad (198)$$

Observe that since P_0 and Z satisfy (132),

$$\csc\left(\frac{\sqrt{P_0 - 1}}{\sqrt{Z}}\right) = \sqrt{\frac{P_0^3 - P_0^2 + 4Z}{(P_0 - 1)P_0^2}}. \quad (199)$$

In first order, the (194) becomes

$$u_1'' - \phi_1'' = \mu_1 u_0, \quad -Z\phi_1'' + \phi_1 = P_0 u_1 + u_0. \quad (200)$$

Write $\phi_1 = \psi_1 + \phi_0/P_0$ where ψ_1 solves $-Z\psi_1'' + \psi_1 = P_0 u_1$. Thus, we may write the first order equation as

$$u_1'' - \psi_1'' = \mu_1 u_0 - \frac{1}{Z}u_0 + \frac{\phi_0}{P_0 Z}. \quad (201)$$

Since the operator $u_1 \mapsto u_1'' - \psi_1''$ (which is $S_C(P_0)$) is self adjoint, the right hand side must be orthogonal to the kernel of the operator, which is spanned by u_0 . Thus, μ_1 solves:

$$\int_{-1/2}^{1/2} \left(\mu_1 u_0 - \frac{1}{Z}u_0 + \frac{\phi_0}{P_0 Z} \right) u_0 dx = 0. \quad (202)$$

Computing the integral and solving for μ_1 , we obtain

$$\mu_1 = \frac{3(P_0 - 1)(P_0^2 - 12Z)}{P_0 Z (3P_0^2 - 60Z + 2)}. \quad (203)$$

Using Lemma 4.7, we obtain an asymptotic form for μ_1 in large Z :

$$\mu_1 = \frac{1}{Z} + O(1/Z^2). \quad (204)$$

Thus, for sufficiently large Z , $\mu'(P_0) = \mu_1 > 0$.

Lemma 4.2 gives the value of P_2 . In large Z , this expands as

$$P_2 = \frac{\pi^2}{48}Z + O(1). \quad (205)$$

Thus, for large Z , $P_2 > 0$. Thus,

$$\lambda(V) = -\frac{\pi^2}{24}V^2 + O\left(\frac{V^4}{Z}\right), \quad (206)$$

so for large Z and small V , the largest real part of the eigenvalues of $T_C(V)$ is negative. \square

We conclude with a technical lemma used in the proof of Lemma 5.5:

Lemma 5.7. Suppose $f : [-1/2, 1/2] \rightarrow \mathbb{R}$ is C^2 . Let $\mathcal{B} = \{v_1, v_2, v_3, \dots\}$ where $v_n(x) = \sin(n\pi x)$ for n odd, and $v_n(x) = \cos(n\pi x)$ for n even. Then there exists $C > 0$ such that

$$\sum_{n=1}^{\infty} |\langle v_m, f v_n \rangle_{L^2}| < C \|f\|_{L^1} \quad \text{and} \quad \sum_{m=1}^{\infty} |\langle v_m, f v_n \rangle_{L^2}| < C \|f\|_{L^1}. \quad (207)$$

Proof. Decompose f as a Fourier series: $f = \sum_{k=1}^{\infty} a_k v_k$. Since f is C^2 -smooth, $|a_k| < \|f''\|_{L^1}/k^2$. Then we can use some product-to-sum trigonometric identities to see that

$$f v_n = \sum_{k=1}^{\infty} a_k v_k v_n = \sum_{k=1}^{\infty} \frac{a_k}{2} (r_{n,k} v_{k+n} + s_{n,k} v_{|k-n|}), \quad (208)$$

where the coefficients $r_{n,k}$ and $s_{n,k}$ are either 1 or -1 and are determined by the parities of n and k . The sign of each coefficient is not important, so we do not endeavor to give them explicitly. Thus,

$$\sum_{n=1}^{\infty} |\langle v_m, f v_n \rangle_{L^2}| = \sum_{n=1}^{\infty} \left| \sum_{k=1}^{\infty} \frac{a_k}{2} \langle v_m, r_{n,k} v_{k+n} + s_{n,k} v_{|k-n|} \rangle \right| \quad (209)$$

$$\leq \sum_{n=1}^{\infty} \sum_{k=1}^{\infty} \frac{|a_k|}{2} (|\langle v_m, v_{k+n} \rangle| + |\langle v_m, v_{|k-n|} \rangle|) \quad (210)$$

$$= \frac{1}{4} \sum_{n=1}^{\infty} |a_{n+m}| + |a_{|n-m|}| \quad (211)$$

$$\leq \frac{3}{4} \sum_{n=1}^{\infty} |a_n| \quad (212)$$

$$\leq \frac{3\|f''\|_{L^1}}{4} \sum_{n=1}^{\infty} \frac{1}{n^2} \quad (213)$$

$$= \frac{\pi^2}{8} \|f''\|_{L^1}. \quad (214)$$

Thus the result for the sum over n holds. The proof for the sum over m is identical. \square

Condition (i): T_C generates a strongly continuous semigroup, see Appendix C. Here we show that the linearized operator T_C defined by (154) generates a strongly continuous semigroup. We will make use of the Hille-Yosida Theorem [33]. We will first prove a supporting proposition.

Proposition 5.8. There exists $V^*, Z^*, \lambda_0 > 0$ such that if $|V| < V^*$ and $Z > Z^*$, then all eigenvalues of for all $\lambda > 0$ and $u \in \tilde{X}_C^2$

$$(\lambda - \lambda_0) \|u\|_{L^2} \leq \|(\lambda I - T_C)u\|_{L^2}. \quad (215)$$

Proof. We calculate the norm via the inner product:

$$\begin{aligned} \|(\lambda I - T_C)u\|_{L^2}^2 &= \langle (\lambda I - T_C)u, (\lambda I - T_C)u \rangle_{L^2} \\ &= \lambda^2 \|u\|_{L^2}^2 + \|T_C u\|_{L^2}^2 - 2\lambda \langle u, T_C u \rangle_{L^2}. \end{aligned}$$

