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EMERGENCE OF TRAVELING WAVES AND THEIR STABILITY IN A FREE BOUNDARY MODEL OF CELL MOTILITY

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Abstract. We consider a 2D free boundary model of cell motility, inspired by the 1D contraction-driven cell motility model due to P. Recho, T. Putelat, and L. Truskinovsky [Phys. Rev. Lett. 111 (2013), p. 108102]. The key ingredients of the model are the Darcy law for overdamped motion of the acto-myosin network, coupled with the advection-diffusion equation for myosin density. These equations are supplemented with the Young-Laplace equation for the pressure and no-flux condition for the myosin density on the boundary, while evolution of the boundary is subject to the acto-myosin flow at the edge.

The focus of the work is on stability analysis of stationary solutions and translationally moving traveling wave solutions. We study stability of radially symmetric stationary solutions and show that at some critical radius a pitchfork bifurcation occurs, resulting in emergence of a family of traveling wave solutions. We perform linear stability analysis of these latter solutions with small velocities and reveal the type of bifurcation (sub- or supercritical). The main result of this work is an explicit asymptotic formula for the stability determining eigenvalue in the limit of small traveling wave velocities.

1. Introduction

Cell motility, i.e. self-sustained motion of living cells using metabolic energy, is a fundamental process involved in a variety of biological phenomena, e.g. wound healing, tissue remodeling (physiological or pathological), immune response, metastatic tumor cell migration etc. In the general context of soft matter physics the interest to the phenomenon led to a recent development of the so-called "Active gel physics", see [24]. Experimental studies of cell motility are often performed on keratocyte cells that are widely considered as a case study example thanks to their fast and persistent migration and stable shape. These cells, found in fish skin and human corneas, are of particular interest due to their medical relevance as key players in wound healing (e.g., in retina). From the modeling perspective keratocytes are also advantageous because of their flat shape that allows one to use 2D mathematical models.

The two leading mechanisms of cell motility are protrusion generated by polymerization of actin filaments (more precisely, filamentous actin or F-actin) and contraction due to myosin motors [18], [20]. The goal of this work is to study the contraction-driven cell motility, since contractile stresses caused by myosin motors prevail in cell polarization and initiation of motion [27]. To this end we introduce

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and investigate a 2D model with free boundary that generalizes the 1D free boundary model proposed in [26], [27]. Despite of its simplicity this 1D model captures the bifurcation of stationary solutions to traveling waves, which is the signature property of cell motility. While mathematical analysis in the 2D case is obviously much more involved than in the 1D case, especially in a free boundary setting, the results of the bifurcation analysis of the 2D model agrees with findings of [26], [27] for the 1D case. In particular, both models exhibit a supercritical bifurcation. However, modeling of the important phenomenon of cell shape evolution requires consideration beyond the 1D setting, and results of this work capture breaking of the shape symmetry, as depicted in Fig. 2, which is an important biological phenomenon, see, e.g., [2] and [31]. Moreover, the main results of the work, in particular the explicit asymptotic formula (7.10) for the eigenvalue that decides on stability, and the asymptotic expansion of the corresponding eigenvector provide a new insight for both 1D and 2D models.

Various 2D free boundary models for cell motility were introduced in, e.g., [2], [7], [6], while [12] proposes a model of motion with fixed shape. The problems in [7] and [6] model the polymerization driven cell motion when myosin contraction is dominated by polymerization, which naturally complements present work. These models extend the classical Hele-Shaw model by adding fundamental active matter features such as the presence of persistent motion modeled by traveling wave solutions. The Keller-Segel system with free boundaries as a model for contraction driven motility was first introduced in [26], in the 1D setting. Its 2D counterpart introduced and analyzed numerically in [2] accounts for both polymerization and myosin contraction. A simplified version of this model was studied analytically in [5], where the traveling wave solutions were established. Notice that the Keller-Segel system in fixed domains appears in various chemotaxis models and it has been extensively studied in mathematical literature (see, e.g., the review paper [4], also see [8] for traveling waves in the 1D flux-limited Keller-Segel model).

Traveling wave solutions were also addressed in other 1D and 2D free boundary problems of cell motility, e.g. [10], [21]. Besides, we mention closely related free boundary problems in tumor growth models. However, in these models the area of domain undergoes significant changes and no persistent motion was established (see, e.g., [14], [23], and [19]).

While in the model [2] the kinematic condition on the free boundary contains its curvature, in the present work we assume continuity of the flow at the cell edge following the 1D model introduced in [26]. Still a term proportional to the curvature appears in the force balance on the boundary since we adapt the Young-Laplace equation for the pressure. This provides the same regularizing effect as in the 2D Hele-Shaw model.

The main purpose of this work is to study stability questions in the onset of motion. Specifically, we consider stationary solutions and traveling wave solutions with small velocities. To show emergence of traveling waves we employ bifurcation analysis of the family of radially symmetric stationary solutions, following the idea originally proposed in [16] in the framework of a tumor growth model and followed in many subsequent works on such models, e.g., [15], [17]. While the aforementioned works deal with bifurcation from radial to non-radial stationary solutions via eigenvectors, in the present work we establish existence of traveling wave solutions bifurcating via *generalized* eigenvectors rather than eigenvectors. Similarly to

[15] we use the Crandall-Rabinowitz bifurcation theorem to justify bifurcation to a family of traveling wave solutions parametrized by their velocity V. However, the functional framework for application of this theorem significantly differs from that used for tumor growth models.

The main mathematical novelty of this work is in the study of spectral properties of the generator $\mathcal{A}(V)$ of the evolution semigroup linearized around traveling wave solutions. The spectrum of the operator $\mathcal{A}(V)$ near zero has rather interesting asymptotic behavior in the limit of small traveling wave velocities due to presence of generalized eigenvectors for multiple zero eigenvalue. Specifically, $\mathcal{A}(V)$ has zero eigenvalue with multiplicity five for $V = 0$ that splits into zero eigenvalue with multiplicity four and a (small) simple non zero eigenvalue $\lambda(V) \neq 0$ for $V \neq 0$ whose sign determines stability of traveling waves. The main result of this work is an explicit asymptotic formula (7.9) for $\lambda(V)$, which determines stability of traveling waves in terms of the total myosin mass and a special eigenvalue E describing movability (see Remark 3.1) of stationary solutions.

The outline of the paper is as follows. Section 2 is devoted to the description of the model. In Section 3 we consider the family of stationary radially symmetric solutions with constant myosin densities and study their linear stability via the Fourier analysis. The main finding of this section is in the identification of the eigenvalue $E(R)$ which determines stability of the solution with radius R. In Section 4 we show that at the critical radius $R = R_0$ such that $E(R_0) = 0$ a pitchfork bifurcation occurs. A family of traveling wave solution emerges, these solutions are parametrized by their velocities V. Then, throughout Sections 5–7 we study the asymptotic behavior of the spectrum of the operator $\mathcal{A}(V)$ (obtained by the linearization around the traveling wave solution) in the limit of small velocities V. We restrict the analysis to perturbations possessing axial symmetry of the traveling wave, since the eigenvector corresponding to the eigenvalue $\lambda(V)$ (which determines stability) has this symmetry. Notice that in the space of perturbations with this axial symmetry the multiplicity of the zero eigenvalue equals two. In Section 5 we construct asymptotic expansions that lead to the formula (7.9) for $\lambda(V)$ for small $V \neq 0$. This construction requires a *four term* ansatz for the eigenvector which has an interesting structure: the first two terms are proportional to the eigenvector and the generalized eigenvector of $\mathcal{A}(V)$ for the zero eigenvalue (see pairs m_i, ρ_i, $i = 1, 2$ in (5.9)–(5.10)). Moreover, a solvability condition for the fifth term yields the formula (7.9) for $\lambda(V)$. This formula, despite the technical derivation, is remarkably simple. The principal term in the asymptotic expansion of $\lambda(V)$ is given in terms of two key quantities: the derivative of the eigenvalue $E(R)$ (at the bifurcation point) with respect to the total myosin mass and the derivative $M'(V)$ of the total myosin mass $M(V)$ of the traveling wave solution with respect to the velocity V (see explanation after the main Theorem 8.3). However, its justification is rather involved and requires passing to the invariant subspace complementary to the generalized eigenspace for the zero eigenvalue. To this end in Section 6 we study the generalized eigenvector (corresponding to the zero eigenvalue) of the adjoint operator $\mathcal{A}^*(V)$. It exhibits a singular behavior (it blows up) as $V \to 0$ (actually, after a proper normalization, it converges to an eigenvector of $\mathcal{A}^*(0)$). Section 7 contains the proofs of results obtained in Sections 5 and 6. The main ingredient of these proofs is the demonstration of resolvent convergence and convergence of spectral projectors. An important technical step there is Lemma 7.5 that deals with the resolvent operators and establishes regularity of solutions of the corresponding boundary value problems. Finally, in Section 8 we extend the results for symmetric perturbations to general perturbations of the traveling wave solutions. The key observation there is that infinitesimal shifts of traveling wave solutions in the direction orthogonal to motion and their infinitesimal rotations yield a complementary pair of eigenvector and generalized eigenvector corresponding to the zero eigenvalue.

2. The model

We consider a 2D model of motion of a cell on a flat substrate. The cell occupies a domain $\Omega(t)$ with free boundary. The flow of the acto-myosin network inside the domain $\Omega(t)$ is described by the velocity field u. In the adhesion-dominated regime (overdamped flow, cf. [7], [6]) u obeys Darcy's law

$$-\nabla p = \zeta u \quad \text{in } \Omega(t), \tag{2.1}$$

where $-p$ stands for the scalar stress (p is the pressure) and ζ is the constant effective adhesion drag coefficient. We describe the acto-myosin network by a compressible fluid continuum equation, for incompressible cytoplasm fluid can be squeezed into the dorsal direction in the cell [22]. The main modeling assumption is the following constitutive law for the scalar stress $-p$

$$-p = \mu \operatorname{div} u + km - p_{\mathrm{h}} \quad \text{in } \Omega(t), \tag{2.2}$$

where $\mu \operatorname{div} u$ is the hydrodynamic stress (μ being the effective bulk viscosity of the gel), the term km is the active component of the stress which is proportional to the density $m = m(x, y, t) > 0$ of myosin motors with a constant contractility coefficient $k > 0$, p_{h} is the constant hydrostatic pressure. Throughout this work we assume that the effective bulk viscosity μ and the contractility coefficient k in (2.2) are scaled to $\mu = 1$, $k = 1$. We prescribe the following condition on the boundary

$$p + p_{\mathrm{e}} = \gamma\kappa \quad \text{on } \partial\Omega(t), \tag{2.3}$$

known as the Young-Laplace equation, where κ denotes the curvature (positive if $\Omega(t)$ is convex), $\gamma > 0$ is a constant coefficient and p_{e} is the effective elastic restoring force which describes the mechanism of approximate conservation of the area due to the membrane-cortex tension. The elastic restoring force p_{e} generalizes the one-dimensional nonlocal spring condition introduced in [26], [27], see more recent work [25] which also introduces the cell volume regulating pressure,[1] and we similarly assume the simple linear dependence of $p_{\mathrm{e}} = p_{\mathrm{e}}(|\Omega|)$ on the area[2]:

$$p_{\mathrm{e}} = k_{\mathrm{e}}(|\Omega_{\mathrm{h}}| - |\Omega|)/|\Omega_{\mathrm{h}}|, \tag{2.4}$$

[1]The authors are grateful to L. Truskinovsky for bringing [25] to their attention and helpful discussions on bifurcations during the preparation of the manuscript.

[2]An alternative way to this mean field elasticity approach (used to regularize the minimal model) could be incorporating the Kelvin-Voigt model which accounts for the elastic response at long time scales. To this end one can introduce the intracellular density ϱ, whose transport is governed, e.g., by $\partial_t \varrho + \mathrm{d}iv(\varrho u) = 0$ and modify the constitutive law (2.2) by a term $P(\varrho)$ with appropriate linear or nonlinear function P. For a discussion of different approaches of elastic regularization of the minimal model in 1D case, including also Maxwell model, we address interested reader to [28].

where k_{e} is the inverse compressibility coefficient (characterizing membrane-cortex elastic tension), $|\Omega_{\mathrm{h}}|$ is the area of the reference configuration Ω_{h} in which $p_{\mathrm{e}}=0$ (cf. vertex models [13], [1]).

The evolution of the myosin motors density is described by the advection-diffusion equation

$$\partial_t m = \Delta m - \operatorname{div}(um) \quad \text{in } \Omega(t) \tag{2.5}$$

and no flux boundary condition in the moving domain

$$\partial_\nu m = (u\cdot\nu - V_\nu)m \quad \text{on } \partial\Omega(t), \tag{2.6}$$

where ν stands for the outward pointing normal vector and V_ν is the normal velocity of the domain $\Omega(t)$. Finally, we assume continuity of velocities on the boundary

$$V_\nu = u\cdot\nu, \tag{2.7}$$

so that (2.6) becomes the homogeneous Neumann condition. Combining (2.1)–(2.7) yields a free boundary model of the cell motility investigated in this work. While there are several models of cell motility in literature (both free boundary and phase field models), in this work we perform analytical study of stability of stationary and persistently moving states in the model (2.1)–(2.7).

It is convenient to introduce the potential for the velocity field u using (2.1):

$$u = \nabla\phi = -\nabla\frac{1}{\zeta}p, \quad \phi := -\frac{1}{\zeta}(p - p_{\mathrm{h}}), \tag{2.8}$$

and rewrite problem (2.1)–(2.7) in the form

$$\Delta\phi + m = \zeta\phi \quad \text{in } \Omega(t), \tag{2.9}$$

$$\zeta\phi = p_*(|\Omega(t)|) - \gamma\kappa \quad \text{on } \partial\Omega(t), \tag{2.10}$$

$$V_\nu = \partial_\nu\phi \quad \text{on } \partial\Omega(t), \tag{2.11}$$

$$\partial_t m = \Delta m - \operatorname{div}(m\nabla\phi) \quad \text{in } \Omega(t), \tag{2.12}$$

$$\partial_\nu m = 0 \quad \text{on } \partial\Omega(t), \tag{2.13}$$

where we introduced the notation

$$p_*(|\Omega|) := p_{\mathrm{h}} + p_{\mathrm{e}}(|\Omega|) = p_{\mathrm{h}} - k_{\mathrm{e}}(|\Omega| - |\Omega_{\mathrm{h}}|)/|\Omega_{\mathrm{h}}| \tag{2.14}$$

for the sum of the hydrostatic pressure p_{h} and the effective elastic restoring force p_{e}. We consider the coefficient k_{e} to be sufficiently large so that it penalizes changes of the area. For instance, it prevents from shrinking of Ω to a point or from infinite expanding. The precise lower bound on $k_{\mathrm{e}}/|\Omega_{\mathrm{h}}|$ is given below in (3.17).

Remark 2.1. Evolution problem (2.9)–(2.13) is naturally considered in the phase space of two unknowns $m(x,y,t)$ and $\Omega(t)$, while the potential $\phi(x,y,t)$ is regarded as auxiliary unknown function determining evolution of the free boundary. Instantaneously ϕ is defined as the unique solution of the elliptic problem (2.9)–(2.10), while its normal derivative $\partial_\nu\phi$ determines normal velocity of the boundary $\partial\Omega(t)$.

Following [9] one can establish local (in time) existence of a solution of (2.9)–(2.13) and its uniqueness in appropriate Hölder spaces. Indeed, introducing $\sigma_1 := \phi - p_*(|\Omega|)/\zeta$ one rewrites (2.9)–(2.13) as a Hele-Shaw type problem

$$\Delta\sigma_1 = \mathcal{H}(\phi, m) \quad \text{in } \Omega(t), \quad \sigma_1 = -\frac{\gamma}{\zeta}\kappa \text{ and } V_\nu = \partial_\nu\sigma_1 \quad \text{on } \partial\Omega \tag{2.15}$$

with the source term $\mathcal{H}(\phi, m) = \zeta\phi - m$, where $\phi = \sigma_1 + p_*(|\Omega|)/\zeta$ and m solves (2.12)–(2.13). Then similarly to [9] the above problem can be treated with the help of the Banach fixed-point theorem. Notice also that every solution of (2.9)–(2.13) enjoys an important feature of conservation of the total mass of myosin $M = \int_{\Omega(t)} m(x, y, t)dxdy$, as follows from (2.11)–(2.13).

Remark 2.2. Observe that if the initial data have reflection symmetry with respect to the x-axis then solutions of problem (2.9)–(2.13) also have this symmetry. We adopt this symmetry assumption throughout Sections 3–7 in the spectral analysis of linearized problems and in the bifurcation analysis. Subsequently we relax this assumption in Theorem 8.3 (see Section 8) to obtain a complete characterization of linear stability of traveling wave solutions.

3. Linear stability analysis of radially symmetric stationary solutions

In the class of radially symmetric stationary solutions of problem (2.9)–(2.13) for a given radius $R > 0$ there exists the unique radial solution with constant myosin density and it is given by

$$\Omega = B_R, \quad m_0 = p_*(\pi R^2) - \gamma/R, \quad \zeta\phi_0 = p_*(\pi R^2) - \gamma/R, \tag{3.1}$$

and we assume that R is such that $p_*(\pi R^2) - \gamma/R > 0$ to have the density $m_0 > 0$.

To describe evolution of perturbations of (3.1), it is convenient to use the polar coordinate system (r, φ),

$$\Omega = \{(x = r\cos\varphi, y = r\sin\varphi); 0 \le r < R + \rho(\varphi, t)\}. \tag{3.2}$$

Then linearizing problem (2.9)–(2.13) around a radially symmetric reference stationary solution (3.1), we get the following problem

$$\Delta\phi + m = \zeta\phi \quad \text{in } B_R, \tag{3.3}$$

$$\phi = \frac{p'_*(\pi R^2)R}{\zeta}\int_{-\pi}^{\pi} \rho d\varphi + \frac{\gamma}{R^2\zeta}(\partial^2_{\varphi\varphi}\rho + \rho) \quad \text{on } \partial B_R, \tag{3.4}$$

$$\partial_t\rho = \partial_r\phi \quad \text{on } \partial B_R, \tag{3.5}$$

$$\partial_t m = \Delta m - m_0\Delta\phi \quad \text{in } B_R, \quad \partial_r m = 0 \quad \text{on } \partial B_R, \tag{3.6}$$

which can be rewritten in the operator form

$$\frac{d}{dt}U = \mathcal{A}_{\rm ss}(R)U, \tag{3.7}$$

where $U = (m, \rho)$, and $\mathcal{A}_{\rm ss}(R)$ is the following operator

$$(\mathcal{A}_{\rm ss}(R)U)_m = \Delta m - m_0\Delta\phi \quad \text{in } B_R, \quad (\mathcal{A}_{\rm ss}(R)U)_\rho = \partial_r\phi \quad \text{on } \partial B_R. \tag{3.8}$$

Here ϕ solves the time independent problem (3.3)–(3.4) for given m and ρ, and (3.8) defines an unbounded operator in $L^2(B_R) \times L^2(\partial B_R)$ whose domain is $H^2(B_R) \cap \{m; \partial_r m = 0 \text{ on } \partial B_R\} \times H^3(\partial B_R)$.

Operator $\mathcal{A}_{\rm ss}(R)$ has a compact resolvent (as one can prove following the lines of the proof of Lemma 7.5), therefore its spectrum is discrete. Thanks to the radial symmetry of the problem, the study of spectral properties of $\mathcal{A}_{\rm ss}(R)$ amounts to the Fourier analysis. Moreover we will consider only perturbations possessing the reflection symmetry with respect to the x-axis. That is we consider Fourier modes $m = \hat{m}(r)\cos n\varphi$ and $\rho = \hat{\rho}\cos n\varphi$ for integer $n \ge 0$. Notice that the operator

$\mathcal{A}_{\rm ss}(R)$ always has zero eigenvalue with multiplicity at least two and eigenvectors $(m=0, \rho=\cos\varphi)$ and $(m=2\pi R p_*'(\pi R^2)+\gamma/R^2, \rho=1)$. Indeed, $\mathcal{A}_{\rm ss}(R)$ is obtained by linearizing problem (2.9)–(2.13) around the radially symmetric stationary reference solution with radius R, while stationary solutions (3.1) and their shifts along x-axis form a smooth two parameter family of stationary solutions of the nonlinear problem (2.9)–(2.13), thus taking derivatives of these solutions with respect to the parameters yields two linearly independent eigenvectors of the linearized operator. The first of these eigenvectors represents infinitesimal shifts in the x-direction of a solution (3.1) when R is fixed, and the second one is obtained by taking derivative in R when the position (center of the disk) is fixed at the origin. Next we introduce the eigenvalue $E(R)$ describing movability of stationary solutions. It will be shown that at the critical radius when $E(R)$ crosses zero a family of traveling wave solutions emerges.

Notice that within the mode $(m,\rho)=(\hat{m}(r)\cos\varphi, \hat{\rho}\cos\varphi)$ the eigenvalue problem for $\hat{m}(r)$ decouples from $\hat{\rho}$ since (3.4) becomes the homogeneous Dirichlet condition. Thus the auxiliary function ϕ in this case does not depend on ρ and is the unique solution of

$$\Delta\phi + m = \zeta\phi \quad \text{in } B_R, \quad \phi = 0 \quad \text{on } \partial B_R. \tag{3.9}$$

The eigenvalue problem then reduces to $\lambda m = \Delta m + m_0 m - m_0\zeta\phi$ in B_R, $\partial_r m = 0$ on ∂B_R, and if $\lambda \neq 0$ then one retrieves the ρ-component of the eigenvector by setting $\rho = \partial_r\phi/\lambda$. The reduced eigenvalue problem is self-adjoint and therefore admits variational formulation. The first (maximal) eigenvalue is the solution of the minimization problem[3]

$$E(R) = -\inf\left\{ E_\zeta(m) \Big/ \int_{B_R} m^2 dxdy; m\in H^1(B_R), m=\hat{m}(r)\cos\varphi \right\}, \tag{3.10}$$
$$\text{where } E_\zeta(m) = \int_{B_R} \left(|\nabla m|^2 - m_0 m^2 + m_0\zeta|\nabla\phi|^2 + m_0\zeta^2\phi^2\right) dxdy$$

and ϕ is the unique solution of (3.9). Minimizing the Rayleigh quotient in (3.10) yields a minimizer m that satisfies $\Delta m + m_0 m - m_0\zeta\phi = E(R)m$ in B_R and $\partial_r m = 0$ on ∂B_R. As already mentioned, in the case when $E(R)\neq 0$ one obtains the ρ-component of the eigenvector by setting $\rho = \partial_r\phi|_{r=R}/E(R)$. If $E(R)=0$, then the pair $(m,0)$ is a generalized eigenvector of $\mathcal{A}_{\rm ss}(R)$ while $\mathcal{A}_{\rm ss}(R)(m,0) = (0, \partial_r\phi|_{r=R})$ is an eigenvector (corresponding to infinitesimal shifts).

Problem (3.10) admits separation of variables in polar coordinates and thus can be reduced to an eigenvalue problem for a 1D system, leading to an integro-differential equation. However, the sign of the eigenvalue $E(R)$ can be determined via the solution of simple problem (3.11) below, explicitly given in terms of a Bessel's function (see Theorem 4.1).

Remark 3.1. The Fourier mode with $(m,\rho)=(\hat{m}(r)\cos\varphi, \hat{\rho}\cos\varphi)$ is the only mode that corresponds to motion (when the geometrical center of mass of Ω changes). There are infinitely many eigenvectors within this Fourier mode. In particular, it contains the eigenvector $(0,\cos\varphi)$ (infinitesimal shifts) corresponding to the zero

[3]Technically $E(R)$, given by formula (3.23), depends also on the physical parameter $\zeta > 0$ which is considered fixed throughout the work, with the only exception occurring in the proof of Lemma 3.3 (where it is explicitly stated), and therefore omitted to shorten the notation.

eigenvalue. Then $E(R)$ is the largest of the remaining eigenvalues. That is why $E(R)$ describes movability of the stationary solutions.

Lemma 3.2. *Assume that $m_0 < \zeta$ and $E(R) = 0$, then $E(R)$ is a simple eigenvalue of the variational problem* (3.10), *and the solution $\Psi(r)$ of*

$$\frac{1}{r}(r\Psi'(r))' - \frac{1}{r^2}\Psi(r) + (m_0 - \zeta)\Psi(r) = m_0 r \quad 0 \le r < R, \quad \Psi(0) = \Psi(R) = 0 \tag{3.11}$$

satisfies the additional boundary condition

$$\Psi'(R) = 1. \tag{3.12}$$

Proof. Let m be a minimizer of (3.10). Then the function m and the solution ϕ of (3.9) are of the form $m = \hat{m}(r)\cos\varphi$, $\phi = \hat{\phi}(r)\cos\varphi$, and since $\Delta(m - m_0\phi) = 0$, we have $m = m_0(\phi - Cr\cos\varphi)$. Clearly $C \neq 0$, therefore we can assume that $C = 1$, multiplying m and ϕ by a (same) constant if necessary. Then separating variables in (3.9) leads to (3.11), i.e. $\hat{\phi} = \Psi(r)$, and since $\partial_r m = 0$ on ∂B_R we obtain (3.12). Simplicity of the eigenvalue $E(R) = 0$ follows from the uniqueness of the solution of (3.11). □

Lemma 3.3. *Assume that $m_0 < \zeta$, then $E(R) > 0$, $E(R) = 0$ or $E(R) < 0$ if and only if $\Psi'(R) > 1$, $\Psi'(R) = 1$ or $\Psi'(R) < 1$, correspondingly, where $\Psi(r)$ is the solution of* (3.11).

