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A PDE model for bleb formation and interaction with linker proteins

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The aim of this paper is to further develop mathematical models for bleb formation in cells, including cell membrane interactions with linker proteins. This leads to nonlinear reaction–diffusion equations on a surface coupled to fluid dynamics in the bulk. We provide a detailed mathematical analysis and investigate some singular limits of the model, connecting it to previous literature. Moreover, we provide numerical simulations in different scenarios, confirming that the model can reproduce experimental results on bleb initiation.

Keywords: cell blebbing, surface PDEs, fluid–structure interaction, free boundary problems.

1. Introduction

Bleb formation or ‘blebbing’ is a biological process during which the cell membrane of a eucaryotic cell is disconnected from the cell cortex. The inflowing cytosol pushes out the free membrane part which builds a protrusion called a bleb. Due to regeneration mechanisms of the cell the membrane connection to the cortex is restored and the protrusion is healed after some time. Despite these phases seem to be well established the particular cause for the transition from one phase to the other or the initialization of the whole process are still subject to debate. Blebbing has been related to many interesting biological processes such as mitosis (Boss, 1955), cell spreading (Breiter-Hahn *et al.*, 1990) and apoptosis (Robertson *et al.*, 1978). It has also been noticed as migration mechanism, especially in embryonic (Concha & Adams, 1998; Hofreiter, 1943) and cancer cells. Nevertheless, according to Charras *et al.* (2008), the lamellipodia migration mechanism had received a lot more interest and the authors found it necessary to emphasize the importance of deeper investigations into bleb formation. Following their promotion effort has been made to derive bio-physical models and develop an understanding of this phenomenon by numerical means focusing on fluid–membrane interaction (Strychalski & Guy, 2013, 2016; Young & Mitran, 2010), on membrane dynamics including linker influence Lim *et al.* (2012) or on linker kinetics Alert *et al.* (2015). There has also been effort in enhanced mechanical modelling (Woolley *et al.*, 2014) and on developing models of a full bleb life cycle in three dimensions (Manakova *et al.*, 2016).

In this work we propose a model for bleb formation in three dimensions taking into account the following aspects:

- elastic properties of the membrane described via Canham–Helfrich energies;
- forces of the actin cortex exerted on the membrane via linker proteins;
- activation and deactivation of linker proteins as well as possible movement of the proteins;
- intracellular fluid–dynamics and the corresponding fluid–structure interaction.

A key issue of the cell blebbing phenomenon is the fact that there are actually two free boundaries, the membrane and the cortex that strongly interact via linker proteins. We describe the membrane by a height relative to the cell cortex, which is subject to forces exerted by a surrounding fluid as well as proteins that connect the cell membrane with the cell cortex and act like springs (cf. [Alert *et al.*, 2015](#)). We take into account that these proteins may disconnect by introducing a ripping rate function whose steepness is controlled by a small parameter ϑ . This way we rediscover the model of [Lim *et al.* \(2012\)](#) by ignoring movement of the linker proteins and passing to the limit $\vartheta \searrow 0$.

Besides the detailed mathematical modelling we provide a detailed analysis of the model in the case of small deformations of the membrane relative to the cortex, where a linearization of the mechanics applies. The key nonlinearities we focus on are hence due to the presence of the linker proteins. Besides well posedness of the time-dependent model we prove the existence of stationary solution and show that some critical pressure (e.g. arising from cortex contraction) is necessary and sufficient to form a bleb, which we define as a deformation above a critical height of the membrane relative to the cortex at which linkers are ripping off. As mentioned above we study singular limits and show that the models of [Alert *et al.* \(2015\)](#) and [Lim *et al.* \(2012\)](#) arise as special cases respectively scaling limits of our model. Moreover, we provide a numerical study of the bleb initiation by a critical pressure.

The paper is organized as follows: after having fixed some basic notational conventions in Section 2, we derive a fourth-order evolution system of equations in Section 3 starting from first principles. The main result of Section 4 is a global-in-time existence theorem for solutions of this system. The following Section 5 is devoted to proving existence of stationary solutions and studying stability of a particular subclass of stationary solutions by means of nonlinear semigroups. The analytical part of this paper ends with Section 6, in which we pass to the limit $\vartheta \searrow 0$ in the parameter controlling the disconnection rate. Finally, we illustrate some properties of our model numerically by presenting simulations of different biological situations in Section 7 and conclude in Section 8.

2. Preliminaries

General By I_X we denote the identity on the set X . We denote the minimum of two values x and y by $x \wedge y$. Let $F : X \rightarrow Y$ for Banach spaces X and Y ; the Gateaux derivative of F in direction $v \in X$ at $x \in X$, if it exists, written as $\frac{d}{dv}(F)|_x$. The space of Radon measures or regular, countably additive measures on a measurable space $\Omega \subseteq \mathbb{R}^n$ that is absolutely continuous with respect to the Lebesgue measure is $\text{rca}(\Omega)$.

Differential operators and vectorial Sobolev spaces Gradients ∇u (in the weak and strong sense and independent of whether they are on open sets or manifolds) of scalar functions u are column vectors. The Jacobian ∇v of a vector-valued function v is the matrix whose lines are the transposed gradients of the components of v . We write $\mathcal{J}(v) = (\nabla v + (\nabla v)^T)$ for the symmetrized gradient. The set of k -times, $k \geq 0$, weak differentiable, X -valued functions, where X is a vector space, on some open set $\Omega \subseteq \mathbb{R}^3$ is

$H^k(\Omega, X)$. We will also employ the subspaces of mean-value-free functions,

$$H_{\text{mvf}}^k(\Omega) = \left\{ u \in H^k(\Omega) \mid \int_{\Omega} u \, dx = 0 \right\},$$

of functions with time-constant mean value,

$$C_{\text{cmv}}([0, T], X) = \left\{ u \in C([0, T], X) \mid \int_{\Omega} u(t, x) \, dx = \int_{\Omega} u(0, x) \, dx \text{ for a.e. } t \in [0, T] \right\},$$

$T \in [0, \infty)$, of solenoidal functions,

$$H_{\sigma}^k(\Omega) = \overline{\{u \in C^{\infty}(\Omega) \mid \nabla \cdot u = 0\}}^{H^k(\Omega)},$$

and the traces of solenoidal functions,

$$H_{\gamma_0\sigma}^k(\mathcal{M}, \mathbb{R}^3) = \left\{ u \in H^k(\mathcal{M}) \mid \int_{\mathcal{M}} u \cdot \nu_{\mathcal{M}} \, d\sigma^2 = 0 \right\},$$

where $\mathcal{M} \subseteq \mathbb{R}^3$ is some two-dimensional manifold with outer unit normal field $\nu_{\mathcal{M}}$ and σ^2 the Hausdorff measure with Hausdorff dimension two.

Shape derivatives For denoting the shape derivative of a functional \mathcal{W} in directions θ and ϑ we following the notation in [Delfour & Zolésio \(2011\)](#) using $d(\mathcal{W}; \theta)$ for the first and $d^2(\mathcal{W}; \theta, \vartheta)$ for the second shape derivative. We denote by

$$M_{\delta}[v] = \{x + \delta v(x) \mid x \in M\},$$

for a hypersurface M , $\delta \in I \subseteq \mathbb{R}$, I being an interval, and $v : M \rightarrow \mathbb{R}^3$, the perturbation of M by v . In this particular case the shape derivative of the functional \mathcal{W} being defined on $M_{\delta}[v]$ is $d(\mathcal{W}; v) = \frac{d}{d\delta} (\mathcal{W}(M_{\delta}[v])) \Big|_{\delta=0}$.

Differential geometry The notation of this paragraph follows [Amann & Escher \(2006\)](#) and [Barrett et al. \(2020\)](#). With $\text{Diff}^q(X, Y)$ we denote the set of all C^q -diffeomorphisms mapping the Banach space X into the Banach space Y . The set of functions

$$\left\{ \varphi : J \times X \rightarrow Y \mid \forall s \in J : \varphi(s, \cdot) \in \text{Diff}^q(X, Y) \wedge \forall x \in X : \varphi(\cdot, x) \in C^k(J, Y) \right\},$$

where J is a real interval, is denoted by $\text{Diff}^{k,q}(J \times X, Y)$. We call an n -dimensional manifold $\Gamma \subseteq \mathbb{R}^{n+k}$ a real submanifold. The tangent space of a real submanifold at a point $p \in \Gamma$ is denoted by $T_p\Gamma \subseteq \mathbb{R}^{n+k}$.

Let $(\Gamma_s)_{s \in J}$ be a family of real submanifolds in \mathbb{R}^n with a mapping $\mathfrak{X} : J \times \Gamma \rightarrow \bigcup_{s \in J} \Gamma_s$ such that \mathfrak{X}^s is a global parametrization of Γ_s on a reference manifold Γ . We call the set $\mathcal{G}(\Gamma_s; s \in J) = \bigcup_{s \in J} \{s\} \times \Gamma_s$ an *evolving manifold*. If Γ_s are hypersurfaces, then we use the term *evolving hypersurface*. For functions $f^s : \Gamma_s \rightarrow N$, where N is a set, we define the function

$$f : \mathcal{G}(\Gamma_s; s \in J) \rightarrow N, (s, x) \mapsto f^s(x).$$

An evolving manifold $\mathcal{G}(\Gamma_s; s \in J)$ is *smooth* if $T_p \mathcal{G}(\Gamma_s; s \in J) \neq \{0\} \times \mathbb{R}^n$ for all $p \in \mathcal{G}(\Gamma_s; s \in J)$. For such a smooth evolving manifold we denote the velocities $\partial_s(\mathfrak{X}^s)|_r \circ (\mathfrak{X}^r)^{-1}$ by \mathcal{V}^r . If the manifolds are orientable, i.e., there exist smooth outer unit normal fields $\nu_s : \Gamma_s \rightarrow \mathbb{R}^3$, then the velocities can be decomposed in their normal $\mathcal{V}_\nu^s = V_\nu^s \nu_s$, $V_\nu^s = \mathcal{V}_\nu^s \cdot \nu_s$ and tangential \mathcal{V}_t^r components. We define a differential operator

$$\partial_s^\circ(f)|_r = \partial_s(f \circ (s, \theta) \mapsto (s, \mathfrak{X}^s(\theta)))|_r \circ (\mathfrak{X}^r)^{-1}$$

called the *material derivative (of f with respect to \mathfrak{X})*.— The parametrization mapping shall always be given by the context if not stated explicitly.

For any real submanifold $\Gamma \subseteq \mathbb{R}^n$, the *tangential gradient* ∇_Γ of a function $f : \Gamma \rightarrow \mathbb{R}$ at $p \in \Gamma$ is given by

$$\nabla_\Gamma(f)|_p = \mathbb{P}_{T_p \Gamma} \left(\nabla(\bar{f})|_p \right),$$

where \bar{f} is any differentiable extension of f to an open neighbourhood of p in \mathbb{R}^n and $\mathbb{P}_{T_p \Gamma}$ is the orthogonal projection onto the tangent space $T_p \Gamma$ of Γ at p . The projection matrix $1 - \nu_\Gamma(p) \otimes \nu_\Gamma(p)$ and the projection $\mathbb{P}_{T_p \Gamma}$ are identified. This way, we also acquire the *partial tangential derivatives*

$$\partial_{\Gamma,i}(f)|_p = \left(\nabla_\Gamma(f)|_p \right)_i, \quad i \in \{1, \dots, n\}.$$

For a differentiable, orientable real submanifold $\Gamma \subseteq \mathbb{R}^n$ with normal field ν , we denote the *Weingarten map* by $\mathcal{H}^\Gamma : \Gamma \rightarrow \mathbb{R}^{(n,n)}, p \mapsto \nabla_\Gamma(\nu)|_p$. Then, the *mean curvature* of Γ is $H^\Gamma = \text{tr}(\mathcal{H}^\Gamma) = \nabla_\Gamma \cdot \nu$ and the *Gaussian curvature* is $K^\Gamma = \det(\mathcal{H}^\Gamma)$.

Physical dimension and units The sets \mathbb{R}^n , $n \in \mathbb{N}$, are identified with the product sets $\mathbb{R}^n \times \mathcal{D} \times \mathcal{U}$, where \mathcal{D} is the set of all physical dimensions $\mathcal{D} = \{\text{T, L, M, N, } \dots\}$ (meaning time, length, mass, etc.) and \mathcal{U} the set of all physical units. For $x \in \mathbb{R}^n$, we denote by $\langle x \rangle$ its second component (called the physical dimension of x). When we write x , we always refer to the first component.

3. Modelling

As mentioned in the introduction, many details of the process of bleb formation are still subject to research and not fully understood. Therefore, we aim at a rather abstract model following the general description of the process in [Charras et al. \(2008\)](#): the main parts of a eucaryotic cell that are involved in bleb formation are the cell membrane, which is basically a bilayer of lipid molecules, the cell cortex, which is a network of actin fibres, and elastic proteins which connect the cell cortex to the cell membrane. These linker proteins are only stretchable to a certain length above which they disconnect from the membrane. Inside the cell there is a fluid that is called the cytosol and the cell is itself swimming in an extracellular fluid. Caused by mechanisms which have not completely been understood yet, a certain patch of the cell cortex contracts and raises the pressure on the membrane locally. This way, the corresponding membrane patch is pushed so far away from the cortex that most of the linker proteins disconnect. The cytosol that pushes against the free membrane patch now causes the formation of a protrusion which is called a bleb. Over time, the protein linkers are reconnected to the cell membrane causing the membrane patch to be fixed to the cortex again and the bleb to vanish.

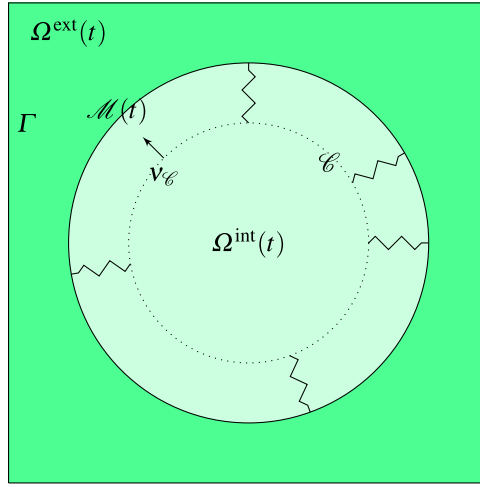


FIG. 1. Cell geometry.

3.1 The fluid system

Let $\mathcal{D} \subseteq \mathbb{R}^3$ be a bounded, connected and open set with sufficiently regular boundary. We require this set to be partitioned into the open connected set Ω_0^{ext} , modelling a reference region exterior to the cell, the open connected set Ω_0^{int} , modelling a reference region interior to the cell, and the boundary \mathcal{M}_0 of Ω_0^{int} , which shall be a two-dimensional orientable C^2 -manifold, modelling the membrane in its initial state; its unit normal field is denoted by $\nu_{\mathcal{M}_0} : \mathcal{M}_0 \rightarrow \mathbb{R}^3$. The region which is occupied by the cell at time $t \in [0, \infty)$ is given as the image $\Omega^{\text{int}}(t) = \Phi(t, \Omega_0^{\text{int}})$ of $\Phi \in \text{Diff}^{1,2}([0, \infty) \times \mathcal{D}, \mathcal{D})$, where $\Phi(0, \cdot) = I_{\mathcal{D}}$. Consequently, the exterior region is $\Omega^{\text{ext}}(t) = \Phi(t, \Omega_0^{\text{ext}})$ and the whole domain is denoted by $\Omega(t) = \Omega^{\text{ext}}(t) \cup \Omega^{\text{int}}(t)$ and $\mathcal{M}(t) = \Phi(t, \mathcal{M}_0)$. Furthermore, the cell cortex is denoted by $\mathcal{C} \subseteq \Omega_0^{\text{int}}$ and is modelled as a sphere which is fixed in time. Figure 1 illustrates a typical geometry compatible with the previous description.

Both the fluid in the inner region, representing the cytosol, and in the outer region with pressures $p^i : \Omega_T^i \rightarrow \mathbb{R}$ and velocities $u^i : \Omega_T^i \rightarrow \mathbb{R}^3$, $i \in \{\text{int}, \text{ext}\}$, are described by incompressible stationary Stokes equations in Eulerian coordinates

$$\mu^i \Delta u^i + \nabla p^i = 0 \tag{3.1a}$$

$$\nabla \cdot u^i = 0, \tag{3.1b}$$

on $\Omega_T^i = \bigcup_{t \in [0, T]} \{t\} \times \Omega^i(t)$ with final time $T > 0$ (time dependency will be brought into the system by boundary conditions). This is justified by small length scales as in [Strychalski & Guy \(2013\)](#). For any functions $g^i : \Omega_T^i \rightarrow X$, $i \in \{\text{int}, \text{ext}\}$, into a vector space X , we associate the function

$$g(t, x) = \begin{cases} g^{\text{ext}}(t, x) & x \in \Omega^{\text{ext}}(t) \\ g^{\text{int}}(t, x) & x \in \Omega^{\text{int}}(t). \end{cases}$$

We further pose a homogeneous Dirichlet boundary condition at the exterior boundary

$$\Gamma = \partial(\Omega(t) \cup \mathcal{M}(t)) = \partial\mathcal{D},$$

which does not change over time,

$$\gamma_0(u^{\text{ext}}) \upharpoonright_{\Gamma} = 0,$$

where γ_0 is the trace operator. For every $t \in [0, \infty)$ let $f_i \in L^2_{\gamma_0\sigma}(\cdot, \mathcal{M}(t), \mathbb{R}^3)$, $\langle f_{i,i} \rangle = \frac{ML}{T^2}$, $i \in \{1, 2, 3\}$, be a force we will specify below. The stress at the interface $\mathcal{M}(t)$ is subject to a Neumann-type boundary condition:

$$\llbracket \mathbb{T}(t, \cdot) \rrbracket \nu_{\mathcal{M}(t)} = f_i, \quad (3.2)$$

where $\mathbb{T} = \mu \mathcal{J}(u) - pl$ is the Cauchy stress tensor of the interior and exterior fluid and we define $\llbracket g \rrbracket(t, \cdot) = \gamma_0(g \upharpoonright_{\Omega_T^{\text{ext}}}(t, \cdot)) \upharpoonright_{\mathcal{M}(t)} - \gamma_0(g \upharpoonright_{\Omega_T^{\text{int}}}(t, \cdot))$ for any function $g : \Omega_T^{\text{ext}} \cup \Omega_T^{\text{int}} \rightarrow X$. To assure well posedness of the problem we further require

$$\llbracket u \rrbracket = 0 \quad \text{on } \mathcal{M}(t).$$

Taking an energetic point of view we consider a variational formulation of the Stokes equations (3.1) with boundary conditions (3.2) (the no-jump condition is encoded in the solution space):

PROBLEM 3.1 Find $u \in H^1([0, T], H^{-1}(\mathcal{D}, \mathbb{R}^3)) \cap L^2([0, T], H_0^1(\mathcal{D}, \mathbb{R}^3))$ and $p \in L^2([0, T], L^2(\mathcal{D}))$ such that

$$\frac{\mu}{2} (\mathcal{J}(u), \mathcal{J}(\varphi))_{L^2(\mathcal{D}, \mathbb{R}^{(3,3)})} - (p, \nabla \cdot \varphi)_{L^2(\mathcal{D})} = (f_i, \varphi)_{L^2(\mathcal{M}(t), \mathbb{R}^3)} \quad (3.3a)$$

$$(\nabla \cdot u, q)_{L^2(\mathcal{D})} = 0 \quad (3.3b)$$

for all $\varphi \in H_0^1(\mathcal{D}, \mathbb{R}^3)$ and $q \in L^2(\mathcal{D})$.

REMARK 3.2 Another formulation of the Stokes equations includes the term $(\nabla u, \nabla \varphi)_{L^2(\mathcal{D}, \mathbb{R}^{(3,3)})}$ instead of $\frac{1}{2} (\mathcal{J}(u), \mathcal{J}(\varphi))_{L^2(\mathcal{D}, \mathbb{R}^{(3,3)})}$. We observe that, because of u being solenoidal,

$$\left(\nabla u, (\nabla \varphi)^T \right)_{L^2(\mathcal{D}, \mathbb{R}^{(3,3)})} = \left((\nabla u)^T, \nabla \varphi \right)_{L^2(\mathcal{D}, \mathbb{R}^{(3,3)})} = - \left(\nabla \cdot (\nabla u)^T, \varphi \right)_{L^2(\mathcal{D}, \mathbb{R}^3)} = 0,$$

so both expressions are equal. The motivation to use the latter is related to the structure of the employed Neumann boundary conditions.

We introduce a function $h : [0, T] \times \mathcal{C} \rightarrow \mathbb{R}$, $\langle h \rangle = L$, which is intended to give the membrane's height relative to the cortex in normal direction $\nu_{\mathcal{C}}$, i.e.,

$$\mathcal{M}(t) = \{x + h(t, x)\nu_{\mathcal{C}}(x) \mid x \in \mathcal{C}\}. \quad (3.4)$$

We further require $\mathcal{M}(t)$ lying in a sufficiently small tubular neighbourhood of \mathcal{C} (this approach is analogous to Elliott *et al.*, 2017):

CONDITION 3.3 Let $U_\delta(\mathcal{C}) = \{x + \delta v_{\mathcal{C}}(x) \mid x \in \mathcal{C}\}$, $\delta > 0$. Then $\mathcal{M}(t) \subseteq U_\delta(\mathcal{C})$, such that the orthogonal projection

$$\mathbb{P}_{\mathcal{C}} : U_\delta(\mathcal{C}) \rightarrow \mathcal{C}(t), y \mapsto \arg \min_{x \in \mathcal{C}} \|y - x\|_2$$

exists.

Yet there is no guarantee that the mapping in (3.4) is bijective between \mathcal{C} and $\mathcal{M}(t)$ as multiple points in $\mathcal{M}(t)$ may have the same projection point rendering the existence of a function h impossible. Therefore, we also pose an invertibility condition for the parametrization of the membrane over the cortex:

CONDITION 3.4 It shall hold,

$$\partial_t \Phi(t, y) = \partial_t h(t, x) v_{\mathcal{C}}(x) \tag{3.5}$$

for $y \in \mathcal{M}_0$, $x = \mathbb{P}_{\mathcal{C}}(y)$.

Potential energy In view of Condition 3.3, we define a rescaled height $h = \delta \hat{h}$ and we may regard $\mathcal{M}(t)$ as small perturbation of \mathcal{C} by $\hat{h} v_{\mathcal{C}}$ with order of magnitude δ . In particular, we write $\mathcal{M}(t) = \mathcal{C}_\delta [\hat{h}(t, \cdot) v_{\mathcal{C}}]$.

In order to derive a mathematical model, let us turn to the bio-physical properties of the membrane-cortex system just described: the membrane shall consist of lipid molecules arranged in two layers. On the cortex, there are proteins connected to the membrane, therefore called linkers proteins. They are considered stretchable and shall obey Hooke's law for springs, so we can assign the potential energy density functional

$$V(t, h) = \frac{1}{2} \xi \rho_a \|h(t, \cdot)\|_{L^2(\mathcal{C})}^2,$$

where $\xi \in L^\infty(\mathcal{C}, [0, \infty))$, $\langle \xi \rangle = \text{MT}^{-2}$, is a function playing the role of a spring constant in every spatial point and $\rho_a \in L^2(\mathcal{C})$, $\langle \rho_a \rangle = \text{L}^{-2}$, is the density of active linkers (further explanation below, see Section 3.4). There are several models (cf. Seifert, 1997) for the surface energy of membranes. A widely used example is the Helfrich energy (cf. Helfrich, 1973 and Zhon-can & Helfrich, 1989):

$$\mathcal{W}(\mathcal{M}) = \int_{\mathcal{M}} \frac{\kappa}{2} \left(H^{\mathcal{M}} + H_0^{\mathcal{M}} \right)^2 + \kappa_G K^{\mathcal{M}} \, d\sigma^2,$$

where $H^{\mathcal{M}} : \mathcal{M} \rightarrow \mathbb{R}$, $H_0^{\mathcal{M}} \in \mathbb{R}$ and $K^{\mathcal{M}} : \mathcal{M} \rightarrow \mathbb{R}$ are the mean curvature, spontaneous mean curvature and Gaussian curvature of \mathcal{M} , respectively, with bending rigidity κ and Gaussian bending rigidity κ_G .

The second-order expansion of the total energy density of the membrane-cortex system at time $t \in [0, \infty)$ is

$$\begin{aligned} V(t, \delta \hat{h}) + \mathcal{W}(\mathcal{C}_\delta [\hat{h} v_{\mathcal{C}}]) &= V(t, 0) + \mathcal{W}(\mathcal{M}_0) + \delta \left(\frac{d}{d\delta} (V(t, \delta \hat{h})) \Big|_0 \hat{h} + d(\mathcal{W}; \hat{h} v_{\mathcal{C}}) \right) \\ &+ \delta^2 \left(\frac{d^2}{d\delta^2} (V(t, \delta \hat{h})) \Big|_0 (\hat{h}, \hat{h}) + d^2(\mathcal{W}; \hat{h} v_{\mathcal{C}}, \hat{h} v_{\mathcal{C}}) \right) + o(\delta^3) \\ &= \mathcal{W}(\mathcal{M}_0) + \delta d(\mathcal{W}; \hat{h} v_{\mathcal{C}}) + \delta^2 \left(\frac{1}{2} \xi \rho_a \|\hat{h}\|_{L^2(\mathcal{C})}^2 + d^2(\mathcal{W}; \hat{h} v_{\mathcal{C}}, \hat{h} v_{\mathcal{C}}) \right) \\ &+ o(\delta^3), \end{aligned}$$

where we have used that the derivatives of $\mathcal{W}(\mathcal{C}_\delta [\widehat{h}(t, \cdot) v_{\mathcal{C}}])$ with respect to δ at 0 are equal to the shape derivatives of \mathcal{W} in direction $\widehat{h}(t, \cdot) v_{\mathcal{C}}$ at zero. If the cortex was an equilibrium shape of Helfrich's energy, then we would have $d(\mathcal{W}; \widehat{h} v_{\mathcal{C}}) = 0$. However, this may be especially not true if the cortex is contracted due to myosin motor activity. Therefore, we model $d(\mathcal{W}; \widehat{h} v_{\mathcal{C}}) = (\delta p_0, \widehat{h})_{L^2(\mathcal{C})}$ for $p_0 \in L^\infty([0, T], L^\infty(\mathcal{C}))$ interpreting p_0 as a stress that is exerted on the membrane due to the cortex contraction and transmitted by the fluid. The energy functional up to second order therefore is

$$\mathcal{J}(t, \widehat{h}; \delta, \mathcal{C}, \rho_a, \kappa, \kappa_G, \xi) = \mathcal{W}(\mathcal{M}_0) + \delta^2 \left((p_0, \widehat{h})_{L^2(\mathcal{C})} + \frac{1}{2} \rho_a \xi \|\widehat{h}\|_{L^2(\mathcal{C})}^2 + d^2(\mathcal{W}; \widehat{h} v_{\mathcal{C}}, \widehat{h} v_{\mathcal{C}}) \right).$$

REMARK 3.2 Setting $d(\mathcal{W}; \widehat{h} v_{\mathcal{C}}) = (\delta p_0, \widehat{h})_{L^2(\mathcal{C})}$ introduces a mechanism by which an initially flat membrane in a resting fluid may be deformed after all: not considering $d(\mathcal{W}; \widehat{h} v_{\mathcal{C}})$ as a parameter but instead taking the terms that come out of a computation of this shape derivative would only change the coefficients of the $\Delta_{\mathcal{C}} h$ and h terms in the variational principle we will derive below. The resulting equation is homogeneous and therefore does not show any deforming behaviour in case the membrane is initially flat and the fluid velocity zero. The more physical but also rather complex approach for introducing this mechanism would be to relate the pressure p_0 to shape deformations of the cortex and then describe the influence of p_0 on the fluid introducing another surface-bulk coupling this way.