Observe that

$$\langle u, T_C u \rangle_{L^2} \leq -\|u'\|_{L^2}^2 + \|(\phi'(1/2) - \phi)m'_T\|_{L^2}^2 + \|(V - \phi_T)u'\|_{L^2}^2 + \|m_T \phi''\|_{L^2}^2 + \|u \phi_T''\|_{L^2}^2. \quad (216)$$

There exists $C, V^* > 0$ so that $|V| < V^*$ so that (after applying the Poincaré inequality):

$$\begin{aligned} \|(\phi'(1/2) - \phi)m'_T\|_{L^2}^2 &< C|V| \|u\|_{L^2}^2 \\ \|(V - \phi_T)u'\|_{L^2}^2 &< C|V| \|u'\|_{L^2}^2 \\ \|m_T \phi''\|_{L^2}^2 &\leq C \|u\|_{L^2}^2 \\ \|u \phi_T''\|_{L^2}^2 &\leq C|V| \|u\|_{L^2}^2. \end{aligned} \quad (217)$$

Assume V^* is sufficiently small that $C|V| < 1/2$.

$$\langle u, T_C u \rangle_{L^2} \leq -\frac{1}{2} \|u'\|_{L^2}^2 + (1 + C) \|u\|_{L^2}^2. \quad (218)$$

Let $\lambda_0 = 2(1 + C)$ so that $\langle u, T_C u \rangle_{L^2} \leq (\lambda_0/2) \|u\|_{L^2}^2$. Thus,

$$\|(\lambda I - T_C)u\|_{L^2}^2 \geq \lambda^2 \|u\|_{L^2}^2 - \lambda \lambda_0 \|u\|_{L^2}^2 = (\lambda^2 - \lambda \lambda_0) \|u\|_{L^2}^2. \quad (219)$$

If $\lambda > \lambda_0$, then $\lambda^2 - \lambda \lambda_0 \geq \lambda^2 - 2\lambda \lambda_0 + \lambda_0^2 = (\lambda - \lambda_0)^2$. Therefore,

$$\|(\lambda I - T_C)u\|_{L^2} \geq (\lambda - \lambda_0) \|u\|_{L^2}. \quad (220)$$

□

We recall the definition of a closed operator:

Definition 5.9. Let X and Y be Banach spaces and let $B : D(B) \subset X \rightarrow Y$ be a linear operator. Then B is *closed* if for every sequence (x_n) converging to some $x \in X$ such that Bx_n converges to $y \in Y$, it follows that $x \in D(B)$ and $Bx = y$.

An operator is closed if its resolvent $(\lambda I - B)^{-1}$ exists and is bounded for at least one value of $\lambda \in \mathbb{C}$. By Theorem 5.6, the resolvent set of T_C is non-empty, and by Proposition 5.2, the resolvent is compact (and thus bounded) whenever it exists. Therefore, T_C is a closed operator. Thus, we may prove the main result of this section:

Proposition 5.10. *There exists $V^* > 0$ such that if $|V| < V^*$, then A generates a strongly continuous semigroup.*

Proof. We appeal to the Hille-Yosida Theorem [33], which states that if $T_C : X \rightarrow Y$ is a closed, densely defined operator and if there exists $\lambda_0 > 0$ such that

$$\|(\lambda I - T_C)^{-n}\|_{L^2} \leq \frac{1}{(\lambda - \lambda_0)^n}, \quad (221)$$

then T_C generates a strongly continuous semigroup.

It is clear to see that (221) is satisfied due to Proposition 5.8. Therefore, the hypotheses of the Hille-Yosida theorem are satisfied for sufficiently small V^* , so the result holds. □

Since T_C generates a strongly continuous semigroup, the first condition of the Gearhart-Prüss-Griener Theorem is satisfied.

Condition (iii): the resolvent of T_C is uniformly bounded, see appendix C. Now we prove that the resolvent of T_C is uniformly bounded for complex numbers with positive real part. Then we formally establish linear stability in Theorem 5.12.

Proposition 5.11. *There exist $V^*, Z^*, \Gamma > 0$ such that if $0 < |V| < V^*$ and $Z > Z^*$, then the resolvent $\|(\lambda I - T_C)^{-1}\| < \Gamma$ for all $\lambda \in \mathbb{C}$ with $\operatorname{Re} \lambda > 0$.*

Proof. Existence of the resolvent $(\lambda I - T_C)^{-1}$ for all λ with $\operatorname{Re} \lambda > 0$ is established in Theorem 5.6. Assume, to the contrary, that there exists a sequence $(\lambda_k)_{k=1}^\infty \subset \mathbb{C}$ such that $\operatorname{Re} \lambda_k > 0$ for each k and

$$\|(\lambda_k I - T_C)^{-1}\|_{L^2} > k. \quad (222)$$

Then for each k , there exist $v_k \in \tilde{X}^2$ and $w_k \in L^2(-1/2, 1/2)$ such that $(\lambda_k I - T_C)v_k = w_k$, $\|v_k\|_{L^2} = 1$, and $\|w_k\|_{L^2} < 1/k$. We shall consider two cases: (i) the sequence (λ_k) is bounded, and (ii) (λ_k) is unbounded. We will show that in each case, we arrive at a contradiction.

- (i) If the sequence (λ_k) is bounded, then it has a subsequence also called (λ_k) which converges to some $\lambda \in \mathbb{C}$ with $\operatorname{Re} \lambda \geq 0$. By Theorem 5.6, λ is in the resolvent set of T_C . Recall the *first resolvent identity* [32] from which we conclude that for each k ,

$$(\lambda I - T_C)^{-1} - (\lambda_k I - T_C)^{-1} = (\lambda - \lambda_k)(\lambda I - T_C)^{-1}(\lambda_k I - T_C)^{-1}. \quad (223)$$

We calculate:

$$\begin{aligned} \|v_k\|_{L^2} &= \|(\lambda_k I - T_C)^{-1} w_k\|_{L^2} \\ &\leq \| - [(\lambda I - T_C)^{-1} - (\lambda_k I - T_C)^{-1}] w_k \|_{L^2} + \|(\lambda I - T_C)^{-1} w_k\|_{L^2} \\ &\leq \|(\lambda_k - \lambda)(\lambda I - T_C)^{-1}(\lambda_k I - T_C)^{-1} w_k\|_{L^2} + \|w_k\|_{L^2} \|(\lambda I - T_C)^{-1}\| \\ &\leq |\lambda_k - \lambda| \|(\lambda I - T_C)^{-1} v_k\|_{L^2} + \|w_k\|_{L^2} \|(\lambda I - T_C)^{-1}\| \\ &\leq (|\lambda_k - \lambda| \|v_k\|_{L^2} + \|w_k\|_{L^2}) \|(\lambda I - T_C)^{-1}\|_{L^2}. \end{aligned}$$

Since $|\lambda_k - \lambda_0|, \|w_k\|_{L^2} \rightarrow 0$ and $\|v_k\|_{L^2}$ is bounded, we conclude that $\|v_k\|_{L^2} \rightarrow 0$, a contradiction. Therefore, (λ_k) is not bounded.