Proof. Assume that $\Psi'(R) \ge 1$ and consider the test function $m := m_0(\Psi(r) - r)\cos\varphi$. Observe that $\Delta(\Psi(r)\cos\varphi) + m = \zeta\Psi(r)\cos\varphi$, therefore we have, integrating by parts,

$$E(R)\int_{B_R} m^2 dxdy \ge -E_\zeta(m) = -\int_{\partial B_R} m\partial_r m ds$$
$$+ \int_{B_R} (\Delta m + m_0 m - \zeta m_0 \Psi(r)\cos\varphi) m dxdy = \pi R^2 m_0^2(\Psi'(R) - 1) \ge 0.$$

Next we prove that $E(R) \le 0$ if $\Psi'(R) \le 1$. We argue by contradiction. Assume that $E(R) > 0$ and notice that allowing the parameter ζ in (3.23) increase we have a continuous function $E(R, \zeta)$ which becomes negative for sufficiently large ζ. To prove the latter claim observe that otherwise there exists a sequence $\zeta_j \to \infty$ and $m_j = \hat{m}_j(r)\cos\varphi$ such that $\|m_j\|_{L^2(B_R)} = 1$ and $E_{\zeta_j}(m_j) \le 0$. This gives the a priori bound

$$\int_{B_R} |\nabla m_j|^2 dxdy + m_0\zeta_j \int_{B_R} \left(|\nabla\phi_j|^2 + \zeta_j\phi_j^2\right) dxdy \le m_0, \tag{3.13}$$

where $\Delta\phi_j + m_j = \zeta_j\phi_j$ in B_R, $\phi_j = 0$ on ∂B_R. Let us show that $\zeta_j\phi_j - m_j \rightharpoonup 0$ weakly in $L^2(B_R)$. Indeed, multiply the equation $\Delta\phi_j + m_j = \zeta_j\phi_j$ by a test function $v \in C_0^\infty(B_R)$ and integrate over B_R,

$$\int_{B_R} \nabla\phi_j \cdot \nabla v dxdy + \int_{B_R} (\zeta_j\phi_j - m_j) v dxdy = 0. \tag{3.14}$$

Then pass to the limit in this identity as $j \to \infty$. By (3.13) we have $\|\nabla\phi_j\|_{L^2(B_R)} < 1/\sqrt{\zeta_j}$, therefore the first term in (3.14) tends to zero and thus the weak convergence

$\zeta_j\phi_j - m_j \rightharpoonup 0$ is established. It follows from (3.13) that there exists $m^* \in H^1(B_R)$ such that, up to a subsequence, $m_j \to m^*$ strongly in $L^2(B_R)$, consequently

$$\begin{aligned}\liminf_{j\to\infty} \|\zeta_j\phi_j\|^2_{L^2(B_R)} - 1 &= \liminf_{j\to\infty} (\|\zeta_j\phi_j\|^2_{L^2(B_R)} - \|m_j\|^2_{L^2(B_R)}) \\ &= \liminf_{j\to\infty} (\|\zeta_j\phi_j - m_j\|^2_{L^2(B_R)}) \geq 0.\end{aligned}$$

Then (3.13) implies that $\limsup_{j\to\infty} \int_{B_R} |\nabla m_j|^2 dxdy = 0$, i.e. $m^* \equiv$ const. On the other hand m^* admits the representation $m^* = \hat{m}^*(r)\cos\varphi$. Therefore $m^* = 0$ that contradicts the normalization $\|m^*\|_{L^2(B_R)} = 1$.

Thus, $\min E_{\tilde{\zeta}}(m)/\int_{B_R} m^2 dxdy = 0$ for some $\tilde{\zeta} > \zeta$. Then by Lemma 3.2 the solution of

$$\frac{1}{r}(r\tilde{\Psi}'(r))' - \frac{1}{r^2}\tilde{\Psi}(r) + (m_0 - \tilde{\zeta})\tilde{\Psi}(r) = m_0 r \quad 0 \leq r < R, \quad \tilde{\Psi}(0) = \tilde{\Psi}(R) = 0 \tag{3.15}$$

satisfies

$$\tilde{\Psi}'(R) = 1. \tag{3.16}$$

But $-\frac{1}{r}(r(\tilde{\Psi}'(r) - \Psi'(r)))' + \frac{1}{r^2}(\tilde{\Psi}(r) - \Psi(r)) + (\zeta - m_0)(\tilde{\Psi}(r) - \Psi(r)) = (\zeta - \tilde{\zeta})\tilde{\Psi} > 0$ for $0 < r < R$, and $\tilde{\Psi}(0) - \Psi(0) = \tilde{\Psi}(R) - \Psi(R) = 0$. By the maximum principle $\tilde{\Psi}(r) - \Psi(r) > 0$ for $0 < r < R$, therefore $\tilde{\Psi}'(R) < \Psi'(R)$ (due to the Hopf lemma the inequality is strict), i.e. $\Psi'(R) > 1$, contradiction. Lemma 3.3 is proved. □

Remark 3.4. The condition $m_0 < \zeta$ in Lemma 3.2 and Lemma 3.3 is not optimal. It suffices to assume that $m_0 - \zeta$ is less than the first eigenvalue of $-\Delta$ in B_R with the homogeneous Dirichlet boundary condition on ∂B_R. Then a unique solution of the problem (3.11) exists and the maximum principle still holds, along with the Hopf lemma. We nevertheless keep condition $m_0 < \zeta$ to avoid unnecessary technicalities hereafter.

The following result addresses linear stability of radial stationary solutions (3.1).

Theorem 3.5. *Assume that the myosin density m_0 is bounded above by the fourth eigenvalue of the operator $-\Delta$ in B_R with the homogeneous Neumann boundary condition on ∂B_R, also assume that $p'_*(\pi R^2)$ satisfies*

$$p'_*(\pi R^2) < -(\gamma/R + 2m_0)/(2\pi R^2). \tag{3.17}$$

Then $\mathcal{A}_{\rm ss}(R)$ has zero eigenvalue with multiplicity two if $E(R) \neq 0$ or three if $E(R) = 0$ (in this case geometric multiplicity is still two), and all its eigenvalues other than zero or $E(R)$ have negative real parts.

Remark 3.6. In terms of the total myosin mass $M_{\rm ss}(R) = \pi R^2 m_0 = \pi R^2 p_*(\pi R^2) - \pi R\gamma$ of the solution (3.1) condition (3.17) rewrites as

$$M'_{\rm ss}(R) < 0. \tag{3.18}$$

This shows that (locally) stationary solutions can be reparametrized by their total myosin mass.

Theorem 3.5 underscores the role of $E(R)$ as a principal eigenvalue of $\mathcal{A}_{ss}(R)$ and provides a basis for applying the center manifold theory to problem (2.9)–(2.13). In particular, if $E(R) < 0$ then (locally) the center manifold is formed by two parameter family of radial stationary solutions (with different radii and positions), the center space (slow space) is two-dimensional, while the unstable space is null.

Using Theorem 3.5 one can establish stability of the linearized problem (3.3)–(3.6) and then transfer this result to original evolution problem (2.9)–(2.13), taking into account invariance of the problem with respect to shifts and the conservation of total myosin mass property. We do not dwell into this nonlinear stability issue in this work and refer an interested reader to, e.g., paper [3] which addresses nonlinear stability of stationary solutions in (a close) framework of the tumor growth free boundary problem.

For $E(R) > 0$ problem (3.3)–(3.6) is unstable, the same is true for $E(R) = 0$ because of linearly growing solutions.

Proof. Let λ_n be an eigenvalue corresponding to an eigenvector $m = \hat{m}_n(r)\cos n\varphi$, $\rho = \hat{\rho}_n \cos n\varphi$ with $n \geq 2$. Multiply the equation $\lambda_n m = \Delta m + m_0 m - m_0\zeta\phi$ by the complex conjugate $\overline{m}$ of m and integrate over B_R,

$$\lambda_n \int_{B_R} |m|^2 dxdy = -\int_{B_R} |\nabla m|^2 dxdy + m_0 \int_{B_R} |m|^2 dxdy - m_0\zeta \int_{B_R} \phi\overline{m} dxdy. \tag{3.19}$$

Now multiply the equation $\overline{m} = \zeta\overline{\phi} - \Delta\overline{\phi}$ by $m_0\zeta\phi$ and integrate over B_R, then we obtain the following representation for the last term in (3.19):

$$m_0\zeta \int_{B_R} \phi\overline{m} dxdy = m_0\zeta \int_{B_R} \left(|\nabla\phi|^2 + \zeta|\phi|^2\right) dxdy - m_0\zeta \int_{\partial B_R} \phi\partial_r\overline{\phi} ds. \tag{3.20}$$

Since $\partial_r\overline{\phi} = \overline{\lambda}_n\overline{\rho}$ and (by virtue of (3.4)) $\overline{\rho} = \frac{R^2\zeta}{\gamma(1-n^2)}\overline{\phi}$ on ∂B_R, equality (3.19) rewrites as

$$\begin{aligned} \lambda_n \int_{B_R} |m|^2 dxdy + \overline{\lambda}_n \frac{m_0 R^2\zeta^2}{\gamma(n^2-1)} \int_{\partial B_R} |\phi|^2 ds = \int_{B_R} \left(-|\nabla m|^2 + m_0|m|^2\right) dxdy \\ - m_0\zeta \int_{B_R} \left(|\nabla\phi|^2 + \zeta|\phi|^2\right) dxdy. \end{aligned} \tag{3.21}$$

Notice that, thanks to the assumption that m_0 is bounded by the fourth eigenvalue of $-\Delta$ in B_R with homogeneous Neumann boundary condition, we have

$$\int_{B_R} \left(|\nabla m|^2 dxdy - m_0|m|^2\right) dxdy \geq 0. \tag{3.22}$$

Therefore the right hand side of (3.21) is negative, so the real part of λ_n is also negative.

Next we consider eigenvalues whose corresponding eigenvectors have the form $m = \hat{m}(r)\cos\varphi$, $\rho = \hat{\rho}\cos\varphi$. As already mentioned, the operator $\mathcal{A}_{ss}(R)$ always has the eigenvector $(0, \cos\varphi)$ corresponding to the zero eigenvalue, while eigenvalue problem for other eigenvalues is reduced to a self-adjoint one. These eigenvalues can be arranged in nonincreasing order, $E(R) = \lambda_{1,1} \geq \lambda_{1,2} \geq \dots$ and described by the Courant minimax principle,

$$\lambda_{1,j} = -\sup_{codim(S)=j-1} \inf_{m\in S} \frac{E_\zeta(m)}{\int_{B_R} m^2 dxdy}, \tag{3.23}$$

where S is a subspace of $\left\{m \in H^1(B_R), m = \hat{m}(r)\cos\varphi\right\}$. Then we have

$$-\lambda_{1,2} > \sup_{codim(S)=1} \inf_{m\in S} \frac{|\nabla m|^2 dxdy}{\int_{B_R} m^2 dxdy} - m_0 \tag{3.24}$$

(since

$$\inf\left\{\int_{B_R}\left(|\nabla\phi|^2+\zeta\phi^2\right)dxdy;\ \phi \text{ solves (3.9)}, \|m\|_{L^2(B_R)}=1, \|m\|_{H^1(B_R)}\leq C\right\}>0$$

$\forall C>0$, the inequality in (3.24) is strict). Notice that by Proposition 3.7 the first term in the right hand side of (3.24) is greater than or equal to the fourth eigenvalue of $-\Delta$ in B_R with the homogeneous Neumann condition on ∂B_R. Thus all eigenvalues, but possibly $E(R)$, are negative and minimizers of (3.23) for $j>1$ yield m-components of eigenvectors. The same holds for $j=1$ if $E(R)\neq 0$, otherwise we obtain a generalized eigenvector $(m,0)$, $\mathcal{A}_{\rm ss}(R)(m,0)=\hat{\phi}'(R)(0,\cos\varphi)$, where $\hat{\phi}(r)=\phi/\cos\varphi$ and ϕ is the solution of (3.9).

Consider finally an eigenvalue λ_0 corresponding to a radially symmetric eigenvector. We have, on ∂B_R

$$\phi=(\gamma/R^2+2\pi R p_*'(\pi R^2))\rho/\zeta,\quad \lambda_0\rho=\partial_r\phi. \tag{3.25}$$

Multiply the equation $\lambda_0 m=\Delta m+m_0 m-m_0\zeta\phi$ by $\overline{m}-\langle\overline{m}\rangle$ and add to the equation $-\Delta\overline{\phi}+\zeta\overline{\phi}=\overline{m}$ multiplied by $m_0\zeta(\phi-\langle\phi\rangle)$, where $\langle\overline{m}\rangle$, $\langle\phi\rangle$ denote mean values of $\overline{m}$, ϕ (over B_R). Integrating the result over B_R we obtain,

$$\begin{aligned}\lambda_0\int_{B_R}|m-\langle m\rangle|^2dxdy&=-\int_{B_R}|\nabla m|^2dxdy+m_0\int_{B_R}|m-\langle m\rangle|^2dxdy\\&\quad-m_0\zeta\int_{B_R}\left(|\nabla\phi|^2+\zeta|\phi-\langle\phi\rangle|^2\right)dxdy+m_0\zeta\int_{\partial B_R}(\phi-\langle\phi\rangle)\partial_r\overline{\phi}ds.\end{aligned} \tag{3.26}$$

Assume that $\lambda_0\neq 0$. Then we can evaluate $\langle\phi\rangle$ in terms of ρ, integrating equations $\lambda_0 m=\Delta m+m_0 m-m_0\zeta\phi$ and $-\Delta\phi+\zeta\phi=m$ over B_R and eliminating $\langle m\rangle$:

$$\langle\phi\rangle=\frac{1}{\pi R^2\zeta}(1-m_0/\lambda_0)\int_{\partial B_R}\partial_r\phi ds=\frac{2}{R\zeta}(\lambda_0-m_0)\rho. \tag{3.27}$$

Now we use (3.25) and (3.27) to rewrite the last term in (3.26) as

$$\begin{aligned}m_0\zeta\int_{\partial B_R}(\phi-\langle\phi\rangle)\partial_r\overline{\phi}ds=&-4\pi m_0|\lambda_0|^2|\rho|^2\\&+2\pi m_0\overline{\lambda}_0|\rho|^2\left(\gamma/R+2m_0+2\pi R^2p_*'(\pi R^2)\right).\end{aligned} \tag{3.28}$$

Substitute (3.28) into (3.26), as the result we get

$$\begin{aligned}\lambda_0\int_{B_R}|m-\langle m\rangle|^2dxdy&+2\pi m_0\overline{\lambda}_0|\rho|^2\left(2\lambda_0-\gamma/R-2m_0-2\pi R^2p_*'(\pi R^2)\right)\\&=-\int_{B_R}|\nabla m|^2dxdy+m_0\int_{B_R}|m-\langle m\rangle|^2dxdy\\&\quad-m_0\zeta\int_{B_R}\left(|\nabla\phi|^2+\zeta|\phi-\langle\phi\rangle|^2\right)dxdy.\end{aligned} \tag{3.29}$$

Thanks to the radial symmetry of m the function $m-\langle m\rangle$ is orthogonal (with respect to the standard inner product in $L^2(B_R)$) to the first three eigenfunctions of the operator $-\Delta$ in B_R with the homogeneous Neumann boundary condition on ∂B_R. Therefore $\int_{B_R}|\nabla m|^2dxdy-m_0\int_{B_R}|m-\langle m\rangle|^2dxdy\geq 0$. Thus (3.29) implies that the real part of λ_0 is negative. To complete the proof it remains only to consider the case $\lambda_0=0$. By virtue of (3.26) the m-component of any eigenvector is constant in this case, i.e. the unique (up to multiplication by nonzero constant) eigenvector is $(m = 2\pi R p_*'(\pi R^2) + \gamma/R^2, \rho = 1)$. This eigenvector does not have any associated generalized eigenvector, otherwise integrating the equation $2\pi R p_*'(\pi R^2) + \gamma/R^2 = \Delta m - m_0 \Delta\phi$ over B_R and taking into account the boundary condition $1 = \partial_r \phi$ on ∂B_R we find that

$$0 = \int_{B_R} (2\pi R p_*'(\pi R^2) + \gamma/R^2) dxdy + m_0 \int_{\partial B_R} \partial_r \phi ds$$
$$= \pi R(2\pi R^2 p_*'(\pi R^2) + \gamma/R + 2m_0)$$

contradictory to (3.17). Theorem 3.5 is proved. □

In the proof of Theorem 3.5 we have used the following simple result.

Proposition 3.7. *The eigenfunctions corresponding to the second and the third (if counted with multiplicity) eigenvalues of $-\Delta$ in B_R with the homogeneous Neumann condition on ∂B_R have the form*

$$v_2(r, \varphi) = \hat{v}_2(r) \cos(\varphi + \varphi_0). \tag{3.30}$$

Proof. It suffices to show that $v_2(r, \varphi)$ is not radially symmetric. Let λ_2 denote the corresponding eigenvalue. Assume by contradiction that $v_2(r, \varphi) = \hat{v}_2(r)$, then by straightforward differentiation of the eigenvalue equation one checks that $\hat{v}_2'(r) \cos\varphi$ is an eigenfunction of the equation $-\Delta(\hat{v}_2'(r)\cos\varphi) = \lambda_2 \hat{v}_2'(r) \cos\varphi$ in B_R with the homogeneous Dirichlet condition on ∂B_R. Since each eigenvalue of $-\Delta$ in B_R with the homogeneous Dirichlet condition on ∂B_R is strictly greater than that of $-\Delta$ in B_R with the homogeneous Neumann condition on ∂B_R, λ_2 must be the first eigenvalue of the former operator. However the first eigenfunction is sign preserving, a contradiction. □

4. Bifurcation of traveling waves from the family of stationary solutions

In this section we prove that at the critical radius $R = R_0$ such that $E(R_0) = 0$ radially symmetric stationary solutions (3.1) bifurcate to a family of traveling wave solutions. Notice that for R in a neighborhood of R_0 and at $R = R_0$ the geometric multiplicity of the zero eigenvalue of $\mathcal{A}_{ss}(R)$ is two, and the bifurcation takes place via the generalized eigenvector appearing at R_0.

Consider the ansatz of a traveling wave solution moving with velocity $V > 0$ in x-direction

$$m = m(x - Vt, y),\ \phi = \phi(x - Vt, y),\ \Omega(t) = \Omega + (Vt, 0) \tag{4.1}$$

and substitute it to (2.9)–(2.13) to derive stationary free boundary problem for the unknowns ϕ, Ω and $M > 0$,

$$\Delta\phi + \frac{M}{\int_\Omega e^{\phi - Vx} dxdy} e^{\phi - Vx} = \zeta\phi \quad \text{in } \Omega, \quad \partial_\nu(\phi - Vx) = 0 \quad \text{on } \partial\Omega, \tag{4.2}$$

$$\zeta\phi = p_*(|\Omega|) - \gamma\kappa \quad \text{on } \partial\Omega. \tag{4.3}$$

Indeed, (2.12) yields $-V\partial_x m = \Delta m - \mathrm{div}(m\nabla\phi)$ in Ω while $\partial_\nu \phi = V\nu_x$ on $\partial\Omega$, then, taking into account the boundary condition $\partial_\nu m = 0$, we see that

$$m = \Lambda e^{\phi - Vx}, \quad \text{where } \Lambda := \frac{M}{\int_\Omega e^{\phi - Vx} dxdy}. \tag{4.4}$$

Here unknown constant $M > 0$ represents the total mass of myosin, $M = \int_\Omega m dxdy$.

For radially symmetric stationary solutions (3.1) the total myosin mass $M_{ss}(R)$ is given by

$$M_{\mathrm{ss}}(R) = \pi R^2 p_*(\pi R^2) - \pi\gamma R, \tag{4.5}$$

in terms of the radius R. It is convenient to keep the parameter R in the bifurcation analysis presented below, although the domain Ω is no longer a disk. Then dependence on R will appear implicitly in the parametrization of the boundary $\partial\Omega$, as the radius of the reference disk, and explicitly in $M := M_{ss}(R)$ given by (4.5). We also use the notation $m_{\mathrm{ss}}(R)$ for the densities of stationary solutions (3.1),

$$m_{\mathrm{ss}}(R) := M_{\mathrm{ss}}(R)/(\pi R^2) = p_*(\pi R^2) - \gamma/R,$$

reserving m_0 for the density at $R = R_0$.

We rely on Theorem 1.7 from [11] to get the following result on bifurcation of traveling wave solutions.

Theorem 4.1. *Let R_0 be the critical radius, i.e. $E(R_0) = 0$. Assume also that $m_0 < \zeta$,*

$$p_*'(\pi R_0^2) < -(\gamma/R_0 + 2m_0)/(2\pi R_0^2), \tag{4.6}$$

and

$$F'(R_0) \neq 0, \tag{4.7}$$

where

$$F(R) := \frac{R^3}{\Theta(R)}\left(\frac{\zeta I_1\left(\sqrt{\Theta(R)}\right)}{\sqrt{\Theta(R)}I_1'\left(\sqrt{\Theta(R)}\right)} - m_{\mathrm{ss}}(R)\right), \quad \Theta(R) = R^2(\zeta - m_{\mathrm{ss}}(R)), \tag{4.8}$$

I_1 is the 1st modified Bessel function of the first kind.

Then stationary solutions (3.1) *at $R = R_0$ bifurcate to a family of traveling wave solutions, i.e. solutions of* (4.2)–(4.3) *parametrized by the velocity V. Moreover for small V, $|V| \leq \overline{V}$ (for some $\overline{V} > 0$), these solutions (both the function ϕ and the domain Ω) are smooth and depend smoothly on the parameter V.*

Proof. As above we consider Ω in polar coordinates, $\Omega = \{0 \leq r < R + \rho(\varphi)\}$. Since $\zeta > m_{\mathrm{ss}}(R_0)$, for sufficiently small ρ, V and R sufficiently close to R_0 there is a unique solution $\Phi = \Phi(x, y; V, R, \rho)$ of (4.2). It depends on three parameters: the scalar parameter V (the prescribed velocity), the radius R via the parametrization of the domain and

$$M := M_{\mathrm{ss}}(R), \text{ where } M_{\mathrm{ss}}(R) \text{ is given by (4.5)},$$

and the functional parameter ρ that describes the shape of the domain Ω or, more precisely, its deviation from the disk B_R. As above we assume the symmetry of the domain with respect to the x-axis and therefore its shape is described by an even function ρ.

The condition (4.3) on the unknown boundary, described by $\rho(\varphi)$, rewrites as

$$p_*(|\Omega|) - \gamma\frac{(R+\rho)(R+\rho-\rho'') + 2(\rho')^2}{((R+\rho)^2 + (\rho')^2)^{3/2}} = \zeta\Phi((R+\rho)\cos\varphi, (R+\rho)\sin\varphi; V, R, \rho). \tag{4.9}$$

To get rid of infinitesimal shifts we will require that

$$\int_{-\pi}^{\pi} \rho(\varphi) \cos\varphi d\varphi = 0. \tag{4.10}$$

Then introducing the function $\mathcal{F}$ which maps from $X = C^2_{\#}(-\pi,\pi) \times \mathbb{R} \times \mathbb{R}$ to $Y = C_{\#}(-\pi,\pi) \times \mathbb{R}$ (where the subscript # means even periodic functions):

$$\mathcal{F}((\rho,V),R) := \left(\gamma \frac{(R+\rho)^2 + 2(\rho')^2 - \rho''(R+\rho)}{\zeta((R+\rho)^2+(\rho')^2)^{3/2}} + \Phi - \frac{p_*(|\Omega|)}{\zeta}, \int_{-\pi}^{\pi} \rho\cos\varphi d\varphi\right), \tag{4.11}$$

we rewrite problem (4.2)–(4.3) in the form

$$\mathcal{F}((\rho,V),R) = 0. \tag{4.12}$$

Next we apply the Crandall-Rabinowitz bifurcation theorem [11] (Theorem 1.7), which guarantees bifurcation of new smooth branch of solutions provided that

(i) $\mathcal{F}(0,R) = 0$ for all R in a neighborhood of R_0;
(ii) there exist continuous $\partial_{(\rho,V)}\mathcal{F}$, $\partial_R\mathcal{F}$, and $\partial^2_{(\rho,V),R}\mathcal{F}$ in a neighborhood of $(\rho,V) = 0$, $R = R_0$;
(iii) the null space $\mathrm{Null}(\partial_{(\rho,V)}\mathcal{F})$ at $(\rho,V) = 0$, $R = R_0$ has dimension one and $\mathrm{Range}(\partial_{(\rho,V)}\mathcal{F})$ at $(\rho,V) = 0$, $R = R_0$ has co-dimension one;
(iv) $(\partial^2_{(\rho,V),R}\mathcal{F})(\rho,V) \notin \mathrm{Range}(\partial_{(\rho,V)}\mathcal{F})$ at $(\rho,V) = 0$, $R = R_0$ for all $(\rho,V) \in \mathrm{Null}(\partial_{(\rho,V)}\mathcal{F})$.