3.2 Connecting the fluid and the membrane model

The fluid system is not closed but subject to external forces f_t . This is exactly where the membrane-cortex system comes into play: the potential energy of this system is considered to be the source of forces acting on the fluid and therefore being transformed into kinetic energy of the fluid. We also take a damping effect due to friction between the fluid particles and the cortex into account with a linear friction model with friction constant c having dimension $\langle c \rangle = \text{MT}^{-1}\text{L}^{-2}$. In order to enforce Condition 3.4 these forces are all directed normally to the cortex, so the tangential part of f_t is zero:

$$f_t = -\frac{d}{d\widehat{h}} \left(\mathcal{J}(t, \widehat{h}; \delta, \mathcal{C}, \kappa, \kappa_G, \xi) \right) \Big|_0 \varphi - \delta^2 (c \partial_t \widehat{h} v_{\mathcal{C}}, \varphi v_{\mathcal{C}})_{L^2(\mathcal{C}; \mathbb{R}^3)}. \quad (3.6)$$

Recalling (3.5) we have the fluid particles at the membrane moving in the direction of the cortex normal. Taking the length of the velocity vector to be the change of the membrane's height in time we have specified the Dirichlet boundary of u at $\mathcal{M}(t)$, and we therefore may express

$$\llbracket \widehat{\mathbb{T}}(t, \cdot) \rrbracket v_{\widehat{\mathcal{M}}(t)} = \mathcal{D}_t \mathcal{N}_t \left(\llbracket \partial_t (\delta \widehat{h}(t, \cdot)) v_{\mathcal{C}} \rrbracket_{\mathfrak{X}} \right),$$

where $[\varphi]_{\mathfrak{X}} = \varphi \circ \mathfrak{X}(t, \cdot)^{-1}$ for $\mathfrak{X}(t, \cdot) := I_{\mathcal{C}} + h(t, \cdot) v_{\mathcal{C}}$ and any function φ with domain \mathcal{C} and

$$\mathcal{D}_t \mathcal{N}_t : H_{\gamma_0 \sigma}^1 \left(\widehat{\mathcal{M}}(t), \mathbb{R}^3 \right) \rightarrow L_{\gamma_0 \sigma}^2 \left(\widehat{\mathcal{M}}(t), \mathbb{R}^3 \right)$$

is the Dirichlet-to-Neumann operator of the Stokes problem Problem 3.1. A definition and references to important properties of this operator is given in Appendix A. By combination of both descriptions of the Neumann data we are going to derive a partial differential equation (PDE) model:

3.3 PDE description of the height function

Approximation of the Dirichlet-to-Neumann operator For sufficiently regular Stokes flow velocity we can make use of the small height condition Condition 3.3 to approximate the time-dependent Dirichlet-to-Neumann operator (see Appendix C) with its stationary version on \mathcal{C} . This way we arrive at a gradient-flow structure

$$\begin{aligned}
 -\frac{d}{dh} \left(\mathcal{J}(t, \hat{h}; \delta, \mathcal{C}, \rho_a, \kappa, \kappa_G, \xi) \right) \Big|_0 \varphi &= \delta^2 \left(c \partial_t \hat{h}(t, \cdot) v_{\mathcal{C}}, \varphi v_{\mathcal{C}} \right)_{L^2(\mathcal{C}, \mathbb{R}^3)} \\
 &\quad + \delta^2 \left(\mathcal{D} \mathcal{N}_0 \left(\partial_t \hat{h} v_{\mathcal{C}} \right), \varphi v_{\mathcal{C}} \right)_{L^2(\mathcal{C}, \mathbb{R}^3)} + o(\delta^3) \\
 &= \delta^2 \left(\left(c I_{H^1(\mathcal{C}, \mathbb{R}^3)} + \mathcal{D} \mathcal{N}_0 \right) \left(\partial_t \hat{h} v_{\mathcal{C}} \right), \varphi v_{\mathcal{C}} \right)_{L^2(\mathcal{C}, \mathbb{R}^3)} + o(\delta^3) \\
 &= \delta^2 \left\langle L \left(\partial_t \hat{h} v_{\mathcal{C}} \right), \varphi v_{\mathcal{C}} \right\rangle_{H^{-\frac{1}{2}}(\mathcal{C}, \mathbb{R}^3)} + o(\delta^3)
 \end{aligned} \tag{3.7}$$

with $L = c I_{H^1(\mathcal{C}, \mathbb{R}^3)} + \mathcal{D} \mathcal{N}_0$ and $\varphi \in H^2(\mathcal{C})$.

Calculating the variation of the potential energy

To derive a full PDE description for h we have to calculate the variation of the potential energy functional. So first, we calculate the first and second shape derivatives of \mathcal{W} . Recall,

$$\mathcal{W}(\mathcal{C}_\delta [\hat{h} v_{\mathcal{C}}]) = \frac{\kappa}{2} \int_{\mathcal{C}_\delta [\hat{h} v_{\mathcal{C}}]} (H^\delta)^2 \, d\sigma^2 + \kappa \int_{\mathcal{C}_\delta [\hat{h} v_{\mathcal{C}}]} H^\delta H_0 \, d\sigma^2 + \int_{\mathcal{C}_\delta [\hat{h} v_{\mathcal{C}}]} \frac{\kappa}{2} H_0^2 + \kappa_G K^\delta \, d\sigma^2,$$

where H^δ is the mean curvature of $\mathcal{C}_\delta [\hat{h} v_{\mathcal{C}}]$

Observe that the integral over the Gaussian curvature is constant in δ due to the Gauss–Bonnet theorem ($\mathcal{C}_\delta [\hat{h} v_{\mathcal{C}_0}]$ is homeomorphic to \mathcal{C}) and therefore vanishes when differentiated in δ . The necessary calculations have been carried out before for the Willmore energy, e.g., in Elliott *et al.* (2017, p. 7):

$$\begin{aligned}
 \frac{1}{2} d^2 \left(\int_{\mathcal{C}} H^2 \, d\sigma^2; \hat{h} v_{\mathcal{C}} \right) &= \int_{\mathcal{C}} \left(\Delta_{\mathcal{C}} \hat{h} + |\mathcal{A}^2 \hat{h}| \right)^2 + 2H \mathcal{H} : 2\hat{h} \nabla_{\mathcal{C}}^2 \hat{h} \\
 &\quad + 2H \nabla_{\mathcal{C}} \hat{h} \cdot \nabla_{\mathcal{C}} \hat{h} + H h \nabla_{\mathcal{C}} \hat{h} \cdot \nabla_{\mathcal{C}} H \\
 &\quad - H^2 \nabla_{\mathcal{C}} \hat{h} \cdot \nabla_{\mathcal{C}} \hat{h} - \frac{5}{2} H^2 \hat{h} \Delta_{\mathcal{C}} \hat{h} \\
 &\quad + \hat{h}^2 \left(2H \operatorname{tr} \left(\mathcal{A}^2 \right) - \frac{5}{2} H^2 |\mathcal{A}^2| + \frac{1}{2} H^4 \right) \, d\sigma^2.
 \end{aligned}$$

The additional calculations use the same techniques and the interested reader may consult the appendix (Corollary 3 and Corollary 5) for details:

$$d^2 \left(\int_{\mathcal{C}} H \, d\sigma^2; \hat{h} v_{\mathcal{C}_0} \right) = \int_{\mathcal{C}} 2\hat{h} \operatorname{tr} \left(\mathcal{A} \nabla_{\mathcal{C}}^2 \hat{h} + \hat{h} \mathcal{A}^2 \right) - \hat{h} H \Delta_{\mathcal{C}} \hat{h} - 3\hat{h}^2 H |\mathcal{A}^2| + H \nabla_{\mathcal{C}} \hat{h} \cdot \nabla_{\mathcal{C}} \hat{h} + \hat{h}^2 H^3 \, d\sigma^2$$

and

$$d^2 \left(\int_{\mathcal{C}} 1 \, d\sigma^2; \widehat{h}v_{\mathcal{C}_0} \right) = \int_{\mathcal{C}} \nabla_{\mathcal{C}} \widehat{h} \cdot \nabla_{\mathcal{C}} \widehat{h} - h^2 |\mathcal{H}|^2 + h^2 H^2 \, d\sigma^2.$$

Spherical cortex shape Significant simplification of these terms is achieved by considering \mathcal{C} to be a sphere with radius R :

$$\frac{1}{2} d^2 \left(\int_{\mathcal{C}} H^2 \, d\sigma^2; \widehat{h}v_{\mathcal{C}} \right) = \int_{\mathcal{C}} (\Delta_{\mathcal{C}} h)^2 - \frac{2}{R^2} \nabla_{\mathcal{C}} h \cdot \nabla_{\mathcal{C}} h \, d\sigma^2$$

(cf. Elliott *et al.*, 2017) and

$$d^2 \left(\int_{\mathcal{C}} H \, d\sigma^2; \widehat{h}v_{\mathcal{C}_0} \right) = \int_{\mathcal{C}} \frac{2}{R} \nabla_{\mathcal{C}} h \cdot \nabla_{\mathcal{C}} h \, d\sigma^2$$

(cf. Corollary 4) and

$$d^2 \left(\int_{\mathcal{C}} 1 \, d\sigma^2; \widehat{h}v_{\mathcal{C}} \right) = \int_{\mathcal{C}} \nabla_{\mathcal{C}} h \cdot \nabla_{\mathcal{C}} h + \frac{2}{R^2} h^2 \, d\sigma^2.$$

Force density equation All together we arrive at the following expression for (3.7):

$$- (\rho_a \xi h, \varphi)_{L^2(\mathcal{C})} - (p_0, \varphi)_{L^2(\mathcal{C})} - a(h, \varphi) = \langle L(\partial_t h v_{\mathcal{C}}), \varphi v_{\mathcal{C}} \rangle_{H^{-\frac{1}{2}}(\mathcal{C}, \mathbb{R}^3)}, \quad (3.8)$$

where

$$a(h, \varphi) = \kappa (\Delta_{\mathcal{C}} h, \Delta_{\mathcal{C}} \varphi)_{L^2(\mathcal{C})} + \gamma (\nabla_{\mathcal{C}} h, \nabla_{\mathcal{C}} \varphi)_{L^2(\mathcal{C}, \mathbb{R}^3)} + \lambda (h, \varphi)_{L^2(\mathcal{C})}$$

with $\gamma = \frac{\kappa}{2} \left(-\frac{4}{R^2} + \frac{2}{R} H_0 + \frac{1}{2} H_0^2 \right)$ and $\lambda = \kappa \frac{2}{R^2} H_0^2$.

REMARK 3.3 The form $a(\cdot, \cdot)$ may not be coercive on $H^2(\mathcal{C})$ nor may it be non-negative. In order to assure at least non-negativity, we make the following considerations:

In case $H_0 \geq 0$, we follow Elliott *et al.* (2017) and derive a Poincaré-type inequality from Courant's min-max principle

$$\int_{\mathcal{C}} h^2 \, d\sigma^2 \leq \frac{R^2}{2} \int_{\mathcal{C}} |\nabla_{\mathcal{C}} h|^2 \, d\sigma^2 \leq \frac{R^4}{4} \int_{\mathcal{C}} (\Delta_{\mathcal{C}} h)^2 \, d\sigma^2,$$

where $\frac{2}{R^2}$ is the second eigenvalue of the Laplace–Beltrami operator, on $\text{span}\{1\}^\perp$, i.e., for all functions with mean zero. As $H^2(\mathcal{C}) = \text{span}\{1\} \oplus \text{span}\{1\}^\perp$ for every $u \in H^2(\mathcal{C})$ there is a constant m (u 's mean value) and u_0 (being mean-value-free) such that $u = m + u_0$. We observe

$$\begin{aligned} a(u, u) &= a(m, m + u_0) + a(u_0, m + u_0) = a(m, m) + 2a(m, u_0) + a(u_0, u_0) \\ &\geq \lambda \|m\|_{L^2(\mathcal{C})}^2 + 2\lambda (m, u_0)_{L^2(\mathcal{C})} + \lambda \|u_0\|_{L^2(\mathcal{C})}^2 \\ &\geq 0. \end{aligned}$$

In case $H_0 < 0$ we need a compatibility condition on H_0 and R . We require $\frac{2}{R}H_0 + \frac{1}{2}H_0^2 \geq 0$. This leads to $\frac{2}{R} + \frac{1}{2}H_0 \leq 0$, and further $H_0 \leq -\frac{4}{R}$.

For coercivity we shall therefore require $H_0 \in (0, \infty) \cup (-\infty, -\frac{4}{R})$.

3.4 Protein linkers

The quantity ρ_a has been mentioned before in modelling the potential energy of the membrane-cortex system. It models the density of linkers that are connected to the membrane. We also take linkers into account that are disconnected and whose density is denoted ρ_i . Both active and inactive linkers are considered to be mobile species diffusing on the cortex. Moreover, they are transformed into each other as result of overstretching above a critical height $h^* \in C(\mathcal{C}, [0, \infty))$, which causes active linkers to disconnect, or regeneration mechanisms connecting inactive linkers to the membrane again. A reaction–diffusion kind of system may be used to model these processes:

$$\partial_t \rho_a - \eta_a \Delta_{\mathcal{C}} \rho_a = k \rho_i - r \left(\frac{h - h^*}{\vartheta} \right) \rho_a \tag{3.9a}$$

$$\partial_t \rho_i - \eta_i \Delta_{\mathcal{C}} \rho_i = -k \rho_i + r \left(\frac{h - h^*}{\vartheta} \right) \rho_a, \tag{3.9b}$$

where $\eta_a, \eta_i \in [0, \infty)$ are the active and inactive linker diffusivities, $k \in [0, \infty)$ a regeneration rate and $r : \mathbb{R} \rightarrow [0, \infty)$ a disconnection rate being Lipschitz continuous and $r \downarrow_{(-\infty, 0)} = 0$ (a typical example is the non-negative part). The disconnection of linkers from the membrane is considered to be a fast process. To account for this, a (small) parameter $\vartheta \in (0, \infty)$ is used for rescaling the argument of r . (In Section 6, we analyse the solution’s behaviour when $\vartheta \searrow 0$.) For the sake of readability we may use the abbreviation

$$r_{\vartheta}(h) = r \left(\frac{h - h^*}{\vartheta} \right)$$

in the following.

REMARK 3.4 Approaching the linker movement by a reaction–diffusion model is motivated by the work of [Alert & Casademunt \(2016\)](#). They consider the following equation for the membrane height h and linker density ρ_a (we adopt the notation of this work for their parameters and quantities):

$$c \partial_t h = p_0 - \xi h \rho_a \tag{3.10a}$$

$$\partial_t \rho_a = k (\rho_0 - \rho_a) - k_{\text{off}}(h) \rho_a \tag{3.10b}$$

with a maximal linker density ρ_0 and a disconnection rate k_{off} . However, there is an important new aspect to the model presented here: the concept of inactive linkers is not present in (3.10), but a gauge protein density ρ_0 is assumed of which a part is connected ρ_a and $\rho_0 - \rho_a$ is disconnected. As consequence of this condition their approach is limited to scenarios where the cortex is intact. Nevertheless, it has also been observed ([Charras et al., 2008](#)) that bleb formation may be triggered by cortex disruption (leading to a hole in the cortex). This case is contained in our active–inactive linker setting with $\rho_a(0, x) \equiv \rho_i(0, x) = 0$ for $x \in D$, where D is the area of the hole in the cortex (cf. Section 7.3).

Indeed, (3.10) is a specialization of our model: set $\eta_a = \eta_i = \eta$ and $\rho_a(0, \cdot) + \rho_i(0, \cdot) \equiv \rho_0$. Adding (3.9a) and (3.9b) we get

$$\partial_t(\rho_a + \rho_i) + \eta \Delta_{\mathcal{C}}(\rho_a + \rho_i) = 0,$$

which is solved by $\rho_a + \rho_i \equiv \rho_0$. This way we can express $\rho_i = \rho_0 - \rho_a$ giving (3.10).

After having derived a PDE model for the blebbing phenomenon we will deal analytically with the following issues in the next sections:

1. global-in-time existence of weak solutions (Section 4),
2. existence of stationary solutions and their stability (Section 5),
3. convergence of stationary solutions to a singular limit when $\vartheta \searrow 0$,
4. and rediscovering the model for bleb formation proposed in [Lim et al. \(2012\)](#) (Section 6).

4. Time-dependent solutions

In the following three chapters, we analyse a variational formulation of (3.8), (3.9a) and (3.9b) having the following strong equivalent for sufficiently regular h, ρ_a, ρ_i :

$$L(\partial_t h v_{\mathcal{C}}) \cdot v_{\mathcal{C}} + \kappa \Delta_{\mathcal{C}}^2 h - \gamma \Delta_{\mathcal{C}} h + \lambda h = -\xi \rho_a h + p_0 \quad (4.1a)$$

$$\partial_t \rho_a - \eta_a \Delta_{\mathcal{C}} \rho_a = k \rho_i - r_{\vartheta}(h) \rho_a \quad (4.1b)$$

$$\partial_t \rho_i - \eta_i \Delta_{\mathcal{C}} \rho_i = -k \rho_i + r_{\vartheta}(h) \rho_a, \quad (4.1c)$$

where we write $r_{\vartheta}(h) = r\left(\frac{h-h^*}{\vartheta}\right)$. Let us summarize the properties of the parameters involved:

- κ and λ are non-negative constants, whereas γ is also a constant but not necessarily non-negative.
- The operator L in front of the time derivative is the sum of the identity and the Dirichlet-to-Neumann operator of the Stokes problem.
- The function ξ is in $L^\infty([0, T], L^\infty(\mathcal{C}))$ as well as the pressure p_0 . Also, ξ is assumed to be non-negative a.e.
- The repairing rate k is a non-negative constant.
- The diffusivities η_a, η_i are taken to be positive.
- The disconnection rate r is assumed to be non-negative and Lipschitz; the corresponding steepness parameter ϑ shall be non-negative as well.
- The critical height h^* is a non-negative $L^\infty([0, T], L^\infty(\mathcal{C}))$ function.

For better readability we introduce the following forms: $b_a(\rho_a, \sigma_a) = \eta_a (\nabla_{\mathcal{C}} \rho_a, \nabla_{\mathcal{C}} \sigma_a)_{L^2(\mathcal{C}, \mathbb{R}^3)}$ and $b_i(\rho_i, \sigma_i) = \eta_i (\nabla_{\mathcal{C}} \rho_i, \nabla_{\mathcal{C}} \sigma_i)_{L^2(\mathcal{C}, \mathbb{R}^3)}$.

PROBLEM 4.1 Find

$$h \in L^2_{\text{cmv}}([0, T], H^2(\mathcal{C})) \cap H^1([0, T], H^1_{\text{mvf}}(\mathcal{C})),$$

$$\rho_a, \rho_i \in L^2([0, T], H^1(\mathcal{C})) \cap H^1([0, T], H^{-1}(\mathcal{C}))$$

such that

$$(L(\partial_t h v_{\mathcal{C}}), \varphi v_{\mathcal{C}})_{L^2(\mathcal{C})} + a(h, \varphi) = -(\rho_a \xi h, \varphi)_{L^2(\mathcal{C})} + (p_0, \varphi)_{L^2(\mathcal{C})} \quad (4.2a)$$

$$\langle \partial_t \rho_a, \sigma_a \rangle_{H^{-1}(\mathcal{C})} + b_a(\rho_a, \sigma_a) = k(\rho_i, \sigma_a)_{L^2(\mathcal{C})} - (r_{\vartheta}(h) \rho_a, \sigma_a)_{L^2(\mathcal{C})} \quad (4.2b)$$

$$\langle \partial_t \rho_i, \sigma_i \rangle_{H^{-1}(\mathcal{C})} + b_i(\rho_i, \sigma_i) = -k(\rho_i, \sigma_i)_{L^2(\mathcal{C})} + (r_{\vartheta}(h) \rho_a, \sigma_i)_{L^2(\mathcal{C})} \quad (4.2c)$$

for all $\varphi \in H^2(\mathcal{C})$, $\sigma_a \in H^1(\mathcal{C})$ and $\sigma_i \in H^1(\mathcal{C})$ and initial values $h(0, \cdot) \in L^2(\mathcal{C})$, $\rho_a(0, \cdot) \in L^2(\mathcal{C}, [0, \infty))$, $\rho_i(0, \cdot) \in L^2(\mathcal{C}, [0, \infty))$.

The antisymmetric structure of the linker equations allows for a simple conclusion:

LEMMA 4.2 (Mass conservation). Let ρ_a and ρ_i be parts of a solution to Problem 4.1 in the strong sense. Then, there exists $m_0 \in [0, \infty)$ such that for almost all $t \in [0, \infty)$

$$\int_D \rho_a(t, x) + \rho_i(t, x) \, dx = m_0.$$

Proof. Add (4.1b) and (4.1c), integrated over D , to achieve

$$\int_D \partial_t(\rho_a + \rho_i) \, dx = \int_D \eta_a \Delta_D \rho_a + \eta_i \Delta_D \rho_i \, dx.$$

Then, with the divergence theorem on closed manifolds, we get

$$\int_D \partial_t(\rho_a + \rho_i) \, dx = 0.$$

The integral and the weak differential operator commute, so $\int_D \rho_a + \rho_i \, dx$ is constant almost everywhere in time. Considering the non-negativity of the initial values the claim follows. \square

4.1 Global-in-time existence

In the following we refer to

- the initial values $\rho_a^0 = \rho_a(0, \cdot)$, $\rho_i^0 = \rho_i(0, \cdot)$, $h^0 = h(0, \cdot)$,
- the coefficients κ , γ , λ , the pressure p_0 , the critical height h^* , the linkers spring constant ξ , the function r with its Lipschitz constant L_r , the parameter ϑ , the repairing rate k ,
- the positive definite, self-adjoint operator $L = S^2$, and the constant $\mathcal{E} > 0$ such that $\mathcal{E} \|u\|_{H^1(\mathcal{C})}^2 \leq (Lu, u)_{L^2(\mathcal{C})}$

as the *data of Problem 4.1*.

We set

$$X_T = L^\infty([0, T], H^1(\mathcal{C})), \quad Y_T = L^\infty([0, T], L^2(\mathcal{C}))$$

and define the operator

$$F_T : X_T \times Y_T \times Y_T \rightarrow X_T \times Y_T \times Y_T$$

such that a triple $(\bar{h}, \bar{\rho}_a, \bar{\rho}_i) \in X_T \times Y_T \times Y_T$ is mapped to $(H_T(\bar{\rho}_a), G_T(\bar{h}))$ with $H_T : Y_T \rightarrow X_T$ such that $H_T(\bar{\rho}_a)$ solves

$$(L(\partial_t h v_{\mathcal{C}}), \varphi v_{\mathcal{C}})_{L^2(\mathcal{C}; \mathbb{R}^3)} + a(h, \varphi) = -(\bar{\rho}_a \xi h, \varphi)_{L^2(\mathcal{C})} + (p_0, \varphi)_{L^2(\mathcal{C})} \quad (4.3)$$

and $G_T : X_T \rightarrow Y_T \times Y_T$ such that $G_T(\bar{h})$ solves

$$(\partial_t \rho_a, \sigma_a)_{H^{-1}(\mathcal{C})} + b_a(\rho_a, \sigma_a) = k(\rho_i, \sigma_a)_{L^2(\mathcal{C})} - (r_{\vartheta}(\bar{h}) \rho_a, \sigma_a)_{L^2(\mathcal{C})} \quad (4.4a)$$

$$(\partial_t \rho_i, \sigma_i)_{H^{-1}(\mathcal{C})} + b_i(\rho_i, \sigma_i) = -k(\rho_i, \sigma_i)_{L^2(\mathcal{C})} + (r_{\vartheta}(\bar{h}) \rho_a, \sigma_i)_{L^2(\mathcal{C})} \quad (4.4b)$$

for all $\varphi \in H^2(\mathcal{C})$, and $\sigma_a, \sigma_i \in H^1(\mathcal{C})$ with initial data h^0, ρ_a^0, ρ_i^0 .

REMARK 4.3 (Well defined). The unique existence of a solution to (4.4) follows by standard parabolic PDE theory. Existence and uniqueness of solutions to (4.3) may be shown by employing a Petrov–Galerkin-type approximation argument. (We refer the interested reader to Appendix B.) Hence, F_T is well defined.

We aim at a Banach-type fixed point argument. To this end the following *a priori* estimates are derived, which will give us Lipschitz continuity of the map F_T . We will then show that F_T is contractive in a rescaled topology of X_T and Y_T by introducing the rescaled L^∞ norms

$$|u| = \text{ess sup}_{0 \leq s \leq T} (e^{-\beta s} \|u\|(s)),$$

$\|\cdot\| \in \{\|\cdot\|_{L^2(\mathcal{C})}, \|\cdot\|_{H^1(\mathcal{C})}\}$, for a constant $\beta > 0$ that we may choose with respect to the problem data and T . In the following, X_T and Y_T are equipped with their corresponding rescaled norms. We will not state the rescaling constant explicitly since, from now on, the rescaling factor of every rescaled norm we deal with shall be $e^{-\beta t}$ if not stated otherwise.

REMARK 4.4 We will make use of the following interpolation embedding, which is a specialization of [Amann \(2000\)](#), Theorem 3.1 for $\theta \in [0, 1]$ and $m \in [0, \infty)$:

$$L^2([0, T], H^m(\mathcal{C})) \cap H^1([0, T], H^{-m}(\mathcal{C})) \cong H^\theta([0, T], (H^m(\mathcal{C}), H^{-m}(\mathcal{C}))_{\theta, 2})$$

isometrically. Choosing $\theta = \frac{1}{4}$ and $m = 1$ we have

$$H^{\frac{1}{4}}([0, T], X) \hookrightarrow L^4([0, T], X),$$

$$(H^1(\mathcal{C}), H^{-1}(\mathcal{C}))_{\frac{1}{4}, 2} \cong H^{\frac{1}{2}}(\mathcal{C}) \hookrightarrow L^3(\mathcal{C});$$

hence

$$L^2([0, T], H^1(\mathcal{C})) \cap H^1([0, T], H^{-1}(\mathcal{C})) \hookrightarrow L^4([0, T], L^3(\mathcal{C})), \quad (4.5)$$

A priori estimates There will be a lot of constants in the following estimates, so for ease of notation and in the sake of readability, we will slightly abuse notation and write $C(\xi, \mathcal{E}, \dots)$ or similar for an expression that only depends on the problem data; it does not necessarily denote the same expression in every occurrence. For convenience, we abbreviate $\bar{h} = \int_D h \, dx$.

LEMMA 4.5 Let $\bar{\rho}_a \in Y_T$, $\bar{\rho}_a \geq 0$ a.e. and $T > 0$. The following bound holds for $h = H_T(\bar{\rho}_a)$:

$$\|h\|_{L^\infty([0,T],H^1(\mathcal{C}))}^2 \leq C(T, \mathcal{E}, \xi, |\mathcal{C}|) \left(\|S((h^0 - \bar{h}_0)v_{\mathcal{C}})\|_{L^2(\mathcal{C})}^2 + \|p_0\|_{L^\infty([0,T],L^2(\mathcal{C}))}^2 + \bar{h}_0^2 \right). \quad (4.6)$$

Proof. (i) We observe that because the mean value of h is constant in time, we have $\bar{h} = \bar{h}_0$ and $L(\partial_t h v_{\mathcal{C}}) = L(\partial_t (h - \bar{h}_0)v_{\mathcal{C}})$. As $\int_{\mathcal{C}} L(\partial_t h v_{\mathcal{C}}) \cdot v_{\mathcal{C}} \, dx = 0$, we have $\int_{\mathcal{C}} L(\partial_t h v_{\mathcal{C}}) \cdot \bar{h}_0 v_{\mathcal{C}} \, dx = 0$, so by testing (4.3) with $\varphi = h$, we achieve

$$\begin{aligned} \frac{1}{2} \partial_t \|S((h - \bar{h}_0)v_{\mathcal{C}})\|_{L^2(\mathcal{C}, \mathbb{R}^3)}^2 + \kappa \|\Delta_{\mathcal{C}} h\|_{L^2(\mathcal{C})}^2 + \gamma \|\nabla_{\mathcal{C}} h\|_{L^2(\mathcal{C}, \mathbb{R}^3)}^2 + \lambda \|h\|_{L^2(\mathcal{C})}^2 \\ = -(\bar{\rho}_a \xi h, h)_{L^2(\mathcal{C})} + (p_0, h)_{L^2(\mathcal{C})} \\ \leq (p_0, h)_{L^2(\mathcal{C})}, \end{aligned}$$

where we dropped the term $-(\bar{\rho}_a \xi h, h)_{L^2(\mathcal{C})}$ because of its non-positivity. We note that

$$\mathcal{E} \|u\|_{L^2(\mathcal{C})}^2 \leq \mathcal{E} \|u\|_{H^1(\mathcal{C})}^2 \leq \mathcal{E} \|uv_{\mathcal{C}}\|_{H^1(\mathcal{C}, \mathbb{R}^3)}^2 \leq (L(uv_{\mathcal{C}}), uv_{\mathcal{C}})_{L^2(\mathcal{C}, \mathbb{R}^3)} \leq \|S(uv_{\mathcal{C}})\|_{L^2(\mathcal{C}, \mathbb{R}^3)}^2$$

for $u \in H_{\text{mvf}}^1(\mathcal{C})$; therefore,

$$\sqrt{\mathcal{E}} \|h - \bar{h}_0\|_{H^1(\mathcal{C})} \leq \|S((h - \bar{h}_0)v_{\mathcal{C}})\|_{L^2(\mathcal{C})}$$

leading to

$$\|h\|_{H^1(\mathcal{C})}^2 \leq 2 \|\bar{h}_0\|_{H^1(\mathcal{C})}^2 + 2\mathcal{E}^{-1} \|S((h - \bar{h}_0)v_{\mathcal{C}})\|_{L^2(\mathcal{C})}^2.$$

With this simple observation the remaining right-hand side term is bounded by employing the Cauchy–Schwartz and then the Young inequality:

$$\begin{aligned} \frac{1}{2} \partial_t \|S((h - \bar{h}_0)v_{\mathcal{C}})\|_{L^2(\mathcal{C}, \mathbb{R}^3)}^2 + \kappa \|\Delta_{\mathcal{C}} h\|_{L^2(\mathcal{C})}^2 + \gamma \|\nabla_{\mathcal{C}} h\|_{L^2(\mathcal{C}, \mathbb{R}^3)}^2 + \lambda \|h\|_{L^2(\mathcal{C})}^2 \\ \leq \frac{1}{2} \|p_0\|_{L^2(\mathcal{C})}^2 + |\mathcal{C}| \bar{h}_0^2 + \frac{1}{\mathcal{E}} \|S((h - \bar{h}_0)v_{\mathcal{C}})\|_{L^2(\mathcal{C})}^2. \end{aligned} \quad (4.7)$$

The Grönwall inequality then gives us the bound:

$$\begin{aligned} \|S((h - \bar{h}_0)v_{\mathcal{C}})\|_{L^2(\mathcal{C}, \mathbb{R}^3)}^2(t) &\leq \|S((h^0 - \bar{h}_0)v_{\mathcal{C}})\|_{L^2(\mathcal{C})}^2 e^{t2\mathcal{E}^{-1}} + \int_0^t e^{(t-s)2\mathcal{E}^{-1}} \left(\|p_0\|_{L^2(\mathcal{C})}^2 + 2|\mathcal{C}|\bar{h}_0^2 \right) ds \\ &\leq C(\mathcal{E}, \xi, |\mathcal{C}|) \left(\|S((h^0 - \bar{h}_0)v_{\mathcal{C}})\|_{L^2(\mathcal{C})}^2 + T(\|p_0\|_{L^\infty([0,T], L^2(\mathcal{C}))}^2 + \bar{h}_0^2) \right). \end{aligned} \quad (4.8)$$