- (ii) If the sequence (λ_k) is unbounded, then it has a subsequence also called (λ_k) such that $\lambda_k \rightarrow \infty$. There exists corresponding sequences (v_k) and (w_k) such that

$$w_k = (\lambda_k I - T_C)v_k, \quad \|v_k\|_{L^2} = 1, \quad \|w_k\|_{L^2} \leq 1/k. \quad (224)$$

We calculate the inner product

$$\begin{aligned} \langle w_k, v_k \rangle_{L^2} &= \lambda_k + \|v'_k\|_{L^2} + \int_{-1/2}^{1/2} (V - \phi'_T) v'_k \bar{v}_k dx \\ &\quad + \int_{-1/2}^{1/2} m'_T (\phi'_k(1/2) - \phi'_k) \bar{v}_k dx - \int_{-1/2}^{1/2} \phi''_T |v_k|^2 dx - \int_{-1/2}^{1/2} m_T \phi''_k \bar{v}_k dx \end{aligned} \quad (225)$$

Since (v_k) is L^2 -bounded, by Proposition 6.1 in Appendix A, the last three integrals in (225) are uniformly bounded:

$$\left| \int_{-1/2}^{1/2} m'_T (\phi'_k(1/2) - \phi'_k) \bar{v}_k dx - \int_{-1/2}^{1/2} \phi''_T |v_k|^2 dx - \int_{-1/2}^{1/2} m_T \phi''_k \bar{v}_k dx \right| < C \quad (226)$$

for some $C > 0$ independent of k .

Taking the real part of (225), we find using the Cauchy-Schwartz inequality and the Poincaré inequality that

$$\operatorname{Re} \langle w_k, v_k \rangle \geq \operatorname{Re} \lambda_k + \|v'_k\|_{L^2} - \frac{1}{\pi} \|V - \phi'_T\|_{L^\infty} \|v'_k\|_{L^2}^2 - C. \quad (227)$$

Assuming V^* is sufficiently small that if $|V| < V^*$, then $\|V - \phi'_T\|_{L^\infty} < \pi$, we conclude that $\operatorname{Re} \langle w_k, v_k \rangle \geq \operatorname{Re} \lambda_k - C$. On the other hand, $\operatorname{Re} \langle w_k, v_k \rangle \leq |\langle w_k, v_k \rangle| < 1/k$. Since $\operatorname{Re} \lambda_k > 0$, we conclude that $(\operatorname{Re} \lambda_k)$ is bounded. Furthermore, since all terms in (227) have been shown to be bounded except those involving $\|v'_k\|$, we conclude that (v'_k) must be bounded as well.

Now taking the imaginary part of (225), we find that

$$\operatorname{Im} \langle w_k, v_k \rangle \geq \operatorname{Im} \lambda_k - \frac{1}{\pi} \|V - \phi'_T\|_{L^\infty} \|v'_k\|_{L^2}^2 - C. \quad (228)$$

Once again, all terms in this equation are known to be bounded in k except $\operatorname{Im} \lambda_k$, so we conclude that $(\operatorname{Im} \lambda_k)$ is bounded also, a contradiction.

Since (λ_k) can be neither bounded nor unbounded, we conclude that no such sequence (λ_k) can exist, and so $(\lambda I - T_C)^{-1}$ is uniformly bounded. That is, there exists $\Gamma > 0$ such that

$$\|(\lambda I - T_C)^{-1}\| < \Gamma. \quad (229)$$

□

Now that we have in place all the results proving the conditions of the Gearhart-Prüss-Greiner Theorem, we may apply it to prove linear stability.

Theorem 5.12. *There exist $V^*, Z^*, \Gamma, \sigma > 0$ such that if $|V| < V^*$ and $Z > Z^*$ then T_C generates a strongly continuous semigroup $\{S(t) : t \geq 0\}$ satisfying*

$$\|S(t)\| < \Gamma e^{-\sigma t}. \quad (230)$$

Proof. We need to satisfy the three hypotheses of the Gearhart-Prüss-Greiner Theorem 8.1.

- (i) is satisfied for sufficiently small V^* due to Proposition 5.10
- (ii) is satisfied for sufficiently small V^* and sufficiently large Z^* due to Theorem 5.6.
- (iii) is satisfied due to Proposition 5.11.

Thus, the desired result holds. □

Finally we can now prove that traveling wave solution m_T to model C are asymptotically stable. Specifically, we will prove the following theorem:

Theorem 5.13. *Fix $V \in \mathbb{R}$ and $Z > 0$, and let $m(x, t)$ be a solution to (44) with $m(0, x) = m_0(x)$. Let m_T denote the traveling wave solution to (44) with velocity V . There exist $V^*, Z^* > 0$ independent of V and Z and $\varepsilon > 0$ depending on V and Z such that if $|V| < V^*$, $Z > Z^*$ and*

$$\|m_0 - m_T\|_{H^1} < \varepsilon, \quad (231)$$

then

$$\lim_{t \rightarrow \infty} \|m(\cdot, t) - m_T\|_{L^2} = 0. \quad (232)$$

To prove Theorem 5.13, we follow the same strategy as proving Theorem 3.1. We decompose F_C as a sum of its linearization T_C about m_T and its “nonlinear part”. Since the nonlinearity in F_C is quadratic (that is, the Keller-Segel term $(m\phi')'$), the nonlinear part about the traveling wave $m = m_T$ is the same as the nonlinear part about the stationary state $m = 1$. Thus,

$$F_C(m_T + u) = T_C u + \Psi(u), \quad (233)$$

where Ψ is given by (61). Thus, we may directly apply Proposition 3.7. We will prove a version of 3.8 for T_C showing that the linear part of F_C dominates the nonlinear part in a neighborhood of m_T . Finally, the proof of Theorem 5.13 is identical to the proof of Theorem 3.1.