It is easy to see that condition (i) is satisfied, and condition (ii) can be verified as in [5]. To verify (iii) we begin with calculating $\mathcal{L} := \partial_{(\rho,V)}\mathcal{F}$ at $(\rho,V) = 0$. Linearizing (4.11) around $(\rho,V) = 0$ we get

$$\begin{aligned}\mathcal{L} : (\rho,V) \mapsto \Big(&-\frac{\gamma}{R^2\zeta}(\rho''+\rho) + V\partial_V\Phi(R\cos\varphi, R\sin\varphi; 0, R, 0) \\ &+ \langle\partial_\rho\Phi,\rho\rangle\big|_{(\rho,V)=0} - \frac{p'_*(\pi R^2)}{\zeta}\int_{-\pi}^{\pi} R\rho d\varphi, \int_{-\pi}^{\pi}\rho\cos\varphi d\varphi\Big),\end{aligned} \tag{4.13}$$

where $\langle\partial_\rho\Phi,\rho\rangle\big|_{(\rho,V)=0}$ denotes the Gateaux derivative of Φ at $(\rho,V) = 0$, and $\partial_V\Phi(x,y;0,R,0) =: \Phi^0_V(x,y)$ is the unique solution of the problem

$$\Delta\Phi^0_V + m_{\mathrm{ss}}(R)(\Phi^0_V - x) = \zeta\Phi^0_V \quad \text{in } B_R, \quad \partial_\nu\Phi^0_V = \nu_x \quad \text{on } \partial B_R, \tag{4.14}$$

the latter problem being obtained by taking derivative with respect to V in (4.2) (when $\Omega = B_R$) at $V = 0$. To calculate $\langle\partial_\rho\Phi,\rho\rangle\big|_{(\rho,V)=0}$ observe that for $V = 0$ the solution of (4.2) is given by $\phi = M_{\mathrm{ss}}(R)/(\zeta|\Omega|)$, therefore

$$\langle\partial_\rho\Phi,\rho\rangle\big|_{(\rho,V)=0} = -\frac{1}{\zeta\pi R} m_{ss}(R)\int_{-\pi}^{\pi}\rho d\varphi.$$

Notice that the solution Φ^0_V of (4.14) can be found in polar coordinates via separation of variables $\Phi^0_V = \hat{\Phi}^0_V(r,R)\cos\varphi$, this yields the following problem for $\hat{\Phi}^0_V(r,R)$:

$$\begin{aligned}&\frac{1}{r}\partial_r\left(r\partial_r\hat{\Phi}^0_V\right) - \frac{1}{r^2}\hat{\Phi}^0_V + (m_{ss}(R)-\zeta)\hat{\Phi}^0_V = m_{ss}(R)r \quad 0 \le r < R,\\ &\hat{\Phi}^0_V(0,R) = 0, \quad \partial_r\hat{\Phi}^0_V(R,R) = 1.\end{aligned} \tag{4.15}$$

The operator $\mathcal{L}$ has a bounded inverse when $\hat{\Phi}_V^0(R,R)\neq 0$ and R is sufficiently close to R_0, as can be verified by Fourier analysis. Indeed, this operator[4] has the eigenvalue $-\frac{1}{\zeta R}\left(\gamma/R+2m_{ss}(R)+2\pi R^2 p_*'(\pi R^2)\right)$ which is strictly positive by virtue of the assumption (4.6), the corresponding eigenvector is $(\rho=1, V=0)$; $\mathcal{L}$ has a pair of (either real or imaginary) eigenvalues $\pm\sqrt{\pi\hat{\Phi}_V^0(R,R)}$ whose corresponding eigenvectors form the subspace $span\{(\cos\varphi,0),(0,1)\}$; also $\mathcal{L}$ has eigenvalues $\frac{\gamma}{R^2\zeta}(n^2-1)$, $2\leq n\in\mathbb{Z}_+$ whose corresponding eigenvectors are $(\cos n\varphi, 0)$. In the case $\hat{\Phi}_V^0(R,R)=0$, in particular for $R=R_0$ (by Lemma 3.2 $\hat{\Phi}_V^0(R,R)=0$ when $R=R_0$) the null space of $\mathcal{L}$ is one-dimensional (it is $span\{(\rho=0,V=1)\}$) and its range consists of all the pairs $(f,C)\in C_\#(-\pi,\pi)\times\mathbb{R}$ such that $\int_{-\pi}^{\pi}f(\varphi)\cos\varphi d\varphi=0$. Thus, condition (iii) is satisfied.

It remains to verify the transversality condition (iv). We check if $\partial_R\mathcal{L}(0,1)\big|_{R=R_0}$ does not belong to the range of the operator $\mathcal{L}$, where

(4.16)
$$\partial_R\mathcal{L}\big|_{R=R_0}\colon(\rho,V)\mapsto\left(\frac{2\gamma}{R_0^3\zeta}(\rho''+\rho)+V\frac{d}{dR}\hat{\Phi}_V^0(R,R)\Big|_{R=R_0}\cos\varphi+Z\int_{-\pi}^{\pi}\rho d\varphi, 0\right)$$

with some constant $Z=Z(R)$. Since the range of $\mathcal{L}$ (described above) is all (f,C) such that $\int_{-\pi}^{\pi}f(\varphi)\cos\varphi d\varphi=0$, we must have a nonzero coefficient in front of $\cos\varphi$ in (4.16) to satisfy condition (iv). Thus this (transversality) condition can be equivalently restated as

$$\frac{d}{dR}\hat{\Phi}_V^0(R,R)\Big|_{R=R_0}\neq 0. \tag{4.17}$$

In order to check (4.17) introduce $\psi(r,R):=\hat{\Phi}_V^0(Rr,R)$, this change of variable reduces (4.15) to the following problem:

$$\begin{aligned}&\frac{1}{r}\partial_r\left(r\partial_r\psi\right)-\frac{1}{r^2}\psi+R^2(m_{ss}(R)-\zeta)\psi=R^3 m_{ss}(R)r \quad 0\leq r<1,\\ &\psi(0,R)=0,\quad \partial_r\psi(r,R)=R.\end{aligned}$$

The solution of this problem is given by

$$\psi(r,R)=\frac{R^3}{\Theta(R)}\left(\frac{\zeta I_1\left(\sqrt{\Theta(R)}r\right)}{\sqrt{\Theta(R)}I_1'\left(\sqrt{\Theta(R)}\right)}-m_{ss}(R)r\right),\quad \Theta(R)=R^2(\zeta-m_{ss}(R)),$$

so that condition (4.17) writes as (4.7). □

Remark 4.2. By virtue of Lemma 3.3, the necessary bifurcation condition $E(R_0)=0$ is equivalent to the condition (3.12) (with $R=R_0$), which, in turn, is equivalent to the condition $\hat{\Phi}_V^0(R_0,R_0)=0$ for the solution $\hat{\Phi}_V^0(r,R_0)$ of (4.15). Thus we have $E(R_0)=0 \Leftrightarrow F(R_0)=0$, i.e. both the necessary bifurcation condition and the

[4] More precisely, a realization of $\mathcal{L}$ as an operator acting in the same space, e.g. $H^2_\#(-\pi,\pi)\times\mathbb{R}$.

transversality condition write in terms of the function F (given by (4.8)) as follows

$$F(R_0) = 0, \; F'(R_0) \neq 0. \tag{4.18}$$

Moreover, we show below, see (4.22), that $F'(R_0) \neq 0$ iff $E'(R_0) \neq 0$.

Remark 4.3. Let $\Phi = \Phi(x, y, V)$, $\Omega(V) = \{(r\cos\varphi, \sin\varphi); 0 \leq r < R_0 + \rho_{\rm tw}(\varphi, V)\}$ and $M(V)$ be solutions of (4.2)–(4.3), given via the construction in the proof of Theorem 4.1. Then, by Theorem 1.18 in [11], the solutions depend smoothly on the parameter V and the first term in the asymptotic expansion of $\rho_{\rm tw}$ is of order V^2, i.e. $\|\rho_{\rm tw}\|_{C^2((-\pi,\pi])} \leq CV^2$, also $M'(0) = \Lambda'(0) = 0$, so that $\Lambda(V) = \Lambda(0) + O(V^2)$, where

$$\Lambda(V) := \frac{M(V)}{\int_{\Omega(V)} e^{\Phi(x,y,V) - Vx} dxdy}, \quad \Lambda(0) = m_0 e^{-m_0/\zeta}.$$

Combining this with elliptic estimates one can improve bounds for $\rho_{\rm tw}$ to

$$\|\rho_{\rm tw}\|_{C^j((-\pi,\pi])} \leq CV^2 \quad \forall j \in \mathbb{Z}_+ \tag{4.19}$$

with C depending only on j, and derive the following expansion for Φ,

$$\Phi(x, y, V) = m_0/\zeta + V\Phi_V^0(x, y) + V^2\tilde{\Phi}(x, y, V), \tag{4.20}$$

where Φ_V^0 is the unique solution of (4.14), $\Phi_V^0 = \hat{\Phi}_V^0(r, R_0)\cos\varphi$, while functions $\tilde{\Phi}$ and their derivatives with respect to the parameter V are uniformly (in V) bounded in $C^j(\overline{\Omega(V)})$ $\forall j \in \mathbb{Z}_+$. Note that Φ_V^0 extends as the solution of $\Delta\Phi_V^0 + m_0(\Phi_V^0 - x) = \zeta\Phi_V^0$ to the entire space $\mathbb{R}^2$, being the product of the solution $\hat{\Phi}_V^0(r, R_0)$ of (4.15) and $\cos\varphi$.

The following technical lemma provides new formulas for $F'(R_0)$ and $E'(R_0)$ important in the subsequent analysis. These formulas show, in particular, that $F'(R_0) = 0$ iff $E'(R_0) = 0$.

Lemma 4.4. *Assume that $m_0 < \zeta$ and $E(R_0) = 0$, then*

$$F'(R_0) = \frac{1}{\zeta}(\zeta + m_0 - (m_0R_0)^2) - \frac{\gamma/R_0^3 + 2\pi p'_*(\pi R_0^2)}{\pi\zeta} \int_{B_{R_0}} |\nabla(\Phi_V^0 - x)|^2 dxdy. \tag{4.21}$$

Moreover,

$$E'(R_0) = -\frac{R_0\pi\zeta F'(R_0)}{m_0 \int_{B_{R_0}} (\Phi_V^0 - x)^2 dxdy}, \tag{4.22}$$

where Φ_V^0 is the solution of (4.14) *with $R = R_0$.*

Proof. In polar coordinates function Φ_V^0 can be represented as $\Phi_V^0 = \hat{\Phi}_V^0(r,R)\cos\varphi$ with $\hat{\Phi}_V^0(r,R)$ solving (4.15). Taking derivative in (4.15) with respect to the parameter R we obtain that $\partial_R \hat{\Phi}_V^0(r,R)\big|_{R=R_0} =: \hat{\Phi}_{V,R}^0(r)$ satisfies the equation

$$\frac{1}{r}\partial_r\left(r\partial_r\hat{\Phi}_{V,R}^0\right)-\frac{1}{r^2}\hat{\Phi}_{V,R}^0+(m_0-\zeta)\hat{\Phi}_{V,R}^0=-m_{\mathrm{ss}}'(R_0)(\hat{\Phi}_V^0-r)\quad 0\le r<R_0, \tag{4.23}$$

with boundary conditions

$$\hat{\Phi}_{V,R}^0(0)=0,\quad \partial_r\hat{\Phi}_{V,R}^0(R_0)=-\partial_{rr}^2\hat{\Phi}_V^0(R_0,R_0)=1/R_0-m_0R_0. \tag{4.24}$$

Multiply (4.23) by the function $-r(\zeta-m_0)\hat{\Phi}_V^0(r,R_0)-m_0r^2$ and integrate to get, using (4.15),

$$\begin{aligned} R_0\left(m_0(m_0R_0^2-1)+\zeta\hat{\Phi}_{V,R}^0(R_0)\right)=&\zeta m_{\mathrm{ss}}'(R_0)\int_0^R\left(\hat{\Phi}_V^0-r\right)\hat{\Phi}_V^0 r dr\\ &-m_0m_{\mathrm{ss}}'(R_0)\int_0^{R_0}\left(\hat{\Phi}_V^0-r\right)^2 r dr. \end{aligned}\tag{4.25}$$

Then observe that $\hat{\Phi}_V^0(r,R)-r$ satisfies

$$\frac{1}{r}\partial_r\left(r\partial_r\left(\hat{\Phi}_V^0-r\right)\right)-\frac{1}{r^2}(\hat{\Phi}_V^0-r)=-m_0(\hat{\Phi}_V^0-r)+\zeta\hat{\Phi}_V^0;$$

multiply this latter equation by $-m_{\mathrm{ss}}'(R_0)(\hat{\Phi}_V^0-r)r$, integrate and add to (4.25). As a result we obtain

$$\begin{aligned} R_0\zeta(\hat{\Phi}_{V,R}^0(R_0)+1)&=R_0\zeta-m_0R_0(m_0R_0^2-1)\\ &\quad-m_{\mathrm{ss}}'(R_0)\int_0^{R_0}\left(\left(\partial_r\hat{\Phi}_V^0-1\right)^2+\frac{1}{r^2}\left(\hat{\Phi}_V^0-r\right)^2\right)rdr\\ &=R_0\left(\zeta+m_0-(m_0R_0)^2\right)-\frac{\gamma/R_0^2+2\pi R_0p_*'(\pi R_0^2)}{\pi}\int_{B_{R_0}}|\nabla(\Phi_V^0-x)|^2dxdy. \end{aligned}$$

Since $\frac{d}{dR}\hat{\Phi}_V^0(R,R)\big|_{R=R_0}=\hat{\Phi}_{V,R}^0(R_0)+\partial_r\hat{\Phi}_V^0(R_0,R_0)=\hat{\Phi}_{V,R}^0(R_0)+1$, the left hand side of the above relation is equal to $R\zeta F'(R)$. Thus (4.21) is proved.

To calculate the derivative of $E(R)$ at $R=R_0$, notice that since $E(R_0)=0$ is a simple (see Lemma 3.2) eigenvalue of the problem (3.10), one can choose a smooth family of eigenfunctions $m(x,y,R)=\hat{m}(r,R)\cos\varphi$ such that for R in a neighborhood of R_0 it holds

$$E(R)m=\Delta m+m_{\mathrm{ss}}(R)m-\zeta m_{\mathrm{ss}}(R)\phi\quad\text{in } B_R,\quad \partial_r m=0\quad\text{on }\partial B_R, \tag{4.26}$$

where $\phi=\phi(x,y,R)$ is the unique solution of problem (3.9), and $m(x,y,R_0)=m_0(\Phi_V^0-x)$. Differentiating (4.26) in R at $R=R_0$ we find that $\partial_R m(x,y,R)\big|_{R=R_0}$ $=: \hat{m}_R(r)\cos\varphi$ satisfies

$$E'(R_0)m=m_{\mathrm{ss}}'(R_0)m-\zeta m_{\mathrm{ss}}'(R_0)\phi+(\Delta+m_0)(\hat{m}_R(r)\cos\varphi)-\zeta m_0\phi_R\quad\text{in } B_{R_0}, \tag{4.27}$$

where $m=m_0(\Phi_V^0-x)$, $\phi=\phi(x,y,R_0)=\Phi_V^0$, $\phi_R=\partial_R\phi(x,y,R)\big|_{R=R_0}$, and

$$\partial_r\hat{m}_R(R_0)=-\partial_{rr}^2\hat{m}(R_0,R_0)=-m_0\partial_{rr}^2\hat{\Phi}_V^0=\frac{m_0}{R_0}\partial_r\hat{\Phi}_V^0-m_0^2R_0=\frac{m_0}{R_0}-m_0^2R_0. \tag{4.28}$$

Now multiply (4.27) by $\Phi_V^0 - x$ and integrate over B_{R_0}:

$$
\begin{aligned}
E'(R_0)m_0 \int_{B_{R_0}} (\Phi_V^0 - x)^2 dxdy &= -\zeta m_0 \int_{B_{R_0}} (\Phi_V^0 - x)\phi_R dxdy \\
&- \int_{\partial B_{R_0}} \partial_r \hat{m}_R(R_0)\frac{x^2}{R_0} ds + \int_{B_{R_0}} \left(\Delta\Phi_V^0 + m_0(\Phi_V^0 - x)\right)\hat{m}_R(r)\frac{x}{r} dxdy \\
&+ m'_{\mathrm{ss}}(R_0)\int_{B_{R_0}} \left(m_0(\Phi_V^0 - x) - \zeta\Phi_V^0\right)(\Phi_V^0 - x)dxdy.
\end{aligned}
\tag{4.29}
$$

Since $\Delta\Phi_V^0 + m_0(\Phi_V^0 - x) = \zeta\Phi_V^0$ in B_{R_0} and $\partial_r(\Phi_V^0 - x) = 0$ on ∂B_{R_0}, the last line in (4.29) rewrites as $m'_{\mathrm{ss}}(R_0)\int_{B_{R_0}} |\nabla(\Phi_V^0 - x)|^2 dxdy$, while the second term in the second line can be written as $\zeta\int_{B_{R_0}} \Phi_V^0(-\Delta\phi_R + \zeta\phi_R)dxdy$, where we have used the equation $\Delta\phi_R + \hat{m}_R(r)\cos\varphi = \zeta\phi_R$ in B_{R_0}. Then integrating by parts,

$$
\int_{B_{R_0}} \Phi_V^0(-\Delta\phi_R + \zeta\phi_R)dxdy = \int_{\partial B_{R_0}} \phi_R \frac{x}{R_0} ds - \int_{B_{R_0}} \phi_R(-\Delta\Phi_V^0 + \zeta\Phi_V^0)dxdy,
$$

we simplify (4.29) to

$$
\begin{aligned}
E'(R_0)m_0 \int_{B_{R_0}} (\Phi_V^0 - x)^2 dxdy =& m'_{\mathrm{ss}}(R_0)\int_{B_{R_0}} |\nabla(\Phi_V^0 - x)|^2 dxdy \\
&+ \int_{\partial B_{R_0}} (\zeta\phi_R x - \partial_r\hat{m}_R(R_0)x^2)/R_0 ds.
\end{aligned}
\tag{4.30}
$$

Similarly to (4.28) one can calculate that $\phi_R = -\partial_r\Phi_V^0 = -x/R_0$ on ∂B_{R_0}. Thus the second term in the right hand side of (4.30) is equal to $-\pi R_0\left(\zeta + m_0 - (m_0R_0)^2\right)$, and calculating $m'_{\mathrm{ss}}(R_0) = \gamma/R_0^2 + 2\pi R_0 p'_*(\pi R_0^2)$ completes the proof of Lemma 4.4. □

5. Asymptotic expansions of eigenvectors of the problem linearized around traveling wave solutions with small velocities

Let $R = R_0$ be the critical radius, i.e. $E(R) = 0$. By Theorem 4.1 there exist a family of traveling wave solutions emanating from the radially symmetric stationary solution (3.1) with the radius R. They are parametrized by their velocities V, and hereafter we consider for small $V \neq 0$ the linear evolution problem obtained via linearization of (2.9)–(2.13) around the traveling wave solution with velocity V. More precisely, we are interested in stability of this problem and therefore study spectral properties of the generator $\mathcal{A}(V)$ (given by (5.1)–(5.5)) of the corresponding semigroup. In this section we construct asymptotic expansions of an eigenvector corresponding to a small eigenvalue $\lambda(V)$ whose sign determines stability of the traveling wave solution. These expansions will be justified in Section 7. Throughout this section, and Sections 6 and 7, we assume that conditions of Theorem 4.1 are satisfied.

It is convenient to pass from the polar coordinates to the parametrization of domains via the signed distance ρ from the reference domain $\Omega(V)$. More precisely, given a solution $\phi = \Phi(x, y, V)$, $\Omega = \Omega(V)$ of problem (4.2)-(4.3), we consider problem (2.9)–(2.13) in the frame moving with constant velocity V in x-direction so that the pair $(\Lambda e^{\Phi(x,y,V)-Vx}, \Omega(V))$ represents a stationary solution. We describe perturbations of $\Omega(V)$ by the function ρ such that the boundary of the perturbed domain Ω is given by $\partial\Omega = \{(x(s), y(s)) + \rho(s,t)\nu(s);\ (x(s), y(s)) \in \partial\Omega(V)\}$, where s is the arc length parametrization of $\partial\Omega(V)$ and $\nu(s)$ denotes the outward pointing unit normal to $\partial\Omega(V)$. Perturbations of the myosin density $m = \Lambda e^{\Phi(x,y,V)-Vx}$ and auxiliary function $\phi = \Phi(x, y, V)$ are described, with a slight abuse of notation, by functions $m(x, y, t)$ and $\phi(x, y, t)$. Then the linearized problem writes as, see Appendix A,

$$\Delta\phi + m = \zeta\phi \quad \text{in } \Omega(V), \tag{5.1}$$

$$\zeta(\phi + V\nu_x\rho) = p'_*(|\Omega(V)|)\int_{\partial\Omega(V)} \rho(s)ds + \gamma(\rho'' + \kappa^2\rho) \quad \text{on } \partial\Omega(V), \tag{5.2}$$

$$\partial_t\rho = (\mathcal{A}(V)(m,\rho))_\rho := \frac{\partial\phi}{\partial\nu} + \frac{\partial^2\Phi}{\partial\nu^2}\rho - \left(\frac{\partial\Phi}{\partial\tau} + V\nu_y\right)\rho' \quad \text{on } \partial\Omega(V), \tag{5.3}$$

(5.4)
$$\partial_t m = (\mathcal{A}(V)(m,\rho)))_m := \Delta m + V\partial_x m - \operatorname{div}\left(\Lambda e^{\Phi-Vx}\nabla\phi + m\nabla\Phi\right) \quad \text{in } \Omega(V),$$

$$\partial_\nu m + \Lambda e^{\Phi-Vx}\left(\frac{\partial^2\Phi}{\partial\nu^2}\rho - \left(\frac{\partial\Phi}{\partial\tau} + V\nu_y\right)\rho'\right) = 0 \quad \text{on } \partial\Omega(V). \tag{5.5}$$

Here and in what follows ρ', ρ'' denote derivatives of ρ with respect to the arc length s, κ is the curvature of $\partial\Omega(V)$, and $\partial/\partial\tau$ denotes the tangential derivative on $\partial\Omega(V)$. The linearized operator $\mathcal{A}(V)$ appearing in (5.1)–(5.5) is well defined on smooth $m \in L^2(\Omega(V))$, $\rho \in L^2(\partial\Omega(V))$ such that (5.5) holds. It can be extended to the closed operator in $L^2(\Omega(V)) \times L^2(\partial\Omega(V))$ whose domain is the set of pairs (m, ρ) from $H^2(\Omega(V)) \times H^3(\partial\Omega(V))$ satisfying (5.5).

Since traveling wave solutions bifurcate from radial stationary solutions the spectrum of the operator $\mathcal{A}(V)$ for small V is close to the spectrum of the operator $\mathcal{A}(0) = \mathcal{A}_{ss}(R)$ (this fact will be proved in Theorem 7.6). The latter operator has zero eigenvalue with multiplicity at least three, in fact the multiplicity is exactly equal to three as will be shown in Section 6, Lemma 6.1. Therefore in order to study stability of traveling wave solutions it is crucial to investigate what happens with zero eigenvalue for small $V \neq 0$. Observe that for all V the operator $\mathcal{A}(V)$ has zero eigenvalue with multiplicity at least two, this multiple zero eigenvalue appears because of translational invariance of problem (2.9)–(2.13) and existence of a continuum of traveling waves with close velocities, see Appendix A. The operator $\mathcal{A}(V)$ has the eigenvector

$$W_1 = (m_1, \rho_1), \quad m_1 = -\Lambda(V)\partial_x e^{\Phi(x,y,V)-Vx},\ \rho_1 = \nu_x \tag{5.6}$$

corresponding to the infinitesimal shifts along the x-axis, and the generalized eigenvector

$$W_2 = (m_2, \rho_2), \quad m_2 = \partial_V\left(\Lambda(V)e^{\Phi(x,y,V)-Vx}\right),\ \rho_2 = \partial_{\tilde V}\tilde\rho\big|_{\tilde V=V} \tag{5.7}$$

that satisfies $\mathcal{A}(V)W_2 = W_1$, where $\tilde\rho$ describes the boundary of the traveling wave with velocity $\tilde V$ via the signed distance to $\partial\Omega(V)$. And these two vectors for small $V \neq 0$ exhaust the generalized eigenspace corresponding to zero eigenvalue. Moreover, it will be shown that zero eigenvalue of multiplicity three at $V = 0$ splits into zero eigenvalue of multiplicity two and a small nonzero eigenvalue $\lambda = \lambda(V)$ for $V \neq 0$. The asymptotic behavior of $\lambda(V)$ as $V \to 0$ is studied below. The main difficulty in this analysis comes from the fact that the eigenvector corresponding to $\lambda(V)$ merges as $V \to 0$ with the eigenvector W_1. Moreover, the next term in the expansion of this eigenvector is proportional to W_2. That is why the asymptotic problem for $\lambda(V)$ is a kind of singularly perturbed problem.