With the positive definiteness of L we even have

$$\|h\|_{H^1(\mathcal{C})}^2(t) \leq C(\mathcal{E}, \xi, |\mathcal{C}|) \left(\|S((h^0 - \bar{h}_0)v_{\mathcal{C}})\|_{L^2(\mathcal{C})}^2 + T(\|p_0\|_{L^\infty([0,T], L^2(\mathcal{C}))}^2 + \bar{h}_0^2) + \bar{h}_0^2 \right).$$

This finishes the proof. \square

LEMMA 4.6 Let $T > 0$ and $\bar{h} \in X_T$. The following *a priori* bounds hold for $(\rho_a, \rho_i) = G_T(\bar{h})$:

- (i) $\|\rho_a\|_{L^\infty([0,T], L^2(\mathcal{C}))}^2 + \|\rho_i\|_{L^\infty([0,T], L^2(\mathcal{C}))}^2 \leq \left(\|\rho_a^0\|_{L^2(\mathcal{C})}^2 + \|\rho_i^0\|_{L^2(\mathcal{C})}^2 \right) e^{Tk + C(k, \rho_i) \|r_{\vartheta}(\bar{h})\|_{L^2([0,T], L^4(\mathcal{C}))}^2},$
(ii)

$$\begin{aligned} \|\rho_a\|_{L^2([0,T], H^1(\mathcal{C}))}^2 + \|\partial_t \rho_a\|_{L^2([0,T], H^{-1}(\mathcal{C}))}^2 &\leq C(k, \eta_a, \eta_i) \left(\|\rho_a^0\|_{L^2(\mathcal{C})}^2 + \|\rho_i^0\|_{L^2(\mathcal{C})}^2 \right) \\ &\cdot \left(1 + Tk + \|r_{\vartheta}(\bar{h})\|_{L^2([0,T], L^4(\mathcal{C}))}^2 \right) e^{Tk + C(k, \eta_i) \|r_{\vartheta}(\bar{h})\|_{L^2([0,T], L^4(\mathcal{C}))}^2}. \end{aligned}$$

Proof. (i) We test (4.4a) by $\sigma_a = \rho_a$:

$$\frac{1}{2} \partial_t \|\rho_a\|_{L^2(\mathcal{C})}^2 + \eta_a \|\nabla_{\mathcal{C}} \rho_a\|_{L^2(\mathcal{C}, \mathbb{R}^3)}^2 = k(\rho_i, \rho_a)_{L^2(\mathcal{C})} - (r_{\vartheta}(\bar{h}) \rho_a, \rho_a)_{L^2(\mathcal{C})}$$

and (4.4b) by $\sigma_i = \rho_i$:

$$\frac{1}{2} \partial_t \|\rho_i\|_{L^2(\mathcal{C})}^2 + \eta_i \|\nabla_{\mathcal{C}} \rho_i\|_{L^2(\mathcal{C}, \mathbb{R}^3)}^2 = -k(\rho_i, \rho_i)_{L^2(\mathcal{C})} + (r_{\vartheta}(\bar{h}) \rho_a, \rho_i)_{L^2(\mathcal{C})}$$

and add the equations leaving out the non-positive term $-(r_{\vartheta}(\bar{h}) \rho_a, \rho_a)_{L^2(\mathcal{C})}$ on the right-hand side ($r_{\vartheta} \geq 0$ by assumption):

$$\begin{aligned} \frac{1}{2} \partial_t \left(\|\rho_a\|_{L^2(\mathcal{C})}^2 + \|\rho_i\|_{L^2(\mathcal{C})}^2 \right) + \eta_a \|\nabla_{\mathcal{C}} \rho_a\|_{L^2(\mathcal{C}, \mathbb{R}^3)}^2 + \eta_i \|\nabla_{\mathcal{C}} \rho_i\|_{L^2(\mathcal{C}, \mathbb{R}^3)}^2 + k \|\rho_i\|_{L^2(\mathcal{C})}^2 \\ \leq k(\rho_i, \rho_a)_{L^2(\mathcal{C})} + (r_{\vartheta}(\bar{h}) \rho_a, \rho_i)_{L^2(\mathcal{C})} \\ \leq \frac{k}{2} \left(\|\rho_a\|_{L^2(\mathcal{C})}^2 + \|\rho_i\|_{L^2(\mathcal{C})}^2 \right) + \\ + \frac{\|r_{\vartheta}(\bar{h})\|_{L^4(\mathcal{C})}^2 \|\rho_a\|_{L^2(\mathcal{C})}^2}{4\varepsilon} + \varepsilon \|\rho_i\|_{L^4(\mathcal{C})}^2. \end{aligned} \quad (4.9)$$

We may absorb $\varepsilon \|\rho_i\|_{L^4(\mathcal{C})}^2$ on the left choosing ε small enough. The Grönwall inequality now implies

$$\|\rho_a\|_{L^2(\mathcal{C})}^2(t) + \|\rho_i\|_{L^2(\mathcal{C})}^2(t) \leq \left(\|\rho_a^0\|_{L^2(\mathcal{C})}^2 + \|\rho_i^0\|_{L^2(\mathcal{C})}^2 \right) e^{tk + C(k, \eta_i) \|r_\vartheta(\bar{h})\|_{L^2([0, T], L^4(\mathcal{C}))}^2}$$

thus giving the claimed $L^\infty - L^2$ bound.

(ii) We start again with (4.9), drop $\eta_i \|\nabla_{\mathcal{C}} \rho_i\|_{L^2(\mathcal{C})}^2 + k \|\rho_i\|_{L^2(\mathcal{C})}^2$ on the left, integrate in time and then also drop $\|\rho_a\|_{L^2(\mathcal{C})}^2(t) + \|\rho_i\|_{L^2(\mathcal{C})}^2(t)$ on the left:

$$2\eta_a \|\nabla_{\mathcal{C}} \rho_a\|_{L^2([0, T], L^2(\mathcal{C}, \mathbb{R}^3))}^2 \leq \left(Tk + C(k, \eta_i) \|r_\vartheta(\bar{h})\|_{L^2([0, T], L^4(\mathcal{C}))}^2 \right) \left(\|\rho_a\|_{L^\infty([0, T], L^2(\mathcal{C}))}^2 + \|\rho_i\|_{L^\infty([0, T], L^2(\mathcal{C}))}^2 \right).$$

We further test (4.4a) by $\sigma_a \in H^1(\mathcal{C})$ with $\|\sigma_a\|_{H^1(\mathcal{C})} \leq 1$ such that $\langle \rho_a, \sigma_a \rangle_{H^{-1}(\mathcal{C})} \geq 0$ w.l.o.g., shift the gradient term to the right and use the Hölder inequality on the right-hand side terms:

$$\langle \partial_t \rho_a, \sigma_a \rangle_{H^{-1}(\mathcal{C})} \leq \eta_a \|\nabla_{\mathcal{C}} \rho_a\|_{L^2(\mathcal{C})} + k \|\rho_i\|_{L^2(\mathcal{C})} + \|r_\vartheta(\bar{h})\|_{L^4(\mathcal{C})} \|\rho_a\|_{L^2(\mathcal{C})}.$$

Squaring the inequality and integrating in time we obtain

$$\begin{aligned} \int_0^T \langle \partial_s \rho_a, \sigma_a \rangle_{H^{-1}(\mathcal{C})}^2 ds &\leq C(k, \eta_a) \left(\|\nabla_{\mathcal{C}} \rho_a\|_{L^2([0, T], L^2(\mathcal{C}))}^2 + \|\rho_i\|_{L^2([0, T], L^2(\mathcal{C}))}^2 \right. \\ &\quad \left. + \int_0^T \|r_\vartheta(\bar{h})\|_{L^4(\mathcal{C})}^2(s) \|\rho_a\|_{L^2(\mathcal{C})}^2(s) ds \right) \\ &\leq C(k, \eta_a) \left(\|\nabla_{\mathcal{C}} \rho_a\|_{L^2([0, T], L^2(\mathcal{C}))}^2 + \|\rho_i\|_{L^2([0, T], L^2(\mathcal{C}))}^2 \right. \\ &\quad \left. + \|\rho_a\|_{L^\infty([0, T], L^2(\mathcal{C}))}^2 \|r_\vartheta(\bar{h})\|_{L^2([0, T], L^4(\mathcal{C}))}^2 \right). \end{aligned}$$

□

LEMMA 4.7 Given a time $T > 0$ there exist constants $M_1 > 0$, $M_2 > 0$, depending on the data of Problem 4.1 such that the operator F_T maps the set

$$\begin{aligned} K_T = \{ (u, v, w) \in X_T \times Y_T \times Y_T \mid &\|u\|_{L^\infty([0, T], H^1(\mathcal{C}))}^2 \leq M_1, \\ &\|v\|_{L^\infty([0, T], L^2(\mathcal{C}))}^2 + \|w\|_{L^\infty([0, T], L^2(\mathcal{C}))}^2 \leq M_2, \\ &v, w \geq 0 \text{ a.e.} \}, \end{aligned}$$

into itself for initial data $h^0, \rho_a^0 \geq 0, \rho_i^0 \geq 0$ a.e.

Proof. We choose M_1 as the expression on the right-hand side of the equation in Lemma 4.5. The bound M_2 then directly follows with Lemma 4.6 by setting $M_2 = N \left(\|\rho_a^0\|_{L^2(\mathcal{C})}^2 + \|\rho_i^0\|_{L^2(\mathcal{C})}^2 \right) e^{T(k + \tilde{N} \frac{M_1 L_T}{\vartheta})}$ for some sufficiently large $N, \tilde{N} \in [0, \infty)$.

We may consider (4.4a) and (4.4b) as reaction–diffusion system with right-hand side

$$f(\rho_a, \rho_i) = \begin{pmatrix} f_1(\rho_a, \rho_i) \\ f_2(\rho_a, \rho_i) \end{pmatrix} = \begin{pmatrix} k\rho_i - r_{\vartheta}(\bar{h})\rho_a \\ -k\rho_i + r_{\vartheta}(\bar{h})\rho_a \end{pmatrix}.$$

According to Pierre (2010, Lemma 1.1) quasi-positivity of f is sufficient to guarantee preservation of non-negativity. We see immediately that for $r_1, r_2 \geq 0, f_1(0, r_2) = kr_2 \geq 0$ and $f_2(r_1, 0) = r_{\vartheta}(\bar{h})r_1 \geq 0$, so ρ_a and ρ_i are non-negative since the initial data are non-negative. Therefore, $F_T(K_T) \subseteq K_T$. \square

To apply Banach's fixed point theorem we have to show that there is a $\beta > 0$ such that F_T is a contraction for an arbitrarily chosen $T > 0$. To this purpose we choose an arbitrary pair of arguments $u = (\bar{h}^1, \bar{\rho}_a^1, \bar{\rho}_i^1), v = (\bar{h}^2, \bar{\rho}_a^2, \bar{\rho}_i^2)$ and derive a bound on the difference of $(h^1, \rho_a^1, \rho_i^1) = F_T(u)$ and $(h^2, \rho_a^2, \rho_i^2) = F_T(v)$ in the rescaled norm:

$$|F_T(u) - F_T(v)|_{X_T \times Y_T \times Y_T} \leq L|u - v|_{X_T \times Y_T \times Y_T},$$

where $L \in [0, 1)$. For ease of notation we abbreviate $h_{\Delta} = h^1 - h^2, \rho_{a\Delta} = \rho_a^1 - \rho_a^2$ and $\rho_{i\Delta} = \rho_i^1 - \rho_i^2$.

LEMMA 4.8 There is a β (depending only on problem data) such that the following estimate holds:

$$|h_{\Delta}|_{L^{\infty}([0, T], H^1(\mathcal{C}))} \leq L_h |\bar{\rho}_{a\Delta}|_{L^{\infty}([0, T], L^2(\mathcal{C}))} \quad (4.10)$$

for some $L_h \in [0, 1)$.

Proof. Subtracting (4.3) for the two different arguments one achieves (using the linearity of L):

$$\begin{aligned} & (L((\partial_t h_{\Delta}) \nu_{\mathcal{C}}), \varphi \nu_{\mathcal{C}})_{L^2(\mathcal{C}, \mathbb{R}^3)} + \kappa (\Delta_{\mathcal{C}} h_{\Delta}, \Delta_{\mathcal{C}} \varphi)_{L^2(\mathcal{C})} + \gamma (\nabla_{\mathcal{C}} h_{\Delta}, \nabla_{\mathcal{C}} \varphi)_{L^2(\mathcal{C}, \mathbb{R}^3)} \\ & + \lambda (h_{\Delta}, \varphi)_{L^2(\mathcal{C})} = - \left(\bar{\rho}_a^1 \xi h^1, \varphi \right)_{L^2(\mathcal{C})} + \left(\bar{\rho}_a^2 \xi h^2, \varphi \right)_{L^2(\mathcal{C})}. \end{aligned} \quad (4.11)$$

(i) We then test by $\varphi = h_{\Delta}$ and insert a suitable zero expression on the right-hand side. (Note that h_{Δ} is mean-value-free as $\bar{h}^1 = \bar{h}_0 = \bar{h}^2$.)

$$\begin{aligned} & \frac{1}{2} \partial_t \|S(h_{\Delta} \nu_{\mathcal{C}})\|_{L^2(\mathcal{C}, \mathbb{R}^3)}^2 + \kappa \|\Delta_{\mathcal{C}} h_{\Delta}\|_{L^2(\mathcal{C})}^2 + \gamma \|\nabla_{\mathcal{C}} h_{\Delta}\|_{L^2(\mathcal{C}, \mathbb{R}^3)}^2 + \lambda \|h_{\Delta}\|_{L^2(\mathcal{C})}^2 \\ & = - \left(\bar{\rho}_{a\Delta} \xi h^1, h_{\Delta} \right)_{L^2(\mathcal{C})} - \left(\bar{\rho}_a^2 \xi h_{\Delta}, h_{\Delta} \right)_{L^2(\mathcal{C})}. \end{aligned} \quad (4.12)$$

The last term on the right-hand side is non-positive, so we drop it. We apply the Hölder and then Young inequality and use the positive definiteness of L :

$$\begin{aligned} \frac{1}{2} \partial_t \|S(h_{\Delta} v_{\mathcal{C}})\|_{L^2(\mathcal{C}, \mathbb{R}^3)}^2 + \kappa \|\Delta_{\mathcal{C}} h_{\Delta}\|_{L^2(\mathcal{C})}^2 + \gamma \|\nabla_{\mathcal{C}} h_{\Delta}\|_{L^2(\mathcal{C}, \mathbb{R}^3)}^2 + \lambda \|h_{\Delta}\|_{L^2(\mathcal{C})}^2 \\ \leq \frac{1}{2} \|\bar{\rho}_{a\Delta}\|_{L^2(\mathcal{C})}^2 \|\xi h^1\|_{L^4(\mathcal{C})}^2 + \frac{1}{2} \|h_{\Delta}\|_{L^4(\mathcal{C})}^2 \\ \leq \frac{1}{2} C(\mathcal{E}, \mathcal{C}, \xi) \left(\|\bar{\rho}_{a\Delta}\|_{L^2(\mathcal{C})}^2 \|h^1\|_{L^4(\mathcal{C})}^2 + \|S(h_{\Delta} v_{\mathcal{C}})\|_{L^2(\mathcal{C})}^2 \right). \end{aligned}$$

With the Grönwall inequality we obtain

$$\|S(h_{\Delta} v_{\mathcal{C}})\|_{L^2(\mathcal{C}, \mathbb{R}^3)}^2(t) \leq C(\mathcal{E}, \mathcal{C}, \xi) e^{TC(\mathcal{E}, \mathcal{C}, \xi)} \int_0^t \|\bar{\rho}_{a\Delta}\|_{L^2(\mathcal{C})}^2(s) \|h^1\|_{L^4(\mathcal{C})}^2(s) ds.$$

By multiplying the inequality with $e^{-\beta t}$ and inserting $e^{-\beta s} e^{\beta s}$ under the right-hand side time integral we arrive at

$$\begin{aligned} e^{-\beta t} \|S(h_{\Delta} v_{\mathcal{C}})\|_{L^2(\mathcal{C}, \mathbb{R}^3)}^2(t) &\leq C(T, \mathcal{E}, \mathcal{C}, \xi) e^{-\beta t} \int_0^t e^{-\beta s} e^{\beta s} \|\bar{\rho}_{a\Delta}\|_{L^2(\mathcal{C})}^2(s) \|h^1\|_{L^4(\mathcal{C})}^2(s) ds \\ &\leq C(T, \mathcal{E}, \mathcal{C}, \xi) |\bar{\rho}_{a\Delta}|_{L^\infty([0, T], L^2(\mathcal{C}))}^2 \int_0^t e^{\beta(s-t)} \|h^1\|_{L^4(\mathcal{C})}^2(s) ds. \end{aligned}$$

Observe

$$\int_0^t e^{\beta(s-t)} \|h^1\|_{L^4(\mathcal{C})}^2(s) ds \leq \|h^1\|_{L^\infty([0, T], L^4(\mathcal{C}))}^2 \int_0^t e^{\beta(s-t)} ds = \|h^1\|_{L^\infty([0, T], L^4(\mathcal{C}))}^2 \beta^{-1} (1 - e^{-\beta t}),$$

so by choosing β appropriately large, the claimed contraction estimate follows. \square

LEMMA 4.9 The following estimates hold:

$$|\rho_{i\Delta}|_{L^\infty([0, T], L^2(\mathcal{C}))} + |\rho_{a\Delta}|_{L^\infty([0, T], L^2(\mathcal{C}))} \leq L_\ell |\bar{h}_\Delta|_{L^\infty([0, T], L^6(\mathcal{C}))} \quad (4.13)$$

for $L_\ell \in (0, 1)$.

Proof. (i) Subtracting (4.4b) for the two different arguments and inserting a suitable zero expression on the right-hand side we obtain

$$\begin{aligned} \langle \partial_t \rho_{i\Delta}, \sigma_i \rangle_{H^{-1}(\mathcal{C})} + \eta_i \langle \nabla_{\mathcal{C}} \rho_{i\Delta}, \nabla_{\mathcal{C}} \sigma_i \rangle_{L^2(\mathcal{C}, \mathbb{R}^3)} = -k \langle \rho_{i\Delta}, \sigma_i \rangle_{L^2(\mathcal{C})} \\ + \left(\left(r_{\vartheta}(\bar{h}^1) - r_{\vartheta}(\bar{h}^2) \right) \rho_{a\Delta}^1, \sigma_i \right)_{L^2(\mathcal{C})} + \left(r_{\vartheta}(\bar{h}^2) \rho_{a\Delta}, \sigma_i \right)_{L^2(\mathcal{C})}. \end{aligned}$$

By choosing $\sigma_i = \rho_{i\Delta}$ we find

$$\begin{aligned} \frac{1}{2} \partial_t \|\rho_{i\Delta}\|_{L^2(\mathcal{C})}^2 + \eta_i \|\nabla_{\mathcal{C}} \rho_{i\Delta}\|_{L^2(\mathcal{C}, \mathbb{R}^3)}^2 + k \|\rho_{i\Delta}\|_{L^2(\mathcal{C})}^2 \leq & \left((r_{\vartheta}(\bar{h}^1) - r_{\vartheta}(\bar{h}^2)) \rho_a^1, \rho_{i\Delta} \right)_{L^2(\mathcal{C})} \\ & + \left(r_{\vartheta}(\bar{h}^2) \rho_{a\Delta}, \rho_{i\Delta} \right)_{L^2(\mathcal{C})}. \end{aligned}$$

We apply the Hölder inequality on the right-hand side and then use Young's inequality with a parameter ε so small that $\varepsilon \|\rho_{i\Delta}\|_{L^4(\mathcal{C})}^2$ can be absorbed by the H^1 norm on the left:

$$\begin{aligned} \frac{1}{2} \partial_t \|\rho_{i\Delta}\|_{L^2(\mathcal{C})}^2 + \alpha \|\rho_{i\Delta}\|_{H^1(\mathcal{C})}^2 \leq & \frac{1}{4\varepsilon} \left\| (r_{\vartheta}(\bar{h}^1) - r_{\vartheta}(\bar{h}^2)) \right\|_{L^4(\mathcal{C})}^2 \|\rho_a^1\|_{L^2(\mathcal{C})}^2 \\ & + \frac{1}{4\varepsilon} \left\| r_{\vartheta}(\bar{h}^2) \right\|_{L^4(\mathcal{C})}^2 \|\rho_{a\Delta}\|_{L^2(\mathcal{C})}^2, \end{aligned} \quad (4.14)$$

where α is some positive constant.

Next, we subtract (4.4a) for the two different arguments and insert a suitable zero expression on the right-hand side to obtain

$$\begin{aligned} \langle \partial_t \rho_{a\Delta}, \sigma_a \rangle_{H^{-1}(\mathcal{C})} + \eta_a (\nabla_{\mathcal{C}} \rho_{a\Delta}, \nabla_{\mathcal{C}} \sigma_a)_{L^2(\mathcal{C}, \mathbb{R}^3)} = & k (\rho_{i\Delta}, \sigma_a)_{L^2(\mathcal{C})} \\ & + \left((r_{\vartheta}(\bar{h}^2) - r_{\vartheta}(\bar{h}^1)) \rho_a^1, \sigma_a \right)_{L^2(\mathcal{C})} - \left(r_{\vartheta}(\bar{h}^2) \rho_{a\Delta}, \sigma_a \right)_{L^2(\mathcal{C})}. \end{aligned}$$

Testing with $\sigma_a = \rho_{a\Delta}$ leads to

$$\begin{aligned} \frac{1}{2} \partial_t \|\rho_{a\Delta}\|_{L^2(\mathcal{C})}^2 + \eta_a \|\nabla_{\mathcal{C}} \rho_{a\Delta}\|_{L^2(\mathcal{C}, \mathbb{R}^3)}^2 = & k (\rho_{i\Delta}, \rho_{a\Delta})_{L^2(\mathcal{C})} + \left((r_{\vartheta}(\bar{h}^2) - r_{\vartheta}(\bar{h}^1)) \rho_a^1, \rho_{a\Delta} \right)_{L^2(\mathcal{C})} \\ & - \left(r_{\vartheta}(\bar{h}^2) \rho_{a\Delta}, \rho_{a\Delta} \right)_{L^2(\mathcal{C})} \leq k (\rho_{i\Delta}, \rho_{a\Delta})_{L^2(\mathcal{C})} + \left((r_{\vartheta}(\bar{h}^2) - r_{\vartheta}(\bar{h}^1)) \rho_a^1, \rho_{a\Delta} \right)_{L^2(\mathcal{C})}. \end{aligned}$$

Applying the Hölder and then the Young inequality on the right-hand side terms we obtain

$$\begin{aligned} \frac{1}{2} \partial_t \|\rho_{a\Delta}\|_{L^2(\mathcal{C})}^2 + \eta_a \|\nabla_{\mathcal{C}} \rho_{a\Delta}\|_{L^2(\mathcal{C}, \mathbb{R}^3)}^2 \leq & \frac{k}{2} \left(\|\rho_{i\Delta}\|_{L^2(\mathcal{C})}^2 + \|\rho_{a\Delta}\|_{L^2(\mathcal{C})}^2 \right) \\ & + \frac{1}{2} \left\| (r_{\vartheta}(\bar{h}^2) - r_{\vartheta}(\bar{h}^1)) \right\|_{L^6(\mathcal{C})}^2 \|\rho_a^1\|_{L^3(\mathcal{C})}^2 + \frac{1}{2} \|\rho_{a\Delta}\|_{L^2(\mathcal{C})}^2. \end{aligned} \quad (4.15)$$

We add (4.15) and (4.14) leaving out all non-negative terms on the left-hand sides:

$$\begin{aligned} \frac{1}{2} \left(\partial_t \|\rho_{a\Delta}\|_{L^2(\mathcal{C})}^2 + \partial_t \|\rho_{i\Delta}\|_{L^2(\mathcal{C})}^2 \right) &\leq \frac{1}{2} \left\| \left(r_{\vartheta}(\bar{h}^2) - r_{\vartheta}(\bar{h}^1) \right) \right\|_{L^6(\mathcal{C})}^2 \left\| \rho_a^1 \right\|_{L^3(\mathcal{C})}^2 \\ &\quad + \frac{1}{4\varepsilon} \left\| \left(r_{\vartheta}(\bar{h}^1) - r_{\vartheta}(\bar{h}^2) \right) \right\|_{L^4(\mathcal{C})}^2 \left\| \rho_a^1 \right\|_{L^2(\mathcal{C})}^2 \\ &\quad + \frac{k}{2} \left(\|\rho_{i\Delta}\|_{L^2(\mathcal{C})}^2 + \|\rho_{a\Delta}\|_{L^2(\mathcal{C})}^2 \right) + \frac{1}{4\varepsilon} \left\| r_{\vartheta}(\bar{h}^2) \right\|_{L^4(\mathcal{C})}^2 \|\rho_{a\Delta}\|_{L^2(\mathcal{C})}^2 \\ &\quad + \frac{1}{2} \|\rho_{a\Delta}\|_{L^2(\mathcal{C})}^2. \end{aligned}$$

The Grönwall inequality now implies

$$\|\rho_{a\Delta}\|_{L^2(\mathcal{C})}^2(t) + \|\rho_{i\Delta}\|_{L^2(\mathcal{C})}^2(t) \leq C(\eta_i, \mathcal{C}, \vartheta, L_r) \int_0^t e^{-(t-s)C(k, \mathcal{C}, \eta_i) \|r_{\vartheta}(\bar{h}^2)\|_{L^4(\mathcal{C})}^2} \|\bar{h}_{\Delta}\|_{L^6(\mathcal{C})}^2 \left\| \rho_a^1 \right\|_{L^3(\mathcal{C})}^2 ds.$$

We multiply the inequality by $e^{-\beta t}$ and insert $e^{-\beta s} e^{\beta s}$ under the right-hand side time integral:

$$\begin{aligned} e^{-\beta t} \left(\|\rho_{a\Delta}\|_{L^2(\mathcal{C})}^2(t) + \|\rho_{i\Delta}\|_{L^2(\mathcal{C})}^2(t) \right) &\leq C(\eta_i, \mathcal{C}, \vartheta, L_r) e^{TC(k, \mathcal{C}, \eta_i) \|r_{\vartheta}(\bar{h}^2)\|_{L^\infty([0, T], L^4(\mathcal{C}))}^2} \\ &\quad \cdot e^{-\beta t} \int_0^t e^{\beta s} e^{-\beta s} \|\bar{h}_{\Delta}\|_{L^6(\mathcal{C})}^2 \left\| \rho_a^1 \right\|_{L^3(\mathcal{C})}^2 ds \\ &\leq C(\eta_i, \mathcal{C}, \vartheta, L_r) e^{TC(k, \mathcal{C}, \eta_i) \|r_{\vartheta}(\bar{h}^2)\|_{L^\infty([0, T], L^4(\mathcal{C}))}^2} \\ &\quad \cdot \|\bar{h}_{\Delta}\|_{L^\infty([0, T], L^6(\mathcal{C}))}^2 \int_0^t e^{\beta(s-t)} \left\| \rho_a^1 \right\|_{L^3(\mathcal{C})}^2 ds \\ &\leq C(\eta_i, \mathcal{C}, \vartheta, L_r) e^{TC(k, \mathcal{C}, \eta_i) \|r_{\vartheta}(\bar{h}^2)\|_{L^\infty([0, T], L^4(\mathcal{C}))}^2} \\ &\quad \cdot \|\bar{h}_{\Delta}\|_{L^\infty([0, T], L^6(\mathcal{C}))}^2 \left(\int_0^t e^{2\beta(s-t)} ds \right)^{\frac{1}{2}} \left(\int_0^t \left\| \rho_a^1 \right\|_{L^3(\mathcal{C})}^4 ds \right)^{\frac{1}{2}}. \end{aligned}$$

Due to the *a priori* bounds on ρ_a^1 and the interpolation mentioned in Remark 4.4 we know that

$$\left(\int_0^t \left\| \rho_a^1 \right\|_{L^3(\mathcal{C})}^4 ds \right)^{\frac{1}{2}} = \left\| \rho_a^1 \right\|_{L^4([0, T], L^3(\mathcal{C}))}^2$$

is also bounded. Hence, choosing β large enough (depending only on problem data and T), we obtain the claimed contractive estimate. \square

THEOREM 4.10 (i) Given any $T > 0$ Problem 4.1 has a unique weak solution in K_T .

(ii) Therefore, given the fact that the bounds in K_T include only problem data, Problem 4.1 is well posed in terms of the definition of Hadamard.

Proof. Let $T > 0$ arbitrarily chosen and define K_T as above. It is clear that K_T is closed in $X_T \times Y_T \times Y_T$. The fixed point operator F_T maps K_T into itself according to Lemma 4.7. Furthermore, F_T is a contraction due to Lemmas 4.8 4.9, so the Banach fixed point theorem applies on F_T and guarantees the existence of (h, ρ_a, ρ_i) such that $F_T(h, \rho_a, \rho_i) = (h, \rho_a, \rho_i)$ what immediately implies that (h, ρ_a, ρ_i) is a weak solution of Problem 4.1. Banach's fixed point theorem also guarantees uniqueness of such a fixed point, so the weak solution is unique. \square

5. Stationary solutions

In this section we deal with solutions (h, ρ_a, ρ_i) of Problem 4.1 with $\partial_t h \stackrel{a.e.}{=} \partial_t \rho_a \stackrel{a.e.}{=} \partial_t \rho_i \stackrel{a.e.}{=} 0$, which we call *stationary solutions*. From now on we only consider the case where $a(\cdot, \cdot)$ is coercive (cf. Remark 3.3) and ξ, h^* and p_0 shall be time independent. As pointed out in Remark 3.3 the coercivity requirement puts restrictions on the spontaneous mean curvature, i.e., $H_0 \in (-\infty, -\frac{4}{R}) \cup (0, \infty)$. Physically speaking this means that we either consider a membrane whose natural tendency is to form a concave shape (negative curvature) with a curvature of an absolute value of at least $\frac{4}{R}$ or a strictly convex shape (positive curvature). Apart from this all assumptions on the parameters are the same as in the previous section. The associated stationary problem reads:

PROBLEM 5.1 (Stationary variational problem). Find $h \in H^2(\mathcal{C}), \rho_a, \rho_i \in H^1(\mathcal{C}, [0, \infty))$ such that it holds

$$\kappa (\Delta_{\mathcal{C}} h, \Delta_{\mathcal{C}} \varphi)_{L^2(\mathcal{C})} + \gamma (\nabla_{\mathcal{C}} h, \nabla_{\mathcal{C}} \varphi)_{L^2(\mathcal{C}, \mathbb{R}^3)} + \lambda (h, \varphi)_{L^2(\mathcal{C})} = - (\xi \rho_a h, \varphi)_{L^2(\mathcal{C})} + (p_0, \varphi)_{L^2(\mathcal{C})} \quad (5.1a)$$

$$\eta_a (\nabla_{\mathcal{C}} \rho_a, \nabla_{\mathcal{C}} \sigma_a)_{L^2(\mathcal{C}, \mathbb{R}^3)} = k (\rho_i, \sigma_a)_{L^2(\mathcal{C})} - (r_{\vartheta}(h) \rho_a, \sigma_a)_{L^2(\mathcal{C})} \quad (5.1b)$$

$$\eta_i (\nabla_{\mathcal{C}} \rho_i, \nabla_{\mathcal{C}} \sigma_i)_{L^2(\mathcal{C}, \mathbb{R}^3)} = -k (\rho_i, \sigma_i)_{L^2(\mathcal{C})} + (r_{\vartheta}(h) \rho_a, \sigma_i)_{L^2(\mathcal{C})} \quad (5.1c)$$

for all $\varphi \in H^2(\mathcal{C}), \sigma_a, \sigma_i \in H^1(\mathcal{C})$.