Lemma 5.14. *Let $T, \delta > 0$ and let u be a solution to*

$$\begin{cases} \partial_t u = T_C u + \Psi(u) & -1/2 < x < 1/2, 0 < t < T \\ u' = 0 & x = \pm 1/2, t > 0. \end{cases} \quad (234)$$

There exist $V^, U^* > 0$ such that if $\|u'(0, \cdot)\|_{L^2} < \delta$, $|V| < V^*$, and $\|u(\cdot, t)\|_{L^2} < U^*$ for all $0 \leq t \leq T$, then*

$$\|u'(\cdot, t)\|_{L^2} \leq \delta \quad (235)$$

for all $0 \leq t \leq T$.

Proof. Write the evolution equation (44) as

$$\partial_t u - u'' = Bu + \Psi(m). \quad (236)$$

Where B is defined by

$$Bu = (\phi'(1/2) - \phi')m'_T + (V - \phi'_T)u' - m_T\phi'' - u\phi''_T, \quad \begin{cases} -Z\phi'' + \phi = Pu \\ \phi(-1/2) = \phi(1/2) \\ \phi'(-1/2) = \phi'(1/2). \end{cases} \quad (237)$$

Now square both sides and integrate to obtain

$$\|Bu + \Psi(u)\|_{L^2}^2 = \int_{-1/2}^{1/2} \Psi^2(u) dx \quad (238)$$

$$= \int_{-1/2}^{1/2} (\partial_t u)^2 - 2(\partial_t u)u'' + (u'')^2 dx \quad (239)$$

$$= \|\partial_t u\|_{L^2}^2 + 2 \int_{-1/2}^{1/2} (\partial_t u)u' dx + \|m''\|_{L^2}^2 \quad (240)$$

$$= \|\partial_t u\|_{L^2}^2 + \frac{d}{dt} \|u'\|_{L^2}^2 + \|u''\|_{L^2}^2. \quad (241)$$

Thus,

$$\frac{d}{dt} \|u'\|_{L^2}^2 \leq \|Bu + \Psi(u)\|_{L^2}^2 - \|u''\|_{L^2}^2 \quad (242)$$

$$\leq 2\|Bu\|_{L^2}^2 + 2\|\Psi(u)\|_{L^2}^2 - \|u''\|_{L^2}^2. \quad (243)$$

From Lemma 3.7, there exists C_1 independent of u , V , and Z such that

$$\|\Psi(u)\|_{L^2} \leq C_1 \|u\|_{L^2} \|u\|_{H^1}. \quad (244)$$

Observe that due to 6.1, if $|V| < V^*$ is small enough, there exist C_2, C_3 depending only on Z such that

$$\|Bu\|_{L^2} \leq C_2 V^* \|u'\|_{L^2} + C_3 \|u\|_{L^2}. \quad (245)$$

Since $\int_{-1/2}^{1/2} u dx = 0$ and $u'(\pm 1/2, t) = 0$, we may apply the Poincaré inequality to both u and u' with a Poincaré constant of π :

$$\pi \|u\|_{L^2} \leq \|u'\|_{L^2} \quad \text{and} \quad \pi \|u'\|_{L^2} \leq \|u''\|_{L^2}. \quad (246)$$

Thus,

$$\frac{d}{dt} \|u'\|_{L^2}^2 \leq 2C_1^2 \|u\|_{L^2}^2 \|u\|_{H^1}^2 + 4C_2^2 (V^*)^2 \|u'\|_{L^2}^2 + 4C_3^2 \|u\|_{L^2}^2 - \|u''\|_{L^2}^2 \quad (247)$$

$$\leq 2C_1^2 \left(1 + \frac{1}{\pi}\right)^2 \|u\|_{L^2}^2 \|u'\|_{L^2}^2 + 4C_2^2 (V^*)^2 \|u'\|_{L^2}^2 + 4C_3^2 \|u\|_{L^2}^2 - \|u''\|_{L^2}^2 \quad (248)$$

$$\leq -(\pi^2 - 4C_1^2 \|u\|_{L^2}^2 - 4C_2^2 (V^*)^2) \|u'\|_{L^2}^2 + 4C_3^2 \|u\|_{L^2}^2. \quad (249)$$

Without loss of generality, we may assume that

$$V^* \leq \frac{\pi}{4C_2} \quad \text{and} \quad U^* \leq \frac{\pi}{4C_1}. \quad (250)$$

Then, if $\|u\|_{L^2} \leq U^*$ for all $0 < t < T$,

$$\frac{d}{dt} \|u'\|_{L^2}^2 \leq -R_1 \|u'\|_{L^2}^2 + R_2 \quad (251)$$

where

$$R_1 = \pi^2 - 4C_1^2(U^*)^2 - 4C_2^2(V^*)^2 \geq \frac{\pi^2}{2} \quad \text{and} \quad R_2 = 4C_3^2(U^*)^2. \quad (252)$$

We now introduce a new variable:

$$q(t) = \|u'(\cdot, t)\|_{L^2}^2 - \frac{R_2}{R_1}. \quad (253)$$

Then q satisfies $q' \leq -R_1 q$. By Grönwall's inequality,

$$q(t) \leq q(0)e^{-R_1 t}. \quad (254)$$

We conclude that if $q(0) < 0$, then $q(t) < 0$ for all $t > 0$. Thus, if $|V| < V^*$ and $\|u\|_{L^2} \leq U^*$, and if

$$\|u'(\cdot, 0)\|_{L^2} < \sqrt{\frac{R_2}{R_1}}, \quad \text{then} \quad \|u'(\cdot, t)\|_{L^2} < \sqrt{\frac{R_2}{R_1}} \quad (255)$$

for all $t > 0$. Letting U^* be sufficiently small that

$$\sqrt{\frac{R_2}{R_1}} \leq \frac{\sqrt{8}}{\pi} C_3 U^* < \delta, \quad (256)$$

the desired result holds. \square

With Lemma 5.14 in place, we may duplicate the proof of Theorem 3.1 in order to prove the nonlinear stability of traveling waves via Theorem 5.13.