We seek the eigenvalue λ and the eigenvector (m,ρ) in the form

$$\lambda(V) = \hat{\lambda}V^2 + \dots, \tag{5.8}$$

$$m = m_1 + \hat{\lambda}V^2 m_2 + V^3 m_3 + V^4 m_4 + V^5 m_5 + \dots, \tag{5.9}$$

$$\rho = \rho_1 + \hat{\lambda}V^2\rho_2 + V^3\rho_3 + V^4\rho_4 + V^5\rho_5 + \dots \tag{5.10}$$

with unknown $\hat{\lambda}$, m_k, ρ_k $(k=3,4,5)$ which do not depend on V, and will be found via perturbation expansion in V. In contrast, m_1, m_2, ρ_1, and ρ_2 are expressed in terms of the traveling wave solution via (5.6) and (5.7), and *do depend* on V. These two terms belong to the domain of the operator $\mathcal{A}(V)$ (which depends on V) and even with ansatz $W_1 + \hat{\lambda}V^2 W_2$, truncated to two terms, we have

$$\mathcal{A}(V)(W_1 + \hat{\lambda}V^2 W_2) = \hat{\lambda}V^2(W_1 + \hat{\lambda}V^2 W_2) - \hat{\lambda}^2 V^4 W_2.$$

This suggests that in order to identify $\hat{\lambda}$ we have to satisfy the eigenvalue equation up to the order $O(V^5)$. Regarding the auxiliary function ϕ (which appears in the definition of $\mathcal{A}(V)$) it is convenient now to consider ϕ as an independent unknown, seeking it in the form

$$\phi = -\partial_x\Phi + \hat{\lambda}V^2\partial_V\Phi + V^3\phi_3 + V^4\phi_4 + V^5\phi_5 + \dots. \tag{5.11}$$

Substitute expansions (5.8)–(5.11) into the equations

$$\lambda\rho = \frac{\partial\phi}{\partial\nu} + \frac{\partial^2\Phi}{\partial\nu^2}\rho - \left(\frac{\partial\Phi}{\partial\tau} + V\nu_y\right)\rho' \quad \text{on } \partial\Omega(V), \tag{5.12}$$

$$\lambda m = \Delta m + V\partial_x m - \operatorname{div}(\Lambda e^{\Phi - Vx}\nabla\phi) - \operatorname{div}(m\nabla\Phi) \quad \text{in } \Omega(V), \tag{5.13}$$

along with (5.1) and boundary conditions (5.2), (5.5), and collect term of the order V^3 and V^4 (as already mentioned above the lower order terms vanish).

First we collect terms of the order V^3, replacing $\Omega(V)$ by the disk B_R (it approximates $\Omega(V)$ to the order V^2, see Remark 4.3). This leads to the following problem for m_3, ϕ_3 and ρ_3,

$$\Delta\phi_3 + m_3 = \zeta\phi_3 \quad \text{in } B_R, \tag{5.14}$$

$$\partial_r\phi_3 = 0, \quad \zeta\phi_3 = p_*'(\pi R^2)R\int_{-\pi}^{\pi}\rho_3 d\varphi + \frac{\gamma}{R^2}(\partial^2_{\varphi\varphi}\rho_3 + \rho_3) \quad \text{on } \partial B_R, \tag{5.15}$$

$$\Delta m_3 - m_0\Delta\phi_3 = 0 \quad \text{in } B_R, \quad \partial_r m_3 = 0 \quad \text{on } \partial B_R. \tag{5.16}$$

Thus, up to the eigenvector corresponding to the infinitesimal shifts of the disk B_R,

$$\rho_3 = \alpha, \ \zeta\phi_3 = \alpha(\gamma/R^2 + 2\pi R p_*'(\pi R^2)), \ m_3 = \zeta\phi_3. \tag{5.17}$$

The unknown parameter α will be determined by considering higher order terms in (5.1)–(5.2), (5.5), (5.12)–(5.13).

Next we collect terms of the order V^4 arriving at the following problem for m_4, ϕ_4 and ρ_4,

$$\Delta\phi_4 + m_4 = \zeta\phi_4 \quad \text{in } B_R, \tag{5.18}$$

$$\Delta m_4 - m_0\Delta\phi_4 = \hat{\lambda}^2 m_0(\Phi_V^0 - x) + \alpha(\gamma/R^2 + 2\pi R p_*'(\pi R^2))\Delta\Phi_V^0 \quad \text{in } B_R, \tag{5.19}$$

$$\zeta\left(\phi_4 + \alpha\partial_r\Phi_V^0\right) = p_*'(\pi R^2)R\int_{-\pi}^{\pi}\rho_4(\varphi)d\varphi + \frac{\gamma}{R^2}(\partial^2_{\varphi\varphi}\rho_4 + \rho_4) \quad \text{on } \partial B_R, \tag{5.20}$$

$$\partial_r m_4 + \alpha m_0\partial^2_{rr}\Phi_V^0 = 0 \quad \text{on } \partial B_R, \tag{5.21}$$

$$\partial_r\phi_4 + \alpha\partial^2_{rr}\Phi_V^0 = 0 \quad \text{on } \partial B_R. \tag{5.22}$$

To determine solvability of (5.18)–(5.22) observe that after adding $\alpha m_0\partial_r\Phi_V^0$ to m_4 and $\alpha\partial_r\Phi_V^0$ to ϕ_4, the problem is transformed to the form $\mathcal{A}_{ss}(R)(m_4{+}\alpha m_0\partial_r\Phi_V^0, \rho_4)$ $= (f(r)\cos\varphi, \varrho\cos\varphi)$ with some function $f(r)$ and a constant ϱ. Then (f,ϱ) has to be orthogonal to solutions of the adjoint homogeneous problem (see Section 6, the adjoint operator $\mathcal{A}^*_{\rm ss}(R)$ is given by (6.3), (6.4)–(6.6) with $V=0$)

$$\Delta\tilde{m} + \tilde{\phi} = 0 \quad \text{in } B_R, \quad \partial_r\tilde{m} = 0 \quad \text{on } \partial B_R, \tag{5.23}$$

$$\Delta\tilde{\phi} - \zeta\tilde{\phi} - m_0\Delta\tilde{m} = 0 \quad \text{in } B_R, \tag{5.24}$$

with boundary conditions

$$\tilde{\rho} - m_0\tilde{m} + \tilde{\phi} = 0 \text{ on } \partial B_R, \tag{5.25}$$

$$-\frac{\gamma}{R}(\partial^2_{\varphi\varphi}\partial_r\tilde{\phi} + \partial_r\tilde{\phi}) - \frac{R}{\zeta}p_*'(\pi R^2)\int_{-\pi}^{\pi}\partial_r\tilde{\phi}d\varphi = 0 \quad \text{on } \partial B_R. \tag{5.26}$$

This problem has a nontrivial solution given by $\tilde{m} = \Phi_V^0 - x$ in B_R and $\tilde{\rho} = m_0\tilde{m} - \tilde{\phi}$ on ∂B_R, with $\tilde{\phi} = -(\zeta - m_0)\Phi_V^0 - m_0 x$ (note that actually $\tilde{\rho} = 0$). Then in order to identify the unknown α multiply (5.19) by $\tilde{m}$ and integrate over B_R,

(5.27)
$$\int_{B_R}(\Delta m_4 - m_0\Delta\phi_4)\tilde{m}dxdy = \hat{\lambda}^2 m_0\int_{B_R}(\Phi_V^0 - x)^2 dxdy$$
$$+ \alpha(\gamma/R^2 + 2\pi R p_*'(\pi R^2))\int_{B_R}(\Phi_V^0 - x)\Delta(\Phi_V^0 - x)dxdy.$$

The left hand side of (5.27) rewrites as follows, using integration by parts and (5.18), (5.21)–(5.22), (5.23)–(5.24),

$$\int_{B_R}(\Delta m_4 - m_0\Delta\phi_4)\tilde{m}dxdy = \int_{B_R}(\Delta\phi_4 - (\zeta - m_0)\phi_4)\tilde{\phi}dxdy$$
$$= \int_{\partial B_R}(\partial_r\phi_4\tilde{\phi} - \partial_r\tilde{\phi}\phi_4)ds.$$

The traces of functions $\partial_r\phi_4$, ϕ_4, $\tilde{\phi}$ and $\partial_r\tilde{\phi}$ on ∂B_R are given by $\partial_r\phi_4 = \alpha(1/R - m_0R)\cos\varphi$, $\phi_4 = -\alpha\cos\varphi$, $\tilde{\phi} = -m_0R\cos\varphi$ and $\partial_r\tilde{\phi} = -\zeta\cos\varphi$, therefore

$$\begin{aligned}\int_{B_R}(\Delta m_4 - m_0\Delta\phi_4)\tilde{m}dxdy &= -m_0\pi R^2\alpha(1/R - m_0R) - \alpha\zeta\pi R \\ &= \alpha\pi R((m_0R)^2 - m_0 - \zeta).\end{aligned} \tag{5.28}$$

Thus combining (5.28) with (5.27) we get the following relation between $\hat\lambda$ and α,

$$\alpha R\left(\pi\left(\zeta+m_0-(m_0R)^2\right)-\left(\gamma/R^3+2\pi p_*'(\pi R^2)\right)\int_{B_R}|\nabla(\Phi_V^0-x)|^2dxdy\right)$$
$$=-\hat\lambda^2 m_0\int_{B_R}(\Phi_V^0-x)^2dxdy,$$

or, by Lemma 4.4,

$$\alpha E'(R)=\hat\lambda^2. \tag{5.29}$$

Besides the solution ($\tilde m=\Phi_V^0-x,\tilde\rho=0$) the problem (5.23)–(5.26) has exactly one linearly independent solution ($\tilde m=1,\tilde\rho=m_0$). Since $(f(r)\cos\varphi,\varrho\cos\varphi)$ is orthogonal to $(1,m_0)$ (with respect to the pairing (6.1)) there is a solution of (5.18)–(5.22). Moreover, if we require additionally that m_4 has zero mean value and $\int_{-\pi}^{\pi}\rho_4\cos\varphi d\varphi=0$ then $\rho_4=0$ and both m_4 and ϕ_4 are represented in the form of products of radially symmetric functions and $\cos\varphi$. Then separating variables in (5.18)–(5.19) we see that m_4 and ϕ_4 extend as solutions of (5.18)–(5.19) to the entire plane $\mathbb{R}^2$.

Thus we have constructed a four term ansatz of the eigenvector, and functions m_k, ϕ_k, $k=3,4$ are defined on $\Omega(V)$. However this ansatz is not in the domain of the operator $\mathcal{A}(V)$ as the boundary condition (5.5) is not exactly satisfied, but with accuracy of the order V^5. This is why we introduce a correcting term m_5^{c} such that

$$\partial_\nu m_5^{\mathrm{c}}=-\frac{1}{V}\partial_\nu m_4-\frac{\Lambda(V)}{V^2}e^{\Phi-Vx}\partial^2_{\nu\nu}\Phi\rho_3\quad\text{on }\partial\Omega(V). \tag{5.30}$$

In view of (5.21), bounds (4.19) and the expansion (4.20) (see Remark 4.3) one can show that the right hand side of (5.30) defines functions uniformly bounded in $C^j(\partial\Omega(V))$ $\forall j\in\mathbb{Z}_+$. Therefore we can define m_5^{c} in $\Omega(V)$, e.g., by solving the equation $\Delta m_5^{\mathrm{c}}=m_5^{\mathrm{c}}$ with the boundary condition (5.30), then we set

$$W_{ans}:=(m_1,\rho_1)+\hat\lambda V^2(m_2,\rho_2)+V^3(m_3,\alpha)+V^4(m_4+Vm_5^{\mathrm{c}},0), \tag{5.31}$$

where $m_1=-\Lambda(V)\partial_x e^{\Phi-Vx}$, $\rho_1=\nu_x$, $m_2=\partial_V(\Lambda(V)e^{\Phi-\tilde Vx})$, $\rho_2=\partial_{\tilde V}\tilde\rho_{\mathrm{tw}}(s,\tilde V)\big|_{\tilde V=V}$ and $\tilde\rho_{\mathrm{tw}}$ stands for the parametrization of $\partial\Omega(\tilde V)$ via the signed distance to $\partial\Omega(V)$. The (corrected) four term ansatz given by (5.31) is in domain of the operator $\mathcal{A}(V)$, and introducing the unique solution ϕ_5^{c} of

$$\Delta\phi_5^{\mathrm{c}}+m_5^{\mathrm{c}}=\zeta\phi_5^{\mathrm{c}}\quad\text{in }\Omega(V)$$

with the boundary condition

$$\zeta\phi_5^{\mathrm{c}}=\frac{1}{V^2}\left(p_*'(|\Omega(V)|)\int_{\partial\Omega(V)}\rho_3ds+\gamma\kappa^2\rho_3-\zeta(\phi_3+V\nu_x\rho_3)\right)-\frac{\zeta}{V}\phi_4\quad\text{on }\partial\Omega(V),$$

we can calculate the components of $\mathcal{A}(V)W_{ans} - \hat{\lambda}V^2 W_{ans}$:

(5.32)

$$\begin{aligned}\frac{1}{V^5}\Big(\mathcal{A}(V)W_{ans} - \hat{\lambda}V^2 W_{ans}\Big)_m = &\Delta m_5^{\mathrm{c}} + V\partial_x m_5^{\mathrm{c}} - \operatorname{div}(\Lambda e^{\Phi - Vx}\nabla\phi_5^{\mathrm{c}}) - \operatorname{div}(m_5^{\mathrm{c}}\nabla\Phi)\\ &+ \frac{1}{V}\left(\Delta m_4 + V\partial_x m_4 - \operatorname{div}(\Lambda e^{\Phi - Vx}\nabla\phi_4) - \operatorname{div}(m_4\nabla\Phi)\right)\\ &+ \frac{1}{V^2}\left(\Delta m_3 + V\partial_x m_3 - \operatorname{div}(\Lambda e^{\Phi - Vx}\nabla\phi_3) - \operatorname{div}(m_3\nabla\Phi)\right)\\ &- \frac{\hat{\lambda}}{V}\left(\hat{\lambda}\partial_V(\Lambda(V)e^{\Phi - Vx}) + Vm_3 + V^2 m_4 + V^3 m_5^{\mathrm{c}}\right),\end{aligned}$$

(5.33)

$$\begin{aligned}\frac{1}{V^5}\left(\mathcal{A}(V)W_{ans} - \hat{\lambda}V^2 W_{ans}\right)_\rho = &\partial_\nu\phi_5^{\mathrm{c}} + \frac{1}{V}\partial_\nu\phi_4 + \frac{1}{V^2}\partial_\nu\phi_3\\ &+ \frac{1}{V^2}\partial^2_{\nu\nu}\Phi\rho_3 - \frac{\hat{\lambda}}{V}\left(\hat{\lambda}\partial_{\tilde{V}}\tilde{\rho}_{\mathrm{tw}}\big|_{\tilde{V}=V} + V\rho_3\right).\end{aligned}$$

Thanks to (5.15), (5.20) we have $\|\phi_5^{\mathrm{c}}\|_{C^j(\partial\Omega(V))} \le C_j\ \forall j \in \mathbb{Z}_+$, and since $\Delta\phi_5^{\mathrm{c}} + m_5^{\mathrm{c}} = \zeta\phi_5^{\mathrm{c}}$ in $\Omega(V)$ one can show that $\|\phi_5^{\mathrm{c}}\|_{C^j(\overline{\Omega(V)})} \le C_j\ \forall j \in \mathbb{Z}_+$ by elliptic estimates. Furthermore, since m_3, ϕ_3 are constants the third line of (5.32) simplifies to $-m_3\Delta\Phi/V^2$ and substituting Δm_4 from (5.19) we obtain after rearranging terms,

(5.34)

$$\begin{aligned}\frac{1}{V^5}\Big(\mathcal{A}(V)W_{ans} - \hat{\lambda}V^2 W_{ans}\Big)_m = &\Delta m_5^{\mathrm{c}} + V\partial_x m_5^{\mathrm{c}} - \operatorname{div}(\Lambda e^{\Phi - Vx}\nabla\phi_5^{\mathrm{c}}) - \operatorname{div}(m_5^{\mathrm{c}}\nabla\Phi)\\ &- \frac{\hat{\lambda}^2}{V}\left(\partial_V\left(\Lambda(V)e^{\Phi - Vx}\right) - m_0(\Phi_V^0 - x)\right)\\ &+ \frac{1}{V}\left(V\partial_x m_4 - \operatorname{div}\left((\Lambda e^{\Phi - Vx} - m_0)\nabla\phi_4\right) - \operatorname{div}(m_4\nabla\Phi)\right)\\ &- \hat{\lambda}(m_3 + Vm_4 + V^2 m_5^{\mathrm{c}}) + \frac{m_3}{V^2}\left(V\Delta\Phi_V^0 - \Delta\Phi\right),\end{aligned}$$

(5.35)

$$\frac{1}{V^5}\Big(\mathcal{A}(V)W_{ans} - \hat{\lambda}V^2 W_{ans}\Big)_\rho = \partial_\nu\phi_5^{\mathrm{c}} + \frac{1}{V}\partial_\nu\phi_4 + \frac{1}{V^2}\partial^2_{\nu\nu}\Phi\rho_3 - \frac{\hat{\lambda}}{V}\Big(\hat{\lambda}\partial_{\tilde{V}}\tilde{\rho}_{\mathrm{tw}}\big|_{\tilde{V}=V} + V\rho_3\Big).$$

Assuming that there exist next terms $V^5 m_5$ and $V^5\rho_5$ of the asymptotic expansions we have $\mathcal{A}(V)(m_5,\rho_5) = -\frac{1}{V^5}(\mathcal{A}(V)W_{ans} - \hat{\lambda}V^2 W_{ans}) + \hat{\lambda}V^2(m_5,\rho_5) + \dots = -\frac{1}{V^5}(\mathcal{A}(V)W_{ans} + \dots$. Since the null space of the adjoint operator $\mathcal{A}^*(V)$ contains $(1, \Lambda(V)e^{\Phi - Vx})$ (see Section 6) we will require that

$$\begin{aligned}I(\hat{\lambda}, V) := &\int_{\Omega(V)}\Big(\mathcal{A}(V)W_{ans} - \hat{\lambda}V^2 W_{ans}\Big)_m\,dxdy\\ &+ \Lambda(V)\int_{\partial\Omega(V)}\Big(\mathcal{A}(V)W_{ans} - \hat{\lambda}V^2 W_{ans}\Big)_\rho e^{\Phi - Vx}\,ds = 0.\end{aligned}$$

Then resolving the equation $I(\hat\lambda, V) = 0$ we will identify $\hat\lambda$. To this end write $I(\hat\lambda, V)$ in the following form, integrating by parts and using (5.30), (5.35):

(5.36)
$$
\begin{aligned}
I(\hat\lambda, V) &= \frac{1}{V}\int_{\partial\Omega(V)} (\Lambda(V)e^{\Phi - Vx}\partial_\nu\phi_4 - \partial_\nu m_4)\, ds - \int_{\partial\Omega(V)} \hat\lambda\rho_3\Lambda(V)e^{\Phi-Vx}\, ds \\
&+ \int_{\Omega(V)} (V\partial_x m_5^{\mathrm{c}} - \operatorname{div}(m_5^{\mathrm{c}}\nabla\Phi))\, dxdy + \frac{1}{V}\int_{\Omega(V)} \left(\hat\lambda^2 m_0(\Phi_V^0 - x) + m_3\Delta\Phi_V^0\right) dxdy \\
&+ \frac{1}{V}\int_{\Omega(V)} \left(V\partial_x m_4 - \operatorname{div}((\Lambda e^{\Phi - Vx} - m_0)\nabla\phi_4) - \operatorname{div}(m_4\nabla\Phi)\right) dxdy \\
&- \hat\lambda\int_{\Omega(V)} \left(m_3 + Vm_4 + V^2 m_5^{\mathrm{c}}\right) dxdy \\
&- \frac{\hat\lambda^2}{V}\left(\int_{\Omega(V)} \partial_V(\Lambda(V)e^{\Phi - Vx})\, dxdy + \int_{\partial\Omega(V)} \Lambda(V)e^{\Phi - Vx}\partial_{\tilde V}\tilde\rho_{\mathrm{tw}}\big|_{\tilde V = V} ds\right).
\end{aligned}
$$

This formula is further simplified by noticing that the first term in the second line of (5.36) is zero thanks to the fact that $\partial_\nu\Phi = V\nu_x$ on $\partial\Omega(V)$. Also, observing that, by virtue of (5.19) (see also (5.17)) the integrand in the second term equals $\Delta m_4 - m_0\Delta\phi_4$, then collecting all the terms with the prefactor $\frac{1}{V}$ except the last line, we see that these terms cancel each other. Finally, notice that the last line of (5.36) is equal to $-\frac{\hat\lambda^2}{V}M'(V)$. Thus

$$
I(\hat\lambda, V) = -\hat\lambda\alpha\pi R(2m_0 + \gamma/R + 2\pi R^2 p_*'(\pi R^2) + O(V)) - \frac{\hat\lambda^2}{V}M'(V), \tag{5.37}
$$

and substituting α from (5.29) we obtain that the equation $I(\hat\lambda, V) = 0$ has nonzero solution

$$
\hat\lambda(V) = -\frac{1}{V}M'(V)E'(R)\frac{1}{\pi R\,(2m_0 + \gamma/R + 2\pi R^2 p_*'(\pi R^2) + O(V))} \tag{5.38}
$$

for sufficiently small V, provided that $M'(V) \neq 0$ when $V \neq 0$. Moreover, in the nondegenerate case, when $M''(0) \neq 0$, the solution $\hat\lambda(V)$ has nonzero finite limit

$$
\hat\lambda = -M''(0)E'(R)/M_{\mathrm{ss}}'(R). \tag{5.39}
$$

If $M''(0) = 0$ but $M'(V) \neq 0$ for small $V \neq 0$ there still exists a nonzero solution $\hat\lambda(V)$ of the equation $I(\hat\lambda, V) = 0$ and we can repeat the above construction observing that in this case m_k, ρ_k, ϕ_k, $k = 3, 4$ and m_5^{c}, ϕ_5^{c} contain the small factor $\alpha = O\left((M'(V)/V)^2\right)$.

We summarize the results of the above construction of asymptotic expansions in the following

Lemma 5.1. *Assume that $M'(V) \neq 0$ for small $V \neq 0$, and let $\hat\lambda(V)$ be a nonzero solution of the equation $I(\hat\lambda, V) = 0$. Then the vector W_{ans} given by (5.31) is in* *the domain of* $\mathcal{A}(V)$ *and*

$$W_{\rm ans} = (-\Lambda(V)\partial_x e^{\Phi - Vx}, \nu_x) + W_{\rm cor}, \quad \|W_{cor}\|_{L^2} = O(V^2), \tag{5.40}$$

$$\|\mathcal{A}(V)W_{\rm ans} - \hat\lambda(V)V^2 W_{ans}\|_{L^2} \le C|M'(V)|^2|V|^3, \tag{5.41}$$

$$\langle \mathcal{A}(V)W_{\rm ans} - \hat\lambda(V)V^2 W_{\rm ans}, W_1^*\rangle_{L^2} = 0, \tag{5.42}$$

where $\langle\,\cdot,\cdot\rangle_{L^2}$ *denotes the pairing defined by* (6.1) *and* $\|\cdot\|_{L^2}$ *is the corresponding norm,* $W_1^* = (1, \Lambda(V)e^{\Phi - Vx})$. *Moreover, there is a unique solution* $\hat\lambda(V) \neq 0$ *of* $I(\hat\lambda, V) = 0$ *for sufficiently small* $V \neq 0$ *and it is given by the asymptotic formula*

$$\hat\lambda(V) = -E'(R)\frac{M'(V)}{VM'_{\rm ss}(R)}(1 + O(V)) \quad \text{as } V \to 0. \tag{5.43}$$

Proof. For simplicity consider the nondegenerate case, when $M''(0) \neq 0$, otherwise one just has to take into account that all the terms in (5.34)–(5.35) contain the small factor $\alpha = \hat\lambda^2(V)/E'(R) = O\left((M'(V)/V)^2\right)$.