5.1 Basic properties

LEMMA 5.2 Let h and ρ_a be parts of a solution to Problem 5.1. If $\rho_a \geq 0$ a.e., then $\|h\|_{L^2(\mathcal{C})}$ is bounded by a constant depending only on $\kappa, \gamma, \lambda, p_0$ and the domain \mathcal{C} .

Proof. Testing (5.1a) with h we obtain

$$\kappa \|\Delta_{\mathcal{C}} h\|_{L^2(\mathcal{C})}^2 + \gamma \|\nabla_{\mathcal{C}} h\|_{L^2(\mathcal{C}, \mathbb{R}^3)}^2 + \lambda \|h\|_{L^2(\mathcal{C})}^2 + (\xi h \rho_a, h)_{L^2(\mathcal{C})} = (p_0, h)_{L^2(\mathcal{C})}.$$

Due to the coercivity assumption on $a(\cdot, \cdot)$ we stated at the beginning of the section we further have

$$\alpha \|h\|_{H^2(\mathcal{C})}^2 + (\xi h \rho_a, h)_{L^2(\mathcal{C})} \leq \frac{1}{4\varepsilon} \|p_0\|_{L^2(\mathcal{C})}^2 + \varepsilon \|h\|_{L^2(\mathcal{C})}^2$$

for some $\alpha > 0$. Choosing ε small enough (depending on \mathcal{C} and κ, γ , and λ) such that $\varepsilon \|h\|_{L^2(\mathcal{C})}^2$ may be absorbed on the left-hand side we derive

$$\tilde{\alpha} \|h\|_{H^2(\mathcal{C})}^2 \leq \frac{1}{4\varepsilon} \|p_0\|_{L^2(\mathcal{C})}^2$$

with $\tilde{\alpha} > 0$. Since α also depends only on $\mathcal{C}, \kappa, \gamma$ and λ the claim now directly follows. \square

The special structure of (5.1b) and (5.1c) also gives the following:

LEMMA 8 Let $\rho_a, \rho_i \in H^1(\mathcal{C}_0)$ be parts of a solution to Problem 5.1. Then

$$\eta_a \rho_a + \eta_i \rho_i = \rho_0$$

for $\rho_0 \in [0, \infty)$.

Proof. Testing (5.1b) and (5.1c) with the same $\sigma \in C_c^\infty(\mathcal{C})$ and adding both we get

$$(\eta_a \nabla_{\mathcal{C}} \rho_a + \eta_i \nabla_{\mathcal{C}} \rho_i, \nabla_{\mathcal{C}} \sigma)_{L^2(\mathcal{C}, \mathbb{R}^3)} = 0.$$

On closed Riemannian manifolds all weak solutions of this problem are smooth and only differ up to a constant. Therefore,

$$\eta_a \rho_a + \eta_i \rho_i = \rho_0 \text{ a.e.}$$

for a constant $\rho_0 \in [0, \infty)$ since $\rho_a, \rho_i \geq 0$ a.e. □

With the previous results we are in the position to state the following observation:

LEMMA 5.3 Let h be part of a solution to Problem 5.1 with non-negative linker densities. If p_0 is pointwise a.e. large enough, then there exists a set M with two-dimensional Hausdorff measure non-zero such that $(h(x) - h^*) \upharpoonright_M > 0$ for a.e. $x \in \mathcal{C}$.

Proof. Choose an arbitrary function $p_0 \in L^2(\mathcal{C}, [0, \infty))$ and consider the problem of finding $h^s \in H^2(\mathcal{C})$, for $s \in [0, \infty)$, such that

$$\kappa (\Delta_{\mathcal{C}} h^s, \Delta_{\mathcal{C}} \varphi)_{L^2(\mathcal{C})} + \gamma (\nabla_{\mathcal{C}} h^s, \nabla_{\mathcal{C}} \varphi)_{L^2(\mathcal{C}, \mathbb{R}^3)} + \lambda (h^s, \varphi)_{L^2(\mathcal{C})} + \frac{\rho_0}{\eta_a} (\xi h^s, \varphi)_{L^2(\mathcal{C})} = s (p_0, \varphi)_{L^2(\mathcal{C})} \quad (5.2)$$

for all $\varphi \in H^2(\mathcal{C})$, where ρ_0 is the constant of Lemma 8. We note, $h^s \stackrel{a.e.}{=} s h^1$, which directly implies

$$\sup_{x \in \mathcal{C}} h^s(x) = s \sup_{x \in \mathcal{C}} h^1(x).$$

Assume $h^1 \leq 0$. Testing (5.2) with h^1 we find $\|h^1\|_{H^2(\mathcal{C})} \leq 0$, so $h^1 \stackrel{a.e.}{=} 0$, which is no solution to (5.2). Therefore, there exists $x \in \mathcal{C}$ such that $h^1(x) > 0$, so $\sup_{x \in \mathcal{C}} h^1 > 0$.

Since h^s is continuous, there exists $x^* \in \mathcal{C}$ such that $h^s(x^*) = \sup_{x \in \mathcal{C}} h^s(x)$. Choose s^* large enough such that $h^{s^*}(x^*) > h^*$; then, we have a ball $B_\delta(x^*) \subseteq \mathcal{C}$ (in the induced subtopology of \mathcal{C}), $\delta > 0$, where $h^{s^*}(x) > h^*$, $x \in B_\delta(x^*)$, which is a set of non-zero two-dimensional Hausdorff measure.

Now assume h being part of a stationary solution to Problem 5.1 with pressure $s^* p_0$ and being lower or equal h^* almost everywhere. Then (5.1c) becomes

$$\eta_i (\nabla_{\mathcal{C}} \rho_i, \nabla_{\mathcal{C}} \sigma_i)_{L^2(\mathcal{C}, \mathbb{R}^3)} + k (\rho_i, \sigma_i)_{L^2(\mathcal{C})} = 0,$$

so $\rho_i \stackrel{a.e.}{=} 0$. Consequently, $\eta_a \rho_a \stackrel{a.e.}{=} \rho_0$ for some $\rho_0 \geq 0$ (cf. Lemma 8). Therefore, h fulfils (5.2) for s^* . However, this contradicts the observation $h \upharpoonright_{B_\delta(x^*)} > h^*$ made above and the claim must be true. □

Elimination and reconstruction of the inactive linker density Motivated by Lemma 8, we introduce two auxiliary variational problems, which are parametrized by m_0 (recall Lemma 4.1) or ρ_0 , respectively, such that for every stationary solutions of Problem 4.1 there is an auxiliary problem that is fulfilled by it and whose solutions allow for construction of a solution of Problem 5.1. In case $\eta_a \geq \eta_i$ we will employ

PROBLEM 5.4 (Auxiliary problem). Let $m_0 \in [0, \infty)$. Find $h \in H^2(\mathcal{C})$ and $\rho_a \in H^1(\mathcal{C})$ such that

$$a(h, \varphi) + (\xi h \rho_a, \varphi)_{L^2(\mathcal{C})} = (p_0, \varphi)_{L^2(\mathcal{C})} \quad (5.3a)$$

$$b_a(\rho_a, \sigma) + \left(\left(\frac{k\eta_a}{\eta_i} + r_\vartheta(h) \right) \rho_a, \sigma \right)_{L^2(\mathcal{C})} = \frac{k}{|\mathcal{C}|} \left(\left(\left(\frac{\eta_a}{\eta_i} - 1 \right) \int_{\mathcal{C}} \rho_a \, dx + m_0 \right), \sigma \right)_{L^2(\mathcal{C})} \quad (5.3b)$$

for all $\varphi \in H^2(\mathcal{C})$ and $\sigma \in H^1(\mathcal{C})$.

In case $\eta_i > \eta_a$, we will use

PROBLEM 5.6 (Auxiliary problem). Let $\rho_0 \in \mathbb{R}$. Find $h \in H^2(\mathcal{C})$ and $\rho_a \in H^1(\mathcal{C})$ such that

$$a(h, \varphi) + (\xi h \rho_a, \varphi)_{L^2(\mathcal{C})} = (p_0, \varphi)_{L^2(\mathcal{C})} \quad (5.4a)$$

$$b_a(\rho_a, \sigma) + \left(\left(\frac{k\eta_a}{\eta_i} + r_\vartheta(h) \right) \rho_a, \sigma \right)_{L^2(\mathcal{C})} = \frac{k}{\eta_i} (\rho_0, \sigma)_{L^2(\mathcal{C})} \quad (5.4b)$$

for all $\varphi \in H^2(\mathcal{C})$ and $\sigma \in H^1(\mathcal{C})$.

LEMMA 5.5 (i) For all stationary solutions (h, ρ_a, ρ_i) of Problem 4.1 with total linker mass m_0 Problem 5.6 is fulfilled with $\rho_0 = \frac{\eta_i}{|\mathcal{C}|} \left(\left(\frac{\eta_a}{\eta_i} - 1 \right) \int_{\mathcal{C}} \rho_a \, dx + m_0 \right)$ (and therefore also Problem 5.4).

(ii) In case $\eta_i \leq \eta_a$ all solutions (h, ρ_a) of Problem 5.4 (with parameter m_0) can be extended to a solution (h, ρ_a, ρ_i) of Problem 5.1 such that $\eta_a \rho_a + \eta_i \rho_i \equiv \text{const}$ and $\int_{\mathcal{C}} \rho_a + \rho_i \, dx = m_0$. If $\rho_a \geq 0$ a.e., then $\rho_i \geq 0$ a.e.

(iii) In case $\eta_i > \eta_a$ all solutions (h, ρ_a) of Problem 5.6 (with parameter ρ_0) can be extended to a solution (h, ρ_a, ρ_i) of Problem 5.1 such that $\eta_a \rho_a + \eta_i \rho_i \equiv \rho_0$. If $\rho_a \geq 0$ a.e., then $\rho_i \geq 0$ a.e.

Proof. (i) Let h, ρ_a and ρ_i be stationary solutions of Problem 4.1. According to Lemma 4.1 it holds

$$m_0 = \int_{\mathcal{C}} \rho_a + \rho_i \, dx. \quad (5.5)$$

Additionally, due to Lemma 8, we have

$$\rho_0 = \eta_a \rho_a + \eta_i \rho_i. \quad (5.6)$$

Inserting (5.5) into the integrated version of (5.6) gives an equation for ρ_0 :

$$\begin{aligned} \rho_0 &= \frac{1}{|\mathcal{C}|} \left(\eta_a \int_{\mathcal{C}} \rho_a \, dx + \eta_i \int_{\mathcal{C}} \rho_i \, dx \right) = \frac{1}{|\mathcal{C}|} \left(\eta_a \int_{\mathcal{C}} \rho_a \, dx + \eta_i \left(m_0 - \int_{\mathcal{C}} \rho_a \, dx \right) \right) \\ &= \frac{\eta_i}{|\mathcal{C}|} \left(\frac{\eta_a}{\eta_i} \int_{\mathcal{C}} \rho_a \, dx + m_0 - \int_{\mathcal{C}} \rho_a \, dx \right) = \frac{\eta_i}{|\mathcal{C}|} \left(\left(\frac{\eta_a}{\eta_i} - 1 \right) \int_{\mathcal{C}} \rho_a \, dx + m_0 \right). \end{aligned}$$

Inserting this expression and $\rho_i = \frac{1}{\eta_i}(\rho_0 - \eta_a \rho_a)$ into (5.1b) we get

$$\eta_a (\nabla_{\mathcal{E}} \rho_a, \nabla_{\mathcal{E}} \sigma_a)_{L^2(\mathcal{E})} + \left(\left(\frac{k\eta_a}{\eta_i} + r_{\vartheta}(h) \right) \rho_a, \sigma_a \right)_{L^2(\mathcal{E})} = \frac{k}{|\mathcal{E}|} \left(\left(\frac{\eta_a}{\eta_i} - 1 \right) \int_{\mathcal{E}} \rho_a \, dx + m_0 \right) \int_{\mathcal{E}} \sigma_a \, dx.$$

(ii) Now let (h, ρ_a) be a solution of Problem 5.4. Choose

$$\rho_0 = \frac{\eta_i}{|\mathcal{E}|} \left(\left(\frac{\eta_a}{\eta_i} - 1 \right) \int_{\mathcal{E}} \rho_a \, dx + m_0 \right)$$

and set

$$\rho_i = \frac{1}{\eta_i} (\rho_0 - \eta_a \rho_a).$$

We know

$$\eta_a (\nabla_{\mathcal{E}} \rho_a, \nabla_{\mathcal{E}} \sigma_a)_{L^2(\mathcal{E})} + \left(\left(\frac{k\eta_a}{\eta_i} + r_{\vartheta}(h) \right) \rho_a, \sigma_a \right)_{L^2(\mathcal{E})} = \frac{k}{\eta_i} \rho_0 \int_{\mathcal{E}} \sigma_a \, dx,$$

so

$$\begin{aligned} \eta_a (\nabla_{\mathcal{E}} \rho_a, \nabla_{\mathcal{E}} \sigma_a)_{L^2(\mathcal{E})} + (r_{\vartheta}(h) \rho_a, \sigma_a)_{L^2(\mathcal{E})} &= \frac{k}{\eta_i} \left((\rho_0 - \eta_a \rho_a, \sigma_a)_{L^2(\mathcal{E})} \right) \\ &= k (\rho_i, \sigma_a)_{L^2(\mathcal{E})} \end{aligned}$$

and ρ_a satisfies (5.1b). We further calculate the following:

$$\nabla_{\mathcal{E}} \rho_i = \nabla_{\mathcal{E}} \left(\frac{1}{\eta_i} (\rho_0 - \eta_a \rho_a) \right) = -\nabla_{\mathcal{E}} \left(\frac{\eta_a}{\eta_i} \rho_a \right),$$

so

$$\eta_i \nabla_{\mathcal{E}} \rho_i = -\eta_a \nabla_{\mathcal{E}} \rho_a.$$

and ρ_i fulfils (5.1c).

A small computation shows

$$\int_{\mathcal{E}} \rho_a + \rho_i \, dx = \int_{\mathcal{E}} \frac{1}{\eta_i} (\rho_0 - \eta_a \rho_a) + \rho_a \, dx = \frac{|\mathcal{E}|}{\eta_i} \rho_0 + \left(1 - \frac{\eta_a}{\eta_i} \right) \int_{\mathcal{E}} \rho_a \, dx = m_0.$$

Furthermore, if $\rho_a \geq 0$ a.e., then a standard maximum principle guarantees non-negativity of ρ_i .

(iii) The reconstruction of ρ_i is just the same as in (ii) with ρ_0 being directly given. \square

REMARK 5.6 In the case $\eta_i > \eta_a$ the total linkers' mass is given by

$$m_0 = \int_{\mathcal{E}} \rho_a + \frac{1}{\eta_i} (\rho_0 - \eta_a \rho_a) \, dx = \int_{\mathcal{E}} \left(1 - \frac{\eta_a}{\eta_i} \right) \rho_a + \frac{1}{\eta_i} \rho_0 \, dx.$$

It is not hard to see that

$$\frac{|\mathcal{C}|}{\eta_i} \rho_0 \leq m_0 \leq \frac{|\mathcal{C}|}{\eta_a} \rho_0$$

(the latter inequality being due to $\int_{\mathcal{C}} \rho_a \, dx \leq \frac{1}{\eta_a} \int_{\mathcal{C}} \rho_0 \, dx$) implying that there are stationary solutions with arbitrary small (but non-negative) or arbitrary large mass. We conjecture existence of stationary solutions for *all* non-negative masses m_0 . However, it is not clear how a surjective map from ρ_0 to m_0 can be defined—not even a continuous map, so the mean value theorem is not directly applicable; hence, a rigorous argument is still missing.

5.2 Fixed point argument

THEOREM 5.7 There exists a solution (h, ρ_a, ρ_i) to Problem 5.1 with $\rho_a, \rho_i \geq 0$ a.e.

Proof. 1.) Let $\eta_a \geq \eta_i$. According to Lemma 5.5, it is sufficient to prove existence of solutions (h, ρ_a) of Problem 5.4 where $\rho_a \geq 0$ a.e.

Fix $m_0 \geq 0$ and let

$$K = \left\{ (h, \rho_a) \in L^\infty(\mathcal{C}) \times L^1(\mathcal{C}) \left| \begin{aligned} \|h\|_{L^\infty(\mathcal{C})} &\leq C \|p_0\|_{L^2(\mathcal{C})}, \\ 0 &\leq \rho_a \text{ a. e.}, \int_{\mathcal{C}} \rho_a \, dx \leq m_0 \end{aligned} \right. \right\},$$

where C is a constant depending on the constant in Lemma 5.2 and the embedding constant of $H^2(\mathcal{C}) \xrightarrow{\text{cont}} L^\infty(\mathcal{C})$. K is clearly convex and bounded. K is also closed: let $(h^n, \rho_a^n)_{n \in \mathbb{N}}$ be a sequence in K that converges in $L^\infty(\mathcal{C}) \times L^1(\mathcal{C})$. Hence, for all $n \in \mathbb{N}$,

$$\int_{\mathcal{C}} \rho_a^n \, dx \leq m_0,$$

and, as $L^1(\mathcal{C})$ -convergence implies convergence of the integrals $\int_{\mathcal{C}} \rho_a^n \, dx \xrightarrow{n \rightarrow \infty} \int_{\mathcal{C}} \rho_a \, dx$, the inequality is preserved in the limit. Furthermore, for all $x \in \mathcal{C}$ and all $\varepsilon > 0$,

$$\int_{B_\varepsilon(x)} \rho_a^n \, d\xi \geq 0,$$

so, due to $L^1(\mathcal{C})$ -convergence,

$$\int_{B_\varepsilon(x)} \rho_a \, d\xi \geq 0$$

which finally gives (using the Lebesgue point property)

$$\rho_a \geq 0 \text{ a.e.}$$

We now define

$$F : K \rightarrow H^2(\mathcal{C}) \times H^1(\mathcal{C}) \subseteq L^\infty(\mathcal{C}) \times L^1(\mathcal{C})$$

(based on Problem 5.4) with $(h, \rho_a) = F(\bar{h}, \bar{\rho}_a)$ being the functions satisfying

$$a(h, \varphi) + (\xi h \bar{\rho}_a, \varphi)_{L^2(\mathcal{C})} = (p_0, \varphi)_{L^2(\mathcal{C})} \tag{5.7a}$$

$$b_a(\rho_a, \sigma) + \left(\left(\frac{k\eta_a}{\eta_i} + r_\vartheta(\bar{h}) \right) \rho_a, \sigma \right)_{L^2(\mathcal{C})} = \frac{k}{|\mathcal{C}|} \left(\left(\frac{\eta_a}{\eta_i} - 1 \right) \int_{\mathcal{C}} \bar{\rho}_a \, dx + m_0 \right) \int_{\mathcal{C}} \sigma \, dx \tag{5.7b}$$

for all $\varphi \in H^2(\mathcal{C})$ and all $\sigma \in H^1(\mathcal{C})$.

It holds $F(K) \subseteq K$: in order to show non-negativity of ρ_a , we test (5.7b) with $(\rho_a)^-$:

$$\eta_a \|\nabla_{\mathcal{C}}(\rho_a)^-\|_{L^2(\mathcal{C})}^2 + \frac{k\eta_a}{\eta_i} \|(\rho_a)^-\|_{L^2(\mathcal{C})}^2 \leq -\frac{k}{|\mathcal{C}|} \left(\left(\frac{\eta_a}{\eta_i} - 1 \right) \int_{\mathcal{C}} \bar{\rho}_a \, dx + m_0 \right) \int_{\mathcal{C}} (\rho_a)^- \, dx.$$

By assumption $\eta_a \geq \eta_i$ and the right-hand side is always ≤ 0 , which implies $(\rho_a)^- = 0$ a.e. The appropriate *a priori* bound of ρ_a is obtained by testing (5.7b) with 1 and leaving out the gradient term on the left-hand side:

$$\frac{k\eta_a}{\eta_i} \int_{\mathcal{C}} \rho_a \, dx \leq k \left(\left(\frac{\eta_a}{\eta_i} - 1 \right) \int_{\mathcal{C}} \bar{\rho}_a \, dx + m_0 \right) \leq k \left(\left(\frac{\eta_a}{\eta_i} - 1 \right) m_0 + m_0 \right).$$

Dividing both sides by $k\frac{\eta_a}{\eta_i}$ leads to the claimed bound. The bound of h follows directly with the non-negativity of $\bar{\rho}_a$ and Lemma 5.2.

F is continuous: let $(\bar{h}^n, \bar{\rho}_a^n)_{n \in \mathbb{N}}$ be a sequence that converges in K . Take an arbitrary subsequence $F(\bar{h}^{n_k}, \bar{\rho}_a^{n_k}) = (h^{n_k}, \rho_a^{n_k})$. We have the *a priori* bound

$$\|h^{n_k}\|_{H^2(\mathcal{C})} \leq (D(\mathcal{C}, \kappa, \gamma) + 1) \|p_0\|_{L^2(\mathcal{C})}$$

immediately by Lemma 5.2. We also observe

$$\frac{k}{|\mathcal{C}|} \left(\left(\frac{\eta_a}{\eta_i} - 1 \right) \int_{\mathcal{C}} \bar{\rho}_a \, dx + m_0 \right) \int_{\mathcal{C}} \rho_a^{n_k} \, dx \leq \frac{k^2 \eta_a^2}{4\varepsilon \eta_i^2} m_0^2 + \varepsilon \left(\int_{\mathcal{C}} \rho_a^{n_k} \, dx \right)^2 \leq \frac{k^2 \eta_a^2}{4\varepsilon \eta_i^2} m_0^2 + \varepsilon \int_{\mathcal{C}} (\rho_a^{n_k})^2 \, dx.$$

We can choose ε small enough such that $\frac{\varepsilon}{|\mathcal{C}|} < \frac{k\eta_a}{\eta_i}$, so $\varepsilon \int_{\mathcal{C}} (\rho_a^{n_k})^2 \, dx$ can be absorbed on the left-hand side of (5.7b), which gives a uniform bound of $\|\rho_a^{n_k}\|_{H^1(\mathcal{C})}$. So by weak compactness, there are subsequences $h^{n_{k_\ell}}, \rho_a^{n_{k_\ell}}, \bar{h}^{n_{k_\ell}}, \bar{\rho}_a^{n_{k_\ell}}$ such that the integrals in (5.7) converge and we have for the limits

$$F(\bar{h}, \bar{\rho}_a) = (h, \rho_a). \tag{5.8}$$

Due to unique solvability of (5.7), \bar{h} and $\bar{\rho}_a$ are the same limits for all subsequences $\bar{h}^{n_{k_l}}$ and $\bar{\rho}_a^{n_{k_l}}$, respectively, so h^n and ρ_a^n converge to $F(\bar{h}, \bar{\rho}_a)$. However, this implies that F is continuous.

$F(K)$ is relatively compact: choose a sequence $(h^n, \rho_a^n) = F(\bar{h}^n, \bar{\rho}_a^n)$. From the previous calculations, we have a bound of $\|\rho_a^n\|_{H^1(\mathcal{C})}$ and know that $\|h^n\|_{H^2(\mathcal{C})}$ is bounded *a priori*. The compact embeddings $H^1(\mathcal{C}) \xrightarrow{\text{comp}} L^1(\mathcal{C})$ and $H^2(\mathcal{C}) \xrightarrow{\text{comp}} L^\infty(\mathcal{C})$ directly give us a convergent subsequence $(h^{n_k}, \rho_a^{n_k})$ in $L^\infty(\mathcal{C}) \times L^1(\mathcal{C})$.

With these properties of K and F , Schauder's fixed point theorem applies, so F has a fixed point in K . This fixed point (h, ρ_a) is a solution of Problem 5.4, which then may be extended to a solution (h, ρ_a, ρ_i) of Problem 5.1 due to Lemma 5.5.

2.) In case $\eta_a < \eta_i$, the proof is similar: we choose $\rho_0 > 0$ and set

$$K = \left\{ (h, \rho_a) \in L^\infty(\mathcal{C}) \times L^1(\mathcal{C}) \mid \|h\|_{L^\infty(\mathcal{C})} \leq C \|p_0\|_{L^2(\mathcal{C})}, \right. \\ \left. 0 \leq \rho_a \text{ a.e.}, \int_{\mathcal{C}} \rho_a \, dx \leq \frac{|\mathcal{C}|}{\eta_a} \rho_0 \right\}$$

and define

$$F : K \rightarrow H^2(\mathcal{C}) \times H^1(\mathcal{C}) \subseteq L^\infty(\mathcal{C}) \times L^1(\mathcal{C})$$

(based on Problem 5.6) with $(h, \rho_a) = F(\bar{h}, \bar{\rho}_a)$ being the functions satisfying

$$a(h, \varphi) + (\xi h \bar{\rho}_a, \varphi)_{L^2(\mathcal{C})} = (p_0, \varphi)_{L^2(\mathcal{C})}$$

$$b_a(\rho_a, \sigma) + \left(\left(\frac{k\eta_a}{\eta_i} + r_\vartheta(\bar{h}) \right) \rho_a, \sigma \right)_{L^2(\mathcal{C})} = \frac{k}{\eta_i} \rho_0 \int_{\mathcal{C}} \sigma \, dx$$

for all $\varphi \in H^2(\mathcal{C})$ and all $\sigma \in H^1(\mathcal{C})$. □

5.3 Local exponential stability of non-critical stationary solutions

In this section we will be concerned with the local stability of stationary solutions for a specific ripping interpolation function $r_\vartheta(h) = \left(\frac{h-h^*}{\vartheta}\right)^+$ for solutions below the critical height h^* . We are going to make a linearized stability argument using nonlinear semigroup theory (for an introduction see, e.g., Barbu, 1976). Note that, due to Lemma 5.2, there are stationary solutions $\bar{h} < h^*$ a.e. for sufficiently small ρ_0 . Without loss of generality we set $\xi \stackrel{a.e.}{=} 1$. Observe that the operator

$$\mathcal{L}: H^1_{\text{mvf}}(\mathcal{C}) \rightarrow L^2_{\text{mvf}}(\mathcal{C}) \\ x \mapsto L(xv_{\mathcal{C}}) \cdot v_{\mathcal{C}}$$

is invertible as it is linear and its kernel is zero-dimensional (to see this, one may test with x and use the positive definiteness of L).

In the following we will be concerned with a strong version of Problem 4.1:

PROBLEM 5.8 Find $h \in H^1([0, T], H^2(\mathcal{C})) \cap L^2([0, T], H^6(\mathcal{C}))$ and $\rho_a, \rho_i \in H^1([0, T], L^2(\mathcal{C})) \cap L^2([0, T], H^2(\mathcal{C}))$ such that

$$\partial_t \begin{pmatrix} h \\ \rho_a \\ \rho_i \end{pmatrix} = \mathcal{A}(h, \rho_a, \rho_i) + F(h, \rho_a, \rho_i) + G \tag{5.10}$$

with the operator

$$\begin{aligned} \mathcal{A}: H^6(\mathcal{C}) \times H^2(\mathcal{C}) \times H^2(\mathcal{C}) &\rightarrow H^2(\mathcal{C}) \times L^2(\mathcal{C}) \times L^2(\mathcal{C}) \\ (h, \rho_a, \rho_i) &\mapsto \begin{pmatrix} \mathcal{L}^{-1}(-\kappa \Delta_{\mathcal{C}}^2 h + \gamma \Delta_{\mathcal{C}} h + \lambda h) \\ \eta_a \Delta_{\mathcal{C}} \rho_a \\ \eta_i \Delta_{\mathcal{C}} \rho_i \end{pmatrix}, \end{aligned}$$

which is densely defined and closed, the nonlinearity

$$\begin{aligned} F: H^6(\mathcal{C}) \times H^2(\mathcal{C}) \times H^2(\mathcal{C}) &\rightarrow H^6(\mathcal{C}) \times H^2(\mathcal{C}) \times H^2(\mathcal{C}) \\ (h, \rho_a, \rho_i) &\mapsto \begin{pmatrix} -\mathcal{L}^{-1}(h \rho_a) \\ k \rho_i - r_{\vartheta}(h) \rho_a \\ -k \rho_i + r_{\vartheta}(h) \rho_a \end{pmatrix} \end{aligned}$$

and inhomogeneity

$$G: \mathcal{C} \rightarrow [0, \infty), x \mapsto \begin{pmatrix} \mathcal{L}^{-1} p_0(x) \\ 0 \\ 0 \end{pmatrix},$$

for initial data $\rho_a(0, \cdot), \rho_i(0, \cdot) \in L^2(\mathcal{C}, [0, \infty))$, $h(0, \cdot) \in H^2(\mathcal{C})$ and $p_0 \in H^1(\mathcal{C})$.