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6 Appendix A

Here we show the Proposition which controls the solution ϕ to (32), (35)-(36).

Proposition 6.1. *Let $u \in L^0([-1/2, 1/2])$. Then there exists a unique solution $\phi \in W^{2,p}(-1/2, 1/2)$ for any $1 \leq p \leq \infty$ satisfying $-Z\phi'' + \phi = Pu$ with periodic boundary conditions on $(-1/2, 1/2)$. Moreover, ϕ satisfies the following for any $1 \leq p \leq \infty$:*

- $\|\phi\|_{L^p} \leq P\|u\|_{L^p},$
- $\|\phi'\|_{L^\infty} \leq \frac{P}{2Z}\|u\|_{L^2},$
- $\|\phi''\|_{L^p} \leq \frac{2P}{Z}\|u\|_{L^p}.$

Proof. The solution ϕ can be calculated explicitly using a Green's function:

$$\phi(x) = \frac{P}{2\sqrt{Z} \sinh\left(\frac{1}{2\sqrt{Z}}\right)} \int_{-1/2}^{1/2} G(x, y) u(y) dy, \quad G(x, y) = \begin{cases} \cosh\left(\frac{1/2+(y-x)}{\sqrt{Z}}\right) & y < x \\ \cosh\left(\frac{1/2+(x-y)}{\sqrt{Z}}\right) & y > x. \end{cases} \quad (257)$$

By Young's Integral inequality [67], $\|\phi\|_{L^p} \leq C\|u\|_{L^p}$ where

$$C = \sup_{|x| \leq 1/2} \frac{P}{2\sqrt{Z} \sinh\left(\frac{1}{2\sqrt{Z}}\right)} \int_{-1/2}^{1/2} |G(x, y)| dy = \sup_{|y| \leq 1/2} \frac{P}{2\sqrt{Z} \sinh\left(\frac{1}{2\sqrt{Z}}\right)} \int_{-1/2}^{1/2} |G(x, y)| dx. \quad (258)$$

We calculate

$$\frac{P}{2\sqrt{Z} \sinh\left(\frac{1}{2\sqrt{Z}}\right)} \int_{-1/2}^{1/2} |G(x, y)| dy \quad (259)$$

$$= \frac{P}{2\sqrt{Z} \sinh\left(\frac{1}{2\sqrt{Z}}\right)} \left(\int_{-1/2}^x \cosh\left(\frac{1/2 + y - x}{\sqrt{Z}}\right) dy + \int_x^{1/2} \cosh\left(\frac{1/2 + x - y}{\sqrt{Z}}\right) dy \right) \quad (260)$$

$$= \frac{P}{2 \sinh\left(\frac{1}{2\sqrt{Z}}\right)} \left(\sinh\left(\frac{1}{2\sqrt{Z}}\right) + \sinh\left(\frac{x}{\sqrt{Z}}\right) - \sinh\left(\frac{x}{\sqrt{Z}}\right) + \sinh\left(\frac{1}{2\sqrt{Z}}\right) \right) \quad (261)$$

$$= P. \quad (262)$$

We conclude that $\|\phi\|_{L^p} \leq P\|u\|_{L^p}$. Next, since G is continuous and differentiable in x except where $x = y$,

$$\phi'(x) = \frac{P}{2\sqrt{Z} \sinh\left(\frac{1}{2\sqrt{Z}}\right)} \int_{-1/2}^{1/2} \frac{d}{dx} G(x, y) u(y) dy. \quad (263)$$

Therefore, using Hölder's inequality for p and its Hölder conjugate q ,

$$\|\phi'\|_{L^\infty} \leq \frac{P}{2\sqrt{Z} \sinh\left(\frac{1}{2\sqrt{Z}}\right)} \|u\|_{L^p} \sup_{|x| \leq 1/2} \left\| \frac{d}{dx} G(x, \cdot) \right\|_{L^q}. \quad (264)$$

Since $|\frac{d}{dx} G(x, y)| \leq \frac{1}{\sqrt{Z}} \sinh\left(\frac{1}{2\sqrt{Z}}\right)$, we conclude that $\|\phi'\|_{L^\infty} \leq \frac{P}{2Z} \|u\|_{L^p}$. Finally, since $\phi'' = -\frac{P}{Z}u + \frac{1}{Z}\phi$, we have

$$\|\phi''\|_{L^p} \leq \frac{P}{Z} \|u\|_{L^p} + \frac{1}{Z} \|\phi\|_{L^p} \leq \frac{2P}{Z} \|u\|_{L^p}. \quad (265)$$

□

7 Appendix B

Here we formulate the Crandall-Rabinowitz Theorem [21].

Theorem 7.1. *Let X and Y be Banach spaces, and let $\mathcal{F} : X \times \mathbb{R} \rightarrow Y$ be an operator with the following properties:*

- $\mathcal{F}(0, t) = 0$ for all t .
- $D_x \mathcal{F}$, $D_t \mathcal{F}$, and $D_{xt} \mathcal{F}$ exist and are continuous.
- The dimension of the null space and co-dimension of the range of $D_x \mathcal{F}(0, 0)$ are both 1.
- If $x_0 \neq 0$ is in the null space of $D_x \mathcal{F}(0, 0)$, then $D_{xt} \mathcal{F}(0, 0)x_0$ is not in the range of $D_x \mathcal{F}(0, 0)$.

Then there exists a neighborhood $U \subset X \times \mathbb{R}$ of $(0, 0)$, $\varepsilon > 0$ and functions $\sigma : (-\varepsilon, \varepsilon) \rightarrow X$ and $s : (-\varepsilon, \varepsilon) \rightarrow \mathbb{R}$ with $\sigma \neq 0$ such that $\sigma(0) = 0$, $s(0) = 0$, and

$$\mathcal{F}^{-1}(0) \cap U = (\{(0, t) : t \in \mathbb{R}\} \cup \{(\sigma(\alpha), s(\alpha)) : |\alpha| < \varepsilon\}) \cap U. \quad (266)$$

Moreover, if \mathcal{F}_{xx} exists and is continuous, then σ is continuously differentiable and $\sigma'(0)$ spans the null space of $D_x \mathcal{F}(0, 0)$.