First notice that (5.40) follows immediately from the definition (5.31) of W_{ans}. To prove (5.41) it suffices to show that right hand sides of (5.34)–(5.35) are uniformly bounded. To this end one can use the representation (4.20) for Φ and the representation $\Lambda(V) = m_0 e^{-m_0/\zeta} + V^2\tilde\Lambda(V)$ for $\Lambda(V)$ (where $\tilde\Lambda(V)$ and its derivatives are bounded), see Remark 4.3, and derive that $\Lambda(V)e^{\Phi - Vx} = m_0 + VO(1)$, $\partial_V\left(\Lambda(V)e^{\Phi - Vx}\right) = m_0(\Phi_V^0 - x) + VO(1)$, $|\nabla\Phi| = VO(1)$, $\Delta\Phi = V\Delta\Phi_V^0 + V^2O(1)$, where $O(1)$ stands for various uniformly bounded functions. This readily implies that ρ-component of $\frac{1}{V^5}\left(\mathcal{A}(V)W_{ans} - \hat\lambda(V)V^2 W_{ans}\right)$ is bounded. Next, regarding (5.35) consider first the sum of two middle terms, $\frac{1}{V}(\partial_\nu\phi_4 + \frac{1}{V}\partial^2_{\nu\nu}\Phi\rho_3)$, and write it, by using (4.20), as $\frac{1}{V}(\partial_\nu\phi_4 + \partial^2_{\nu\nu}\Phi_V^0\rho_3) + \partial^2_{\nu\nu}\tilde\Phi\rho_3$. Recall that $\rho_3 = \alpha$ and ϕ_4 satisfies (5.22) on ∂B_R. Then, passing to polar coordinates we see that $|\partial_\nu\phi_4 + \partial^2_{\nu\nu}\Phi_V^0\rho_3| \le |\partial_r\phi_4 + \partial^2_{rr}\Phi_V^0\rho_3| + CV^2 \le C_1V^2$ on $\partial\Omega(V)$. Also, if $\rho_{\rm tw}(\varphi, V) + R$ is the radial coordinate of a point on $\partial\Omega(V)$ then $\partial_{\tilde V}\tilde\rho_{\rm tw}\big|_{\tilde V = V} = \partial_V\rho_{\rm tw}(\varphi, V)(\nu_x\cos\varphi + \nu_y\sin\varphi)$ and since $|\partial_V\rho_{\rm tw}(\varphi, V)| \le C|V|$ the last term in (5.35) is also bounded. This completes the proof of (5.41). Finally, (5.42) is nothing but the equation $I(\hat\lambda, V) = 0$, while the asymptotic formula (5.43) was derived above (see (5.38)). Lemma 5.1 is proved. □

6. Adjoint operator and its generalized eigenvector

As usual in the spectral analysis of non-self-adjoint boundary value problems, the adjoint operator plays an important role. To define the adjoint operator $\mathcal{A}^*(V)$ with respect to the pairing

$$\langle (m,\rho), (\tilde m, \tilde\rho)\rangle_{L^2} = \int_{\Omega(V)} m\tilde m\, dxdy + \int_{\partial\Omega(V)} \rho\tilde\rho\, ds, \tag{6.1}$$

assume that $(\tilde m, \tilde\rho)$ belongs to the domain of $\mathcal{A}^*(V)$ and $\tilde\rho \in C^\infty(\partial\Omega(V))$, $\tilde m \in C^\infty(\overline{\Omega(V)})$, then $\forall\ m \in C^\infty(\overline{\Omega(V)})$ and $\rho \in C^\infty(\partial\Omega(V))$ such that (m,ρ) belongs to the domain of $\mathcal{A}(V)$ we have $\langle (m,\rho), \mathcal{A}^*(V)(\tilde m, \tilde\rho)\rangle_{L^2} = \langle \mathcal{A}(V)(m,\rho), (\tilde m, \tilde\rho)\rangle_{L^2}$.

Next, using integration by parts we write

$$\langle \mathcal{A}(V)(m,\rho),(\tilde m,\tilde\rho)\rangle_{L^2} = \int_{\partial\Omega(V)} \left(\partial_\nu\phi + \partial^2_{\nu\nu}\Phi\rho\right)\tilde\rho\, ds - \int_{\partial\Omega(V)} \left(\partial_\tau\Phi + V\nu_y\right)\rho'\tilde\rho\, ds$$
$$+ \int_{\Omega(V)} \left(\Delta m + V\partial_x m - \operatorname{div}(m\nabla\Phi)\right)\tilde m\, dxdy - \int_{\Omega(V)} \operatorname{div}\left(\Lambda e^{\Phi - Vx}\nabla\phi\right)\tilde m\, dxdy$$
$$= \int_{\partial\Omega(V)} \left(\partial_\nu\phi + \partial^2_{\nu\nu}\Phi\rho\right)\tilde\rho\, ds + \int_{\partial\Omega(V)} \rho\left(\left(\partial_\tau\Phi + V\nu_y\right)\tilde\rho\right)'\, ds$$
$$+ \int_{\partial\Omega(V)} \left(\Lambda e^{\Phi - Vx}\left(\left(\partial_\tau\Phi + V\nu_y\right)\rho' - \partial^2_{\nu\nu}\Phi\rho\right)\tilde m - m\partial_\nu\tilde m - \Lambda e^{\Phi - Vx}\partial_\nu\phi\tilde m\right) ds$$
$$+ \int_{\Omega(V)} m\left(\Delta\tilde m + \nabla\Phi\cdot\nabla\tilde m - V\partial_x\tilde m\right)\, dxdy - \int_{\Omega(V)} \phi \operatorname{d}\!iv\left(\Lambda e^{\Phi - Vx}\nabla\tilde m\right)\, dxdy,$$

where we have used the boundary condition (5.5) for $\partial_\nu m$ and $\partial_\nu\Phi = V\nu_x$ on $\partial\Omega(V)$. To eliminate ϕ and its derivatives, multiply (5.1) by an auxiliary function $\tilde\phi$, to be defined later, and integrate over $\Omega(V)$ to obtain that

$$\int_{\partial\Omega(V)} \left(\partial_\nu\phi\tilde\phi - \phi\partial_\nu\tilde\phi\right) ds + \int_{\Omega(V)} \left(\phi\Delta\tilde\phi + m\tilde\phi - \zeta\phi\tilde\phi\right)\, dxdy = 0;$$

then we can rewrite $\langle \mathcal{A}(V)(m,\rho),(\tilde m,\tilde\rho)\rangle_{L^2}$ as

(6.2)
$$\langle \mathcal{A}(V)(m,\rho),(\tilde m,\tilde\rho)\rangle_{L^2} = \int_{\partial\Omega(V)} \partial_\nu\phi\left(\tilde\phi + \tilde\rho - \Lambda e^{\Phi - Vx}\tilde m\right)\, ds$$
$$+ \int_{\Omega(V)} \phi\left(\Delta\tilde\phi - \zeta\tilde\phi - \operatorname{d}\!iv\left(\Lambda e^{\Phi - Vx}\nabla\tilde m\right)\right)\, dxdy$$
$$+ \int_{\Omega(V)} m\left(\Delta\tilde m + \nabla\Phi\cdot\nabla\tilde m - V\partial_x\tilde m + \tilde\phi\right)\, dxdy - \int_{\partial\Omega(V)} m\partial_\nu\tilde m\, ds$$
$$+ \int_{\partial\Omega(V)} \rho\left(\partial^2_{\nu\nu}\Phi(\tilde\rho - \tilde m\Lambda e^{\Phi - Vx}) + \left(\left(\partial_\tau\Phi + V\nu_y\right)\left(\tilde\rho - \tilde m\Lambda e^{\Phi - Vx}\right)\right)'\right)\, ds$$
$$- \int_{\partial\Omega(V)} \phi\partial_\nu\tilde\phi ds.$$

Define now the auxiliary function $\tilde\phi$ as the unique solution of the problem

$$\Delta\tilde\phi - \zeta\tilde\phi - \operatorname{d}\!iv(\Lambda e^{\Phi - Vx}\nabla\tilde m) = 0 \quad \text{in } \Omega(V), \quad \tilde\phi = \Lambda e^{\Phi - Vx}\tilde m - \tilde\rho \quad \text{on } \partial\Omega(V), \tag{6.3}$$

this choice of $\tilde\phi$ nullifies the first two terms in the right hand side of (6.2). Notice also that using boundary condition (5.2) and integrating by parts the last term in the right hand side of (6.2) can be written in the form

$$-\int_{\partial\Omega(V)} \phi\partial_\nu\tilde\phi ds = \int_{\partial\Omega(V)} \rho\left((V\nu_x - \frac{\gamma\kappa^2}{\zeta})\partial_\nu\tilde\phi - \frac{\gamma}{\zeta}\partial^2_{\tau\tau}\partial_\nu\tilde\phi\right) ds$$
$$- \frac{p'_*(|\Omega(V)|)}{\zeta}\int_{\partial\Omega(V)} \partial_\nu\tilde\phi\, ds \int_{\partial\Omega(V)} \rho\, ds.$$

Thus, we conclude by density of smooth functions from the domain of $\mathcal{A}(V)$ in $L^2(\Omega(V)) \times L^2(\partial\Omega(V))$ that

$$\partial_\nu\tilde m = 0 \quad \text{on } \partial\Omega(V), \tag{6.4}$$

and components of $\mathcal{A}^*(V)$ are given by

$$(\mathcal{A}^*(V)(\tilde{m},\tilde{\rho}))_{\tilde{m}} = \Delta\tilde{m} + \nabla\Phi\cdot\nabla\tilde{m} - V\partial_x\tilde{m} + \tilde{\phi} \quad \text{in } \Omega(V), \tag{6.5}$$

$$\begin{aligned}(\mathcal{A}^*(V)(\tilde{m},\tilde{\rho}))_{\tilde{\rho}} &= \partial^2_{\nu\nu}\Phi(\tilde{\rho} - \tilde{m}\Lambda e^{\Phi - Vx}) + \big((\partial_\tau\Phi + V\nu_y)(\tilde{\rho} - \tilde{m}\Lambda e^{\Phi-Vx})\big)' \\ &+ \big(V\nu_x - \frac{\gamma\kappa^2}{\zeta}\big)\partial_\nu\tilde{\phi} - \frac{\gamma}{\zeta}\partial^2_{\tau\tau}\partial_\nu\tilde{\phi} - \frac{p_*'(|\Omega(V)|)}{\zeta}\int_{\partial\Omega(V)}\partial_\nu\tilde{\phi}\,ds \quad \text{on } \partial\Omega(V).\end{aligned} \tag{6.6}$$

Observe that the definition of $\mathcal{A}^*(V)$ admits an important simplification. Namely, one can express the action of the operator $\mathcal{A}^*(V)$ in terms of the only function $\tilde{\phi}$ as follows. In view of (6.3) we have

$$(\mathcal{A}^*(V)(\tilde{m},\tilde{\rho}))_{\tilde{m}} = \frac{1}{\Lambda(V)e^{\Phi-Vx}}(\Delta\tilde{\phi} - \zeta\tilde{\phi}) + \tilde{\phi}, \tag{6.7}$$

and, due to the boundary condition $\tilde{\phi} = \Lambda e^{\Phi-Vx}\tilde{m} - \tilde{\rho}$ on $\partial\Omega(V)$, (6.6) rewrites as

$$\begin{aligned}(\mathcal{A}^*(V)(\tilde{m},\tilde{\rho}))_{\tilde{\rho}} =& -\partial^2_{\nu\nu}\Phi\tilde{\phi} - \partial_\tau\left(\tilde{\phi}\partial_\tau\Phi\right) - V\nu_y'\tilde{\phi} - V\nu_y\partial_\tau\tilde{\phi} \\ &+ V\nu_x\partial_\nu\tilde{\phi} - \frac{\gamma\kappa^2}{\zeta}\partial_\nu\tilde{\phi} - \frac{\gamma}{\zeta}\partial^2_{\tau\tau}\partial_\nu\tilde{\phi} - \frac{p_*'(|\Omega(V)|)}{\zeta}\int_{\partial\Omega(V)}\partial_\nu\tilde{\phi}\,ds.\end{aligned} \tag{6.8}$$

Moreover, since

$$\mathrm{d}iv(\Lambda e^{\Phi-Vx}\nabla\tilde{m}) = \Delta\tilde{\phi} - \zeta\tilde{\phi} \quad \text{in } \Omega(V), \quad \partial_\nu\tilde{m} = 0 \quad \text{on } \partial\Omega(V), \tag{6.9}$$

the following additional condition

$$\int_{\partial\Omega(V)}\partial_\nu\tilde{\phi}\,ds = \zeta\int_{\Omega(V)}\tilde{\phi}\,dxdy \tag{6.10}$$

must be satisfied by $\tilde{\phi}$. Then one can reconstruct $\tilde{m}$, up to an additive constant, by solving (6.9).

The following equivalent form of (6.8) is obtained by using the equation and the boundary conditions from (4.2)–(4.3),

$$\begin{aligned}(\mathcal{A}^*(V)(\tilde{m},\tilde{\rho}))_{\tilde{\rho}} =& (\Lambda(V)e^{\Phi-Vx} - \zeta\Phi)\tilde{\phi} + (\gamma\kappa'/\zeta - V\nu_y)\,\partial_\tau\tilde{\phi} \\ &+ V\nu_x\partial_\nu\tilde{\phi} - \frac{\gamma\kappa^2}{\zeta}\partial_\nu\tilde{\phi} - \frac{\gamma}{\zeta}\partial^2_{\tau\tau}\partial_\nu\tilde{\phi} - \frac{p_*'(|\Omega(V)|)}{\zeta}\int_{\partial\Omega(V)}\partial_\nu\tilde{\phi}\,ds.\end{aligned} \tag{6.11}$$

When $V=0$ the operator $\mathcal{A}^*(0)$ coincides with the adjoint operator $\mathcal{A}^*_{\rm ss}(R)$ of $\mathcal{A}_{\rm ss}(R)$ at the critical radius $R=R_0$.

Lemma 6.1. *The algebraic multiplicity of the zero eigenvalue of $\mathcal{A}^*_{\rm ss}(R)$ (and $\mathcal{A}_{\rm ss}(R)$) is equal to three, while its geometric multiplicity is equal to two.*

Proof. Consider an element $(\tilde{m},\tilde{\rho})$ of the null space of $\mathcal{A}^*_{\rm ss}(R)$, then, passing to the parametrization of ∂B_R via the angle φ, we have problem (5.23)–(5.26). This problem has the following solution: $\tilde{m}=1$, $\rho = m_0$ with $\tilde{\phi}=0$, while any other linearly independent solution corresponds to a nonzero function $\tilde{\phi}$. It follows from (5.23)–(5.24) that $\tilde{\phi}$ satisfies $\Delta\tilde{\phi} + (m_0-\zeta)\tilde{\phi} = 0$ in B_R therefore it is completely determined by its normal derivative $\partial_r\tilde{\phi}$ on ∂B_R. Moreover, $\partial_r\tilde{\phi}$ satisfies (5.26), while all linearly independent (even and periodic) solutions of this equation are $\partial_r\tilde{\phi} = \cos\varphi$ and, possibly, $\partial_r\tilde{\phi}=1$. Even though $\partial_r\tilde{\phi}=1$ might satisfy (5.26) (for some particular values of parameters), this choice of $\partial_r\tilde{\phi}$ is inconsistent with the boundary condition in (5.23) as can be seen by integrating equations in (5.23)–(5.24) over B_R. On the other hand assuming $\partial_r\tilde{\phi} = -\zeta\cos\varphi$ on ∂B_R does lead to the triple $\tilde{\phi} = -(\zeta - m_0)\Phi_V^0 - m_0 x$, $\tilde{m} = \Phi_V^0 - x$ and $\tilde{\rho} = 0$ satisfying (5.23)–(5.26). Thus the null space of $\mathcal{A}^*_{ss}(R)$ is of dimension two, therefore the operator $\mathcal{A}_{ss}(R)$ also has a two-dimensional null space. Recall that $\mathcal{A}_{ss}(R)$ has two eigenvectors $(2\pi R p_*'(\pi R^2) + \gamma/R^2, 1)$ and $(0, \cos\varphi)$ corresponding to zero eigenvalue, and the generalized eigenvector $(\Phi_V^0 - x, 0)$. We claim that the algebraic multiplicity of zero eigenvalue is three. Otherwise there is a generalized eigenvector W such that $\mathcal{A}_{ss}(R)W = (2\pi R p_*'(\pi R^2) + \gamma/R^2, 1)$ or $\mathcal{A}_{ss}(R)W = (\Phi_V^0 - x, 0)$. Both cases are impossible, in the first one

$$0 = \langle W, \mathcal{A}^*_{ss}(R)(1, m_0)\rangle_{L^2} = \langle \mathcal{A}_{ss}(R)W, (1, m_0)\rangle_{L^2} = 2\pi^2 R^3 p_*'(\pi R^2) + \pi\gamma + 2\pi R m_0$$

contradictory to (4.6); in the second case

$$0 = \langle W, \mathcal{A}^*_{ss}(R)(\Phi_V^0 - x, 0)\rangle_{L^2} = \langle \mathcal{A}_{ss}(R)W, (\Phi_V^0 - x, 0)\rangle_{L^2} = \int_{B_R} (\Phi_V^0 - x)^2\, dxdy.$$

Thus, the algebraic multiplicity of zero eigenvalue of $\mathcal{A}_{ss}(R)$ is equal to three, and the same holds for $\mathcal{A}^*_{ss}(R)$. Lemma 6.1 is proved. □

While the generalized eigenspace of $\mathcal{A}(V)$ corresponding to the zero eigenvalue is explicitly given in terms of the solutions $\phi = \Phi(x, y, V)$, $\Omega = \Omega(V)$ of the free boundary problem (4.2)–(4.3), for the operator $\mathcal{A}^*(V)$ we know explicitly only the eigenvector

$$W_1^* = (1, \Lambda(V)e^{\Phi - Vx}) \tag{6.12}$$

that is related to the conservation of the total myosin mass in the linearized problem. While this eigenvector does not have any associated generalized eigenvector for $V = 0$ (see proof of Lemma 6.1), such a generalized eigenvector appears for $V \neq 0$ and it exhibits singular behavior for small velocities. Namely, we will show that if $\mathcal{A}^*(V)(\tilde{m}, \tilde{\rho}) = (1, \Lambda(V)e^{\Phi - Vx})$ then $(\tilde{m}, \tilde{\rho})$ blows up as $1/V$, when $V \to 0$. This is why it is natural to renormalize this generalized eigenvector and write the problem in the form $\mathcal{A}^*(V)(\tilde{m}, \tilde{\rho}) = Vk(1, \Lambda(V)e^{\Phi - Vx})$, assuming that $(\tilde{m}, \tilde{\rho})$ is bounded.

Consider the ansatz

$$\tilde{m} = \Phi_V^0 - x + V\tilde{m}_1 + \dots, \quad \tilde{\rho} = V\tilde{\rho}_1 + \dots, \tag{6.13}$$

assuming the expansion $\tilde{\phi} = -(\zeta - m_0)\Phi_V^0 - m_0 x + V\tilde{\phi}_1 + \dots$ for the solution of (6.3), and substitute (6.13) in the equation $\mathcal{A}^*(V)(\tilde{m}, \tilde{\rho}) = Vk(1, \Lambda(V)e^{\Phi - Vx})$ with unknown for the moment constant k. Collecting the leading order terms, they are of the order V, in the corresponding problems we obtain (as above we replace $\Omega(V)$ by the disk B_R which approximates $\Omega(V)$ to the order V^2),

$$\Delta\tilde{m}_1 + \tilde{\phi}_1 = k - |\nabla(\Phi_V^0 - x)|^2 \quad \text{in } B_R, \quad \partial_r\tilde{m}_1 = 0 \quad \text{on } \partial B_R, \tag{6.14}$$

$$\Delta\tilde{\phi}_1 - \zeta\tilde{\phi}_1 = m_0\Delta\tilde{m}_1 + m_0 \mathrm{div}\left((\Phi_V^0 - x)\nabla(\Phi_V^0 - x)\right) \quad \text{in } B_R, \tag{6.15}$$

$$\tilde{\phi}_1 = m_0\tilde{m}_1 + m_0 R^2\cos^2\varphi - \tilde{\rho}_1 \quad \text{on } \partial B_R, \tag{6.16}$$

$$\begin{aligned} -\frac{\gamma}{R^2\zeta}(\partial_r\tilde{\phi}_1 + \partial^2_{\varphi\varphi}\partial_r\tilde{\phi}_1) - \frac{p_*'(\pi R^2)}{\zeta}\int_{-\pi}^{\pi}\partial_r\tilde{\phi}_1 R\, d\varphi = \zeta\cos^2\varphi \\ +m_0(k - \partial^2_{rr}\Phi_V^0 R\cos\varphi - \cos 2\varphi) \text{ on } \partial B_R. \end{aligned} \tag{6.17}$$

Introduce a solution f of $\Delta f = \mathrm{d}iv\left((\Phi_V^0 - x)\nabla(\Phi_V^0 - x)\right)$ in B_R, $\partial_r f = 0$ on ∂B_R, then we can rewrite problem (6.14)-(6.17) in the operator form:

$$\begin{aligned}\mathcal{A}^*_{ss}(R)(\tilde{m}_1 + f, \tilde{\rho}_1 - m_0 f - m_0 R^2\cos^2\varphi) \\ = (k + (\Phi_V^0 - x)\Delta(\Phi_V^0 - x), m_0(k - \partial^2_{rr}\Phi_V^0 R\cos\varphi - \cos 2\varphi) + \zeta\cos^2\varphi),\end{aligned}$$

and since the null space of $\mathcal{A}^*_{\rm ss}(R)$ is nonzero, we can use solvability conditions to identify k. Indeed, the operator $\mathcal{A}_{ss}(R)$ has the eigenvector $(\gamma/R^2 + 2\pi R p'_*(\pi R^2), 1)$ in its null space, and we necessarily have

$$\begin{aligned}(\gamma/R^2 + 2\pi R p'_*(\pi R^2))\left(\pi R^2 k - \int_{B_R}|\nabla(\Phi_V^0 - x)|^2\,dxdy\right) \\ + \int_{-\pi}^{\pi}\left(k m_0 + (m_0 - m_0^2 R^2)\cos^2\varphi + \zeta\cos^2\varphi\right)R\,d\varphi = 0.\end{aligned}$$

This yields, after rearranging terms and using (4.5), (4.21)–(4.22),

$$k = -\frac{\pi R\zeta F'(R)}{M'_{\rm ss}(R)} = m_0\frac{E'(R)}{M'_{\rm ss}(R)}\int_{B_R}(\Phi_V^0 - x)^2 dxdy =: k_0. \tag{6.18}$$

Then solving (6.17) we find

$$\partial_r\tilde{\phi}_1 = A\cos 2\varphi + B = 2A\cos^2\varphi + (B - A) \quad \text{on } \partial B_R, \tag{6.19}$$

where

$$A = \frac{R^2\zeta}{6\gamma}\left(\zeta - m_0 - m_0^2R^2\right), \quad B = -\zeta\frac{2k_0m_0 + m_0 - m_0^2R^2 + \zeta}{2\left(\gamma/R^2 + 2\pi R p'_*(\pi R^2)\right)}. \tag{6.20}$$

Also, eliminating $\tilde{m}_1$ from (6.14)–(6.15) we have that $\tilde{\phi}_1$ satisfies

$$\frac{1}{m_0}\left(\Delta\tilde{\phi}_1 - \zeta\tilde{\phi}_1\right) + \tilde{\phi}_1 = k_0 + (\Phi_V^0 - x)\Delta(\Phi_V^0 - x) \quad \text{in } B_R. \tag{6.21}$$

The unique solution of this equation with boundary condition (6.19) is represented as the sum of a radially symmetric function and the product of another radially symmetric function with $\cos 2\varphi$, therefore it extends as a solution of (6.21) to the entire $\mathbb{R}^2$. Thus the function

$$\tilde{\phi} = -(\zeta - m_0)\Phi_V^0 - m_0 x + V\tilde{\phi}_1 \tag{6.22}$$

is well defined on $\Omega(V)$. One can define $\tilde{m}_1$ by solving (6.14) and then $\tilde{\rho}_1$ by (6.16), completing the construction of the ansatz (6.13). The properties of $\tilde{\phi}$ needed for the justification of the ansatz (6.13) are collected in

Lemma 6.2. *The function $\tilde{\phi}$ given by* (6.22) *satisfies for small V*

$$\left\|\Delta\tilde{\phi} - \zeta\tilde{\phi} + \Lambda(V)e^{\Phi - Vx}\tilde{\phi} - k_0V\Lambda(V)e^{\Phi - Vx}\right\|_{C^j(\overline{\Omega}(V))} = O(V^2) \quad \forall j \in \mathbb{Z}_+, \tag{6.23}$$

$$\left\|\partial_\nu\tilde{\phi} - \left(-\zeta\nu_x + 2AV\nu_x^2 + V(B - A)\right)\right\|_{C^j(\partial\Omega(V))} = O(V^2) \quad \forall j \in \mathbb{Z}_+, \tag{6.24}$$

and

$$\int_{\partial\Omega(V)}\partial_\nu\tilde{\phi}\,ds - \zeta\int_{\Omega(V)}\tilde{\phi}\,dxdy = O(V^2). \tag{6.25}$$

Proof. Bound (6.23) follows from the construction of $\tilde\phi$ and representation (4.20) for $\Phi - Vx$ in conjunction with the formula $\Lambda(V) = \Lambda(0) + O(V^2)$ (see Remark 4.3). To verify (6.24) one passes to polar coordinates and uses (6.19) together with the bound (4.19). Finally, (6.25) follows from the construction of $\tilde\phi$ (recall that $\int_{\partial B_R} \partial_r\tilde\phi\, ds - \zeta\int_{B_R}\tilde\phi\, dxdy = 0$) and (4.19). □

Remark 6.3. Using (4.21) and (6.18) one can derive the following formula for B, cf. (6.20),

$$B = -\frac{\zeta}{2M'_{ss}(R)}\Big(\pi R^2\left(\zeta + m_0 - m_0^2R^2\right) + 2m_0\int_{B_R}|\nabla(\Phi_V^0 - x)|^2\, dxdy\Big),$$

which shows that B is well defined even if the denominator in (6.20) is zero.