REMARK 5.9 Well posedness of this problem follows with sufficient regularity of initial data and the inhomogeneity almost by standard techniques as presented, e.g., in [Evans \(2002, Chapter 7\)](#): Using a Galerkin approach we take existing solutions h, ρ_a, ρ_i of Problem 4.1 and express them with eigenfunctions $(w_k)_{k \in \mathbb{N}}$ of $\Delta_{\mathcal{C}}$ constituting a Schauder basis of $L^2(\mathcal{C})$. We obtain the projections $h^m(t, \cdot) = \sum_{k=0}^m a_k(t) w_k$, $\rho_a^m(t, \cdot) = \sum_{k=0}^m b_k(t) w_k$ and $\rho_i^m(t, \cdot) = \sum_{k=0}^m c_k(t) w_k$. The projected height equation is

$$(L(\partial_t h^m v_{\mathcal{C}}), \varphi v_{\mathcal{C}})_{L^2(\mathcal{C})} + a(h^m, \varphi) = -(\pi_m(h \rho_a), \varphi)_{L^2(\mathcal{C})} + (p_0^m, \varphi)_{L^2(\mathcal{C})}$$

for $\varphi \in \text{span}\{w_1, \dots, w_m\}$, where π_m is the projection into $\text{span}\{w_1, \dots, w_m\}$. We differentiate in time and test by $\partial_t h^m$. Integrating in time then gives an energy estimate of the $L^2([0, T], H^2(\mathcal{C}))$ norm of $\partial_t h^m$ (the nonlinearity on the right-hand side is uniformly controlled due to the already established *a priori* bounds of the solutions). $L^2(\mathcal{C})$ regularity for $\partial_t \rho_a$ and $\partial_t \rho_i$ is established by testing the projected equations with $\partial_t \rho_a^m$ and $\partial_t \rho_i^m$, respectively. Control of the nonlinearities also helps with establishing increased spatial regularity.

This result makes us confident that existence theory of (4.1) might as well be developed using nonlinear semigroups.

LEMMA 5.10 A stationary solution to Problem 5.8 is locally exponentially stable iff it is an exponentially stable stationary solution to the corresponding linearized system (see below).

Proof. Due to [Desch & Schappacher \(1986, Theorem 2.1\)](#) the claim follows if we can show differentiability in $H^2(\mathcal{C}) \times L^2(\mathcal{C})^2$ of the nonlinear C_0 semigroup generated by $\mathcal{A} + F$.

Applying Theorem 3.3 in Jamal *et al.* (2014), it is sufficient to show Fréchet differentiability of F in $H^2(\mathcal{C}) \times L^2(\mathcal{C}) \times L^2(\mathcal{C})$ on a sufficiently small ball around a stationary solution $(\bar{h}, \bar{\rho}_a, \bar{\rho}_i)$ with $\bar{h} < h^*$ a.e. and the Lipschitz continuity of the derivative therein. Indeed, its Fréchet derivative is

$$\frac{d}{d(h, \rho_a, \rho_i)} F(h_\Delta, \rho_{a\Delta}, \rho_{i\Delta}) = \begin{pmatrix} \mathcal{L}^{-1}(-\rho_a h_\Delta - h \rho_{a\Delta}) \\ k \rho_{i\Delta} \\ -k \rho_{i\Delta} \end{pmatrix}$$

for $(h, \rho_a, \rho_i) \in B_r(\bar{h}, \bar{\rho}_a, \bar{\rho}_i)$, $r > 0$, where r is chosen sufficiently small such that $h < h^*$ a.e. (This is possible because $H^2(\mathcal{C}) \xrightarrow{\text{cont}} L^\infty(\mathcal{C})$.)

Note, as \mathcal{L}^{-1} is linear and bounded, we may drop it in the following calculations without loss of generality. Consider for $(h_\Delta, \rho_{a\Delta}, \rho_{i\Delta})$ the difference quotient

$$\begin{aligned} & \frac{\|(h + h_\Delta)(\rho_a + \rho_{a\Delta}) - h\rho_a - \rho_a h_\Delta - h\rho_{a\Delta}\|_{H^2(\mathcal{C})}}{\|h\|_{H^2(\mathcal{C}) \times L^2(\mathcal{C}) \times L^2(\mathcal{C})}} + \\ & \frac{\|k(\rho_i + \rho_{i\Delta}) - r_\vartheta(h + h_\Delta)(\rho_a + \rho_{a\Delta}) - k\rho_i + r_\vartheta(h)(\rho_a) - k\rho_{i\Delta}\|_{L^2(\mathcal{C})}}{\|h\|_{H^2(\mathcal{C}) \times L^2(\mathcal{C}) \times L^2(\mathcal{C})}} + \\ & \frac{\|-k(\rho_i + \rho_{i\Delta}) + r_\vartheta(h - h_\Delta)(\rho_a + \rho_{a\Delta}) + k\rho_i - r_\vartheta(h)\rho_a + k\rho_{i\Delta}\|_{L^2(\mathcal{C})}}{\|h\|_{H^2(\mathcal{C}) \times L^2(\mathcal{C}) \times L^2(\mathcal{C})}}. \end{aligned}$$

After straightforward simplifications we obtain

$$\frac{\|h_\Delta \rho_{a\Delta}\|_{H^2(\mathcal{C})}}{\|h\|_{H^2(\mathcal{C}) \times L^2(\mathcal{C}) \times L^2(\mathcal{C})}} + 2 \frac{\|r_\vartheta(h + h_\Delta)(\rho_a + \rho_{a\Delta})\|_{L^2(\mathcal{C})}}{\|h\|_{H^2(\mathcal{C}) \times L^2(\mathcal{C}) \times L^2(\mathcal{C})}}.$$

(Since $h < h^*$ a.e., $r_\vartheta(h)$ vanishes a.e.) Again, we use the imbedding $H^2(\mathcal{C}) \xrightarrow{\text{cont}} L^\infty(\mathcal{C})$ to conclude that if h_Δ is small enough, $h + h_\Delta < h^*$ a.e., so the last term vanishes and all together the difference quotient goes to zero as $(h_\Delta, \rho_{a\Delta}, \rho_{i\Delta}) \xrightarrow{H^2(\mathcal{C})} 0$; hence, F is Fréchet differentiable. \square

For a stationary solution $(\bar{h}, \bar{\rho}_a, \bar{\rho}_i)$ of Problem 5.8 with $\bar{\rho}_a, \bar{\rho}_i \geq 0$ a. e. and with mass $\int_{\mathcal{C}} \bar{\rho}_a + \bar{\rho}_i dx = m_0$ and $\bar{h} < h^*$ a.e., the linearized system of Problem 5.8 is declared as

PROBLEM 5.11 Find $h_\Delta \in H^1([0, T], H^2(\mathcal{C})) \cap L^2([0, T], H^6(\mathcal{C}))$ and $\rho_{a\Delta}, \rho_{i\Delta} \in H^1([0, T], L^2(\mathcal{C})) \cap L^2([0, T], H^2(\mathcal{C}))$ such that

$$\partial_t \begin{pmatrix} h_\Delta \\ \rho_{a\Delta} \\ \rho_{i\Delta} \end{pmatrix} = \mathcal{A}(h_\Delta, \rho_{a\Delta}, \rho_{i\Delta}) + d(F)|_{\bar{h}, \bar{\rho}_a, \bar{\rho}_i}(h_\Delta, \rho_{a\Delta}, \rho_{i\Delta})$$

or, equivalently,

$$\partial_t(h_\Delta) + \mathcal{L}^{-1}(\kappa \Delta_{\mathcal{C}}^2 h_\Delta - \gamma \Delta_{\mathcal{C}} h_\Delta + \lambda h_\Delta) = -\mathcal{L}^{-1}(\bar{\rho}_a h_\Delta + \bar{h} \rho_{a\Delta}) \quad (5.11a)$$

$$\partial_t(\rho_{a\Delta}) - \eta_a \Delta_{\mathcal{C}} \rho_{a\Delta} = k \rho_{i\Delta} \quad (5.11b)$$

$$\partial_t(\rho_{i\Delta}) - \eta_i \Delta_{\mathcal{C}} \rho_{i\Delta} = -k \rho_{i\Delta} \quad (5.11c)$$

with initial values

$$h_{\Delta}(0) = h^0 - \bar{h}, \quad \rho_{a\Delta}(0) = \rho_a^0 - \bar{\rho}_a, \quad \rho_{i\Delta}(0) = \rho_i^0 - \bar{\rho}_i, \quad (5.12)$$

such that $\rho_a^0, \rho_i^0 \geq 0$.

We start by showing that the inactive linkers decay exponentially:

LEMMA 5.12 Let $\rho_{i\Delta} \in H^2(\mathcal{C})$ be part of a triple solving Problem 5.11. Then,

$$\|\rho_{i\Delta}(t)\|_{L^2(\mathcal{C})} \leq \exp(-\omega t) \|\rho_{i\Delta}(0)\|_{L^2(\mathcal{C})}$$

for $\omega \in (0, \infty)$.

Proof. The operator

$$A: H^2(\mathcal{C}) \longrightarrow L^2(\mathcal{C}), u \mapsto -\eta_i \Delta_{\mathcal{C}} u + ku$$

is self-adjoint and its resolvent $R_{\lambda}(A)$ is bounded by $\frac{1}{\lambda+k\wedge\eta_i}$ for all $\lambda > -k\wedge\eta_i$: we have the energy estimate $k \wedge \eta_i \|u\|_{H^1(\mathcal{C})}^2 \leq \eta_i (\nabla_{\mathcal{C}} u, \nabla_{\mathcal{C}} u)_{L^2(\mathcal{C})} + k(u, u)_{L^2(\mathcal{C})} = c_i(u, u)$, so the bilinear form $c_i + \lambda(u, u)_{L^2(\mathcal{C})}$ is coercive for all $\lambda > -k\wedge\eta_i$, so $c_i(u, \varphi) + \lambda(u, \varphi)_{L^2(\mathcal{C})} = (f, \varphi)_{L^2(\mathcal{C})}$ has unique solution for all $f \in L^2(\mathcal{C})$. As $u = R_{\lambda}(A)f$ we have the estimate $\|R_{\lambda}(A)f\|_{L^2(\mathcal{C})} \leq \frac{1}{\lambda+k\wedge\eta_i} \|f\|_{L^2(\mathcal{C})}$.

Therefore, $\sigma(A) \subseteq (-\infty, -k]$. So A generates an analytic semigroup T (Engel & Nagel, 2000, p. 105, Corollary 3.7). This also implies the growth bound of the solution $\rho_{i\Delta}(t) = T(t)\rho_{i\Delta}(0)$ (Renardy & Rogers, 2004, p. 416, Theorem 12.33). \square

Despite equations (5.11b) and (5.11c) looking very symmetric their decaying behaviour is not. To show exponential decay for the active linkers we require an additional condition: the initial values (5.12) to be chosen such that $\int_{\mathcal{C}} \rho_a^0 + \rho_i^0 dx = m_0$, so $\int_{\mathcal{C}} \rho_{a\Delta} + \rho_{i\Delta} dx = 0$, which we call the *mass conservation property*.

LEMMA 5.13 Let $\rho_{a\Delta}$ be part of a triple solving Problem 5.11. Then,

$$\left| \int_{\mathcal{C}} \rho_{a\Delta} dx \right| \leq D \exp(-\omega t)$$

where $\omega > 0$ is the same as in Lemma 5.12 and $D \in (0, \infty)$.

Proof. From the mass conservation property we have

$$\int_{\mathcal{C}} \rho_{a\Delta} + \rho_{i\Delta} dx = 0,$$

so, using Lemma 5.12, we find

$$\left| \int_{\mathcal{C}} \rho_{a\Delta} dx \right| \leq \int_{\mathcal{C}} |\rho_i| dx \leq D' \|\rho_i\|_{L^2(\mathcal{C})} \leq D \exp(-\omega t)$$

for $D', D \in (0, \infty)$. \square

For $\|\rho_{a\Delta}(t, \cdot)\|_{L^2(\mathcal{C})}$ we have at least a time-uniform bound:

LEMMA 5.14 Let $\rho_{a\Delta}$ be part of a triple solving Problem 5.11. Then $\rho_{a\Delta}$ is bounded in $\|\cdot\|_{L^2(\mathcal{C})}$ uniformly for all $t \in [0, \infty)$.

Proof. The operator

$$B : H^2(\mathcal{C}) \rightarrow L^2(\mathcal{C}), \rho_{a\Delta} \mapsto -\eta_a \Delta_{\mathcal{C}} \rho_{a\Delta}$$

is self-adjoint and its resolvent $R_\lambda(B)$ is bounded by $\frac{1}{\lambda}$ for $\lambda > 0$. Therefore, $\sigma(B) \subseteq (-\infty, 0]$ and so it generates a strongly continuous (even analytic) semigroup bounded by 1. As $\rho_{a\Delta}$ solves (5.11b), it has representation as

$$\rho_{a\Delta}(t) = T(t)\rho_{a\Delta}(0) + k \int_0^t T(s-t)\rho_{i\Delta}(s) ds,$$

where T is the semigroup generated by B . Consequently,

$$\|\rho_{a\Delta}(t)\|_{L^2(\mathcal{C})} \leq \|\rho_{a\Delta}(0)\|_{L^2(\mathcal{C})} + k \int_0^t \exp(-\omega s) \|\rho_i(0)\|_{L^2(\mathcal{C})} ds,$$

so we finally have

$$\|\rho_{a\Delta}(t)\|_{L^2(\mathcal{C})} \leq \|\rho_{a\Delta}(0)\|_{L^2(\mathcal{C})} - k \frac{\|\rho_i(0)\|_{L^2(\mathcal{C})}}{\omega} (\exp(-\omega t) - 1).$$

□

Combining these lemmas we even find exponential decay for the active linkers:

LEMMA 5.15 Let $\rho_{a\Delta}$ be part of a triple solving Problem 5.11. Then

$$\|\rho_{a\Delta}\|_{L^2(\mathcal{C})} \leq E_a \exp(-\alpha_a t)$$

for $\alpha_a, E_a \in (0, \infty)$.

Proof. Test (5.11b) with $\rho_{a\Delta}$ to get

$$\frac{1}{2} \partial_t \|\rho_{a\Delta}\|_{L^2(\mathcal{C})}^2 + \eta_a \|\nabla_{\mathcal{C}} \rho_{a\Delta}\|_{L^2(\mathcal{C})}^2 = k (\rho_{i\Delta}, \rho_{a\Delta})_{L^2(\mathcal{C})}.$$

Next, we apply Poincaré's inequality (Neumann type) and Young's inequality (the modulus ε is specified below):

$$\frac{1}{2} \partial_t \|\rho_{a\Delta}\|_{L^2(\mathcal{C})}^2 \leq \frac{k^2}{4\varepsilon} \|\rho_{i\Delta}\|_{L^2(\mathcal{C})}^2 + \varepsilon \|\rho_{a\Delta}\|_{L^2(\mathcal{C})}^2 - \frac{\eta_a}{\Pi} \left\| \rho_{a\Delta} - \int_{\mathcal{C}} \rho_{a\Delta} dx \right\|_{L^2(\mathcal{C})}^2, \quad (5.13)$$

where Π is the appropriate Poincaré constant. Observe, due to Lemma 5.13, that

$$\left| \left\| \rho_{a\Delta} - \int_{\mathcal{C}} \rho_{a\Delta} dx \right\|_{L^2(\mathcal{C})} - \|\rho_{a\Delta}\|_{L^2(\mathcal{C})} \right| \leq \left\| \int_{\mathcal{C}} \rho_{a\Delta} dx \right\|_{L^2(\mathcal{C})} \leq C_1 \exp(-\omega t)$$

for a constant $C_1 \geq 0$. Therefore,

$$\left\| \rho_{a\Delta} - \int_{\mathcal{C}} \rho_{a\Delta} \, dx \right\|_{L^2(\mathcal{C})} = \|\rho_{a\Delta}\|_{L^2(\mathcal{C})} + \delta(t)$$

with $|\delta(t)| \leq C_2 \exp(-\omega t)$ for some $C_2 \geq 0$. Squaring the terms, it follows

$$\left\| \rho_{a\Delta} - \int_{\mathcal{C}} \rho_{a\Delta} \, dx \right\|_{L^2(\mathcal{C})}^2 = \|\rho_{a\Delta}\|_{L^2(\mathcal{C})}^2 + 2\delta(t) \|\rho_{a\Delta}\|_{L^2(\mathcal{C})} + \delta(t)^2,$$

so, as $\|\rho_{a\Delta}\|_{L^2(\mathcal{C})}$ is bounded (cf. Lemma 5.14), we have

$$\left\| \rho_{a\Delta} - \int_{\mathcal{C}} \rho_{a\Delta} \, dx \right\|_{L^2(\mathcal{C})}^2 = \|\rho_{a\Delta}\|_{L^2(\mathcal{C})}^2 + \zeta(t)$$

with $|\zeta(t)| \leq C_3 \exp(-\omega t)$ for some $C_3 \geq 0$.

Substitution into (5.13) gives

$$\begin{aligned} \frac{1}{2} \partial_t \|\rho_{a\Delta}\|_{L^2(\mathcal{C})}^2 &\leq \frac{k^2}{4\varepsilon} \|\rho_{i\Delta}\|_{L^2(\mathcal{C})}^2 + \left(\varepsilon - \frac{\eta_a}{\Pi}\right) \|\rho_{a\Delta}\|_{L^2(\mathcal{C})}^2 - \frac{\eta_a}{\Pi} \zeta(t) \\ &\leq C_4 \left(\frac{k^2}{4\varepsilon} \|\rho_{i\Delta}(0)\|_{L^2(\mathcal{C})}^2 + \frac{\eta_a}{\Pi} \right) \exp(-\omega t) + \left(\varepsilon - \frac{\eta_a}{\Pi}\right) \|\rho_{a\Delta}\|_{L^2(\mathcal{C})}^2, \end{aligned}$$

where $C_4 \geq 0$.

Set $E(\varepsilon) = 2C_4 \left(\frac{k^2}{4\varepsilon} \|\rho_{i\Delta}(0)\|_{L^2(\mathcal{C})}^2 + \frac{\eta_a}{\Pi} \right)$, $\beta(\varepsilon) = 2\left(\varepsilon - \frac{\eta_a}{\Pi}\right)$ and apply Gronwall's inequality:

$$\begin{aligned} \|\rho_{a\Delta}\|_{L^2(\mathcal{C})}^2 &\leq \|\rho_{a\Delta}(0)\|_{L^2(\mathcal{C})}^2 \exp(\beta(\varepsilon)t) + \int_0^t E(\varepsilon) \exp(-\omega s) \exp(\beta(\varepsilon)(t-s)) \, ds \\ &= \|\rho_{a\Delta}(0)\|_{L^2(\mathcal{C})}^2 \exp(\beta(\varepsilon)t) + \exp(\beta(\varepsilon)t) \int_0^t E(\varepsilon) \exp(-(\omega + \beta(\varepsilon))s) \, ds. \end{aligned}$$

The parameter ε is still free, and we choose it such that $-\omega < \beta(\varepsilon) < 0$. With $E_a = \|\rho_{a\Delta}(0)\|_{L^2(\mathcal{C})}^2 + \int_0^t E(\varepsilon) \exp(-(\omega + \beta(\varepsilon))s) \, ds$ and $\alpha_a = -\beta(\varepsilon)$ the claim follows. \square

The last step to showing local exponential stability of Problem 5.2 is showing exponential decay of the height difference:

LEMMA 5.16 Let h_Δ be part of a triple solving Problem 5.11. Then

$$\|h_\Delta\|_{H^2(\mathcal{C})} \leq E_h \exp(-\alpha_h t)$$

for $E_h, \alpha_h \in (0, \infty)$.

Proof. First, we observe that for stationary solutions with $\bar{h} < h^*$ a.e., there are no inactive linkers, i.e., $\bar{\rho}_i \stackrel{a.e.}{=} 0$. (This can be seen in the last paragraph of the proof to Lemma 5.3: since $r_\vartheta(\bar{h}) = 0$, the right-hand side of the inactive linkers equation is zero and therefore testing with $\bar{\rho}_i$ shows that $\|\bar{\rho}_i\|_{H^1(\mathcal{C})}^2 = 0$.) This has the critical implication that $\bar{\rho}_a$ is constant in space (see Lemma 8). Second, recall that the operator L is positive and self-adjoint, so we have positive square root $S^2 = L$. We apply \mathcal{L} on both sides of (5.11a) and test with h_Δ . Then, we make use of Young's inequality and leave out the terms of the bilinear form on the left-hand side

$$\begin{aligned} \frac{1}{2} \partial_t \|Sh_\Delta\|_{L^2(\mathcal{C})}^2 &\leq (-\bar{\rho}_a + \varepsilon) \|h_\Delta\|_{L^2(\mathcal{C})}^2 + \frac{1}{4\varepsilon} \|\bar{h}\|_{L^\infty(\mathcal{C})}^2 \|\rho_{a\Delta}\|_{L^2(\mathcal{C})}^2 \\ &\leq \beta(\varepsilon) \|Sh_\Delta\|_{L^2(\mathcal{C})}^2 + E(\varepsilon) \exp(-2\alpha_a t), \end{aligned}$$

where $E(\varepsilon) = \frac{E_a^2 \|\bar{h}\|_{L^\infty(\mathcal{C})}^2}{4\varepsilon}$ and $\beta(\varepsilon) = \varepsilon^{-1}(\varepsilon - \bar{\rho}_a)$.

Application of Grönwall's inequality leads to

$$\begin{aligned} \|Sh_\Delta\|_{L^2(\mathcal{C})}^2(t) &\leq 2 \|S(h_\Delta(0))\|_{L^2(\mathcal{C})}^2 \exp(\beta(\varepsilon)t) + \int_0^t E(\varepsilon) \exp(-2\alpha_a s) \exp(\beta(\varepsilon)(t-s)) ds \\ &= 2 \|S(h_\Delta(0))\|_{L^2(\mathcal{C})}^2 \exp(\beta(\varepsilon)t) + \exp(\beta(\varepsilon)t) \int_0^t E(\varepsilon) \exp(-(\alpha_a + \beta(\varepsilon))s) ds. \end{aligned}$$

As in the proof of Lemma 5.15 we choose ε such that $-2\alpha_a < \beta(\varepsilon) < 0$. Going back to (5.11a) we find

$$a(h_\Delta, h_\Delta) \leq -\frac{1}{2} \partial_t \|Sh_\Delta\|_{L^2(\mathcal{C})}^2 - \bar{\rho}_a \|h_\Delta\|_{L^2(\mathcal{C})}^2(t) + \|\bar{h}\|_{L^\infty(\mathcal{C})}(t) \|\rho_{a\Delta}\|_{L^2(\mathcal{C})}(t) \|h_\Delta\|_{L^2(\mathcal{C})}(t).$$

We see that the right-hand side consists only of exponentially decaying terms, which gives the decay rate for h_Δ in $\|\cdot\|_{H^2(\mathcal{C})}$. \square

THEOREM 5.17 Every stationary solution $(\bar{h}, \bar{\rho}_a, \bar{\rho}_i)$ of Problem 5.8 with $\bar{h} < h^*$ a.e. is locally exponentially stable under disturbance that fulfils the mass equality condition, i.e., a solution (h, ρ_a, ρ_i) of Problem 5.8 in a sufficiently small neighbourhood of $(\bar{h}, \bar{\rho}_a, \bar{\rho}_i)$ with $\int_{\mathcal{C}} \rho_a^0 + \rho_i^0 dx = \int_{\mathcal{C}} \bar{\rho}_a + \bar{\rho}_i dx$ converges exponentially fast in time to $(\bar{h}, \bar{\rho}_a, \bar{\rho}_i)$.

Proof. The linearized problem of Problem 5.8 in a sufficiently small neighbourhood around $(\bar{h}, \bar{\rho}_a, \bar{\rho}_i)$ is Problem 5.11. Due to Lemma 5.10 we only need to show exponential stability of Problem 5.11 in zero. However, this follows from the results in Lemmas 5.12, 5.15 and 5.16 and we are finished. \square

6. Singular limits

We are going to have a closer look at stationary solutions in the limit $\vartheta \searrow 0$. This way we also rediscover the model of Lim *et al.* (2012) as specialization of our model. Henceforth, we restrict to the special disconnection rate $r_\vartheta(h) = \left(\frac{h-h^*}{\vartheta}\right)^+$.

6.1 Singular limit of the stationary system

THEOREM 6.1 Let $(h^\vartheta, \rho_a^\vartheta, \rho_i^\vartheta)$ be a solution to Problem 5.1 for the parameter ϑ . For every $(\vartheta_n)_{n \in \mathbb{N}}$ with $\lim_{n \rightarrow \infty} \vartheta_n = 0$ there exists a subsequence $(\vartheta_{n_k})_{k \in \mathbb{N}}$ with $h^{\vartheta_{n_k}} \xrightarrow{H^2(\mathcal{C})} h^0$, $\rho_a^{\vartheta_{n_k}} \xrightarrow{H^1(\mathcal{C})} \rho_a^0$ and $\rho_i^{\vartheta_{n_k}} \xrightarrow{H^1(\mathcal{C})} \rho_i^0$ such that

$$a(h^0, \varphi) = -(\xi h^0 \rho_a^0, \varphi)_{L^2(\mathcal{C})} + (p_0, \varphi)_{L^2(\mathcal{C})} \tag{6.1a}$$

$$b_a(\rho_a^0, \sigma_a) = k(\rho_i^0, \sigma_a)_{L^2(\mathcal{C})} - (r_0, \sigma_a)_{L^2(\mathcal{C})} \tag{6.1b}$$

$$b_i(\rho_i^0, \sigma_i) = -k(\rho_i^0, \sigma_i)_{L^2(\mathcal{C})} + (r_0, \sigma_i)_{L^2(\mathcal{C})} \tag{6.1c}$$

for all $\varphi \in H^2(\mathcal{C})$, $\sigma_a, \sigma_i \in C_c(\mathcal{C})$, where $r_0 \in \text{rca}(\mathcal{C})$. (We identify a Radon measure and its density function w.r.t. the Lebesgue measure in the following.) Moreover,

$$(h^* - h^0)^+ r_0 = 0 \tag{6.2}$$

a.e.

Proof. Let $(\vartheta_n)_{n \in \mathbb{N}}$ be a zero sequence. Lemma 8 and the non-negativity of solutions of Problem 5.1 (cf. Theorem 5.7) implies boundedness of $\|\rho_a^{\vartheta_n}\|_{L^\infty(\mathcal{C})}$ and $\|\rho_i^{\vartheta_n}\|_{L^\infty(\mathcal{C})}$ independent of ϑ_n . By testing (5.11b) with $\rho_a^{\vartheta_n}$ we derive an $H^1(\mathcal{C})$ bound on $\rho_a^{\vartheta_n}$ uniformly w.r.t. ϑ_n (the critical term including r_{ϑ_n} can be dropped due to its non-positivity). We employ Lemma 8 again; this time to see that $\eta_a \nabla_{\mathcal{C}} \rho_a^{\vartheta_n} = -\eta_i \nabla_{\mathcal{C}} \rho_i^{\vartheta_n}$ and conclude that the $H^1(\mathcal{C})$ norm of $\rho_i^{\vartheta_n}$ is as well bounded uniformly w.r.t. ϑ_n . Lemma 5.2 assures the boundedness of $\|h^{\vartheta_n}\|_{H^2(\mathcal{C})}$ independently of ϑ_n .

In $H^1(\mathcal{C})^2$ the theorem of Banach–Alaoglu gives us a weakly convergent subsequence $(\rho_a^{\alpha_n}, \rho_i^{\alpha_n})_{n \in \mathbb{N}}$ to $(\rho_a^0, \rho_i^0) \in H^1(\mathcal{C})^2$ as well as going to another subsequence $(h^{\beta_n})_{n \in \mathbb{N}}$ of $(h^{\alpha_n})_{n \in \mathbb{N}}$ does in $H^2(\mathcal{C})$. We use the Rellich–Kondrachov theorem to single out another subsequence $(\rho_a^{\gamma_n})_{n \in \mathbb{N}}$ converging in $L^2(\mathcal{C})$ to ρ_a^0 (since weak convergence in $H^1(\mathcal{C})$ implies weak convergence in $L^2(\mathcal{C})$ to the same limit). Analogously, we have convergence of a subsequence $(h^{\delta_n})_{n \in \mathbb{N}}$ to h^0 in $L^2(\mathcal{C})$, which includes another subsequence $(h^{\zeta_n})_{n \in \mathbb{N}}$ converging pointwise to h^0 .

Due to weak convergence

$$a(h^{\zeta_n}, \varphi) \xrightarrow{n \rightarrow \infty} a(h^0, \varphi)$$

for any $\varphi \in H^2(\mathcal{C})$. Moreover,

$$\begin{aligned} \left| (h^0 \rho_a^0 - h^{\zeta_n} \rho_a^{\zeta_n}, \varphi)_{L^2(\mathcal{C})} \right| &\leq \left| (h^0 (\rho_a^0 - \rho_a^{\zeta_n}), \varphi)_{L^2(\mathcal{C})} \right| + \left| (\rho_a^{\zeta_n} (h^0 - h^{\zeta_n}), \varphi)_{L^2(\mathcal{C})} \right| \\ &\leq \|h^0\|_{L^\infty(\mathcal{C})} \|\rho_a^0 - \rho_a^{\zeta_n}\|_{L^2(\mathcal{C})} \|\varphi\|_{L^2(\mathcal{C})} + \|h^0 - h^{\zeta_n}\|_{L^2(\mathcal{C})} \|\rho_a^{\zeta_n} \varphi\|_{L^2(\mathcal{C})}, \end{aligned}$$

so we have

$$(h^{\zeta_n} \rho_a^{\zeta_n}, \varphi)_{L^2(\mathcal{C})} \xrightarrow{n \rightarrow \infty} (h^0 \rho_a^0, \varphi)_{L^2(\mathcal{C})}$$

and (6.1a) holds.