8 Appendix C

Here we formulate the the Gearhart-Prüss-Greiner Theorem [33].

Theorem 8.1. (Gearhart-Prüss-Greiner) *Let X be a Hilbert space, and let $L : D(L) \rightarrow X$ be a linear operator, where the domain $D(L)$ of L is a dense subspace of X . If the following hold*

- (i) the semigroup $(S(t))_{t \geq 0}$ generated by L is strongly continuous,
- (ii) The resolvent set of L contains $\{z \in \mathbb{C} : \operatorname{Re} z > 0\}$, and
- (iii) The resolvent $(\lambda I - L)^{-1}$ is uniformly bounded on the above set, i.e.,

$$\sup_{\operatorname{Re} \lambda > 0} \|(\lambda I - L)^{-1}\|_X < \infty, \quad (267)$$

then there exists $\Gamma, \sigma > 0$ such that

- (a) For each λ in the spectrum $\sigma(S(t))$, $|\lambda| < e^{-\sigma t}$, and
- (b) For each $t \geq 0$, $\|S(t)\|_X \leq \Gamma e^{-\sigma t}$.

References

- [1] Priti Agarwal and Ronen Zaidel-Bar. Diverse roles of non-muscle myosin II contractility in 3D cell migration. *Essays in Biochemistry*, 63(5):497–508, 2019.
- [2] Bruce Alberts, Alexander Johnson, Julian Lewis, Martin Raff, Kieth Roberts, and Peter Walter. Molecular biology of the cell. *OCLC*, 145080076(48122761):57023651, 2002.
- [3] Ricard Alert, Carles Blanch-Mercader, and Jaume Casademunt. Active fingering instability in tissue spreading. *Physical review letters*, 122(8):088104, 2019.
- [4] David Arrowsmith and Colin M Place. *Dynamical systems: differential equations, maps, and chaotic behaviour*, volume 5. CRC Press, 1992.
- [5] Yuto Ashida, Zongping Gong, and Masahito Ueda. Non-hermitian physics. *Advances in Physics*, 69(3):249–435, 2020.
- [6] Bernd Aulbach and Thomas Wanner. The Hartman—Grobman theorem for Carathéodory-type differential equations in Banach spaces. *Nonlinear Analysis: Theory, Methods & Applications*, 40(1-8):91–104, 2000.
- [7] Blake Barker, Jeffrey Humpherys, Gregory Lyng, and Joshua Lytle. Evans function computation for the stability of travelling waves. *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences*, 376(2117):20170184, 2018.
- [8] Erin Barnhart, Kun-Chun Lee, Greg M Allen, Julie A Theriot, and Alex Mogilner. Balance between cell- substrate adhesion and myosin contraction determines the frequency of motility initiation in fish keratocytes. *Proceedings of the National Academy of Sciences*, 112(16):5045–5050, 2015.
- [9] Erin L Barnhart, Greg M Allen, Frank Jülicher, and Julie A Theriot. Bipedal locomotion in crawling cells. *Biophysical journal*, 98(6):933–942, 2010.
- [10] Erin L Barnhart, Kun-Chun Lee, Kinneret Keren, Alex Mogilner, and Julie A Theriot. An adhesion-dependent switch between mechanisms that determine motile cell shape. *PLoS biology*, 9(5):e1001059, 2011.
- [11] Samir Bendoukha, Salem Abdelmalek, and Mokhtar Kirane. The global existence and asymptotic stability of solutions for a reaction–diffusion system. *Nonlinear Analysis: Real World Applications*, 53:103052, 2020.
- [12] Leonid Berlyand, Jan Fuhrmann, and Volodymyr Rybalko. Bifurcation of traveling waves in a keller–segel type free boundary model of cell motility. *Commun. Math. Sci.*, 16(3):735–762, 2018.
- [13] Leonid Berlyand, Mykhailo Potomkin, and Volodymyr Rybalko. Phase-field model of cell motility: Traveling waves and sharp interface limit. *Comptes Rendus Mathématique*, 354(10):986–992, 2016.
- [14] Leonid Berlyand, Mykhailo Potomkin, and Volodymyr Rybalko. Sharp interface limit in a phase field model of cell motility, 2017.
- [15] Justin S Bois, Frank Jülicher, and Stephan W Grill. Pattern formation in active fluids. *Biophysical Journal*, 100(3):445a, 2011.
- [16] Nicolas Bourbaki. *General topology: chapters 5–10*, volume 18. Springer Science & Business Media, 2013.
- [17] Dennis Bray. *Cell movements: from molecules to motility*. Garland Science, 2000.
- [18] Anders E Carlsson and David Sept. Mathematical modeling of cell migration. *Methods in cell biology*, 84:911–937, 2008.
- [19] Paul Cornwell and Christopher KRT Jones. A stability index for travelling waves in activator-inhibitor systems. *Proceedings of the Royal Society of Edinburgh Section A: Mathematics*, 150(1):517–548, 2020.