7. Asymptotic formula for eigenvalues of the operator linearized around traveling wave solutions with small velocities

In this section we justify asymptotic expansions constructed in Section 5. We begin with the generalized eigenvector of the adjoint operator $\mathcal{A}^*(V)$. Recall that $\mathcal{A}^*(V)$ has the eigenvector $W_1^* = (1, \Lambda(V)e^{\Phi - Vx})$ that is related to the total myosin mass conservation property in problem (2.9)–(2.13) and its linearized counterpart (5.1)–(5.5).

Lemma 7.1. *The operator $\mathcal{A}^*(V)$ has a generalized eigenvector $W_2^* = (m_2^*, \rho_2^*)$, $\mathcal{A}^*(V)W_2^* = W_1^*$, whose first component expands when $V \to 0$ as follows,*

$$m_2^* = \frac{1}{k_0V + V^2k_1(V)}(\Phi_V^0 - x + V\tilde m_1) + V\chi \tag{7.1}$$

with bounded $k_1(V)$ and uniformly in V bounded $\chi(\cdot, V)$ (in $C^j(\overline{\Omega(V)})$ $\forall j \in \mathbb{Z}_+$), while $\|\rho_2^*\|_{C^j(\overline{\Omega(V)})} = O(1)$ $\forall j \in \mathbb{Z}_+$. The constant k_0 in (7.1) is given by (6.18), Φ_V^0 is the solution of problem (4.14), and $\tilde m_1$ is a smooth function independent of V (and defined on the entire plane $\mathbb{R}^2$).

Proof. Consider the problem of finding generalized eigenvector in the form

$$\mathcal{A}^*(V)(\tilde m, \tilde\rho) = k(1, \Lambda(V)e^{\Phi - Vx}) \quad \text{(with constant } k \neq 0),$$

then

$$\Delta\tilde\phi - \zeta\tilde\phi + \Lambda e^{\Phi - Vx}\tilde\phi = k\Lambda e^{\Phi - Vx} \quad \text{in } \Omega(V). \tag{7.2}$$

If we waive the condition $k \neq 0$ then solving (7.2) with

$$\begin{aligned} &-\frac{\gamma}{\zeta}\partial^2_{\tau\tau}\partial_\nu\tilde\phi - \frac{\gamma\kappa^2}{\zeta}\partial_\nu\tilde\phi - \frac{p'_*(|\Omega(V)|)}{\zeta}\int_{\partial\Omega(V)}\partial_\nu\tilde\phi\, ds \\ &\quad - \left(\partial^2_{\nu\nu}\Phi + V\nu'_y\right)\tilde\phi - \partial_\tau\left(\tilde\phi\partial_\tau\Phi\right) - V\nu_y\partial_\tau\tilde\phi + V\nu_x\partial_\nu\tilde\phi = k\Lambda e^{\Phi - Vx} \quad \text{on } \partial\Omega(V) \end{aligned} \tag{7.3}$$

and condition (6.10) yields an element of the generalized space of the operator $\mathcal{A}^*(V)$ corresponding to zero eigenvalue. Moreover, if such an element is nontrivial then it never belongs to the linear span of the eigenvector $(1, \Lambda e^{\phi - Vx})$.

The number k can be found in terms of the normal derivative $\partial_\nu\tilde\phi$ on $\partial\Omega(V)$. To this end multiply (7.2) by the solution $\tilde\psi_1$ of the problem

$$\Delta\tilde\psi_1 - \zeta\tilde\psi_1 + \Lambda e^{\Phi - Vx}\tilde\psi_1 = \zeta \quad \text{in } \Omega(V), \quad \partial_\nu\tilde\psi_1 = 0 \quad \text{on } \partial\Omega(V), \tag{7.4}$$

and integrate over $\Omega(V)$. Using integration by parts and condition (6.10) we derive

$$k = \frac{\int_{\partial\Omega(V)} \partial_\nu \tilde{\phi}(1+\tilde{\psi}_1)\,ds}{\Lambda \int_{\Omega(V)} e^{\Phi - Vx}\tilde{\psi}_1\,dxdy}. \tag{7.5}$$

Also, we have $\tilde{\phi} = \tilde{\psi} + k(1+\tilde{\psi}_1)$, where $\tilde{\psi}$ is the solution of the problem

$$\Delta\tilde{\psi} - \zeta\tilde{\psi} + \Lambda e^{\Phi - Vx}\tilde{\psi} = 0 \quad \text{in } \Omega(V), \quad \partial_\nu\tilde{\psi} = \partial_\nu\tilde{\phi} \quad \text{on } \partial\Omega(V). \tag{7.6}$$

Then problem (7.2)–(7.3) with condition (6.10) is reduced to the following integro-differential equation on $\partial\Omega(V)$ for the only unknown $v := \partial_\nu\tilde{\phi}$,

$$\begin{aligned} -\frac{\gamma}{\zeta}\partial^2_{\tau\tau}v - \frac{\gamma\kappa^2}{\zeta}v + \int_{\partial\Omega(V)} Q(s,\tilde{s},V)v(\tilde{s})\,d\tilde{s} \\ + V\nu_x v - \left(\partial^2_{\nu\nu}\Phi + V\nu_y'\right)\tilde{\psi} - \partial_\tau\left(\tilde{\psi}\partial_\tau\Phi\right) - V\nu_y\partial_\tau\tilde{\psi} = 0, \end{aligned} \tag{7.7}$$

where Q is a smooth function and $Q = -p_*'(\pi R^2)/\zeta - m_0/(\pi R^2\zeta) + O(V)$ as $V \to 0$. Observe that (7.7) is a (regular) perturbation of the equation

$$-\frac{\gamma}{\zeta}\partial^2_{\tau\tau}v - \frac{\gamma}{\zeta R^2}v - \int_{\partial B_R}(p_*'(\pi R^2)/\zeta + m_0/(\pi R^2\zeta))v(\tilde{s})\,d\tilde{s} = 0 \quad \text{on } \partial B_R.$$

Under condition (4.6) the latter equation has the only (even) solution $\cos\frac{s}{R}$, up to multiplication by a constant. On the other hand, since the multiplicity of zero eigenvalue of the operator $\mathcal{A}(V)$ is at least two ($\forall V$), and the same holds for $\mathcal{A}^*(V)$, equation (7.7) always has at least one nontrivial solution. Thus, after writing (7.7) in the operator form $\tilde{\mathcal{L}}(V)v = 0$ in $L^2(\partial\Omega(V))$, we see that $\tilde{\mathcal{L}}(V)$ has simple isolated eigenvalue $\lambda = 0$. Then for some $\delta > 0$ and sufficiently small V the operator $(\lambda - \tilde{\mathcal{L}}(V))^{-1}$ is bounded if $0 < |\lambda| \le \delta$ and operator norms $\|(\lambda - \tilde{\mathcal{L}}(V))^{-1}\|$ are uniformly bounded for complex λ with $|\lambda| = \delta$. Therefore, if $\tilde{v}$ is an approximation of an eigenfunction v then we have

$$\tilde{\Pi}_0\tilde{v} - \tilde{v} = \frac{1}{2\pi\mathrm{i}}\oint_{|\lambda|=\delta}(\lambda - \tilde{\mathcal{L}}(V))^{-1}\tilde{\mathcal{L}}(V)\tilde{v}\frac{d\lambda}{\lambda}$$

(this representation is obtained by taking the integral over the circle $|\lambda| = \delta$ of the identity $\frac{1}{\lambda}\tilde{v} = (\lambda - \tilde{\mathcal{L}}(V))^{-1}\tilde{v} - \frac{1}{\lambda}(\lambda - \tilde{\mathcal{L}}(V))^{-1}\tilde{\mathcal{L}}(V)\tilde{v}$), where $\tilde{\Pi}_0$ denotes the spectral projector on the null space of $\tilde{\mathcal{L}}(V)$. Thus

$$\|\tilde{\Pi}_0\tilde{v} - \tilde{v}\|_{L^2(\partial\Omega(V))} \le C\|\tilde{\mathcal{L}}(V)\tilde{v}\|_{L^2(\partial\Omega(V))}$$

and, since the principal term of $\tilde{\mathcal{L}}(V)$ is $-\frac{\gamma}{\zeta}\partial^2_{\tau\tau}\cdot$, one can improve this bound to $\|\tilde{\Pi}_0\tilde{v} - \tilde{v}\|_{H^2(\partial\Omega(V))} \le C\|\tilde{\mathcal{L}}(V)\tilde{v}\|_{L^2(\partial\Omega(V))}$.

Now consider $\tilde{v} := -\zeta\nu_x + 2AV\nu_x^2 + V(B-A)$ (see (6.24)). Introducing the pair $(w, k(w))$ that solves

$$\Delta w - \zeta w + \Lambda e^{\Phi - Vx}w = k(w)\Lambda e^{\Phi - Vx} \quad \text{in } \Omega(V), \quad \partial_\nu w = \tilde{v} \text{ on } \partial\Omega(V),$$

with the additional condition $\int_{\partial\Omega(V)}\partial_\nu w\,ds = \zeta\int_{\Omega(V)} w\,dxdy$, we get by virtue of Lemma 6.2 that $\|w - \tilde{\phi}\|_{C^j(\overline{\Omega(V)})} = O(V^2)$ $\forall j \in \mathbb{Z}_+$, $k(w) = k_0V + O(V^2)$, where $\tilde{\phi}$, k_0 are given by (6.22) and (6.18). Direct calculations show that

$$\|\tilde{\mathcal{L}}(V)\tilde{v}\|_{C(\partial\Omega(V))} = O(V^2).$$

Indeed, observe that $\kappa = \frac{1}{R}+V^2O(1)$, $w = -m_0R\nu_x+VO(1)$, $\partial_\tau w = m_0\nu_y+VO(1)$, $\partial^2_{\nu\nu}\Phi + V\nu_y' = m_0VR\nu_x + V^2O(1)$ and

$$\begin{aligned}\partial_{\tau\tau}(\partial_\nu w) = (-\zeta\nu_x + 2AV\nu_x^2)'' =& \zeta(\kappa\nu_y)' - 4AV(\kappa\nu_x\nu_y)' \\ =& \frac{\zeta}{R^2}\nu_x - \frac{4}{R^2}AV(2\nu_x^2-1) + V^2O(1)\end{aligned}$$

on $\partial\Omega(V)$, where $O(1)$ stands for various uniformly bounded functions on $\partial\Omega(V)$. Then

$$\begin{aligned}\tilde{\mathcal{L}}\tilde{v} = &\Big(m_0^2R^2 + m_0 - \zeta + \frac{6\gamma A}{\zeta R^2}\Big)V\nu_x^2 \\ &- \Big(m_0 + \frac{3\gamma A}{\zeta R^2} + \frac{\gamma B}{\zeta R^2} + 2\pi R\frac{p_*'(\pi R^2)}{\zeta}B + m_0k_0\Big)V + V^2O(1).\end{aligned} \tag{7.8}$$

Both the coefficient in front of $V\nu_x^2$ and the coefficient in front of V in (7.8) vanish by virtue of formulas (6.20) for A and B. Thus we have $\|v-\tilde{v}\|_{H^2(\partial\Omega(V))} \le CV^2$ for a properly normalized solution v of (7.7). Finally, retrieving first the number k and the auxiliary function $\tilde{\phi} = \tilde{\psi} + k(1+\tilde{\psi}_1)$ via (7.4)–(7.6) for $\partial_\nu\phi = v$ and repeating this procedure with $\tilde{v}$ in place of v, then reconstructing W_2^* and its approximation corresponding to $\tilde{v}$ one completes the proof of Lemma 7.1 (details are left to the reader). $\square$

Asymptotic expansions constructed in Section 5 suggest that the operator $\mathcal{A}(V)$ has a small nonzero eigenvalue $\lambda(V)$ and

$$\lambda(V) = -\frac{E'(R)}{M'_{\rm ss}(R)}VM'(V)(1+O(V)) \quad \text{as } V \to 0. \tag{7.9}$$

Theorem 7.2. *Assume that conditions of Theorem* 4.1 *are satisfied and also that* $M'(V) \neq 0$ *for sufficiently small* $V \neq 0$. *Then the spectrum of the operator* $\mathcal{A}(V)$ *has the following structure near zero:* $\mathcal{A}(V)$ *has a small eigenvalue* $\lambda(V)$ *given by the asymptotic formula* (7.9) *in addition to the zero eigenvalue with multiplicity two whose eigenvector is given by* (5.6) *and generalized eigenvector is given by* (5.7). *Other eigenvalues are bounded away from zero.*

Remark 7.3. In generic case $M''(0) \neq 0$ (for almost all values of the parameters $p_{\rm h}$, $k_{\rm e}$, ζ, and γ). Then formula (7.9) is simplified to

$$\lambda(V) = -V^2\frac{E'(R)}{M'_{\rm ss}(R)}M''(0) + O(V^3) \quad \text{as } V \to 0. \tag{7.10}$$

Remark 7.4. In Theorem 7.2 we tacitly assume that operator $\mathcal{A}(V)$ is restricted to the subspace of vectors that are symmetric with respect to the x-axis, while the general case without any symmetry restrictions on eigenvectors and generalized eigenvectors is considered in Section 8, see Theorem 8.3.

Proof. Let W_2^* be a generalized eigenvector of $\mathcal{A}^*(V)$ corresponding to the eigenvector $W_1^* = (1, \Lambda e^{\Phi - Vx})$, $\mathcal{A}^*(V)W_2^* = W_1^*$. The space $L^2(\Omega(V)) \times L^2(\partial\Omega(V))$ decomposes into the direct sum of invariant subspaces $span\{W_1, W_2\}$ and

$$\mathcal{I}(V) := \{W \in L^2(\Omega(V)) \times L^2(\partial\Omega(V));\ \langle W, W_1^*\rangle_{L^2} = \langle W, W_2^*\rangle_{L^2} = 0\} \tag{7.11}$$

of the operator $\mathcal{A}(V)$, where W_1, W_2 are given by (5.6)–(5.7) (the eigenvector of $\mathcal{A}(V)$ corresponding to the zero eigenvalue and a generalized eigenvector). This induces also the decomposition of the domain

$$D(\mathcal{A}(V)) = \{(m,\rho) \in H^2(\Omega(V)) \times H^3(\partial\Omega(V)) \text{ such that (5.5) holds}\}$$

into the sum $D(\mathcal{A}(V)) = D(\mathcal{A}(V)) \cap \mathcal{I}(V) \oplus span\{W_1, W_2\}$.

Fix a sufficiently small $\delta > 0$ such that $\mathcal{A}_{ss}(R)$ does not have eigenvalues λ with $0 < |\lambda| \le \delta$. Then we claim that for sufficiently small V the operator $(\lambda - \mathcal{A}(V))^{-1}$ exists and is uniformly bounded on $\delta/2 \le |\lambda| \le \delta$. Indeed, assume by contradiction that for a sequence $V_j \to 0$ $\exists W_j \in D(\mathcal{A}(V_j)) \cap \mathcal{I}(V_j)$, $W_j = (m_j, \rho_j)$, with $\|m_j\|^2_{L^2(\Omega(V_j))} + \|\rho_j\|^2_{L^2(\partial\Omega(V_j))} = 1$, such that norms of $U_j = (\lambda_j - \mathcal{A}(V_j))W_j$ in $L^2(\Omega(V_j)) \times L^2(\partial\Omega(V_j))$ tend to zero as $j \to \infty$. We use Lemma 7.5 which provides a priori estimates implying that norms $\|m_j\|_{H^2(\Omega(V_j))}$ and $\|\rho_j\|_{H^3(\partial\Omega(V_j))}$ are uniformly bounded.

Lemma 7.5. *There exists $K = K(\overline{V}) > 0$ such that for all V with $|V| < \overline{V}$ every pair (m,ρ) solving*

$$\Delta\phi + m = \zeta\phi \quad \text{in } \Omega(V), \tag{7.12}$$

$$\zeta(\phi + V\nu_x\rho) = p_*'(|\Omega(V)|)\int_{\partial\Omega(V)} \rho(s)ds + \gamma(\rho'' + \kappa^2\rho) \quad \text{on } \partial\Omega(V), \tag{7.13}$$

$$\varrho + K\rho = \frac{\partial\phi}{\partial\nu} + \frac{\partial^2\Phi}{\partial\nu^2}\rho - \left(\frac{\partial\Phi}{\partial\tau} + V\nu_y\right)\rho' \quad \text{on } \partial\Omega(V), \tag{7.14}$$

$$f + Km = \Delta m + V\partial_x m - \operatorname{div}(\Lambda e^{\Phi - Vx}\nabla\phi) - \operatorname{div}(m\nabla\Phi) \quad \text{in } \Omega(V), \tag{7.15}$$

$$\partial_\nu m + \Lambda e^{\Phi - Vx}\left(\frac{\partial^2\Phi}{\partial\nu^2}\rho - \left(\frac{\partial\Phi}{\partial\tau} + V\nu_y\right)\rho'\right) = 0 \quad \text{on } \partial\Omega(V) \tag{7.16}$$

satisfies the bound

$$\|\rho\|_{H^3(\partial\Omega(V))} + \|m\|_{H^2(\Omega(V))} \le C(\|\varrho\|_{L^2(\Omega(V))} + \|f\|_{L^2(\Omega(V))}). \tag{7.17}$$

Proof. Without loss of generality we can assume that ρ and m are sufficiently smooth. Also, for brevity we suppress hereafter the dependence of the domain Ω on V.

The crucial a priori bound is obtained multiplying equation (7.12) by the harmonic extension $\mathcal{H}(\rho)$ of ρ from $\partial\Omega$ into Ω ($\Delta\mathcal{H}(\rho) = 0$ in Ω, and $\mathcal{H}(\rho) = \rho$ on $\partial\Omega$) and integrating over Ω. This yields, after integrating by parts twice and eliminating ϕ, $\partial_\nu\phi$ from the integrals over the boundary with the help of (7.13) and (7.14),

$$\begin{aligned} K\int_{\partial\Omega}\rho^2\,ds - \frac{\gamma}{\zeta}\int_{\partial\Omega}\rho''\partial_\nu\mathcal{H}(\rho)\,ds &= \int_\Omega(\zeta\phi - m)\mathcal{H}(\rho)\,dxdy \\ &+ \int_{\partial\Omega}\left(\left(\frac{\gamma\kappa^2}{\zeta} - V\nu_x\right)\rho\partial_\nu\mathcal{H}(\rho) + \frac{\partial^2\Phi}{\partial\nu^2}\rho^2 - \left(\frac{\partial\Phi}{\partial\tau} + V\nu_y\right)\rho'\rho - \rho\varrho\right)ds. \end{aligned} \tag{7.18}$$

Next observe that the left hand side of (7.18) represents square of a norm in $H^{3/2}(\partial\Omega)$ when $K > 0$ is sufficiently large. Actually, the second term solely defines a seminorm in $H^{3/2}(\partial\Omega)$ if $\kappa \ge 0$. Indeed, using the Frenet-Serret formulas

$\partial_\tau \nu_x = \kappa\tau_x = -\kappa\nu_y$, $\partial_\tau\nu_y = \kappa\tau_y = \kappa\nu_x$ and the fact that $\Delta\mathcal{H}(\rho) = 0$ we find

(7.19)
$$-\rho''\partial_\nu\mathcal{H}(\rho) = -\partial_\tau(\partial_\tau\mathcal{H}(\rho))\partial_\nu\mathcal{H}(\rho) \\ = \kappa(\partial_\nu\mathcal{H}(\rho))^2 + \partial_\nu\mathcal{H}(\rho)\left(\nu_x^2\partial^2_{xx}\mathcal{H}(\rho) + 2\nu_x\nu_y\partial^2_{xy}\mathcal{H}(\rho) + \nu_y^2\partial^2_{yy}\mathcal{H}(\rho)\right),$$

(7.20)
$$\partial_\tau\mathcal{H}(\rho))\partial_\tau(\partial_\nu\mathcal{H}(\rho)) = \kappa(\partial_\tau\mathcal{H}(\rho))^2 + \nabla\mathcal{H}(\rho)\cdot\partial_\nu\nabla\mathcal{H}(\rho) \\ - \partial_\nu\mathcal{H}(\rho)\left(\nu_x^2\partial^2_{xx}\mathcal{H}(\rho) + 2\nu_x\nu_y\partial^2_{xy}\mathcal{H}(\rho) + \nu_y^2\partial^2_{yy}\mathcal{H}(\rho)\right).$$

Then taking the half-sum of these identities and integrating over $\partial\Omega$ we obtain, using integration by parts and the fact that $\Delta\mathcal{H}(\rho) = 0$,

$$\begin{aligned} -\int_{\partial\Omega}\rho''\partial_\nu\mathcal{H}(\rho)\,ds &= -\frac{1}{2}\int_{\partial\Omega}\rho''\partial_\nu\mathcal{H}(\rho)\,ds + \frac{1}{2}\int_{\partial\Omega}\partial_\tau\mathcal{H}(\rho))\partial_\tau(\partial_\nu\mathcal{H}(\rho))\,ds \\ &= \frac{1}{2}\int_{\partial\Omega}\kappa|\nabla\mathcal{H}(\rho)|^2\,ds + \frac{1}{2}\int_{\partial\Omega}\nabla\mathcal{H}(\rho)\cdot\partial_\nu\nabla\mathcal{H}(\rho)\,ds \\ &= \frac{1}{2}\int_{\partial\Omega}\kappa|\nabla\mathcal{H}(\rho)|^2\,ds + \frac{1}{2}\int_{\Omega}|\nabla^2\mathcal{H}(\rho)|^2\,dxdy. \end{aligned} \tag{7.21}$$

Thus $-\frac{\gamma}{\zeta}\int_{\partial\Omega}\rho''\partial_\nu\mathcal{H}(\rho)\,ds \geq \theta\|\rho\|^2_{H^{3/2}(\partial\Omega)} - C\|\rho\|^2_{L^2(\partial\Omega)}$ with some constants $\theta > 0$ and C that does not depend on ρ, and one derives from (7.18) the following bound

$$\begin{aligned} K\|\rho\|^2_{L^2(\partial\Omega)} + \frac{\theta}{2}\|\rho\|^2_{H^{3/2}(\partial\Omega)} &\leq -\frac{\theta}{4}\|\rho\|^2_{H^{3/2}(\partial\Omega)} + C_1\|\rho\|^2_{L^2(\partial\Omega)} \\ &+ C_1\left(\|\varrho\|^2_{L^2(\partial\Omega)} + \|\rho\|_{L^2(\partial\Omega)}\|\phi\|_{L^2(\Omega)} + \|m\|^2_{L^2(\Omega)}\right). \end{aligned} \tag{7.22}$$

To find a bound for L^2-norm of ϕ, represent ϕ as $\phi = \frac{\gamma}{\zeta}\mathcal{H}(\rho'') + G$, where G is the solution of

$$\Delta G = \zeta G + \gamma\mathcal{H}(\rho'') - m, \tag{7.23}$$

$$\zeta(G + V\nu_x\rho) = p'_*(|\Omega|)\int_{\partial\Omega}\rho(s)ds + \gamma\kappa^2\rho \quad \text{on } \partial\Omega. \tag{7.24}$$

Assume for a moment that a bound for $\|\mathcal{H}(\rho'')\|_{L^2}$ is known, then by elliptic estimates we have

$$\|G\|_{L^2(\Omega)} \leq C(\|\rho\|_{H^1(\partial\Omega)} + \|\mathcal{H}(\rho'')\|_{L^2(\Omega)} + \|m\|_{L^2(\Omega)}). \tag{7.25}$$