To retrieve (6.1b) and (6.1c) test (5.1b) with a smoothed signum $S_\varepsilon \in H^1(\mathcal{C})$ of ρ_a with $S_\varepsilon \xrightarrow{H^1(\mathcal{C})} \text{sgn} \circ \rho_a^{\zeta_n}$. We then have

$$(\nabla_{\mathcal{C}} \rho_a^{\zeta_n}, \nabla_{\mathcal{C}} S_\varepsilon)_{L^2(\mathcal{C})} + \left(r_{\zeta_n} (h^{\zeta_n}) \rho_a^{\zeta_n}, S_\varepsilon \right)_{L^2(\mathcal{C})} = k \left(\rho_i^{\zeta_n}, S_\varepsilon \right)_{L^2(\mathcal{C})}.$$

Therefore,

$$\left(r_{\zeta_n} (h^{\zeta_n}) \rho_a^{\zeta_n}, S_\varepsilon \right)_{L^2(\mathcal{C})} \leq C_1 \left(\left\| \rho_a^{\zeta_n} \right\|_{H^1(\mathcal{C})} \left\| S_\varepsilon \right\|_{H^1(\mathcal{C})} + \left\| \rho_i^{\zeta_n} \right\|_{L^2(\mathcal{C})} \left\| S_\varepsilon \right\|_{L^2(\mathcal{C})} \right)$$

for a constant $C_1 > 0$. So in the limit $\varepsilon \rightarrow 0$ we get the estimate

$$\left\| r_{\zeta_n} (h^{\zeta_n}) \rho_a^{\zeta_n} \right\|_{L^1(\mathcal{C})} \leq C_2$$

for a constant $C_2 > 0$ due to the *a priori* bound on ρ_a and ρ_i . This implies weak- \star -convergence in $\text{rca}(\mathcal{C})$ of a subsequence $r_{\zeta_{n_k}} (h^{\zeta_{n_k}}) \rho_a^{\zeta_{n_k}}$ to a Radon measure $r_0 \in \text{rca}(\mathcal{C})$. As $h^{\zeta_{n_k}}$ and h^* are in $L^\infty(\mathcal{C})$, $(h^* - h^{\zeta_{n_k}})^+ r_{\zeta_{n_k}} (h^{\zeta_{n_k}}) \rho_a^{\zeta_{n_k}} \in \text{rca}(\mathcal{C})$ and $(h^* - h^{\zeta_{n_k}})^+ r_{\zeta_{n_k}} (h^{\zeta_{n_k}}) \rho_a^{\zeta_{n_k}}$ weak- \star -converges to $(h^* - h^0)^+ r_0$ in $\text{rca}(\mathcal{C})$. We observe that

$$\text{supp} \left((h^* - h^{\zeta_{n_k}})^+ \right) \cap \text{supp} \left(r_{\zeta_{n_k}} (h^{\zeta_{n_k}}) \right) = \emptyset,$$

so

$$(h^* - h^{\zeta_{n_k}})^+ r_{\zeta_{n_k}} (h^{\zeta_{n_k}}) \rho_a^{\zeta_{n_k}} = 0$$

and $(h^* - h^0)^+ r_0 = 0$. □

6.2 Model without diffusion

We now turn to the system (5.1) with $\eta_a = \eta_i = 0$, which will lead us to a model of Lim *et al.* (2012) in the Γ -limit $\vartheta \rightarrow 0$. Recall, that a sequence of functionals $F_n : X \rightarrow \mathbb{R}$, $n \in \mathbb{N}$, defined on a topological space Γ -converges to a functional $F : X \rightarrow \mathbb{R}$ iff

- (i) For all $x \in X$ and $x_n \xrightarrow{n \rightarrow \infty} x$, $\liminf_{n \rightarrow \infty} F_n(x_n) \geq F(x)$ and
- (ii) For all $x \in X$ there exists $x_n \xrightarrow{n \rightarrow \infty} x$ such that $\limsup_{n \rightarrow \infty} F_n(x_n) \leq F(x)$.

Vanishing diffusivities have not been treated in our previous existence proofs for the time-dependent or stationary case. We attack this issue by reducing the system (5.1) to minimizing an energy functional. In this order we choose a function $\rho \in H^1(\mathcal{C})$, $\rho \geq 0$ a.e., and formally substitute $\rho_i = \rho - \rho_a$ into (5.1b). This way we obtain the following:

$$r \left(\frac{h - h^*}{\vartheta} \right) \rho_a = k (\rho - \rho_a) \iff \rho_a = \frac{k \rho}{k + r \left(\frac{h - h^*}{\vartheta} \right)} = g_\vartheta \circ h, \quad (6.3)$$

where $g_\vartheta : \mathbb{R} \rightarrow \mathbb{R}, x \mapsto \frac{k\rho}{k+r\left(\frac{x-h^*}{\vartheta}\right)}$. Inserting into (5.1a) we have only one equation left:

$$a(h, \varphi) + (hg_\vartheta \circ h, \varphi)_{L^2(\mathcal{C})} = (p_0, \varphi)_{L^2(\mathcal{C})}, \tag{6.4}$$

whose solutions are the critical points of the following energy functional

$$\begin{aligned} \mathcal{J}_\vartheta : H^2(\mathcal{C}) &\rightarrow \mathbb{R} \\ \mathcal{J}_\vartheta(h) &= \frac{1}{2}a(h, h) + \int_{\mathcal{C}} \int_0^{h(x)} sg_\vartheta(s) \, ds \, dx - \int_{\mathcal{C}} p_0(x)h(x) \, dx. \end{aligned}$$

LEMMA 6.2 There exists a minimizer of \mathcal{J}_ϑ .

Proof. This functional is coercive in the $H^2(\mathcal{C})$ norm:

$$\frac{1}{2}a(h, h) - \int_{\mathcal{C}} p_0(x)h(x) \, dx \geq C_1 \|h\|_{H^2(\mathcal{C})}^2 - \frac{1}{4\varepsilon} \|p_0\|_{L^2(\mathcal{C})}^2 - \varepsilon \|h\|_{L^2(\mathcal{C})}^2,$$

$C_1 > 0$, and we choose ε smaller enough for $\varepsilon \|h\|_{L^2(\mathcal{C})}^2$ to be absorbed by $C_1 \|h\|_{H^2(\mathcal{C})}^2$.

Set $A(h) = \frac{1}{2}a(h, h)$ and $B(h) = \int_{\mathcal{C}} \int_0^{h(x)} sg_\vartheta(s) \, ds \, dx + F(h)$, where

$$F : H^2(\mathcal{C}) \rightarrow \mathbb{R}, \quad h \mapsto - \int_{\mathcal{C}} p_0(x)h(x) \, dx.$$

Note that A is weakly lower semicontinuous in $H^2(\mathcal{C})$. We show that B is weakly continuous in $H^2(\mathcal{C})$, so $A + B$ is weakly lower semicontinuous in $H^2(\mathcal{C})$.

B is continuous in $C_b(\mathcal{C})$: take a sequence $(h_n)_{n \in \mathbb{N}}$ converging in $C_b(\mathcal{C})$ to h . Now observe that for all $\delta > 0$, there exists an $N \in \mathbb{N}$ such that for all $n \geq N$, it holds

$$\begin{aligned} \left| \int_{\mathcal{C}} \int_0^{h(x)} sg_\vartheta(s) \, ds \, dx - \int_{\mathcal{C}} \int_0^{h_n(x)} sg_\vartheta(s) \, ds \, dx \right| &\leq |\mathcal{C}| \sup_{x \in \mathcal{C}} \left| \int_{h_n(x)}^{h(x)} sg_\vartheta(s) \, ds \right| \\ &\leq |\mathcal{C}| \sup_{x \in \mathcal{C}} \left| \int_{h(x) \pm \delta}^{h(x)} sg_\vartheta(s) \, ds \right|, \end{aligned}$$

so

$$\int_{\mathcal{C}} \int_0^{h_n(x)} sg_\vartheta(s) \, ds \, dx \xrightarrow{n \rightarrow \infty} \int_{\mathcal{C}} \int_0^{h(x)} sg_\vartheta(s) \, ds \, dx.$$

Conclusively, $B(h_n) \rightarrow B(h)$ for $n \rightarrow \infty$.

Since $H^2(\mathcal{C}) \xrightarrow{\text{comp}} C_b(\mathcal{C})$, for every sequence $(h_n)_{n \in \mathbb{N}}$ converging weakly in $H^2(\mathcal{C})$ to h , we may take from every subsequence a subsubsequence $(h_{n_k})_{k \in \mathbb{N}}$ that converges in $C_b(\mathcal{C})$ to h' . It holds $h' \stackrel{a.e.}{=} h$ as weak convergence in $H^2(\mathcal{C})$ implies weak convergence in $L^2(\mathcal{C})$ and convergence in $C_b(\mathcal{C})$ implies (strong) convergence in $L^2(\mathcal{C})$. So with the previous result $B(h_n) \xrightarrow{n \rightarrow \infty} B(h)$. \square

With this lemma we have proven that for every $\rho \in H^1(\mathcal{C})$, $\rho \geq 0$ a. e., we find a minimizer h of \mathcal{J}_ϑ with which we may then define $\rho_a = g_\vartheta \circ h$, and further $\rho_i = \rho - \rho_a$ such that (h, ρ_a, ρ_i) solves (5.1) with vanishing diffusivities. It is easily checked that the constructed linker densities are non-negative.

LEMMA 6.3 For $\vartheta \searrow 0$ the energy functional \mathcal{J}_ϑ Γ -converges to

$$\mathcal{J}_0(h) = \frac{1}{2}a(h, h) + \int_{\mathcal{C}} g_0(x) dx - \int_{\mathcal{C}} p_0(x)h(x) dx,$$

where $g_0(x) = \frac{\rho}{2} \min\{h(x)^2, (h^*)^2\}$.

Proof. As the other terms in \mathcal{J}_ϑ are independent of ϑ we only need to consider the functional

$$\mathcal{G}_\vartheta : H^2(\mathcal{C}) \rightarrow \mathbb{R}, \quad h \mapsto \int_{\mathcal{C}} \int_0^{h(x)} sg_\vartheta(s) ds dx.$$

It is first shown that from any $(\vartheta_n)_{n \in \mathbb{N}} \rightarrow 0$ and any $(h_n)_{n \in \mathbb{N}}$ that converges in $H^2(\mathcal{C})$ to h a subsequence such that $\mathcal{G}_n(h_n) \rightarrow \mathcal{G}_0(h)$ can be singled out. (For the sake of notational simplicity, we abbreviate $\mathcal{G}_{\vartheta_n} = \mathcal{G}_n$ and $g_{\vartheta_n} = g_n$.)

In this order, rewrite

$$\begin{aligned} \int_{\mathcal{C}} \int_0^{h_n(x)} sg_n(s) ds dx - \int_{\mathcal{C}} \int_0^{h(x)} sg_0(s) ds dx &= \left(\int_{\mathcal{C}} \int_0^{h_n(x)} sg_n(s) ds dx - \int_{\mathcal{C}} \int_0^{h(x)} sg_n(s) ds dx \right) \\ &\quad + \left(\int_{\mathcal{C}} \int_0^{h(x)} sg_n(s) ds dx - \int_{\mathcal{C}} \int_0^{h(x)} sg_0(s) ds dx \right). \end{aligned}$$

We take a subsequence such that h_{n_k} converges in $C_b(\mathcal{C})$ to h . For any $\delta > 0$ consider a sufficiently large k such that

$$\begin{aligned} \left| \int_{\mathcal{C}} \int_0^{h_{n_k}(x)} sg_{n_k}(s) ds dx - \int_{\mathcal{C}} \int_0^{h(x)} sg_{n_k}(s) ds dx \right| &\leq \int_{\mathcal{C}} \left| \int_{h(x) \pm \delta}^{h(x)} sg_{n_k}(s) ds \right| dx \\ &\leq \int_{\mathcal{C}} \int_{h(x) - \delta}^{h(x)} sg_{n_k}(s) ds dx. \end{aligned}$$

This term converges to zero for $\delta \rightarrow 0$ since $\|g_{n_k}\|_{L^\infty(\mathcal{C})}$ is uniformly (in k) bounded. Now consider

$$\begin{aligned} \int_{\mathcal{C}} \int_0^{h(x)} sg_n(s) ds dx &= \int_{\{x \in \mathcal{C} \mid h(x) \leq h^*\}} \int_0^{h(x)} \rho s ds dx + \int_{\{x \in \mathcal{C} \mid h(x) > h^*\}} \int_0^{h^*} \rho s ds dx \\ &\quad + \int_{\{x \in \mathcal{C} \mid h(x) > h^*\}} \int_{h^*}^{h(x)} sg_n(s) ds dx. \end{aligned}$$

Due to the monotonicity of r , $g_n(s)$ monotonically decreases to zero and $g_n \leq g_1 \in L^1(\mathcal{C})$, the monotone convergence theorem applies, so the last term converges to zero for $n \rightarrow \infty$. Therefore,

$$\begin{aligned} \int_{\mathcal{C}} \int_0^{h(x)} s g_n(s) \, ds \, dx &\xrightarrow{n \rightarrow \infty} \int_{\{x \in \mathcal{C} \mid h(x) \leq h^*\}} \frac{\rho}{2} h(x)^2 \, dx + \int_{\{x \in \mathcal{C} \mid h(x) > h^*\}} \frac{\rho}{2} (h^*)^2 \, dx \\ &= \mathcal{G}_0(h). \end{aligned}$$

Take any clustering point of $\mathcal{G}_n(h_n)$ and a subsequence $\mathcal{G}_{n_k}(h_{n_k})$ converging to it. Using the previous result we single out another subsequence that converges to $\mathcal{G}_0(h)$, which has to be the clustering point, so $\mathcal{G}_0(h) \leq \liminf_{n \rightarrow \infty} \mathcal{G}_{\vartheta_n}(h_n)$.

Choosing an arbitrary h and taking the sequence $h_n = h$ converging to it the previous considerations also lead to $\mathcal{G}_0(h) \geq \limsup_{n \rightarrow \infty} \mathcal{G}_n(h_n)$ and the claimed Γ -limit is shown. \square

LEMMA 6.4 The Euler–Lagrange equation of \mathcal{J}_0 is given by

$$\kappa \Delta_{\mathcal{C}}^2 h - \gamma \Delta_{\mathcal{C}} h + \lambda h + \rho h H \left(1 - \frac{h}{h^*} \right) = p_0$$

for all $h \in H^4(\mathcal{C})$ with $H(x) = \begin{cases} 0 & x \leq 0 \\ 1 & x > 0 \end{cases}$ being the Heaviside function.

Proof. Let h be a stationary point of \mathcal{J}_0 , i.e., $\frac{d}{d\varepsilon} (\mathcal{J}_0(h + \varepsilon v))|_0 = 0$ for all $v \in H^2(\mathcal{C})$. Take an arbitrary $v \in H^2(\mathcal{C})$ and consider $\varepsilon > 0$ small enough such that $h < h^*$ a.e. implies $h + \varepsilon v \leq h^*$ a.e. Then calculate

$$\begin{aligned} &\frac{d}{d\varepsilon} \left(\int_{\mathcal{C}} \min\{(h(x) + \varepsilon v(x))^2, (h^*)^2\} \, dx \right) \Big|_0 \\ &= \frac{d}{d\varepsilon} \left(\int_{\{x \in \mathcal{C} \mid h(x) < h^*\}} (h(x) + \varepsilon v(x))^2 \, dx \right) \Big|_0 + \frac{d}{d\varepsilon} \left(\int_{\{x \in \mathcal{C} \mid h(x) \geq h^*\}} (h^*)^2 \, dx \right) \Big|_0 \\ &= \int_{\{x \in \mathcal{C} \mid h(x) \leq h^*\}} \frac{d}{d\varepsilon} \left((h(x) + \varepsilon v(x))^2 \right) \Big|_0 \, dx = 2 \int_{\{x \in \mathcal{C} \mid h(x) \leq h^*\}} h(x) v(x) \, dx \\ &= 2 \int_D h(x) H \left(1 - \frac{h(x)}{h^*} \right) v(x) \, dx. \end{aligned}$$

The other derivatives are standard and the claim follows. \square

We may summarize the results of this section as follows:

THEOREM 6.5 (i) For a total mass density $\rho \geq 0$ and a ripping parameter $\vartheta > 0$, any minimizer h of \mathcal{J}_{ϑ} constitutes a (variational) solution to Problem 5.1 for $\eta_a = \eta_i = 0$ together with some $\rho_a, \rho_i \in H^1(\mathcal{C})$.

(ii) Sending ϑ to zero minimizers of \mathcal{J}_{ϑ} converge to variational solutions of the model of Lim *et al.* (2012), cf. p. 2, Equation (2) therein.

Proof. (i) Take any ρ and ϑ . Existence of minimizers of \mathcal{J}_ϑ is guaranteed by Problem 6.2. As critical points the minimizers solve (6.4). Defining ρ_a according to (6.3) and $\rho_i = \rho - \rho_a$ we get solutions of Problem 5.1 for $\eta_a = \eta_i = 0$.

(ii) Follows directly from Lemma 6.3 and Lemma 6.4. \square

7. Numerical examples

In this section we discuss results from numerical simulations of the parabolic PDE system we analysed in the previous sections. The predicted bleb size after a typical bleb formation time is compared against heights observed by biologists. Furthermore, we investigate the role of the critical pressure defined in Lim *et al.* (2012) for static systems in the case of our time-dependent PDE system.

7.1 Parameters and initial conditions

As the tabular Table 1 suggests, quite a lot parameters of our model have already been assessed and discussed in the literature. The interested reader may consult the given sources and the references therein as a thorough treatment of these parameters is not in the scope of this work. Nevertheless, the choice of γ requires a comment: we decided to follow Lim *et al.* (2012) and Alert & Casademunt (2016) and set $H_0 = 0$. Despite their choice of $\kappa = 2 \cdot 10^{-19}$ J and $\gamma = -2 \cdot 10^{-6}$ we stay consistent with our computations in Section 3.3, p. (10) and take $\gamma \sim -\frac{\kappa}{R^2}$.

In correspondence to Alert & Casademunt (2016) we choose the linker density $\rho_a(0, \cdot)$ to be 10^{14} m^{-2} and start with $\rho_i(0, \cdot) = 0$, accordingly.

7.2 Discretization

The computations were done on a rectangle $\mathcal{C} = [-0.49\pi, 0.49\pi] \times [0, 2\pi]$ being an approximation of the parameter space of the transformation

$$S: \left[-\frac{\pi}{2}, \frac{\pi}{2}\right] \times [0, 2\pi) \rightarrow \omega_R^2$$

$$(\theta, \phi) \mapsto (R \cos(\theta) \cos(\phi), R \cos(\theta) \sin(\phi), R \sin(\theta))^T$$

TABLE 1 *Parameter configuration*

Parameter	Symbol	Value	Unit	Source
Damping constant	c	$5 \cdot 10^{-3}$	Pa s m^{-1}	(Alert & Casademunt, 2016, p. 1879)
Membrane bending rigidity	κ	$2 \cdot 10^{-19}$	J	Dai & Sheetz (1999)
Surface tension	γ	$-4 \cdot 10^{-9}$	N m^{-1}	see text
Linker spring constant	ξ	10^{-4}	N m^{-1}	Alert & Casademunt (2016)
Linker diffusivities	$\eta_a = \eta_i$	10^{-6}	$\text{m}^2 \text{ s}^{-1}$	Jacobson <i>et al.</i> (2019)
Reconnection rate	k	10^4	s^{-1}	Rognoni <i>et al.</i> (2012)
Critical linkers length	h^*	10^{-9}	m	Lim <i>et al.</i> (2012)
Cortex radius	R	10^{-5}	m	Charras & Paluch (2008)

onto the 2-sphere $\omega_R^2 \subseteq \mathbb{R}^3$ in three dimensions with radius R . The boundary $[-0.49, 0.49] \times \{0\} \cup [-0.49, 0.49] \times \{2\pi\}$ is chosen to be periodic and at $\{-0.49\} \times [0, 2\pi] \cup \{0.49\} \times [0, 2\pi]$ we employ homogeneous Neumann boundary conditions. This domain approximation is a simple approach towards the singularities at the poles of ω_R^2 and there are other more elaborate methods like surface finite elements (cf. [Dzuiik & Elliott, 2013](#)) which can handle such problems. However, we will show that we can in fact recover established results and conclude that this approach is sufficient for studying the bleb height near the equator. The fluid influence is neglected for simplicity setting $L = cI$.

In order to avoid a $H^2(\mathcal{C})$ trial space, but to stick with conformal Galerkin methods, we use a standard splitting of the Δ^2 operator with boundary conditions for h and Δh by introducing $w = -\Delta h$. This leads to the following system:

$$c\partial_t h - \kappa \Delta w + \gamma w = -\xi \rho_a h + p_0$$

$$w + \Delta h = 0$$

$$\partial_t \rho_a - \eta_a \Delta \rho_a = k \rho_i - r_\vartheta(h) \rho_a$$

$$\partial_t \rho_i - \eta_i \Delta \rho_i = -k \rho_i + r_\vartheta(h) \rho_a.$$

In the Galerkin approximation, we employ Lagrangian \mathbb{P}_1 finite elements conforming with the trial space $H^1(\mathcal{C})$ for h , w , ρ_a and ρ_i . The mesh width is denoted by Δx . In this configuration we obtain a semidiscretization of the form

$$cM\partial_t h^{\Delta x} + \kappa Aw^{\Delta x} + \gamma Mw^{\Delta x} = b(\rho_a^{\Delta x}, h^{\Delta x}) + Mp_0^{\Delta x}$$

$$Mw^{\Delta x} - Ah^{\Delta x} = 0$$

$$M\partial_t \rho_a^{\Delta x} + \eta_a A \rho_a^{\Delta x} = kM\rho_i^{\Delta x} - q_\vartheta(h^{\Delta x}, \rho_a^{\Delta x})$$

$$M\partial_t \rho_i^{\Delta x} + \eta_i A \rho_i^{\Delta x} = -kM\rho_i^{\Delta x} + q_\vartheta(h^{\Delta x}, \rho_a^{\Delta x})$$

with a matrices $M, A \in \mathbb{R}^{(N,N)}$, where N is the number of interior nodes and the corresponding basis functions $\{\varphi_i \mid i \in \{1, \dots, N\}\}$ defined there and

$$b(\rho_a^{\Delta x}, h^{\Delta x}) = \left((\xi \rho_a^{\Delta x} h^{\Delta x}, \varphi_i)_{L^2(\mathcal{C})} \right)_{i \in \{1, \dots, N\}},$$

$$q_\vartheta(h^{\Delta x}, \rho_a^{\Delta x}) = \left((\rho_a^{\Delta x} r_\vartheta(h^{\Delta x}), \varphi_i)_{L^2(\mathcal{C})} \right)_{i \in \{1, \dots, N\}}.$$

For implementation of this spatial discretization we used the FEM solver *Netgen/NGSolve* (<https://ngsolve.org>, [Schöberl, 2014](#)).

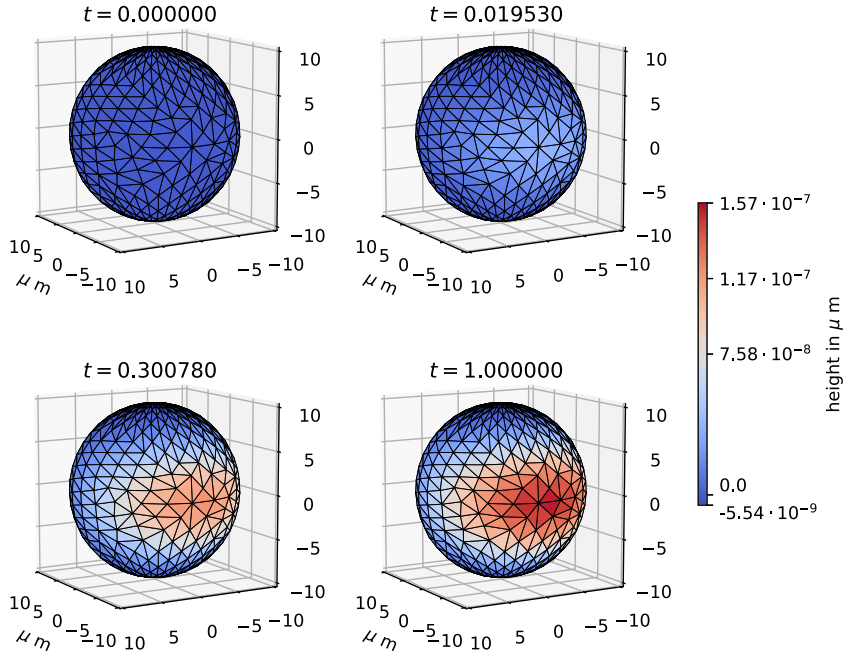


FIG. 2. **Bleb formation over time.** The development of a bleb as a height function with respect to the cortex (which is modelled by a sphere of radius 10^{-5} m) is shown at several points in time (normalized with respect to 30 s) as reaction to an applied pressure that is constant in time. (For details see p. 169.)

Discretization in time is achieved by applying a semi-implicit Euler scheme with time step size $\tau > 0$ and time points $0 = t_1 < t_2 < \dots < t_k < t_{k+1} < \dots < T$, $n \in \mathbb{N}$:

$$c\tau^{-1}M \left(h^{\Delta x, k+1} - h^{\Delta x, k} \right) + \kappa A w^{\Delta x, k+1} + \gamma M w^{\Delta x, k+1} = b \left(\rho_a^{\Delta x, k+1}, h^{\Delta x, k+1} \right) + M p_0^{\Delta x} \quad (7.3a)$$

$$M w^{\Delta x, k+1} - A h^{\Delta x, k+1} = 0 \quad (7.3b)$$

$$\tau^{-1}M \left(\rho_a^{\Delta x, k+1} - \rho_a^{\Delta x, k} \right) + \eta_a A \rho_a^{\Delta x, k+1} = k M \rho_i^{\Delta x, k+1} - q_{\vartheta} \left(h^{\Delta x, k}, \rho_a^{\Delta x, k+1} \right) \quad (7.3c)$$

$$\tau^{-1}M \left(\rho_i^{\Delta x, k+1} - \rho_i^{\Delta x, k} \right) + \eta_i A \rho_i^{\Delta x, k+1} = -k M \rho_i^{\Delta x, k+1} + q_{\vartheta} \left(h^{\Delta x, k}, \rho_a^{\Delta x, k+1} \right). \quad (7.3d)$$

To cope with the implicit terms and the nonlinearities, we use Newton's fixed point iteration.

7.3 Scenarios

For all the simulations we will discuss in the following the parameters of the PDE are as in Fig. 1. The typical expansion time for a bleb to nucleate is about 30 s (Charras & Paluch, 2008), so we normalized the simulation time with respect to this reference quantity. The cortex is modelled (as before in the analytic part) as a sphere with radius $R = 10^{-5}$ m (Charras & Paluch, 2008). **Nucleation of a bleb** We are interested in the (maximal) height of the bleb that is nucleated after this time. It has been observed that the typical height of blebs is about $2 \mu\text{m}$, cf. Charras & Paluch (2008).

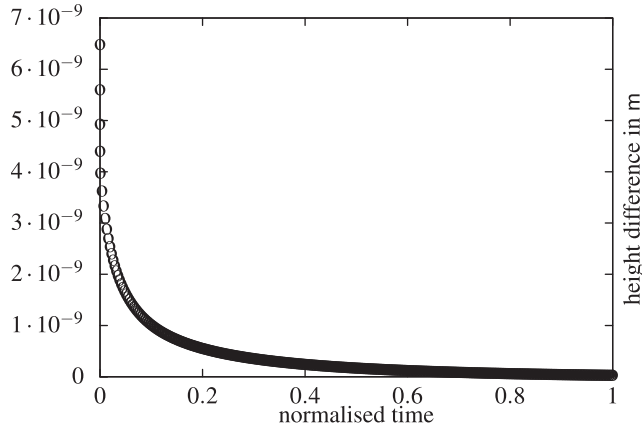


FIG. 3. **Maximal height difference.** The maximum of the height function difference of two preceding time points is plotted against time (normalized with respect to 30 s). (For details see remark 7.1.)

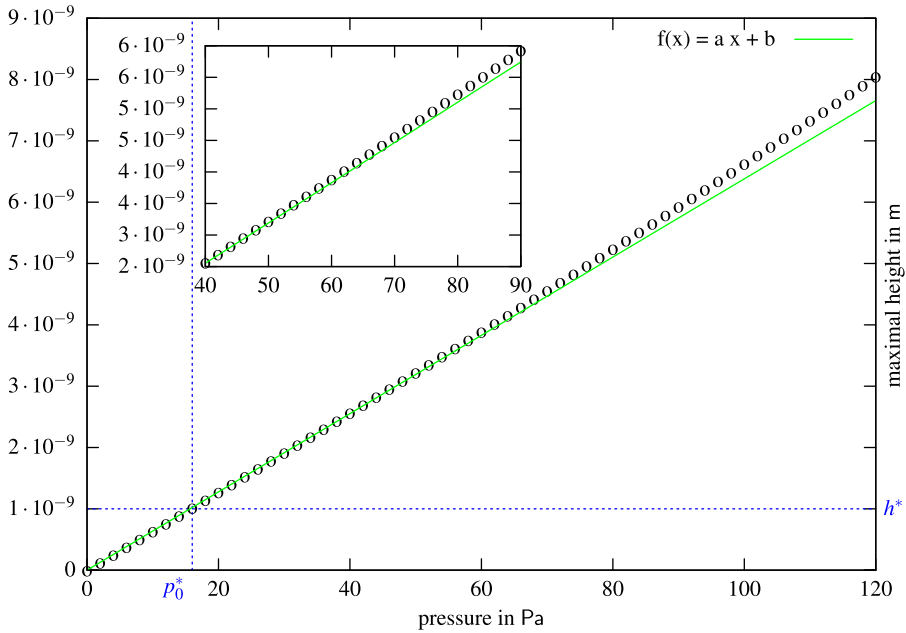


FIG. 4. **Maximal heights after 30 s against the applied pressure.** The maximal height that is reached after $t = 30$ s (black circles) is plotted against a time-constant pressure (abscissa) that has been applied. The green line is a linear function with parameters $a \sim 6.38 \cdot 10^{-11}$, $b \sim 0$ that goes through the first two data samples exactly. The blue labels are the critical pressure $p_0^* = 16$ Pa and the critical height $h^* = 10^{-9}$ m. (For details see p. 175).