- [20] James M Cowan, Jacob J Duggan, Breanne R Hewitt, and Ryan J Petrie. Non-muscle myosin ii and the plasticity of 3d cell migration. *Frontiers in cell and developmental biology*, 10:1047256, 2022.
- [21] Michael G Crandall and Paul H Rabinowitz. Bifurcation from simple eigenvalues. *Journal of Functional Analysis*, 8(2):321–340, 1971.
- [22] Michael G Crandall and Paul H Rabinowitz. Bifurcation, perturbation of simple eigenvalues and linearized stability. 1973.
- [23] Alessandro Cucchi, Antoine Mellet, and Nicolas Meunier. A cahn–hilliard model for cell motility. *SIAM Journal on Mathematical Analysis*, 52(4):3843–3880, 2020.
- [24] Alessandro Cucchi, Antoine Mellet, and Nicolas Meunier. Self polarization and traveling wave in a model for cell crawling migration. *Discrete and dynamical systems*, 42:2381–2407, 2022.
- [25] Noemi David and Benoît Perthame. Free boundary limit of a tumor growth model with nutrient. *Journal de Mathématiques Pures et Appliquées*, 155:62–82, 2021.
- [26] Henry De Belly and Orion D Weiner. Follow the flow: Actin and membrane act as an integrated system to globally coordinate cell shape and movement. *Current Opinion in Cell Biology*, 89:102392, 2024.
- [27] Alberto Dinelli, Jérémy O’Byrne, Agnese Curatolo, Yongfeng Zhao, Peter Sollich, and Julien Tailleur. Non-reciprocity across scales in active mixtures. *Nature Communications*, 14(1):7035, 2023.
- [28] Ronald G Douglas. *Banach algebra techniques in operator theory*, volume 179. Springer Science & Business Media, 2012.
- [29] Bruce K Driver. *Analysis tools with applications*. Springer New York, 2003.
- [30] XinXin Du, Konstantin Doubrovinski, and Miriam Osterfield. Self-organized cell motility from motor-filament interactions. *Biophysical journal*, 102(8):1738–1745, 2012.
- [31] Yu Duan, Jaime Agudo-Canalejo, Ramin Golestanian, and Benoît Mahault. Dynamical pattern formation without self-attraction in quorum-sensing active matter: the interplay between nonreciprocity and motility. *Physical Review Letters*, 131(14):148301, 2023.
- [32] Nelson Dunford and Jacob T Schwartz. *Linear operators, part 1: general theory*, volume 10. John Wiley & Sons, 1988.
- [33] Klaus-Jochen Engel, Rainer Nagel, and Simon Brendle. *One-parameter semigroups for linear evolution equations*, volume 194. Springer, 2000.
- [34] John W Evans. Nerve axon equations: III stability of the nerve impulse. *Indiana University Mathematics Journal*, 22(6):577–593, 1972.
- [35] Isabela C. Fortunato and Raimon Sunyer. The forces behind directed cell migration. *Biophysica*, 2(4):548–563, 2022.
- [36] Avner Friedman and Bei Hu. Asymptotic stability for a free boundary problem arising in a tumor model. *Journal of Differential Equations*, 227(2):598–639, 2006.
- [37] Avner Friedman and Bei Hu. Bifurcation for a free boundary problem modeling tumor growth by stokes equation. *SIAM Journal on Mathematical Analysis*, 39(1):174–194, 2007.
- [38] Luca Giomi and Antonio DeSimone. Spontaneous division and motility in active nematic droplets. *Physical review letters*, 112(14):147802, 2014.
- [39] Rhoda J Hawkins, Renaud Poincloux, Olivier Bénichou, Matthieu Piel, Philippe Chavier, and Raphaël Voituriez. Spontaneous contractility-mediated cortical flow generates cell migration in three-dimensional environments. *Biophysical journal*, 101(5):1041–1045, 2011.
- [40] Jonathon Howard. Mechanics of motor proteins. In *Physics of bio-molecules and cells. Physique des biomolécules et des cellules: session LXXV. 2–27 July 2001*, pages 69–94. Springer, 2002.
- [41] Nikolai Ivanovich Ionkin. The stability of a problem in the theory of heat conduction with nonclassical boundary conditions. *Differentsial’nye Uravneniya*, 15(7):1279–1283, 1979.
- [42] Todd Kapitula. On the stability of traveling waves in weighted L^∞ spaces. *Journal of Differential equations*, 112(1):179–215, 1994.
- [43] Todd Kapitula, Keith Promislow, et al. *Spectral and dynamical stability of nonlinear waves*, volume 457. Springer, 2013.
- [44] Kinneret Keren, Zachary Pincus, Greg M Allen, Erin L Barnhart, Gerard Marriott, Alex Mogilner, and Julie A Theriot. Mechanism of shape determination in motile cells. *Nature*, 453(7194):475–480, 2008.
- [45] Chris Kowall, Anna Marciniak-Czochra, and Finn Münnich. Stability results for bounded stationary solutions of reaction-diffusion-ode systems. *arXiv preprint arXiv:2201.12748*, 2022.