We proceed with derivation of a bound for $\|\mathcal{H}(\rho'')\|_{L^2(\Omega)}$. To this end consider the solution of the Dirichlet problem $\Delta g = \mathcal{H}(\rho'')$ in Ω, $g = 0$ on $\partial\Omega$, along with the functions $\mathcal{H}(\partial_\nu g)$, $\mathcal{H}(\rho')$ and its harmonic conjugate $\mathcal{H}^*(\rho')$ (such that $\partial_\nu\mathcal{H}^*(\rho') = -\partial_\tau\mathcal{H}(\rho') = -\rho''$). We have

$$\int_\Omega|\mathcal{H}(\rho'')|^2\,dxdy = \int_\Omega\mathcal{H}(\rho'')\Delta g\,dxdy \\ = \int_{\partial\Omega}\rho''\partial_\nu g\,ds = -\int_{\partial\Omega}\partial_\nu\mathcal{H}^*(\rho')\mathcal{H}(\partial_\nu g)\,ds = -\int_\Omega\nabla\mathcal{H}^*(\rho')\cdot\nabla\mathcal{H}(\partial_\nu g)\,dxdy,$$

while by elliptic estimates

$$\int_\Omega |\nabla \mathcal{H}(\partial_\nu g)|^2\,dxdy \le C_2\|\partial_\nu g\|_{H^{1/2}(\partial\Omega)} \le C_3\|g\|_{H^2(\Omega)} \le C_4\int_\Omega |\mathcal{H}(\rho'')|^2\,dxdy,$$
$$\int_\Omega |\nabla \mathcal{H}^*(\rho')|^2\,dxdy = \int_\Omega |\nabla \mathcal{H}(\rho')|^2\,dxdy \le C_2\|\rho'\|_{H^{1/2}(\partial\Omega)} \le C_5\|\rho\|_{H^{3/2}(\partial\Omega)}.$$

Thus $\|\mathcal{H}(\rho'')\|^2_{L^2(\Omega)} \le C_4C_5\|\rho\|_{H^{3/2}(\partial\Omega)^2}$, and in view of (7.25) we have

$$\|\phi\|_{L^2(\Omega)} \le C_6\left(\|\rho\|_{H^{3/2}(\partial\Omega)} + \|m\|_{L^2(\Omega)}\right). \tag{7.26}$$

Using (7.26) in (7.22) we see that for $K \ge C_1 + 1$ the following bounds hold,

$$\begin{aligned} \|\rho\|^2_{H^{3/2}(\partial\Omega)} &\le C\left(\|\varrho\|^2_{L^2(\partial\Omega)} + \|m\|^2_{L^2(\Omega)}\right), \\ \|\phi\|^2_{L^2(\Omega)} &\le C\left(\|\varrho\|^2_{L^2(\partial\Omega)} + \|m\|^2_{L^2(\Omega)}\right). \end{aligned} \tag{7.27}$$

It remains to find a bound for m. To this end multiply (7.15) by m and integrate over Ω. Using (7.16), (7.12) and the fact that $\partial_\nu(\Phi - Vx) = 0$ on $\partial\Omega$, we find

$$\begin{aligned} K\int_\Omega m^2\,dxdy + \int_\Omega |\nabla m|^2\,dxdy = &-\int_\Omega fm\,dxdy + \Lambda\int_\Omega \phi\operatorname{div}(m\nabla e^{\Phi - Vx})\,dxdy \\ &+ \int_\Omega \left(V\partial_x m - \nabla m\cdot\nabla\Phi - m\Delta\Phi + \Lambda e^{\Phi-Vx}(m - \zeta\phi)\right)m\,dxdy \\ &- \int_{\partial\Omega} \Lambda e^{\Phi - Vx}\left(\frac{\partial^2\Phi}{\partial\nu^2}\rho - \left(\frac{\partial\Phi}{\partial\tau} + V\nu_y\right)\rho'\right)m\,ds. \end{aligned} \tag{7.28}$$

The right hand side of (7.28) can be estimated with the help of bounds (7.27) and the inequality for traces $\int_{\partial\Omega}|m|^2ds \le C\int_\Omega(|\nabla m|^2 + m^2)\,dxdy$, as the result we get

$$K\int_\Omega m^2\,dxdy + \frac{1}{2}\int_\Omega |\nabla m|^2\,dxdy \le C_7\left(\int_\Omega |m|^2\,dxdy + \int_\Omega |f|^2\,dxdy + \|\varrho\|^2_{L^2(\partial\Omega)}\right). \tag{7.29}$$

Thus for $K \ge \max\{C_1, C_7\} + 1$ we have obtained a bound for H^1-norm of m in terms of L^2-norms of ϱ and f. Then by (7.27) we also have $\|\rho\|_{H^{3/2}(\partial\Omega)} + \|\phi\|_{L^2(\Omega)} \le C\left(|\varrho\|_{L^2(\partial\Omega)} + \|f\|_{L^2(\Omega)}\right)$. Consequently, applying elliptic estimates to problem (7.12), (7.14) one can show that $\|\phi\|_{H^1(\partial\Omega)} \le C\left(\|\varrho\|_{L^2(\partial\Omega)} + \|f\|_{L^2(\Omega)}\right)$. This, in turn implies, in view of equation (7.13), that $\|\rho\|_{H^3(\partial\Omega)} \le C\left(\|\varrho\|_{L^2(\partial\Omega)} + \|f\|_{L^2(\Omega)}\right)$. Finally, one completes the proof of Lemma 7.5 by applying elliptic estimates to (7.12)–(7.13) and (7.15)–(7.16). □

Proof of Theorem 7.2 *(Continued).* Writing the equation $U_j = (\mathcal{A} - \lambda_j(V_j))W_j$ as $\mathcal{A}(V_j))W_j + KW_j = (\lambda_j + K)W_j + U_j$ and applying Lemma 7.5 we see that norms $\|m_j\|_{H^2(\Omega(V))}$ and $\|\rho_j\|_{H^3(\partial\Omega(V))}$ are uniformly bounded. Therefore there exists λ with $\delta/2 \le |\lambda| \le \delta$, a function $\phi \in H^{3/2}(B_R)$ and nontrivial pair $(m,\rho) \in H^2(B_R)\times H^{5/2}(\partial B_R)$ such that, up to a subsequence, $\lambda_j \to \lambda$,

$$\left(\rho_j\left(L_js/(2\pi R)\right), \phi_j\left(x\left(L_js/(2\pi R)\right), y\left(L_js/(2\pi R)\right)\right)\right) \to (\rho(s), \phi(x(s), y(s)))$$

weakly in $H^3(\partial B_R)\times H^1(\partial B_R)$ (where L_j denotes the length of $\partial\Omega(V_j)$) and $m_j \to m$, $\phi_j \to \phi$ strongly in H^1 on every compact subset of B_R. Then passing to the limit in (variational formulation of) problem (5.4)-(5.5) with a smooth test function $v(x,y)$ we find

$$\lambda \int_{B_R} mv dxdy = -\int_{B_R} \nabla m \cdot \nabla v dxdy + m_0 \int_{B_R} (m - \zeta\phi) v dxdy, \tag{7.30}$$

where we have used (5.1) to eliminate $\Delta\phi_j$. Thus $m \in H^2(B_R)$ and m satisfies $\lambda m = \Delta m + m_0(m - \zeta\phi)$ in B_R along with the boundary condition $\partial_\nu m = 0$ on ∂B_R. Passing to the limit in (5.1) with test functions from $C_0^\infty(B_R)$ we get $\Delta\phi = \zeta\phi - m$ in B_R, thus the equation for m rewrites as $\lambda m = \Delta m - m_0 \Delta\phi$ in B_R. Also, taking limit in (5.2) yields $\zeta\phi = p_*'(|B_R|) \int_{\partial B_R} \rho(s) ds + \gamma(\rho'' + \frac{1}{R^2}\rho)$ on ∂B_R. Finally, using a smooth test function $v(x,y)$ in variational formulation of equation (5.1) with boundary condition (5.3) we obtain

(7.31)

$$\begin{aligned} 0 &= -\int_{\Omega(V_j)} \nabla\phi_j \cdot \nabla v \, dxdy + \int_{\Omega(V_j)} (m_j - \zeta\phi_j) v dxdy + \int_{\partial\Omega(V_j)} \lambda_j \rho_j v ds + o(1) \\ &= -\int_{B_R} \nabla\phi \cdot \nabla v \, dxdy + \int_{B_R} (m - \zeta\phi) v dxdy + \int_{\partial B_R} \lambda\rho v ds + o(1), \end{aligned}$$

implying that $\lambda\rho = \partial_r \phi$ on ∂B_R. Thus λ is an eigenvalue of the operator $\mathcal{A}_{ss}(R)$, contradicting the assumption. Repeating this reasoning for $\delta/2$ in place of δ, then $\delta/4$ etc. we conclude that all eigenvalues λ of $\mathcal{A}(V))$ with $|\lambda| \leq \delta$ necessarily converge to zero as $V \to 0$.

To establish convergence of eigenvalues with multiplicities, consider for sufficiently small V spectral projectors on the generalized eigenspaces corresponding to eigenvalues λ with $|\lambda| < \delta$,

$$\Pi_\delta(V) := \frac{1}{2\pi \mathrm{i}} \oint_{|\lambda|=\delta} (\lambda - \mathcal{A}(V))^{-1} \, d\lambda. \tag{7.32}$$

Let us show that restrictions $\Pi_\delta(V)\big|_{\mathcal{I}(V)}$ of $\Pi_\delta(V)$ to $\mathcal{I}(V)$ converge (in the sense described below) to

$$\Pi_0(0) = \frac{1}{2\pi \mathrm{i}} \oint_{|\lambda|=\delta} (\lambda - \mathcal{A}_{ss}(R))^{-1} \, d\lambda \text{ restricted to } \mathcal{I}(0),$$

as $V \to 0$, where

$$\mathcal{I}(0) := \{W \in L^2(B_R) \times L^2(\partial B_R); \langle W, W_1^*|_{V=0}\rangle_{L^2} = \langle W, (\Phi_V^0 - x, 0)\rangle_{L^2} = 0\}$$

(cf. (7.11)). Namely, we claim that for any sequence $V_j \to 0$ and $(m_j, \rho_j) \in \mathcal{I}(V_j)$ such that $\rho_j(L_j s/(2\pi R)) \to \rho$ in $L^2(\partial B_R)$, and $m_j \to m$ in $L^2(\mathbb{R}^2)$ (where we assume m_j and m continued by zero in $\mathbb{R}^2 \setminus \Omega(V_j)$ and $\mathbb{R}^2 \setminus B_R$, correspondingly) the sequence of pairs $(f_j, \varrho_j) := \Pi_\delta(V_j)(m_j, \rho_j)$ converges to $\Pi_0(0)(m, \rho)$ weakly in $H^2(B_R) \times H^3(\partial B_R)$, more precisely this convergence holds for functions f_j extended to B_R (if necessary) by standard reflection through the normal of $\partial\Omega(V)$ and rescaled $\varrho_j = \varrho_j(L_j s/(2\pi R))$. The proof of this claim follows exactly the lines above: we use Lemma 7.5 to get uniform a priori bounds for $(\lambda - \mathcal{A}(V_j))^{-1}(m_j, \rho_j)$ in $H^2(\Omega(V_j)) \times H^3(\partial\Omega(V_j))$ and then pass to limit in variational formulations of corresponding problems with smooth test functions. Moreover, since $(m_j, \rho_j) \in \mathcal{I}(V_j)$ we have $\langle (m_j, \rho_j) W_1^* \rangle_{L^2} = V_j k_0 \langle (m_j, \rho_j), W_2^* \rangle_{L^2} = 0$, therefore passing to the limit we get, by virtue of Lemma 7.1, $\langle (m, \rho) W_1^*|_{V=0} \rangle_{L^2} = \langle (m, \rho), (\Phi_V^0 - x, 0) \rangle_{L^2} = 0$, i.e. $(m, \rho) \in \mathcal{I}(0)$. Thus $\Pi_0(0)(m, \rho) \in \Pi_0(0)\mathcal{I}(0)$.

By Lemma 6.1 we have $\Pi_0(0)\mathcal{I}(0) = span\{W_1|_{V=0}\}$. Therefore the dimension of the space $\Pi_\delta(V)\mathcal{I}(V)$ is at most one for sufficiently small V. Indeed, otherwise there exists a sequence $V_j \to 0$ and elements $W_j, \tilde{W}_j$ of $\Pi_\delta(V_j)\mathcal{I}(V_j)$ that are mutually orthogonal and normalized to one in $L^2(\Omega(V_j)) \times L^2(\partial\Omega(V_j))$. Since $W_j = \Pi_\delta(V_j)W_j$ and $\tilde{W}_j = \Pi_\delta(V_j)\tilde{W}_j$, after extracting a subsequence, if necessary, both W_j and $\tilde{W}_j$ converge strongly in L^2-topology to limits belonging to $\Pi_0(0)\mathcal{I}(0) = span\{W_1|_{V=0}\}$, a contradiction. Furthermore, we construct below

$$W = W_{ans} - \theta W_1 \in \mathcal{I}(V) \quad \text{with } \theta = O(V), \tag{7.33}$$

out of the vectors W_{ans} from Lemma 5.1, then we have

$$\Pi_\delta(V)W \underset{V\to 0}{\longrightarrow} \Pi_0(0)W_1 = W_1 \neq 0. \tag{7.34}$$

Therefore $\mathcal{A}(V)\big|_{\mathcal{I}(V)}$ has for sufficiently small V exactly one simple eigenvalue $\lambda(V)$ with $|\lambda(V)| \leq \delta$, and $\lambda(V) \to 0$ as $V \to 0$. Moreover, by virtue of Lemma 5.1 we get

$$\|\mathcal{A}W - V^2\hat{\lambda}(V)W\|_{L^2} = O(V^2M'(V)). \tag{7.35}$$

Then, since

$$\begin{aligned} 0 =& \frac{1}{2\pi \mathrm{i}} \oint_{|\lambda|=\delta} (\lambda - \mathcal{A}(V))^{-1} \left(\hat{\lambda}(V)V^2 - \mathcal{A}(V)\right) W \, d\lambda \\ &+ \frac{1}{2\pi \mathrm{i}} \oint_{|\lambda|=\delta} (\lambda - \mathcal{A}(V))^{-1} \left(\lambda - \hat{\lambda}(V)V^2\right) W \, d\lambda \\ &= \Pi_\delta(V) \left(\hat{\lambda}(V)V^2 - \mathcal{A}(V)\right) W + \left(\lambda(V) - \hat{\lambda}(V)V^2\right) \Pi_\delta(V)W, \end{aligned}$$

we have

$$|\lambda(V) - \hat{\lambda}(V)V^2| \leq \frac{\|\mathcal{A}(V)W - \hat{\lambda}(V)V^2W\|_{L^2}}{\|\Pi_\delta(V)W\|_{L^2}} = O(V^2M'(V)).$$

It remains to find $\theta = \theta(V)$ such that $W = W_{ast} - \theta W_1 \in \mathcal{I}(V)$. According to Lemma 5.1 we have $\langle \mathcal{A}(V)W - \hat{\lambda}(V)V^2W, W_1^*\rangle_{L^2} = 0$, therefore

$$\hat{\lambda}(V)V^2\langle W, W_1^*\rangle_{L^2} = \langle \mathcal{A}(V)W, W_1^*\rangle_{L^2} = \langle W, \mathcal{A}^*(V)W_1^*\rangle_{L^2} = 0.$$

Thus we only need to choose θ such that $\theta\langle W_1, W_2^*\rangle_{L^2} = \langle W_{ast}, W_2^*\rangle_{L^2}$. Since $\langle \mathcal{A}(V)W_{ast}, W_2^*\rangle_{L^2} = \langle W_{ast}, W_1^*\rangle_{L^2} = \theta\langle W_1, W_1^*\rangle_{L^2} = \theta\langle \mathcal{A}(V)W_2, W_1^*\rangle_{L^2} = 0$, we have $\hat{\lambda}(V)V^2\langle W_{ast}, W_2^*\rangle_{L^2} = \langle \hat{\lambda}(V)V^2W_{ast} - \mathcal{A}(V)W_{ast}, W_2^*\rangle_{L^2}$, while by Lemma 5.1 and Lemma 7.1

$$\begin{aligned} \left|\langle \hat{\lambda}(V)V^2W_{ast} - \mathcal{A}(V)W_{ast}, W_2^*\rangle_{L^2}\right| \leq& \left\|\hat{\lambda}(V)V^2W_{ast} - \mathcal{A}(V)W_{ast}\right\|_{L^2} \\ &\times \|W_2^*\|_{L^2} = O(|M'(V)|^2V^2). \end{aligned}$$

This leads to the bound $\langle W_{ast}, W_2^*\rangle_{L^2} = O(VM'(V))$, and since $\langle W_1, W_2^*\rangle_{L^2} = \langle \mathcal{A}(V)W_2, W_2^*\rangle_{L^2} = \langle W_2, W_1^*\rangle_{L^2} = M'(V)$ we obtain the required bound $|\theta| \leq C|V|$. Theorem 7.2 is completely proved. $\square$

While Theorem 7.2 describes the smallest (in absolute value) nonzero eigenvalue of $\mathcal{A}(V)$, the following Theorem 7.6 shows that all eigenvalues of $\mathcal{A}(V)$ converge to the spectrum of $\mathcal{A}_{ss}(R)$ uniformly in half-planes $\mathbb{C}_K^+ = \{\lambda \in \mathbb{C}; \mathrm{Re}(\lambda) > K\}$.

Theorem 7.6. *Assume that conditions of Theorem* 4.1 *are fulfilled. Let* $\sigma(\mathcal{A}(V))$ *and* $\sigma(\mathcal{A}_{\rm ss}(R))$ *be spectra of operators* $\mathcal{A}(V)$ *and* $\mathcal{A}_{\rm ss}(R)$*, respectively. Then* $\forall K \in \mathbb{R}$ *the distance* $d = \sup\left\{{\rm dist}\,(\lambda, \sigma(\mathcal{A}_{\rm ss}(R)))\,; \lambda \in \sigma(\mathcal{A}(V)) \cap \mathbb{C}^+_K\right\}$ *from* $\sigma(\mathcal{A}(V)) \cap \mathbb{C}^+_K$ *to* $\sigma(\mathcal{A}_{\rm ss}(R))$ *tends to zero as* $V \to 0$*. Moreover, given an eigenvalue* $\lambda \in \sigma(\mathcal{A}_{\rm ss}(R))$*, there is a neighborhood* $\omega \ni \lambda$ *such that the number* $\#\sigma(\mathcal{A}(V)) \cap \omega$ *of eigenvalues of* $\mathcal{A}(V)$ *(counting algebraic multiplicities) in* ω *is less than or equal than the multiplicity of* λ *(as an eigenvalue of* $\mathcal{A}_{\rm ss}(R)$*) for sufficiently small* V*.*

Proof. Observe that arguments applied in Theorem 7.2 in a neighborhood of zero can be readily applied to any complex λ. That is arguing as in Theorem 7.2 one shows that if $\lambda \notin \sigma(\mathcal{A}_{\rm ss}(R))$ then a neighborhood of λ belongs to the resolvent set of $\mathcal{A}(V)$ for sufficiently small V. Next, for $\lambda \in \sigma(\mathcal{A}_{\rm ss}(R))$ one can consider spectral projectors given by the integral $\frac{1}{2\pi i}\oint_{\partial\omega}(\lambda - \mathcal{A}(V))^{-1}\,d\lambda$ (cf. (7.32)) and, reasoning as in Theorem 7.2, prove that $\#\sigma(\mathcal{A}(V)) \cap \omega$ does not exceed the multiplicity of λ for sufficiently small V. It remains to show that $\forall K \in \mathbb{R}$ the eigenvalues of $\mathcal{A}(V)$ whose real parts are larger than K stay uniformly bounded when $V \to 0$.

Let λ be an eigenvalue of $\mathcal{A}(V)$ such that ${\rm Re}(\lambda) > K$. Consider corresponding eigenvector $W = (m, \rho)$ normalized by

$$\int_\Omega |m|^2\,dxdy + \int_{\partial\Omega} |\rho|^2\,ds = 1, \tag{7.36}$$

hereafter for brevity we write Ω in place of $\Omega(V)$. Functions ρ and m satisfy

$$\lambda\rho = \frac{\partial\phi}{\partial\nu} + \frac{\partial^2\Phi}{\partial\nu^2}\rho - \left(\frac{\partial\Phi}{\partial\tau} + V\nu_y\right)\rho' \quad \text{on } \partial\Omega, \tag{7.37}$$

$$\lambda m = \Delta m + V\partial_x m - \Lambda\nabla e^{\Phi - Vx}\cdot\nabla\phi + \Lambda e^{\Phi - Vx}(m - \zeta\phi) - {\rm div}(m\nabla\Phi) \quad \text{in } \Omega, \tag{7.38}$$

along with boundary condition (5.5), the auxiliary function ϕ being a unique solution of (5.1)–(5.2). Consider, as in Lemma 7.5, the harmonic extension $\mathcal{H}(\rho)$ of ρ from $\partial\Omega$ into Ω and multiply (5.1) by the complex conjugate $\mathcal{H}(\overline{\rho})$ of $\mathcal{H}(\rho)$, then integrating over Ω we get (cf. (7.18))

$$\begin{aligned}\lambda\int_{\partial\Omega}|\rho|^2\,ds - \frac{\gamma}{\zeta}\int_{\partial\Omega}\rho''\partial_\nu\mathcal{H}(\overline{\rho})\,ds &= \int_\Omega(\zeta\phi - m)\mathcal{H}(\overline{\rho})\,dxdy \\ &+ \int_{\partial\Omega}\left(\left(\frac{\gamma\kappa^2}{\zeta} - V\nu_x\right)\rho\partial_\nu\mathcal{H}(\overline{\rho}) + \frac{\partial^2\Phi}{\partial\nu^2}|\rho|^2 - \left(\frac{\partial\Phi}{\partial\tau} + V\nu_y\right)\rho'\overline{\rho}\right)ds.\end{aligned} \tag{7.39}$$

Notice that by (7.21), $-\frac{\gamma}{\zeta}{\rm Re}\left(\int_{\partial\Omega}\rho''\partial_\nu\mathcal{H}(\overline{\rho})\,ds\right) \geq \theta\|\rho\|^2_{H^{3/2}(\partial\Omega)} - C\|\rho\|^2_{L^2(\partial\Omega)}$ with some constants $\theta > 0$ and C that does not depend on ρ. Therefore taking real part of (7.39) and estimating various terms in the right hand side of (7.39) as in the proof of Lemma 7.5, we obtain

$$\frac{\theta}{2}\|\rho\|_{H^{3/2}(\partial\Omega)} \leq -{\rm Re}(\lambda)\|\rho\|^2_{L^2(\partial\Omega)} + C_1\left(\|\rho\|^2_{L^2(\partial\Omega)} + \|m\|^2_{L^2(\Omega)}\right) \leq C_1 + |K|, \tag{7.40}$$

where we have also used (7.36) and the inequality $\mathrm{Re}(\lambda) > K$. Next, multiply (7.38) by $\overline{m}$ and integrate over Ω to derive, analogously to (7.28),

(7.41)
$$\lambda \int_\Omega |m|^2\,dxdy + \int_\Omega |\nabla m|^2\,dxdy = \Lambda \int_\Omega \phi \mathrm{div}(\overline{m}\nabla e^{\Phi - Vx})\,dxdy$$
$$+ \int_\Omega \left(V\partial_x m - \nabla m \cdot \nabla\Phi - m\Delta\Phi + \Lambda e^{\Phi - Vx}(m - \zeta\phi)\right)\overline{m}\,dxdy$$
$$- \int_{\partial\Omega} \Lambda e^{\Phi - Vx}\left(\frac{\partial^2\Phi}{\partial\nu^2}\rho - \left(\frac{\partial\Phi}{\partial\tau} + V\nu_y\right)\rho'\right)\overline{m}\,ds.$$

Taking real part of (7.41) one can show (as in the proof of Lemma 7.5) that $\|m\|_{H^1(\Omega)} \leq C$. Now, add (7.39) to (7.41) and collect terms with the factor λ to see that

$$|\lambda| \leq \left|\frac{\gamma}{\zeta}\int_{\partial\Omega} \rho''\partial_\nu\mathcal{H}(\overline{\rho})\,ds\right| + C,$$

i.e. we need only to obtain a bound for the term $\frac{\gamma}{\zeta}\int_{\partial\Omega}\rho''\partial_\nu\mathcal{H}(\overline{\rho})\,ds$. To this end one combines inequalities

$$\left|\int_{\partial\Omega}\rho''\partial_\nu\mathcal{H}(\overline{\rho})\,ds\right| \leq \|\rho''\|_{H^{-1/2}(\partial\Omega)}\|\partial_\nu\mathcal{H}(\overline{\rho})\|_{H^{1/2}(\partial\Omega)} \leq C\|\rho\|^2_{H^{3/2}(\partial\Omega)}$$

with the bound (7.40). □

Remark 7.7. Unlike Theorem 4.1, the above result holds without symmetry assumptions, i.e. it covers all eigenvalues, not necessarily corresponding to eigenvectors with reflection symmetry (with respect to the x-axis).