- [46] Erwin Kreyszig. *Introductory functional analysis with applications*, volume 17. John Wiley & Sons, 1991.
- [47] Karsten Kruse, Jean-Francois Joanny, Frank Jülicher, and Jacques Prost. Contractility and retrograde flow in lamellipodium motion. *Physical biology*, 3(2):130, 2006.
- [48] Rakesh Kumar, Kirankumar R Hiremath, and Sergio Manzetti. A primer on eigenvalue problems of non-self-adjoint operators. *Analysis and Mathematical Physics*, 14(2):21, 2024.
- [49] Yuri Latushkin and Alim Sukhtayev. The algebraic multiplicity of eigenvalues and the Evans function revisited. *Mathematical Modelling of Natural Phenomena*, 5(4):269–292, 2010.
- [50] Veerle Ledoux, Simon JA Malham, Jitse Niesen, and Vera Thümmeler. Computing stability of multidimensional traveling waves. *SIAM Journal on Applied Dynamical Systems*, 8(1):480–507, 2009.
- [51] Alex J Loosley and Jay X Tang. Stick-slip motion and elastic coupling in crawling cells. *Physical Review E—Statistical, Nonlinear, and Soft Matter Physics*, 86(3):031908, 2012.
- [52] Kening Lu. A hartman-grobman theorem for scalar reaction-diffusion equations. *Journal of differential equations*, 93(2):364–394, 1991.
- [53] James D Meiss. *Differential dynamical systems*. SIAM, 2007.
- [54] Alex Mogilner. Mathematics of cell motility: have we got its number? *Journal of mathematical biology*, 58:105–134, 2009.
- [55] Masoud Nickaeen, Igor L Novak, Stephanie Pulford, Aaron Rumack, Jamie Brandon, Boris M Slepchenko, and Alex Mogilner. A free-boundary model of a motile cell explains turning behavior. *PLoS computational biology*, 13(11):e1005862, 2017.
- [56] Ifunanya Nwogbaga and Brian A Camley. Coupling cell shape and velocity leads to oscillation and circling in keratocyte galvanotaxis. *Biophysical Journal*, 122(1):130–142, 2023.
- [57] Takao Ohta, Mitsusuke Tarama, and Masaki Sano. Simple model of cell crawling. *Physica D: Nonlinear Phenomena*, 318:3–11, 2016.
- [58] Lawrence E Payne and Hans F Weinberger. An optimal poincaré inequality for convex domains. *Archive for Rational Mechanics and Analysis*, 5(1):286–292, 1960.
- [59] Robert L Pego and Michael I Weinstein. Eigenvalues, and instabilities of solitary waves. *Philosophical Transactions of the Royal Society of London. Series A: Physical and Engineering Sciences*, 340(1656):47–94, 1992.
- [60] Dmitry E Pelinovsky. Inertia law for spectral stability of solitary waves in coupled nonlinear schrödinger equations. *Proceedings of the Royal Society A: Mathematical, Physical and Engineering Sciences*, 461(2055):783–812, 2005.
- [61] Susanne M Rafelski and Julie A Theriot. Crawling toward a unified model of cell motility: spatial and temporal regulation of actin dynamics. *Annual review of biochemistry*, 73(1):209–239, 2004.
- [62] Pierre Recho, Thibaut Putelat, and Lev Truskinovsky. Contraction-driven cell motility. *Physical review letters*, 111(10):108102, 2013.
- [63] Pierre Recho, Thibaut Putelat, and Lev Truskinovsky. Mechanics of motility initiation and motility arrest in crawling cells. *Journal of the Mechanics and Physics of Solids*, 84:469–505, 2015.
- [64] Pierre Recho and Lev Truskinovsky. Asymmetry between pushing and pulling for crawling cells. *Physical Review E—Statistical, Nonlinear, and Soft Matter Physics*, 87(2):022720, 2013.
- [65] Boris Rubinstein, Ken Jacobson, and Alex Mogilner. Multiscale two-dimensional modeling of a motile simple-shaped cell. *Multiscale Modeling & Simulation*, 3(2):413–439, 2005.
- [66] Walter Rudin. *Functional Analysis*. McGraw-Hill, 1991.
- [67] Bernard Russo. On the Hausdorff-Young theorem for integral operators. 1977.
- [68] Volodymyr Rybalko and Leonid Berlyand. Emergence of traveling waves and their stability in a free boundary model of cell motility. *Transactions of the American Mathematical Society*, 376(03):1799–1844, 2023.
- [69] C Alex Safsten, Volodymyr Rybalko, and Leonid Berlyand. Asymptotic stability of contraction-driven cell motion. *Physical Review E*, 105(2):024403, 2022.
- [70] Björn Sandstede. Chapter 18 - stability of travelling waves. In Bernold Fiedler, editor, *Handbook of Dynamical Systems*, volume 2 of *Handbook of Dynamical Systems*, pages 983–1055. Elsevier Science, 2002.
- [71] Christian H Schreiber, Murray Stewart, and Thomas Duke. Simulation of cell motility that reproduces the force-velocity relationship. *Proceedings of the National Academy of Sciences*, 107(20):9141–9146, 2010.

- [72] Carla A Schwartz and Aiguo Yan. Construction of Lyapunov functions for nonlinear systems using normal forms. *Journal of Mathematical Analysis and Applications*, 216(2):521–535, 1997.
- [73] Shuvasree SenGupta, Carole A Parent, and James E Bear. The principles of directed cell migration. *Nature Reviews Molecular Cell Biology*, 22(8):529–547, 2021.
- [74] Mohamed Shaat and Harold S Park. Chiral nonreciprocal elasticity and mechanical activity. *Journal of the Mechanics and Physics of Solids*, 171:105163, 2023.
- [75] Adam Shellard and Roberto Mayor. All roads lead to directional cell migration. *Trends in cell biology*, 30(11):852–868, 2020.
- [76] PN Shivakumar, JJ Williams, and N Rudraiah. Eigenvalues for infinite matrices. *Linear Algebra and its Applications*, 96:35–63, 1987.
- [77] Elsen Tjhung, Adriano Tiribocchi, Davide Marenduzzo, and Michael E Cates. A minimal physical model captures the shapes of crawling cells. *Nature communications*, 6(1):5420, 2015.
- [78] Lloyd N Trefethen. Spectra and pseudospectra: the behavior of nonnormal matrices and operators. 2020.
- [79] Miguel Vicente-Manzanares, Xuefei Ma, Robert S Adelstein, and Alan Rick Horwitz. Non-muscle myosin ii takes centre stage in cell adhesion and migration. *Nature reviews Molecular cell biology*, 10(11):778–790, 2009.
- [80] Qi Wang, Xiaofeng Yang, David Adalsteinsson, Timothy C Elston, Ken Jacobson, Maryna Kapustina, and M Gregory Forest. Computational and modeling strategies for cell motility. *Computational Modeling of Biological Systems: From Molecules to Pathways*, pages 257–296, 2012.
- [81] Kai Weißenbruch and Roberto Mayor. Actomyosin forces in cell migration: Moving beyond cell body retraction. *Bioessays*, page 2400055, 2024.
- [82] Charles W Wolgemuth, Jelena Stajic, and Alex Mogilner. Redundant mechanisms for stable cell locomotion revealed by minimal models. *Biophysical journal*, 101(3):545–553, 2011.
- [83] Qian Wu, Xianchen Xu, Honghua Qian, Shaoyun Wang, Rui Zhu, Zheng Yan, Hongbin Ma, Yangyang Chen, and Guoliang Huang. Active metamaterials for realizing odd mass density. *Proceedings of the National Academy of Sciences*, 120(21):e2209829120, 2023.
- [84] Yanjun Yang, Mohit Kumar Jolly, and Herbert Levine. Computational modeling of collective cell migration: mechanical and biochemical aspects. *Cell Migrations: Causes and Functions*, pages 1–11, 2019.
- [85] Falko Ziebert and Igor S Aranson. Effects of adhesion dynamics and substrate compliance on the shape and motility of crawling cells. *PloS one*, 8(5):e64511, 2013.
- [86] Falko Ziebert and Igor S Aranson. Computational approaches to substrate-based cell motility. *npj Computational Materials*, 2(1):1–16, 2016.