8. Linear stability analysis of traveling wave solutions with small velocities under perturbations without symmetry assumptions

So far we assumed reflection symmetry with respect to the x-axis of traveling waves (that are solutions $\phi = \Phi(x, y, V)$, $\Omega = \Omega(V)$ of (4.2)–(4.3)) and their perturbations. In this section we consider general perturbations with no symmetry assumptions on the pairs (m, ρ) from the domain of the linearized operator $\mathcal{A}(V)$. We begin with the case $V = 0$, i.e. we consider linearization around the stationary radial solution with the radius $R = R_0$ that satisfies the bifurcation conditions (4.18). The linearized operator $\mathcal{A}(0) = \mathcal{A}_{ss}(R)$ has the same eigenvalues as under the above symmetry assumption, but multiplicities of nonradial eigenvectors double since the odd Fourier modes $m = \hat{m}_n(r)\sin n\varphi$, $\rho = \hat{\rho}_n \sin n\varphi$ are also considered. In particular, $\mathcal{A}_{ss}(R)$ has zero eigenvalue with two eigenvectors corresponding to infinitesimal shifts (in x- and y-directions)

$$(m, \rho) = (0, \nu_x) = (0, \cos\varphi), \quad (m, \rho) = (0, \nu_y) = (0, \sin\varphi), \tag{8.1}$$

and two generalized eigenvectors

$$(m, \rho) = (m_0(\Phi_V^0(x, y) - x), 0), \quad (m, \rho) = (m_0(\Phi_V^0(y, x) - y), 0) \tag{8.2}$$

(cf. (5.7) with $V = 0$), where Φ_V^0 is the unique solution of (4.14). By virtue of Lemma 6.1 the multiplicity of zero eigenvalue equals to five, the complementary eigenvector being $(2\pi R p_*'(\pi R^2) + \gamma/R^2, 1)$. For $V \neq 0$ the generalized eigenspace corresponding to zero eigenvalue is described in

Proposition 8.1. *The operator* $\mathcal{A}(V)$ *defined in* (5.1)-(5.5) *has the zero eigenvalue with multiplicity at least four. There are two eigenvectors* $W_1 = (m_1, \rho_1)$, $W_3 = (m_3, \rho_3)$ *corresponding to infinitesimal shifts,*

$$m_1 := -\Lambda(V)\partial_x e^{\Phi - Vx}, \rho_1 := \nu_x, \quad m_3 := -\Lambda(V)\partial_y e^{\Phi - Vx},\ \rho_3 := \nu_y, \tag{8.3}$$

the generalized eigenvector W_2 *given by* (5.7) *(which is obtained by taking derivative of the traveling wave solution in* V*), and the following generalized eigenvector* $W_4 = (m_4, \rho_4)$,

(8.4)
$$m_4 := -\frac{\Lambda(V)}{V}\partial_\varphi e^{\Phi - Vx} = \frac{\Lambda(V)}{V}(y\partial_x e^{\Phi - Vx} - x\partial_y e^{\Phi - Vx}), \quad \rho_4 := \frac{1}{V}(-y\nu_x + x\nu_y),$$

which represents infinitesimal rotations of the traveling wave solution. The generalized eigenvectors W_2, W_4 *satisfy* $\mathcal{A}(V)W_2 = W_1$, $\mathcal{A}(V)W_4 = W_3$.

Remark 8.2. The eigenvectors W_1, W_3 appear due to translational invariance of the problem (2.9)–(2.13) under shifts of the frame in x and y respectively. This problem is also invariant under rotations. However, equations (4.2)–(4.3) for the traveling wave solutions and corresponding linearized operator are written in the frame that moves with velocity V. That is why rotational invariance gives rise to the generalized eigenvector W_4 rather than eigenvector.

Proof. First we show that $\mathcal{A}(V)W_3 = 0$. Clearly (5.1) is satisfied with $\phi = -\partial_y\Phi$, also $(\mathcal{A}(V)W_3)_m$ (given by (5.4)) equals zero identically. To verify that $(\mathcal{A}(V)W_3)_\rho = 0$ take the tangential derivative of the boundary condition $\partial_\nu\Phi = V\nu_x$ (this amounts to differentiating with respect to the arc length s):

$$-\partial^2_{xx}\Phi\nu_x\nu_y + \partial^2_{xy}\Phi\nu_x^2 - \partial^2_{xy}\Phi\nu_y^2 + \partial^2_{yy}\Phi\nu_x\nu_y - \partial_x\Phi\kappa\nu_y + \partial_y\Phi\kappa\nu_x = -V\kappa\nu_y, \tag{8.5}$$

where we have used the Frenet-Serret formulas $\nu_x' = -\kappa\nu_y$, $\nu_y' = \kappa\nu_x$. Multiply this relation by ν_x and add to its both sides $\partial^2_{\nu\nu}\Phi\nu_y = (\partial^2_{xx}\Phi\nu_x^2 + 2\partial^2_{xy}\Phi\nu_x\nu_y + \partial^2_{yy}\Phi\nu_y^2)\nu_y$ to find

$$0 = \partial_\nu\partial_y\Phi - \partial^2_{\nu\nu}\Phi\nu_y + \kappa\nu_x(\partial_\tau\Phi + V\nu_y) = \partial_\nu\partial_y\Phi - \partial^2_{\nu\nu}\Phi\nu_y + (\partial_\tau\Phi + V\nu_y)\nu_y'.$$

The verification of (5.5) is analogous, while to show (5.2) we differentiate the equality $\zeta\Phi = p_*(|\Omega|) - \gamma\kappa$ in s and obtain $\zeta\partial_\tau\Phi = -\gamma\kappa'$. Then recalling that $\partial_\nu\Phi = V\nu_x$ we derive

$$-\zeta\partial_y\Phi = -\zeta(\partial_\tau\Phi\tau_y + \partial_\nu\Phi\nu_y) = \gamma\kappa'\tau_y - \zeta V\nu_x\nu_y = \gamma(\nu_y'' + \kappa^2\nu_y) - \zeta V\nu_x\nu_y.$$

Clearly, all the above arguments apply to show that W_1 is also an eigenvector. An alternative, more direct proof of this fact is given in Appendix A. It is also shown there that $\mathcal{A}(V)W_2 = W_1$, by taking finite differences to approximate the derivative of the traveling wave solution in V.

We proceed now with the vector W_4. Take the derivative of $\Delta\Phi + \Lambda(V)e^{\Phi - Vx} = \zeta\Phi$ in φ to obtain that (5.1) is satisfied with $\phi = -\partial_\varphi\Phi$. Also, taking the derivative in φ of the equation $-V\partial_x e^{\Phi - Vx} = \Delta e^{\Phi - Vx} - \mathrm{d}iv(e^{\Phi - Vx}\nabla\Phi)$ and using the identities $\partial_\varphi\partial_x\cdot = \partial_x\partial_\varphi\cdot - \partial_y\cdot$, $\partial_\varphi\partial_y\cdot = \partial_y\partial_\varphi\cdot + \partial_x\cdot$ we get $m_3 = \Delta m_4 + Vm_4 - \mathrm{d}iv(m_4\nabla\Phi) + \Lambda(V)\mathrm{d}iv(e^{\Phi - Vx}\nabla\partial_\varphi\Phi)$. Considering equations on the boundary $\partial\Omega(V)$ we provide details only for equation (5.3), the verification of (5.2) and (5.5) being similar. Multiply the equation $\partial_\nu\partial_x\Phi - \partial^2_{\nu\nu}\Phi\nu_x + (\partial_\tau\Phi + V\nu_y)\nu_x' = 0$

by y and subtract the equation $-\partial_\nu\partial_y\Phi+\partial^2_{\nu\nu}\Phi\nu_y-(\partial_\tau\Phi+V\nu_y)\nu'_y=0$ multiplied by x. After simple manipulations we obtain

$$\begin{aligned}0&=-\partial_\nu\partial_\varphi\Phi-\nu_y\partial_x\Phi+\nu_x\partial_y\Phi+\partial^2_{\nu\nu}\Phi(x\nu_y-y\nu_x)+(\partial_\tau\Phi+V\nu_y)(y\nu'_x-x\nu'_y)\\&=-\partial_\nu\partial_\varphi\Phi+\partial_\tau\Phi+\partial^2_{\nu\nu}\Phi(x\nu_y-y\nu_x)+(\partial_\tau\Phi+V\nu_y)\left((y\nu_x-x\nu_y)'-y'\nu_x+x'\nu_y\right),\end{aligned}$$

where x' and y' are derivatives of $x=x(s)$ and $y=y(s)$ in s. Since $x'=\tau_x=-\nu_y$ and $y'=\tau_y=\nu_x$ we finally get

$$-\partial_\nu\partial_\varphi\Phi+\partial^2_{\nu\nu}\Phi(x\nu_y-y\nu_x)-(\partial_\tau\Phi+V\nu_y)(x\nu_y-y\nu_x)'=V\nu_y.$$

Proposition 8.1 is proved. □

While Theorem 7.2 describes all small (in absolute value) eigenvalues of the operator $\mathcal{A}(V)$ in the space of vectors possessing symmetry with respect to the x-axis, Theorem 7.6 and Proposition 8.1 show that in general case, without the said symmetry assumption, the structure of the spectrum of $\mathcal{A}(V)$ near zero is the same as in Theorem 7.2 but the multiplicity of zero eigenvalue changes to four. Then, taking into account Theorem 3.5, we arrive at the following result which summarizes spectral analysis of the operator $\mathcal{A}(V)$.

Theorem 8.3. *Assume that conditions of Theorem* 4.1 *are satisfied, and* $M'(V)\neq 0$ *for sufficiently small* $V\neq 0$. *Then the operator* $\mathcal{A}(V)$ *has for small* $V\neq 0$ *zero eigenvalue and its multiplicity is equal to four. The next smallest in absolute value eigenvalue is* $\lambda(V)\neq 0$, *this eigenvalue is simple and it is given by the asymptotic formula* (7.9). *All other eigenvalues have real parts bounded away from zero. If additionally conditions of Theorem* 3.5 *are satisfied then nonzero eigenvalues other than* $\lambda(V)$ *have negative real parts.*

Notice that under the condition (3.17) the radially symmetric stationary solutions (3.1) with radii R close to the critical radius $R=R_0$ can be reparametrized by their total myosin masses M_{ss}, see Remark 3.6. Then the factor $E'(R)/M'_{ss}(R)$ in the formula (7.9) writes as

$$\frac{E'(R)}{M'_{ss}(R)}=\frac{dE}{dM_{ss}}.$$

Moreover, using Lemma 4.4 one can derive an explicit formula for this factor. Considering the total myosin mass of traveling waves in the companion paper [29] an explicit formula for $M''(0)$ is obtained via asymptotic expansions in the limit of small velocities (see [29], Supplementary Material). Then performing computations

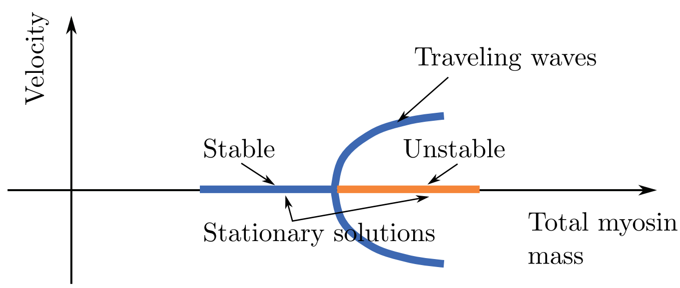

FIGURE 1. Supercritical pitchfork bifurcation.

for factors in formula (7.9) (more precisely, its particular case (7.10)) we see that in a wide range of parameters bifurcation of traveling wave solutions is *always the supercritical pitchfork*, since the real part of the key eigenvalue $\lambda(V)$ is always negative for sufficiently small V. In particular, this holds when the condition (3.17) and conditions of Theorem 3.5 are satisfied. This result agrees with 1D results from [27], where the normal form analysis revealing the structure of the bifurcation was performed for the first time. Also, Fig. 2 (borrowed from [29]) depicts approximate shapes of traveling wave solutions and densities of myosin for small velocities V. The shape becomes asymmetric with increasing V and the myosin accumulates at

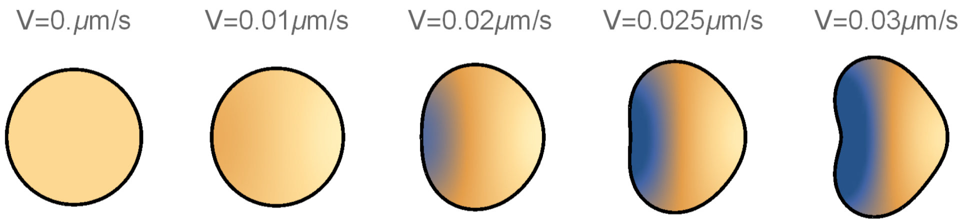

FIGURE 2. Traveling wave solutions with increasing velocities. Motion is to the right. Darker colors correspond to higher myosin density. See [29, Supplementary Material] for parameter values.

the rear. This myosin accumulation is consistent with experimental results from [30].

APPENDIX A. DERIVATION OF THE LINEARIZED OPERATOR

Consider problem (2.9)–(2.13) in the frame moving with constant velocity V in x-direction, and assume that a solution is represented in the perturbative form $m(x, y, t) + \Lambda e^{\Phi(x,y,V)-Vx}$, $\partial\Omega = \{(x(s), y(s)) + \rho(s, t)\nu(s);\ (x(s), y(s)) \in \partial\Omega(V)\}$ with respect to the traveling wave $(\Lambda e^{\Phi(x,y,V)-Vx}, \Omega(V))$ (which is a stationary solution in moving frame), assume also the representation $\phi(x, y, t) + \Phi(x, y, V)$ for the solution of problem (2.9)–(2.10). Hereafter we assume that m, ρ and ϕ are small and smooth enough functions, and the function Φ is extended as a smooth function in a neighborhood of $\Omega(V)$ (such an extension exists thanks to the C^∞ smoothness of the boundary and the function Φ, $\Phi \in C^\infty(\overline{\Omega(V)})$). Then we have

$$-\Delta\phi + \zeta\phi - m = \Delta\Phi - \zeta\Phi + \Lambda e^{\Phi - Vx} \quad \text{in } \Omega, \tag{A.1}$$

$$\zeta\phi = (p_*(|\Omega|) - p_*(|\Omega(V)|)) - (\zeta\Phi - p_*(|\Omega(V)|) + \gamma\kappa) - \gamma(H - \kappa) \quad \text{on } \partial\Omega, \tag{A.2}$$

$$V_N - \frac{\partial\phi}{\partial\nu} = \nabla\phi\cdot(N - \nu) + \frac{\partial\Phi}{\partial N} - VN_x \quad \text{on } \partial\Omega, \tag{A.3}$$

$$\begin{aligned}\partial_t m - \Delta m - V\partial_x m + \operatorname{div}(\Lambda e^{\Phi - Vx}\nabla\phi) + \operatorname{div}(m\nabla\Phi)& \\ = \Lambda\left(\Delta e^{\Phi - Vx} + V\partial_x e^{\Phi - Vx} - \operatorname{div}(e^{\Phi - Vx}\nabla\Phi)\right) - \operatorname{div}(m\nabla\phi)& \quad \text{in } \Omega,\end{aligned} \tag{A.4}$$

$$\partial_\nu m = \nabla m\cdot(\nu - N) - \Lambda\frac{\partial}{\partial N}e^{\Phi - Vx} \quad \text{on } \partial\Omega, \tag{A.5}$$

where N is the outward pointing normal to $\partial\Omega$, V_N denotes the normal velocity of $\partial\Omega$, and H stands for the curvature of $\partial\Omega$. The last term $-VN_x$ in (A.3) appears because of passing to the moving frame. The boundary $\partial\Omega$ is parametrized by the arc length s on $\partial\Omega(V)$ via the map $s \mapsto (x(s), y(s)) + \rho(s,t)\nu(s)$. Therefore considering vectorial line element on $\partial\Omega$ one can calculate the tangent vector T using Frenet-Serre formulas $\nu' = \kappa\tau$, $\tau' = -\kappa\nu$,

$$T = \frac{1}{\sqrt{(\rho')^2 + (1+\kappa\rho)^2}}((1+\kappa\rho)\tau + \rho'\nu), \tag{A.6}$$

and derive that the length element $d\sigma$ on $\partial\Omega$ is given by

$$d\sigma = \sqrt{(\rho')^2 + (1+\kappa\rho)^2}ds.$$

It follows from (A.6) that

$$N = \frac{1}{\sqrt{(\rho')^2 + (1+\kappa\rho)^2}}((1+\kappa\rho)\nu - \rho'\tau). \tag{A.7}$$

Since $dN = HTd\sigma$, one can derive the formula

$$H = \frac{1}{((\rho')^2 + (1+\kappa\rho)^2)^{3/2}}\left(\kappa(1+\rho\kappa)^2 - \rho''(1+\kappa\rho) + \kappa\rho\rho' + 2\kappa(\rho')^2\right) \tag{A.8}$$

for the curvature H. Thus, assuming that ρ, ρ' and ρ'' are small and expanding the right hand side, we obtain after dropping higher order terms,

$$H = \kappa - \rho'' - \kappa^2\rho + \dots, \tag{A.9}$$

this leads to the linear approximation

$$-\gamma(H-\kappa) = \gamma(\rho'' + \kappa^2\rho) + \dots \tag{A.10}$$

of the last term in the right hand side of (A.2). Also, one can show that the linear part of the area change is given by $|\Omega| - |\Omega(V)| = \int_{\partial\Omega(V)} \rho ds + \dots$, so that we have

$$p_*(|\Omega|) - p_*(|\Omega(V)|) = p_*'(|\Omega(V)|\int_{\partial\Omega(V)} \rho ds + \dots. \tag{A.11}$$

Finally taking two terms of the expansion

$$\Phi(x(s) + \rho\nu_x, y(s) + \rho\nu_x, V) = \Phi(x(s), y(s), V) + \partial_\nu\Phi(x(s), y(s), V)\rho + \dots,$$

and recalling that $\partial_\nu\Phi = V\nu_x$, $\zeta\Phi = p_*(|\Omega(V)|) - \gamma\kappa$ on $\partial\Omega(V)$, we obtain

$$-\zeta\Phi(x(s) + \rho\nu_x, y(s) + \rho\nu_y, V) + p_*(|\Omega(V)|) - \gamma\kappa = -\zeta V\nu_x\rho + \dots.$$

Thus, substituting this formula along with (A.10)–(A.11) in (A.2) we obtain the linearized boundary condition (5.2).

Next, the following computations show that (5.3) is in fact linearization of (A.3),

$$V_N = \partial_t\rho N\cdot\nu = \partial_t\rho + \partial_t\rho(N-\nu)\cdot\nu = \partial_t\rho + \dots$$

(from (A.7) one sees that $N - \nu = -\rho'\tau + \dots$),

$$\begin{aligned}
\nabla\phi\cdot(N-\nu) + \frac{\partial\Phi}{\partial N} - VN_x &= \nabla\phi\cdot(N-\nu) \\
&\quad + \frac{\partial\Phi}{\partial\nu}(x(s)+\rho\nu_x, y(s)+\rho\nu_y, V) - \frac{\partial\Phi}{\partial\nu}(x(s), y(s), V) \\
&\quad + \nabla\Phi(x(s)+\rho\nu_x, y(s)+\rho\nu_y, V)\cdot(N-\nu) \\
&\quad + \frac{\partial\Phi}{\partial\nu}(x(s), y(s), V) - V\nu_x - V(N_x - \nu_x) \\
&= \rho\frac{\partial^2\Phi}{\partial\nu^2}(x(s), y(s), V) - \rho'\frac{\partial\Phi}{\partial\tau}(x(s), y(s), V) + V\rho'\tau_x + \dots.
\end{aligned}$$

Writing exactly the same expansion for $\nabla m\cdot(\nu-N)-\Lambda\frac{\partial}{\partial N}e^{\Phi-Vx}$ one can derive the linearized counterpart (5.5) of the boundary condition (A.5). Finally notice that the first term in the right hand side of (A.4) is identically zero, while the right hand side of (A.1) vanishes on $\overline{\Omega(V)}$. Thus in the linear approximation one finds equations (5.4) and (5.1).

Remark that linearized equations (5.1) and (5.4) are derived in the domain Ω rather than $\Omega(V)$. However Ω is a small perturbation of $\Omega(V)$ and one can pass from Ω to $\Omega(V)$ by constructing a diffeomorphic mapping close to the identity map (with the rate controlled by ρ and its derivatives). More detailed derivation of the linearized problem requires also discussion of regularity of solutions that we are not dwelling on. However, the above reasonings, as they are, lead to an alternative proof of the fact that $\mathcal{A}(V)W_1=0$, where $W_1=(-\Lambda\partial_x e^{\Phi-Vx},\nu_x)$, that is more insightful than the formal proof presented in Proposition 8.1. Indeed, consider the solution $\Lambda e^{\Phi(x-\varepsilon,y,V)-V(x-\varepsilon)}$, $\Omega_\varepsilon=\{(x,y);(x-\varepsilon,y)\in\Omega(V)\}$ (a stationary solution of (2.9)–(2.13) in the moving frame), shifted by ε in the x-direction. Here ε is a small parameter and, as above, we assume that Φ is smoothly extended on the exterior of $\overline{\Omega(V)}$. We consider $(\Lambda e^{\Phi(x-\varepsilon,y,V)-V(x-\varepsilon)},\Omega_\varepsilon)$ as a perturbation of $(\Lambda e^{\Phi-Vx},\Omega(V))$, and define $m_\varepsilon:=\frac{\Lambda}{\varepsilon}(e^{\Phi_\varepsilon-V(x-\varepsilon)}-e^{\Phi-Vx})$, $\phi_\varepsilon:=\frac{1}{\varepsilon}(\Phi_\varepsilon-\Phi)$ and $\rho_\varepsilon(s)$ as the scaled by factor $1/\varepsilon$ signed distance from $\partial\Omega_\varepsilon$ to $\partial\Omega(V)$ (s denotes arc length parameter on $\partial\Omega(V)$). Then $m=\varepsilon m_\varepsilon$, $\phi=\varepsilon\phi_\varepsilon$ and $\rho=\varepsilon\rho_\varepsilon$ satisfy the stationary version of (A.1)–(A.5), i.e. with $V_N=0$ and $\partial_t m=0$, so that dividing equalities in (A.1)–(A.5) by ε and passing to the limit as $\varepsilon\to0$ one obtains that $\lim_{\varepsilon\to0}m_\varepsilon=-\Lambda\partial_x e^{\Phi-Vx}$, $\lim_{\varepsilon\to0}\rho_\varepsilon=\nu_x$ is a stationary solution of (5.1)–(5.5) (with $\phi=-\partial_x\Phi$).

Similar arguments can be applied to show that $\mathcal{A}(V)W_2=W_1$, where $W_2=(\partial_{\tilde V}(\Lambda(\tilde V)e^{\Phi-\tilde Vx}),\partial_{\tilde V}\tilde\rho(s,\tilde V))\big|_{\tilde V=V}$. To this end observe that in the frame moving with velocity V the pair $(\Lambda(\tilde V)e^{\Phi-\tilde Vx},\Omega(\tilde V))$ yields a traveling wave solution with velocity $\tilde V-V$. Therefore considering $\varepsilon=\tilde V-V$ as a small parameter, we can employ the above derivation of the linearized problem to find $\mathcal{A}(V)W_2$. Indeed, define

$$m_\varepsilon:=\frac{1}{\varepsilon}\left(\Lambda(V+\varepsilon)e^{\Phi(x,y,V+\varepsilon)-(V+\varepsilon)x}-\Lambda(V)e^{\Phi(x,y,V)-Vx}\right),$$

$$\phi_\varepsilon:=\frac{1}{\varepsilon}\left(\Phi(x,y,V+\varepsilon)-\Phi(x,y,V)\right),\quad \rho_\varepsilon:=\frac{1}{\varepsilon}\tilde\rho(s,V+\varepsilon),$$

then $m=\varepsilon m_\varepsilon$, $\phi=\varepsilon\phi_\varepsilon$ and $\rho=\varepsilon\rho_\varepsilon$ satisfy (A.1)–(A.5) with $V_N=\varepsilon N_x$ and $-\varepsilon\partial_x m-\varepsilon\partial_x(\Lambda(V)e^{\Phi(x,y,V)-Vx})$ in place of $\partial_t m$. After dividing equalities in (A.1)–(A.5) by ε and passing to the limit as $\varepsilon\to0$ one finds that $\mathcal{A}(V)W_2=(-\Lambda\partial_x e^{\Phi-Vx},\nu_x)$, where the auxiliary function $\phi=\partial_V\Phi(x,y,V)$ (appearing in the definition of the operator $\mathcal{A}(V)$) and components of W_2 are obtained as the limits of ϕ_ε and m_ε, ρ_ε. This completes the proof of the fact that W_2 is a generalized eigenvector of $\mathcal{A}(V)$ corresponding to the zero eigenvalue.

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