We prescribe a pressure as the function $x \mapsto 10^3 e^{-\frac{d(x,m)}{2r^2}}$ Pa, where d is the geodesic distance between the argument $x \in S^2$ and a midpoint $m \in S^2$ and r controls the width of the pressure pulse. The pressure is constant in time. The scaling ϑ of the disconnection rate $r_\vartheta(h)$ is still free. A parameter

TABLE 2 *Fitting errors (RMS)*

Pressure (in Pa)	RMS
2	0
4	$4.47 \cdot 10^{-17}$
6	$3.27 \cdot 10^{-17}$
8	$3.50 \cdot 10^{-17}$
10	$3.09 \cdot 10^{-17}$
12	$3.28 \cdot 10^{-17}$
14	$3.16 \cdot 10^{-17}$
16	$2.99 \cdot 10^{-17}$
18	$2.85 \cdot 10^{-14}$
20	$1.11 \cdot 10^{-13}$
22	$2.40 \cdot 10^{-13}$
24	$4.18 \cdot 10^{-13}$
26	$6.45 \cdot 10^{-13}$
28	$9.17 \cdot 10^{-13}$
30	$1.23 \cdot 10^{-12}$
⋮	⋮
120	$5.98 \cdot 10^{-11}$

The tabular shows the root-mean-squared residual errors of the Marquardt–Levenberg algorithm for fitting a linear function into the data sets of the intervals $[0, x]$, where x is the pressure value of the corresponding line. The blue marked lines exhibit a significant jump in the RMS. As the critical pressure was determined before to be 16 Pa this consolidates the hypothesis that above the critical pressure there is a qualitative change in the bleb development. (For details see p. 175).

study shows that with $\vartheta = 1.1 \cdot 10^{-12}$, we may achieve a bleb height of $1.57 \cdot 10^{-7}$, which is about one tenth of the experimentally observed bleb height. With a more elaborate view on the protein distribution at the membrane and especially their behaviour after the critical height h^* is passed, one may achieve better results. For some time points we plotted the membrane height as a heat map on the cortex, see Fig. 2.

REMARK 7.1 Considering the difference between the maximal height of every time step (see Fig. 3) there seems to be numerical indication of a stability property like that rigorously shown in Section 5.3, which does not apply in this case as $H_0 = 0$ and $a(\cdot, \cdot)$ is not coercive.

Critical pressure Lim *et al.* (2012) consider a bleb to form when the the membrane height reaches above the critical height h^* (on a certain interval $I \subseteq \mathbb{R}$) and linker bonds are broken in response. According to this notion of a bleb in their static model they define the *critical pressure* to be the greatest pressure below which the membrane height is beneath the critical height everywhere. We adopt this notion to our (dynamic) model in the sense that the critical pressure p_0^* is the greatest value below which the maximal height of the membrane is beneath the critical height after the nucleation phase of 30 s which is driven by the pressure function

$$p_0(x) = p_0^* \cdot e^{-\frac{d(x,m)}{2r^2}} \text{ Pa.}$$

Passing the critical height triggers the linker disconnection process.

By applying the pressure as previously described and increasing the pressure in steps of 2 Pa we plotted the maximal height after the nucleation phase against the pressure, see Fig. 4. Considering a linear function through the first two data samples gives evidence that the data samples do not grow linearly at least not on the whole pressure range; up to a pressure of about 60 Pa linear growth seems to be a good description. We hypothesize that there is a change in the growing behaviour and that this change occurs at the critical pressure. To give some evidence for this we successively fitted linear functions (with the gnuplot implementation of the Marquardt–Levenberg algorithm) to the data sets of the pressure intervals $[0 : q]$, $q \in \{2, \dots, 120\}$, and assessed the root mean square residuum (RMS), see Fig. 2. We notice that until 16 Pa there is very little change in the RMS. From 16 Pa to 18 Pa there is a specifically large increase of the RMS (three orders of magnitude). Afterwards, the RMS increases readily. Taking a look at, Fig. 4, we see that 16 Pa happens to be the critical pressure which substantiates our hypothesis that reaching the critical pressure triggers a major change in the bleb growth behaviour.

8. Conclusion

We derived a PDE model by balancing the bending, stretching and linker forces coming from the variational derivative of an extended Helfrich energy functional with the stress at the interface between the cytosol and the extracellular fluid. Based on the restriction of only small membrane displacement normal to the cortex we could derive a gradient flow describing the membrane height normal to the cell cortex. Additionally, linker kinetics were incorporated with reaction–diffusion equations where we also introduced the concept of inactive linkers to include the phenomenon of cortex disruption. To our knowledge this effect cannot be modelled with any other model.

For the resulting system we established global-in-time existence and uniqueness of weak solutions by applying the Banach fixed point theorem. The stationary case can also be treated with a fixed point argument, which uses the Schauder fixed point theorem, to establish existence. However, we do not have results about uniqueness or at least classification of stationary solutions.

The *a priori* estimates used in the stationary solution existence proof could be exploited for passing to the limit in the rescaling parameter of the disconnection rate, $\vartheta \searrow 0$. We observed that the model of Lim *et al.* (2012) could be rediscovered this way. The existence of a singular limit in the time-dependent case remains an interesting open question for future research.

Finally, let us mention that so far the model is purely mechanistic and ignores any interaction with external and cell-internal signalling. In particular, the interaction of bleb formation with polarization of protein distributions influencing the mechanical properties will become important in order to fully understand cell migration by blebbing.

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Appendix A. Dirichlet-to-Neumann operator of the stationary Stokes problem

We define the Neumann-to-Dirichlet operator for the stationary Stokes problem

$$\begin{aligned}
 \mu \left(\mathcal{J}(u), \mathcal{J}(\varphi) \right)_{L^2(\mathcal{D}, \mathbb{R}^{3,3})} - (p, \nabla \cdot \varphi)_{L^2(\mathcal{D})} &= (f, \gamma_{\mathcal{M}}(\varphi))_{L^2(\mathcal{M})} \\
 (\nabla \cdot u, q)_{L^2(\mathcal{D})} &= 0 \\
 \gamma_{\Gamma}(u) &= 0 \\
 \gamma_{\mathcal{M}}(u) &= g
 \end{aligned} \tag{A.1}$$

with $u, \varphi \in H^1(\mathcal{D})$, $p, q \in L^2(\mathcal{D})$, and $g \in H_{\gamma_0\sigma}^1(\mathcal{M}, \mathbb{R}^3)$, $f \in L_{\gamma_0\sigma}^2(\mathcal{M}, \mathbb{R}^3)$, where

$$H_{\gamma_0\sigma}^1(\mathcal{M}, \mathbb{R}^3) = \left\{ u \in H^1(\mathcal{M}, \mathbb{R}^3) \mid \int_{\mathcal{M}} uv_{\mathcal{M}} dx = 0 \right\}$$

as function

$$\mathcal{D}\mathcal{N}: H_{\gamma_0\sigma}^1(\mathcal{M}, \mathbb{R}^3) \rightarrow L_{\gamma_0\sigma}^2(\mathcal{M}, \mathbb{R}^3)$$

mapping g to f .

REMARK A.1 For the Stokes problem with mean-value-free pressure p and no restriction on the Neumann data f , the well posedness of this operator follows from (Fabes *et al.*, 1988, Theorem 4.15). However, a unique solution of the above problem is then easily defined by setting $\tilde{p} = p + \int_{\mathcal{M}} f \cdot \nu_{\mathcal{M}} d\sigma^2$.

We further have the following properties

LEMMA A.2

- (i) $\mathcal{D}\mathcal{N}$ is self-adjoint and positive definite.
- (ii) There exists a positive definite operator $S: L_{\gamma_0\sigma}^2(\mathcal{M}, \mathbb{R}^3) \rightarrow L_{\gamma_0\sigma}^2(\mathcal{M}, \mathbb{R}^3)$ such that $S^2 = \mathcal{D}\mathcal{N}$ on the domain of $\mathcal{D}\mathcal{N}$.
- (iii) $\mathcal{D}\mathcal{N}$ is continuous from the $\|\cdot\|_{H^1(\mathcal{M})}$ topology of its domain to the $\|\cdot\|_{L^2(\mathcal{M})}$ topology of its range.

Proof. (i) We may express the Dirichlet-to-Neumann operator as

$$\mathcal{D}\mathcal{N} = \left\{ (g, f) \in \left(L_{\gamma_0\sigma}^2(\mathcal{M}, \mathbb{R}^3) \right)^2 \mid \begin{array}{l} \exists u \in H_{\sigma}^{\frac{3}{2}}(\mathcal{M}), \gamma_{\mathcal{M}}(u) = g: \forall \varphi \in H_{\sigma}^{\frac{3}{2}}(\mathcal{M}): \\ \mu(\mathcal{J}(u), \mathcal{J}(\varphi))_{L^2(\mathcal{D})} = (f, \gamma_{\mathcal{M}}(\varphi))_{L^2(\mathcal{M})} \end{array} \right\}.$$

By form methods (as used e.g. in Fujita *et al.*, 2001, Chapter 7), the claim follows from the coercivity, continuity and symmetry of $(u, \varphi) \mapsto (\mathcal{J}(u), \mathcal{J}(\varphi))_{L^2(\mathcal{D})}$.

(ii) We refer to Sebestyén & Tarcsay (2017, Theorem 2.3).

(iii) This can be directly derived from Fabes *et al.* (1988, Theorem 4.15) and the continuity of the trace operator. \square

Appendix B. Existence and uniqueness of solutions for the height equation

LEMMA B.1 There is exactly one $h \in L^2([0, T], H_{\text{mvf}}^2(\mathcal{C})) \cap H^1([0, T], H_{\text{mvf}}^1(\mathcal{C}))$ satisfying

$$(L(\partial_t h \nu_{\mathcal{C}}, \varphi \nu_{\mathcal{C}}))_{L^2(\mathcal{C})} + a(h, \varphi) = (f(t), \varphi)_{L^2(\mathcal{C})} \quad (\text{B.1})$$

with

$$a(h, \varphi) = \kappa (\Delta_{\mathcal{C}} h, \Delta_{\mathcal{C}} \varphi)_{L^2(\mathcal{C})} + \gamma (\nabla_{\mathcal{C}} h, \nabla_{\mathcal{C}} \varphi)_{L^2(\mathcal{C}, \mathbb{R}^3)} + \lambda (h, \varphi)_{L^2(\mathcal{C})}$$

for almost every $t \in [0, T)$ and all $\varphi \in H^2(\mathcal{C})$, where $f \in C([0, T], L^2(\mathcal{C}))$ and $h(0) = h_0 \in L_0^2(\mathcal{C})$.

Proof. We argue by a Petrov–Galerkin-type approximation:

(1) Let $(\varphi_i)_{i \in \mathbb{N}}$ be an orthonormal Schauder basis of $L^2(\mathcal{C})$ with eigenvalues $(\lambda_i)_{i \in \mathbb{N}}$ (sorted ascendingly) consisting of eigenfunctions of the Laplace–Beltrami operator $\Delta_{\mathcal{C}}$ (due to the divergence theorem and $\partial \mathcal{C} = \emptyset$, the eigenfunctions φ_i , $i \geq 2$, are mean value free; for a spectral theorem on Riemannian manifolds cf. Lablée, 2015, Theorem 4.3.1). For $m \in \mathbb{N}$ we set $h_m(t, x) = \sum_{i=2}^m h_i(t) \varphi_i(x)$ and $f_m(t, x) = \sum_{i=1}^m f_i(t) \varphi_i(x)$. Formally inserting into (B.1) and testing with φ_j , $j \in \{1, \dots, m\}$ we

obtain the finite-dimensional system for the coefficient vectors $\underline{h}_m = (h_i)_{i \in \{2, \dots, m\}}$ and right hand side $\underline{f}_m = (f_j)_{j \in \{1, \dots, m\}}$:

$$M\underline{h}'_m + \kappa A^2 \underline{h}_m + \gamma A \underline{h}_m + \lambda \underline{h}_m = \underline{f}_m, \tag{B.2}$$

where $A = \text{diag}(\lambda_2, \dots, \lambda_m)$ and $M = ((L(\varphi_i \nu_{\mathcal{C}}), \varphi_j \nu_{\mathcal{C}})_{L^2(\mathcal{C})})_{j \in \{1, \dots, m\}, i \in \{2, \dots, m\}}$. Due to the symmetry and positive definiteness of $L(\cdot) \nu_{\mathcal{C}} \cdot \nu_{\mathcal{C}}$ in $L^2(\mathcal{C})$ (see Lemma A.2) the columns of M are linearly independent (M without its last line would be invertible), and well-posedness of (B.2) complemented by the initial condition $\underline{h}(0) = \underline{h}_{0,m} = ((h_0, \varphi_j)_{L^2(\mathcal{C})})_{j \in \{2, \dots, m\}}$ follows by multiplying with the Moore-Penrose pseudo left inverse $(M^T M)^{-1} M^T$ and the Picard–Lindelöf theorem.

(2) Multiplying (B.2) by $h_m = (0, h_i)_{i \in \{2, \dots, m\}}$ in the Euclidean scalar product we obtain

$$(L(h'_m), h_m)_{L^2(\mathcal{C})} + \kappa (\Delta_{\mathcal{C}} h_m, \Delta_{\mathcal{C}} h_m)_{L^2(\mathcal{C})} + \gamma (\nabla_{\mathcal{C}} h_m, \nabla_{\mathcal{C}} h_m)_{L^2(\mathcal{C}, \mathbb{R}^3)} + \lambda (h_m, h_m)_{L^2(\mathcal{C})} = (f, h_m)_{L^2(\mathcal{C})}.$$

Leaving out $a(h_m, h_m)$ (non-negative term, cf. Remark 3.3) and applying the Cauchy–Schwartz inequality on the right we arrive at

$$(L(h'_m), h_m)_{L^2(\mathcal{C})} \leq \frac{1}{2} \|f_m\|_{L^2(\mathcal{C})}^2 + \frac{1}{2} \|h_m\|_{L^2(\mathcal{C})}^2 \leq \frac{1}{2} \|f_m\|_{L^2(\mathcal{C})}^2 + \frac{\theta^{-1}}{2} \|Sh_m\|_{L^2(\mathcal{C})}^2$$

with $L = S^2$. We recall the continuity of L (see Lemma A.2) and observe $(L(h'_m), h_m)_{L^2(\mathcal{C})} = \frac{1}{2} \frac{d}{dt} \|Sh_m\|_{L^2(\mathcal{C})}^2$. By applying the Grönwall inequality we find the bound

$$\theta \|h_m\|_{H^1(\mathcal{C})}^2(t) \leq \|Sh_m\|_{L^2(\mathcal{C})}^2(t) \leq \|Sh_{0,m}\|_{L^2(\mathcal{C})}^2 e^{t\theta^{-1}} + \int_0^t \|f_m\|_{L^2(\mathcal{C})}^2(s) e^{(t-s)\theta^{-1}} ds.$$

Since $h_{0,m}$ and f_m are bounded uniformly in $L^2(\mathcal{C})$ and $L^2([0, T], L^2(\mathcal{C}))$ w.r.t. m , respectively, so is h_m in $L^\infty([0, T], H^1(\mathcal{C}))$. Not leaving out $a(h_m, h_m)$, but integrating in time and using the previously achieved bound, we may further bound $\|\Delta_{\mathcal{C}} h_m\|_{L^2([0, T], L^2(\mathcal{C}))}^2$ uniformly w.r.t. m , eventually giving a bound on h_m in $L^2([0, T], H^2(\mathcal{C}))$ uniformly w. r. t. m . Multiplying (B.2) by $h'_m = (0, h'_i(t))_{i \in \{2, \dots, m\}}$ in the scalar product sense, we see

$$\theta \|h'_m\|_{H^1(\mathcal{C})}^2 \leq (L(h'_m), h'_m)_{L^2(\mathcal{C})} \leq |a(h_m, h'_m)| + |(f_m, h'_m)_{L^2(\mathcal{C})}|.$$

With Young’s inequality, integration in time and the previous bounds we obtain a bound of h'_m in $L^2([0, T], H^1(\mathcal{C}))$ uniformly w.r.t. m . All together there is a subsequence with indices m_k such that h'_{m_k} weakly converges in $H^1(\mathcal{C})$ to $h' \in H^1_{\text{mvf}}(\mathcal{C})$, $L(h'_{m_k})$ converges weakly in $L^2(\mathcal{C})$ to $L(h')$, h_{m_k} weakly converges in $H^2(\mathcal{C})$ to $h \in H^2_{\text{mvf}}(\mathcal{C})$ and f_{m_k} weakly in $L^2(\mathcal{C})$ to f for almost every $t \in [0, T]$. Uniqueness follows with the linearity of the equation. \square

COROLLARY B.2 (i) There is exactly one $h \in L^2([0, T], H^2(\mathcal{C})) \cap H^1([0, T], H^1_{\text{mvf}}(\mathcal{C}))$ satisfying

$$(L(\partial_t h \nu_{\mathcal{C}}), \varphi \nu_{\mathcal{C}})_{L^2(\mathcal{C})} + a(h, \varphi) = (f(t), \varphi)_{L^2(\mathcal{C})}$$

for almost every $t \in [0, T]$ and all $\varphi \in H^2(\mathcal{C})$, where $f \in C([0, T], L^2(\mathcal{C}))$ and $h(0) = h_0 \in L^2(\mathcal{C})$.

(ii) The mean value $\int_{\mathcal{C}} h \, dx$ is constant in time.

Proof. (i) Let $\tilde{f} = f - \lambda \int_{\mathcal{E}} h_0 \, dx$ and $\tilde{h}_0 = h_0 - \int_{\mathcal{E}} h_0 \, dx$. Then consider the solution \tilde{h} of (B.1) with initial data \tilde{h}_0 and right-hand side \tilde{f} . Set $h = \tilde{h} + \int_{\mathcal{E}} h_0 \, dx$ and observe

$$\begin{aligned} (L(\partial_t h v_{\mathcal{E}}), \varphi v_{\mathcal{E}})_{L^2(\mathcal{E})} + a(h, \varphi) &= \left(L(\partial_t \tilde{h} v_{\mathcal{E}}), \varphi v_{\mathcal{E}} \right)_{L^2(\mathcal{E})} + \kappa \left(\Delta_{\mathcal{E}} \tilde{h}, \Delta_{\mathcal{E}} \varphi \right)_{L^2(\mathcal{E})} \\ &\quad + \gamma \left(\nabla_{\mathcal{E}} \tilde{h}, \nabla_{\mathcal{E}} \varphi \right)_{L^2(\mathcal{E})} + \lambda \left(\tilde{h} + \int_{\mathcal{E}} h_0 \, dx, \varphi \right)_{L^2(\mathcal{E})} \\ &= \lambda \left(\int_{\mathcal{E}} h_0 \, dx, \varphi \right)_{L^2(\mathcal{E})} + (\tilde{f}, \varphi)_{L^2(\mathcal{E})} \\ &= (f, \varphi)_{L^2(\mathcal{E})}, \end{aligned}$$

so h is a solution as claimed.

(ii) $\int_{\mathcal{E}} h_0 \, dx$ is constant in time and this is by construction the mean value of h . \square

Appendix C. Taylor approximation of the Dirichlet-to-Neumann operator

We want to show that the Dirichlet-to-Neumann operator $\mathcal{D}\mathcal{N}_t : H^1(\mathcal{M}(t)) \rightarrow L^2(\mathcal{M}(t))$ can be approximated by $\mathcal{D}\mathcal{N}_0 : H^1(\mathcal{M}_0) \rightarrow L^2(\mathcal{M}_0)$ in the sense that for $h = \delta \tilde{h}$ and $\psi = \delta \tilde{\psi}$, it holds

$$\int_{\mathcal{M}(t)} \mathcal{D}\mathcal{N}_t \left([\partial_t h v_{\mathcal{M}_0}]_{\mathcal{X}} \right) \cdot [\psi v_{\mathcal{M}_0}]_{\mathcal{X}} \, dx = \int_{\mathcal{M}_0} \mathcal{D}\mathcal{N}_0 (\partial_t h v_{\mathcal{M}_0}) \cdot \psi v_{\mathcal{M}_0} \, dx + o(\delta^3)$$

for $\psi \in H^1(\mathcal{M}_0)$.

Take u^1 and u^2 as parts of solutions of stationary Stokes problems being continuously differentiable such that

$$\mu \left(\mathcal{J}(u^1), \mathcal{J}(\varphi) \right)_{L^2(\mathcal{D}, \mathbb{R}^{(3,3)})} - (p^1, \nabla \cdot \varphi)_{L^2(\mathcal{D})} = \int_{\mathcal{M}(t)} \mathcal{D}\mathcal{N}_t \left([\partial_t h v_{\mathcal{M}_0}]_{\mathcal{X}} \right) \cdot \gamma_{\mathcal{M}(t)}(\varphi) \, dx \quad (\text{C.1})$$

and

$$\mu \left(\mathcal{J}(u^2), \mathcal{J}(\varphi) \right)_{L^2(\mathcal{D}, \mathbb{R}^{(3,3)})} - (p^2, \nabla \cdot \varphi)_{L^2(\mathcal{D})} = \int_{\mathcal{M}_0} \mathcal{D}\mathcal{N}_0 (\partial_t h v_{\mathcal{M}_0}) \cdot \gamma_{\mathcal{M}_0}(\varphi) \, dx. \quad (\text{C.2})$$

Subtract (C.1) and (C.2) and choose φ as the velocity of a solution of a Stokes problem on \mathcal{D} with Dirichlet boundary data $\psi v_{\mathcal{M}_0}$ on \mathcal{M}_0 , $[\psi v_{\mathcal{M}_0}]_{\mathcal{X}}$ on $\mathcal{M}(t)$ and zero on the rest of the boundary, which is possible under the assumption that $\mathcal{M}(t) \cup \mathcal{M}_0$ is sufficiently regular.

$$\begin{aligned} \mu \left(\mathcal{J}(\tilde{u}), \mathcal{J}(\varphi) \right)_{L^2(\mathcal{D}, \mathbb{R}^{(3,3)})} &= \int_{\mathcal{M}(t)} \mathcal{D}\mathcal{N}_t \left([\partial_t h v_{\mathcal{M}_0}]_{\mathcal{M}(t)} \right) \cdot [\psi v_{\mathcal{M}_0}]_{\mathcal{X}} \, dx \\ &\quad - \int_{\mathcal{M}_0} \mathcal{D}\mathcal{N}_0 (\partial_t h v_{\mathcal{M}_0}) \cdot \psi v_{\mathcal{M}_0} \, dx. \end{aligned}$$

According to Cattabriga (1961, p. 311), $\mathcal{J}(\tilde{u})$ and $\mathcal{J}(\varphi)$ may be bounded by their Dirichlet boundary data. For $x \in \mathcal{M}(t)$, $x_0 \in \mathcal{M}_0$ such that $x = x_0 + \partial_t h(x_0) v_{\mathcal{M}_0}(x_0)$, we have

$$u^2(x) = u^2(x_0) + (x - x_0) \cdot \partial_{x-x_0} \left(u^2 \right) \Big|_{x_0} + o \left(\|x - x_0\|^2 \right). \quad (\text{C.3})$$

By choice $u^2(x) = u^1(x_0)$, so

$$u^2(x) = u^1(x_0) + (x - x_0) \cdot \partial_{x-x_0} (u^2) \Big|_{x_0} + o(\|x - x_0\|_2^2) \quad (\text{C.4})$$

and therefore

$$\tilde{u}(t, x) = (x - x_0) \cdot \partial_{x-x_0} (u^2) \Big|_{x_0} + o(\|x - x_0\|_2^2). \quad (\text{C.5})$$

As $u^2(x_0) = [\partial_t h(t, x_0)]_{\tilde{x}} = \delta [\partial_t \widehat{h}(t, x_0)]_{\tilde{x}}$, $u^2 = o(\delta)$ in a sufficiently small neighbourhood of x_0 , and so $\partial_{x-x_0} (u^2) \Big|_{x_0} = o(\delta)$. With $\|x - x_0\|_2 = o(\delta)$ we have $\|\tilde{u}(t, x)\|_2 = o(\delta^2)$. As the boundary data of φ is of order δ the claim follows.

Appendix D. Differential geometry

This section contains basic differential geometric formulae which are eventually used for calculating the shape derivatives in Section 3.3.

THEOREM D.1 (Transport theorem for surfaces, Barrett *et al.*, 2020, Theorem 32). Let $\mathcal{G}(\Gamma_s; s \in I)$ be a smooth evolving hypersurface in \mathbb{R}^n and $f : \mathcal{G}(\Gamma_s; s \in I) \rightarrow \mathbb{R}$ a function with existing material derivative. Then,

$$\frac{d}{ds} \left(\int_{\Gamma_s} f(s, \cdot) d\sigma^{n-1} \right) \Big|_r = \int_{\Gamma_s} \partial_s^\circ (f)|_r + f^r \nabla_{\Gamma_s} \cdot \mathcal{V}^r d\sigma^{n-1}.$$

LEMMA D.2 (Barrett *et al.*, 2020, Lemma 37). Let $\mathcal{G}(\Gamma_s; s \in I)$ be a smooth evolving manifold in \mathbb{R}^n with normal fields $(\nu_s)_{s \in I}$. It holds

$$\partial_s^\circ (\nu_s)|_r = -(\nabla_{\Gamma_s} \mathcal{V}^r)^T \nu_r.$$

Some simple algebraic observations:

LEMMA D.3 Let Γ be an orientable differentiable real submanifold with normal field ν and $f : \Gamma \rightarrow \mathbb{R}^m$ a function with existing tangential Jacobian. Further, $\mathbb{P}_\Gamma = I - \nu \otimes \nu$. It holds,

$$\nabla_\Gamma f \mathbb{P}_\Gamma = \nabla_\Gamma f \quad (\text{D.1})$$

$$\mathbb{P}_\Gamma (\nabla_\Gamma f)^T = (\nabla_\Gamma f)^T \quad (\text{D.2})$$

$$(\nabla_\Gamma f)^T \mathbb{P}_\Gamma : \nabla_\Gamma g = (\nabla_\Gamma f)^T : \nabla_\Gamma g. \quad (\text{D.3})$$

An analogue of the Schwarz theorem for tangential gradients

LEMMA D.5 (Barrett *et al.*, 2020, Lemma 15). Let $\Gamma \subseteq \mathbb{R}^n$ be a differentiable, orientable real submanifold with normal field ν and $f : \Gamma \rightarrow \mathbb{R}$ a function with existing tangential derivatives up to second order.

$$\nabla_\Gamma^2 (f) - \nabla_\Gamma^2 (f)^T = \nu \otimes (\nabla_\Gamma \nu \nabla_\Gamma f) - (\nabla_\Gamma \nu \nabla_\Gamma f) \otimes \nu$$

This implies

COROLLARY D.6 (Barrett *et al.*, 2020, Lemma 16). Let Γ be a differentiable orientable real submanifold with normal field ν and mean curvature H . It holds,

$$\Delta_\Gamma \nu = \nabla_\Gamma H - \nu \nabla_\Gamma \nu : \nabla_\Gamma \nu.$$

D.1 Commutator rules

LEMMA D.7 (Commutator rule for the tangential gradient, Barrett *et al.*, 2020, Lemma 38). Let $\mathfrak{X} : I \times \mathbb{R}^n \rightarrow \mathbb{R}^{n+k}$, for an interval $I \subseteq \mathbb{R}$, be parametrizations of n -dimensional manifolds Γ_s with an associated material derivative ∂_s° and velocity fields $\mathcal{V}^r = \partial_s (\mathfrak{X}(s, \cdot))|_{r \circ (\mathfrak{X}(r, \cdot))^{-1}}$. Let $f : \mathcal{G}(\Gamma_s; s \in I) \rightarrow \mathbb{R}$ be sufficiently regular. It holds

$$\partial_s^\circ (\nabla_{\Gamma_s} f)|_r = \nabla_{\Gamma_r} (\partial_s^\circ (f)|_r) + \left(\nabla_{\Gamma_r} \mathcal{V}^r - 2 \mathcal{J}_{\Gamma_r}(\mathcal{V}^r) \right) \nabla_{\Gamma_r} f.$$

A similar rule exists for the tangential divergence:

LEMMA D.8 (Commutator rule for the tangential divergence, Barrett *et al.*, 2020, Lemma 38). Let $\mathfrak{X} : I \times \mathbb{R}^n \rightarrow \mathbb{R}^{n+k}$, for an interval $I \subseteq \mathbb{R}$, be parametrizations of n -dimensional manifolds Γ_s with an associated material derivative ∂_s° and velocity fields $\mathcal{V}^r = \partial_s (\mathfrak{X}(s, \cdot))|_{r \circ (\mathfrak{X}(r, \cdot))^{-1}}$. Let $f : \mathcal{G}(\Gamma_s; s \in I) \rightarrow \mathbb{R}^n$ be sufficiently regular. It holds

$$\partial_s^\circ (\nabla_{\Gamma_s} \cdot f)|_r = \nabla_{\Gamma_r} \cdot \partial_s^\circ (f)|_r + \left(\nabla_{\Gamma_r} \mathcal{V}^r - 2 \mathcal{J}_{\Gamma_r}(\mathcal{V}^r) \right) : \nabla_{\Gamma_r} f.$$

We can now derive a commutator rule for the Laplace–Beltrami operator:

LEMMA D.9 (Commutator rule for the Laplace–Beltrami operator). Let $\mathcal{G}(\Gamma_s; s \in I)$, $I \subseteq \mathbb{R}$, be a smooth evolving manifold and $f : \mathcal{G}(\Gamma_s; s \in I) \rightarrow \mathbb{R}$ a function with tangential derivatives up to order two whose material derivative exists and let f be material differentiable itself. It holds,

$$\begin{aligned} \partial_s^\circ (\Delta_{\Gamma_s} (f))|_r &= \Delta_{\Gamma_r} (\partial_s^\circ (f)|_r) + \left(\nabla_{\Gamma_r} \cdot \left(\left(\nabla_{\Gamma_r} \mathcal{V}^r - 2 \mathcal{J}_{\Gamma_r}(\mathcal{V}^r) \right)^T \right) \right) \cdot \nabla_{\Gamma_r} f \\ &\quad + 2 \left(\nabla_{\Gamma_r} \mathcal{V}^r - (\nabla_{\Gamma_r} \mathcal{V}^r)^T - \mathbb{P}_{\Gamma_r} \nabla_{\Gamma_r} \mathcal{V}^r \right) : \nabla_{\Gamma_r}^2 f \\ &\quad + \nabla_{\Gamma_r} \mathcal{V}^r : \nu^r \otimes (\mathcal{H} \nabla_{\Gamma_r} f). \end{aligned}$$

Proof. Commute two times:

$$\begin{aligned} \partial_s^\circ (\Delta_{\Gamma_s} f)|_r &= \partial_s^\circ (\nabla_{\Gamma_s} \cdot \nabla_{\Gamma_s} f)|_r \stackrel{(1)}{=} \nabla_{\Gamma_r} \cdot (\partial_s^\circ (\nabla_{\Gamma_s} f)|_r) + \left(\nabla_{\Gamma_r} \mathcal{V}^r - 2 \mathcal{J}_{\Gamma_r}(\mathcal{V}^r) \right) : \nabla_{\Gamma_r}^2 f \\ &\stackrel{(2)}{=} \nabla_{\Gamma_r} \cdot \left(\nabla_{\Gamma_r} (\partial_s^\circ (f)|_r) + \left(\nabla_{\Gamma_r} \mathcal{V}^r - 2 \mathcal{J}_{\Gamma_r}(\mathcal{V}^r) \right) \nabla_{\Gamma_r}^2 f \right) \\ &\quad + \left(\nabla_{\Gamma_r} \mathcal{V}^r - 2 \mathcal{J}_{\Gamma_r}(\mathcal{V}^r) \right) : \nabla_{\Gamma_r}^2 f \\ &\stackrel{(3)}{=} \Delta_{\Gamma_r} (\partial_s^\circ (f)|_r) + \left(\nabla_{\Gamma_r} \cdot \left(\nabla_{\Gamma_r} \mathcal{V}^r - 2 \mathcal{J}_{\Gamma_r}(\mathcal{V}^r) \right)^T \right) \cdot \nabla_{\Gamma_r} f \\ &\quad + \left(\nabla_{\Gamma_r} \mathcal{V}^r - 2 \mathcal{J}_{\Gamma_r}(\mathcal{V}^r) \right) : \left(\nabla_{\Gamma_r}^2 f \right)^T \\ &\quad + \left(\nabla_{\Gamma_r} \mathcal{V}^r - 2 \mathcal{J}_{\Gamma_r}(\mathcal{V}^r) \right) : \nabla_{\Gamma_r}^2 f \end{aligned}$$

$$\begin{aligned}
& - \left(\nabla_{\Gamma_r} \mathcal{V}^r - 2 \mathcal{J}_{\Gamma_r}(\mathcal{V}^r) \right) : (\mathcal{H}^{\#} \nabla_{\Gamma_r} f) \otimes \nu_r \\
& + \left(\nabla_{\Gamma_r} \mathcal{V}^r - 2 \mathcal{J}_{\Gamma_r}(\mathcal{V}^r) \right) : \nu_r \otimes (\mathcal{H}^{\#} \nabla_{\Gamma_r} f) \\
& \stackrel{(5)}{=} \Delta_{\Gamma_r} (\partial_s^{\circ} (f)|_r) + \left(\nabla_{\Gamma_r} \cdot \left(\nabla_{\Gamma_r} \mathcal{V}^r - 2 \mathcal{J}_{\Gamma_r}(\mathcal{V}^r) \right)^T \right) \cdot \nabla_{\Gamma_r} f \\
& + 2 \left(\nabla_{\Gamma_r} \mathcal{V}^r - (\nabla_{\Gamma_r} \mathcal{V}^r)^T \right) : \left(\nabla_{\Gamma_r}^2 f \right) \\
& - 2 \left(\mathbb{P}_{\Gamma_r} \nabla_{\Gamma_r} \mathcal{V}^r \right) : \nabla_{\Gamma_r}^2 f \\
& + \left(\nabla_{\Gamma_r} \mathcal{V}^r - 2 \mathcal{J}_{\Gamma_r}(\mathcal{V}^r) \right) : \nu_r \otimes (\mathcal{H}^{\#} \nabla_{\Gamma_r} f) \\
& \stackrel{(6)}{=} \Delta_{\Gamma_r} (\partial_s^{\circ} (f)|_r) + \left(\nabla_{\Gamma_r} \cdot \left(\nabla_{\Gamma_r} \mathcal{V}^r - 2 \mathcal{J}_{\Gamma_r}(\mathcal{V}^r) \right)^T \right) \cdot \nabla_{\Gamma_r} f \\
& + 2 \left(\nabla_{\Gamma_r} \mathcal{V}^r - (\nabla_{\Gamma_r} \mathcal{V}^r)^T - \mathbb{P}_{\Gamma_r} \nabla_{\Gamma_r} \mathcal{V}^r \right) : \nabla_{\Gamma_r}^2 f \\
& + \nabla_{\Gamma_r} \mathcal{V}^r : \nu_r \otimes (\mathcal{H}^{\#} \nabla_{\Gamma_r} f)
\end{aligned}$$

(1): Lemma D.8 (2): Lemma D.7 (3): $\nabla \cdot (Av) = (\nabla \cdot A^T) \cdot v + A : (\nabla v)^T$ (4): Lemma D.5 (Schwarz for tangential gradients) (5):

$$\begin{aligned}
\left(\nabla_{\Gamma_r} \mathcal{V}^r - 2 \mathcal{J}_{\Gamma_r}(\mathcal{V}^r) \right) : \nabla_{\Gamma_r}^2 f &= \left(\nabla_{\Gamma_r} \mathcal{V}^r - \mathbb{P}_{\Gamma_r} \nabla_{\Gamma_r} \mathcal{V}^r - (\nabla_{\Gamma_r} \mathcal{V}^r)^T \mathbb{P}_{\Gamma_r} \right) : \nabla_{\Gamma_r}^2 f \\
&= \nabla_{\Gamma_r} \mathcal{V}^r : \nabla_{\Gamma_r}^2 f - \mathbb{P}_{\Gamma_r} \nabla_{\Gamma_r} \mathcal{V}^r : \nabla_{\Gamma_r}^2 f - (\nabla_{\Gamma_r} \mathcal{V}^r)^T \mathbb{P}_{\Gamma_r} : \nabla_{\Gamma_r}^2 f \\
&= \left(\nabla_{\Gamma_r} \mathcal{V}^r - (\nabla_{\Gamma_r} \mathcal{V}^r)^T \right) : \nabla_{\Gamma_r}^2 f - \mathbb{P}_{\Gamma_r} \nabla_{\Gamma_r} \mathcal{V}^r : \nabla_{\Gamma_r}^2 f
\end{aligned}$$

and

$$\begin{aligned}
\left(\nabla_{\Gamma_r} \mathcal{V}^r - 2 \mathcal{J}_{\Gamma_r}(\mathcal{V}^r) \right) : (\mathcal{H}^{\#} \nabla_{\Gamma_r} f) \otimes \nu_r &= \left(\nabla_{\Gamma_r} \mathcal{V}^r - \mathbb{P}_{\Gamma_r} \nabla_{\Gamma_r} \mathcal{V}^r - (\nabla_{\Gamma_r} \mathcal{V}^r)^T \mathbb{P}_{\Gamma_r} \right) : (\mathcal{H}^{\#} \nabla_{\Gamma_r} f) \otimes \nu_r \\
&= \text{tr} \left((\nabla_{\Gamma_r} \mathcal{V}^r)^T (\mathcal{H}^{\#} \nabla_{\Gamma_r} f) \otimes \nu_r \right) \\
&+ \text{tr} \left((\nabla_{\Gamma_r} \mathcal{V}^r)^T \mathbb{P}_{\Gamma_r} (\mathcal{H}^{\#} \nabla_{\Gamma_r} f) \otimes \nu_r \right) \\
&+ \text{tr} \left(\mathbb{P}_{\Gamma_r} \nabla_{\Gamma_r} \mathcal{V}^r (\mathcal{H}^{\#} \nabla_{\Gamma_r} f) \otimes \nu_r \right) \\
&= 0
\end{aligned}$$

by using cyclic shifting. (6):

$$\begin{aligned}
\left(\nabla_{\Gamma_r} \mathcal{V}^r - 2 \mathcal{J}_{\Gamma_r}(\mathcal{V}^r) \right) : \nu_r \otimes (\mathcal{H}^{\#} \nabla_{\Gamma_r} f) &= \left(\nabla_{\Gamma_r} \mathcal{V}^r - \mathbb{P}_{\Gamma_r} \nabla_{\Gamma_r} \mathcal{V}^r - (\nabla_{\Gamma_r} \mathcal{V}^r)^T \mathbb{P}_{\Gamma_r} \right) : \nu_r \otimes (\mathcal{H}^{\#} \nabla_{\Gamma_r} f) \\
&= \nabla_{\Gamma_r} \mathcal{V}^r : \nu_r \otimes (\mathcal{H}^{\#} \nabla_{\Gamma_r} f)
\end{aligned}$$

by the same arguments as in (5). \square

Appendix E. Derivatives

E.1 Material derivative of the mean curvature

LEMMA E.1 (Barrett *et al.*, 2020, Lemma 39). Let $\mathcal{G}(\Gamma_s; s \in I)$ be an orientable, smooth evolving manifold. We then have

$$\partial_s^\circ(H)|_0 = -\Delta_{\Gamma} V_\nu + \Delta_{\Gamma} \nu \cdot \mathcal{V}_\tau - V_\nu |\mathcal{H}|^2.$$

E.2 Second-order derivative of the integral of the mean curvature

LEMMA E.2 Let $\mathcal{G}(\Gamma_s; s \in I)$, $I \subseteq \mathbb{R}$, be a smooth evolving hypersurface in n dimensions. It holds,

$$\begin{aligned} \frac{d^2}{ds^2} \left(\int_{\Gamma_s} H^s d\sigma^{n-1} \right) \Big|_r &= \int_{\Gamma_r} -\partial_s^\circ (V_\nu^s)|_r |\mathcal{H}^s|^2 + 2V_\nu^r \operatorname{tr} \left(\mathcal{H}^s \nabla_{\Gamma_r} \left((\nabla_{\Gamma_r} \mathcal{V}^r)^T \nu_r \right) + \mathcal{H}^s (\nabla_{\Gamma_r} \mathcal{V}^r)^T \mathbb{P}_{\Gamma_r} \mathcal{H}^s \right) \\ &\quad + \left(-\Delta_{\Gamma_r} V_\nu^r + \nabla_{\Gamma_r} H^r \cdot \mathcal{V}_\tau^r - V_\nu^r |\mathcal{H}^s|^2 \right) \nabla_{\Gamma_r} \mathcal{V}^r \\ &\quad + H^r \left(\nabla_{\Gamma_r} \cdot (\partial_s^\circ (\mathcal{V}_\nu^s)|_r) + \left(\nabla_{\Gamma_r} \mathcal{V}^r - 2 \mathcal{J}_{\Gamma_r} (\mathcal{V}^r) \right) : \nabla_{\Gamma_r} \mathcal{V}^r \right) \\ &\quad + \left(-V_\nu^r |\mathcal{H}^s|^2 + H^r \nabla_{\Gamma_r} \cdot \mathcal{V}_\nu^r \right) \nabla_{\Gamma_r} \cdot \mathcal{V}^r d\sigma^{n-1}. \end{aligned}$$

Proof.

$$\begin{aligned} \frac{d^2}{ds^2} \left(\int_{\Gamma_s} H^s d\sigma^{n-1} \right) \Big|_r &\stackrel{(1)}{=} \frac{d}{ds} \left(\int_{\Gamma_s} -\Delta_{\Gamma_s} V_\nu^s + \Delta_{\Gamma_s} \nu_s \cdot \mathcal{V}_\tau^s - V_\nu^s |\mathcal{H}^s|^2 + H^s \nabla_{\Gamma_s} \cdot \mathcal{V}^s d\sigma^{n-1} \right) \Big|_r \\ &\stackrel{(2)}{=} \frac{d}{ds} \left(\int_{\Gamma_s} -\Delta_{\Gamma_s} V_\nu^s + \left(\nabla_{\Gamma_s} H^s - \nu_s |\mathcal{H}^s|^2 \right) \cdot \mathcal{V}_\tau^s - V_\nu^s |\mathcal{H}^s|^2 + H^s \nabla_{\Gamma_s} \cdot \mathcal{V}^s d\sigma^{n-1} \right) \Big|_r \\ &\stackrel{(3)}{=} \frac{d}{ds} \left(\int_{\Gamma_s} -\Delta_{\Gamma_s} V_\nu^s - V_\nu^s |\mathcal{H}^s|^2 + H^s \nabla_{\Gamma_s} \cdot \mathcal{V}^s d\sigma^{n-1} \right) \Big|_r \\ &\stackrel{(4)}{=} \frac{d}{ds} \left(\int_{\Gamma_s} -V_\nu^s |\mathcal{H}^s|^2 + H^s \nabla_{\Gamma_s} \cdot \mathcal{V}^s d\sigma^{n-1} \right) \Big|_r \\ &= \int_{\Gamma_r} -\partial_s^\circ (V_\nu^s)|_r |\mathcal{H}^s|^2 - V_\nu^r \partial_s^\circ (|\mathcal{H}^s|^2) \Big|_r \\ &\quad + \partial_s^\circ (H^s)|_r \nabla_{\Gamma_r} \cdot \mathcal{V}_\nu^r + H^r \partial_s^\circ (\nabla_{\Gamma_s} \cdot \mathcal{V}_\nu^s)|_r \\ &\quad + \left(-V_\nu^r |\mathcal{H}^s|^2 + H^r \nabla_{\Gamma_r} \cdot \mathcal{V}_\nu^r \right) \nabla_{\Gamma_r} \cdot \mathcal{V}^r d\sigma^{n-1} \\ &\stackrel{(5)}{=} \int_{\Gamma_r} -\partial_s^\circ (V_\nu^s)|_r |\mathcal{H}^s|^2 + 2V_\nu^r \operatorname{tr} \left(\mathcal{H}^s \nabla_{\Gamma_r} \left((\nabla_{\Gamma_r} \mathcal{V}^r)^T \nu_r \right) + \mathcal{H}^s (\nabla_{\Gamma_r} \mathcal{V}^r)^T \mathbb{P}_{\Gamma_r} \mathcal{H}^s \right) \end{aligned}$$

$$\begin{aligned}
 & + \partial_s^\circ (H^s)|_r \nabla_{\Gamma_r} \cdot \mathcal{V}_v^r + H^r \partial_s^\circ (\nabla_{\Gamma_s} \cdot \mathcal{V}_v^s)|_r \\
 & + \left(-V_v^r |\mathcal{A}^r|^2 + H^r \nabla_{\Gamma_r} \cdot \mathcal{V}_v^r \right) \nabla_{\Gamma_r} \cdot \mathcal{V} \, d\sigma^{n-1} \\
 & \stackrel{(6)}{=} \int_{\Gamma_r} -\partial_s^\circ (V_v^s)|_r |\mathcal{A}^r|^2 + 2V_v^r \operatorname{tr} \left(\mathcal{A}^r \nabla_{\Gamma_r} \left((\nabla_{\Gamma_r} \mathcal{V}^r)^T v_r \right) + \mathcal{A}^r (\nabla_{\Gamma_r} \mathcal{V}^r)^T \mathbb{P}_{\Gamma_r} \mathcal{A}^r \right) \\
 & + \left(-\Delta_{\Gamma_r} V_v^r + \nabla_{\Gamma_r} H^r \cdot \mathcal{V}_\tau^r - V_v^r |\mathcal{A}^r|^2 \right) \nabla_{\Gamma_r} \cdot \mathcal{V}_v^r \\
 & + H^r \left(\nabla_{\Gamma_r} \cdot (\partial_s^\circ (\mathcal{V}_v^s)|_r) + \left(\nabla_{\Gamma_r} \mathcal{V}^r - 2 \mathcal{J}_{\Gamma_r} (\mathcal{V}^r) \right) : \nabla_{\Gamma_r} \mathcal{V}^r \right) \\
 & + \left(-V_v^r |\mathcal{A}^r|^2 + H^r \nabla_{\Gamma_r} \cdot \mathcal{V}_v^r \right) \nabla_{\Gamma_r} \cdot \mathcal{V} \, d\sigma^{n-1}
 \end{aligned}$$

(1): Lemma E.1

(2): Corollary D.6

(3): integration by parts

(4): divergence theorem for manifolds without boundary

(5): see Elliott *et al.* (2017)

(6): Lemma E.1 and commutator rule for tangential divergence (Lemma 26) □

COROLLARY E.3 In case $\mathcal{V}^s = h\nu \circ (\mathfrak{X}^s)^{-1}$ we have

$$\begin{aligned}
 \frac{d^2}{ds^2} \left(\int_{\Gamma_s} H^s \, d\sigma^{n-1} \right) \Big|_0 &= \int_{\Gamma} 2h \operatorname{tr} \left(\mathcal{A} \nabla_{\Gamma}^2 h + h \mathcal{A}^2 \right) - hH \Delta_{\Gamma} h - 3h^2 H |\mathcal{A}|^2 \\
 & \quad + H \nabla_{\Gamma} h \cdot \nabla_{\Gamma} h + h^2 H^3 \, d\sigma^{n-1}
 \end{aligned}$$

We write $\mathcal{V}^0 = \mathcal{V}$, etc.

Proof.

$$\begin{aligned}
 \frac{d^2}{ds^2} \left(\int_{\Gamma_s} H^s \, d\sigma^{n-1} \right) \Big|_0 & \stackrel{(1)}{=} \int_{\Gamma} -\partial_s^\circ (V_v^s)|_0 |\mathcal{A}^2| + 2V_v \operatorname{tr} \left(\mathcal{A} \nabla_{\Gamma} \left((\nabla_{\Gamma} \mathcal{V})^T v \right) + \mathcal{A} (\nabla_{\Gamma} \mathcal{V})^T \mathbb{P}_{\Gamma} \mathcal{A} \right) \\
 & + \left(-\Delta_{\Gamma} V_v + \nabla_{\Gamma} H \cdot \mathcal{V}_\tau - V_v |\mathcal{A}|^2 \right) \nabla_{\Gamma} \cdot \mathcal{V}_v \\
 & + H \left(\nabla_{\Gamma} \cdot (\partial_s^\circ (V_v^s)|_0) + \left(\nabla_{\Gamma} \mathcal{V} - 2 \mathcal{J}_{\Gamma} (\mathcal{V}) \right) : \nabla_{\Gamma} \mathcal{V} \right) \\
 & + \left(-V_v |\mathcal{A}|^2 + H \nabla_{\Gamma} \cdot \mathcal{V}_v \right) \nabla_{\Gamma} \cdot \mathcal{V} \, d\sigma^{n-1} \\
 & \stackrel{(2)}{=} \int_{\Gamma} 2V_v \operatorname{tr} \left(\mathcal{A} \nabla_{\Gamma} \left((\nabla_{\Gamma} \mathcal{V})^T v \right) + \mathcal{A} (\nabla_{\Gamma} \mathcal{V})^T \mathbb{P}_{\Gamma} \mathcal{A} \right) \\
 & - \left(\Delta_{\Gamma} V_v + V_v |\mathcal{A}|^2 \right) \nabla_{\Gamma} \cdot \mathcal{V}_v \\
 & + H \left(\left(\nabla_{\Gamma} \mathcal{V} - 2 \mathcal{J}_{\Gamma} (\mathcal{V}) \right) : \nabla_{\Gamma} \mathcal{V} \right)
 \end{aligned}$$

$$\begin{aligned}
& + \left(-V_v |\mathcal{H}|^2 + H \nabla_\Gamma \cdot \mathcal{V}_v \right) \nabla_\Gamma \cdot \mathcal{V} d\sigma^{n-1} \\
& \stackrel{(3)}{=} \int_\Gamma 2h \operatorname{tr} \left(\mathcal{H} \nabla_\Gamma \left((v \otimes \nabla_\Gamma h + h \mathcal{H})^T v \right) + \mathcal{H} (v \otimes \nabla_\Gamma h + h \mathcal{H})^T \mathbb{P}_\Gamma \mathcal{H} \right) \\
& - \left(\Delta_\Gamma h + h |\mathcal{H}|^2 \right) h H \\
& + H \left((v \otimes \nabla_\Gamma h - h \mathcal{H}) : (v \otimes \nabla_\Gamma h + h \mathcal{H}) \right) \\
& + \left(-h |\mathcal{H}|^2 + h H^2 \right) h H d\sigma^{n-1} \\
& \stackrel{(4)}{=} \int_\Gamma 2h \operatorname{tr} \left(\mathcal{H} \nabla_\Gamma^2 h + h \mathcal{H}^{\hat{2}} \right) \\
& - h H \left(\Delta_\Gamma h + h |\mathcal{H}|^2 \right) \\
& + H \left(\nabla_\Gamma h \cdot \nabla_\Gamma h - h^2 |\mathcal{H}|^2 \right) \\
& + h H \left(-h |\mathcal{H}|^2 + h H^2 \right) d\sigma^{n-1} \\
& = \int_\Gamma 2h \operatorname{tr} \left(\mathcal{H} \nabla_\Gamma^2 h + h \mathcal{H}^{\hat{2}} \right) - h H \Delta_\Gamma h - 3h^2 H |\mathcal{H}|^2 + H \nabla_\Gamma h \cdot \nabla_\Gamma h + h^2 H^3 d\sigma^{n-1}
\end{aligned}$$

(1): Lemma 29 (2): as $\mathcal{V}^s \circ \mathfrak{X}^s$ is independent of s and (note $\mathfrak{X} = I_\Gamma$)

$$\begin{aligned}
\partial_s^\circ (V_v^s)|_0 & = \partial_s (h v \cdot v_s \circ (I_\Gamma, \mathfrak{X}^s))|_0 = h v \cdot \partial_s (v_s \circ (I_\Gamma, \mathfrak{X}^s)|_0) \\
& = h v \cdot (\nabla_x(\bar{v}) \partial_s(\mathfrak{X}^s)|_0) \\
& = h v \cdot (\nabla_\Gamma(v) \partial_s(\mathfrak{X}^s)|_0) \\
& = h \partial_s(\mathfrak{X}^s)|_0 \cdot \left((\nabla_\Gamma v)^T v \right) \\
& = 0
\end{aligned}$$

due to the symmetry of $\nabla_\Gamma v$.

(3): we have

$$\nabla_\Gamma \mathcal{V} = \nabla_\Gamma (h v) = v \otimes \nabla_\Gamma h + h \mathcal{H}$$

and

$$\nabla_\Gamma \cdot \mathcal{V} = \nabla_\Gamma \cdot (h v) = \nabla_\Gamma h \cdot v + h \nabla_\Gamma \cdot v = h H,$$

as well as

$$\begin{aligned}
\mathbb{P}_\Gamma \nabla_\Gamma \mathcal{V} & = (I - v \otimes v) (v \otimes \nabla_\Gamma h + h \nabla_\Gamma v) = v \otimes \nabla_\Gamma h + h \nabla_\Gamma v - v \otimes \nabla_\Gamma h \\
& \quad - h v \otimes (\nabla_\Gamma v^T v) = h \mathcal{H},
\end{aligned}$$

which implies $(\nabla_\Gamma \mathcal{V})^T \mathbb{P}_\Gamma = h\mathcal{H}$, so

$$2 \mathcal{J}_\Gamma(\mathcal{V}) = \mathbb{P}_\Gamma \nabla_\Gamma \mathcal{V} + (\nabla_\Gamma \mathcal{V})^T \mathbb{P}_\Gamma = 2h\mathcal{H}.$$

(4): observe

$$\nabla_\Gamma \left((v \otimes \nabla_\Gamma h + h\mathcal{H})^T v \right) = \nabla_\Gamma (\nabla_\Gamma h \otimes v) = \nabla_\Gamma^2 h$$

and

$$\begin{aligned} (v \otimes \nabla_\Gamma h + h\mathcal{H})^T \mathbb{P}_\Gamma &= \nabla_\Gamma h \otimes v \mathbb{P}_\Gamma + h\mathcal{H} \\ &= \nabla_\Gamma h \otimes v - \nabla_\Gamma h \otimes v v \otimes v + h\mathcal{H} \\ &= h\mathcal{H} \end{aligned}$$

and

$$\begin{aligned} (v \otimes \nabla_\Gamma h - h\mathcal{H}) : (v \otimes \nabla_\Gamma h + h\mathcal{H}) &= v \otimes \nabla_\Gamma h : v \otimes \nabla_\Gamma h + v \otimes \nabla_\Gamma h : h\mathcal{H} \\ &\quad - h\mathcal{H} : v \otimes \nabla_\Gamma h - h^2 |\mathcal{H}|^2 \\ &= \text{tr}(\nabla_\Gamma h \otimes v v \otimes \nabla_\Gamma h) - h^2 |\mathcal{H}|^2 \\ &= \nabla_\Gamma h \cdot \nabla_\Gamma h - h^2 |\mathcal{H}|^2 \end{aligned}$$

□

COROLLARY E.4 In case $\mathcal{V}^s = hv \circ (\mathfrak{X}^s)^{-1}$ and Γ is a sphere with radius R in \mathbb{R}^3 we have

$$\frac{d^2}{ds^2} \left(\int_{\Gamma_s} H^s d\sigma^{n-1} \right) \Big|_0 = \frac{2}{R} \int_\Gamma \nabla_\Gamma h \cdot \nabla_\Gamma h d\sigma^2$$

Proof.

$$\begin{aligned} \frac{d^2}{ds^2} \left(\int_{\Gamma_s} H^s d\sigma^{n-1} \right) \Big|_0 &= \int_\Gamma 2h \text{tr} \left(\mathcal{H} \nabla_\Gamma^2 h + h\mathcal{H}^2 \right) - hH \Delta_\Gamma h - 3h^2 H |\mathcal{H}|^2 \\ &\quad + H \nabla_\Gamma h \cdot \nabla_\Gamma h + h^2 H^3 d\sigma^{n-1} \\ &\stackrel{(1)}{=} \int_\Gamma 2h \text{tr} \left(\frac{1}{R} \mathbb{P}_\Gamma \nabla_\Gamma^2 h + h \frac{1}{R^3} \mathbb{P}_\Gamma \right) - h \frac{2}{R} \Delta_\Gamma h - h^2 \frac{6}{R^3} \text{tr} \left(\mathbb{P}_\Gamma \right) \\ &\quad + \frac{2}{R} \nabla_\Gamma h \cdot \nabla_\Gamma h + h^2 \frac{8}{R^3} d\sigma^{n-1} \\ &\stackrel{(2)}{=} \frac{2}{R} \int_\Gamma h \text{tr} \left(\nabla_\Gamma^2 h \right) d\sigma^2 - \frac{2}{R} \int_\Gamma h \Delta_\Gamma h d\sigma^2 + \left(\frac{4}{R^3} - \frac{12}{R^3} + \frac{8}{R^3} \right) \int_\Gamma h^2 d\sigma^2 \\ &\quad + \frac{2}{R} \int_\Gamma \nabla_\Gamma h \cdot \nabla_\Gamma h d\sigma^2 \\ &= \frac{2}{R} \int_\Gamma \nabla_\Gamma h \cdot \nabla_\Gamma h d\sigma^2 \end{aligned}$$

(1): $H = \frac{2}{R}$ and $\mathcal{H} = \frac{1}{R}\mathbb{P}_\Gamma$. (2): $\text{tr}(\mathbb{P}_\Gamma) = \text{tr}I_3 - \text{tr}\nu \otimes \nu = 3 - \sum_i \nu_i^2 = 3 - |\nu|^2 = 2$ and cyclic shifting of \mathbb{P}_Γ in the trace \square

E.3 Second-order derivative of the surface area

LEMMA E.5 Let $\mathcal{G}(\Gamma_s; s \in I)$, $I \subseteq \mathbb{R}$, be a smooth orientable evolving hypersurface in \mathbb{R}^n , $n \in \mathbb{N}$. It holds,

$$\frac{d^2}{ds^2} \left(\int_{\Gamma_s} 1 \, d\sigma^2 \right) \Big|_0 = \int_{\Gamma} \nabla_\Gamma \cdot \left(\partial_r^\circ(\mathcal{V}) \Big|_0 \right) + \left(\nabla_\Gamma \mathcal{V} - 2 \mathcal{J}_\Gamma(\mathcal{V}) \right) : \nabla_\Gamma \mathcal{V} + \left(\nabla_\Gamma \cdot \mathcal{V} \right)^2 d\sigma^2.$$

Proof. Apply the surface transport theorem (Theorem D.1) two times

$$\frac{d}{dr} \left(\frac{d}{ds} \left(\int_{\Gamma_s} 1 \, d\sigma^2 \right) \Big|_r \right) \Big|_0 = \frac{d}{dr} \left(\int_{\Gamma} \nabla_{\Gamma_r} \cdot \mathcal{V}^r \, d\sigma^2 \right) \Big|_0 = \int_{\Gamma} \partial_r^\circ(\nabla_{\Gamma_r} \cdot \mathcal{V}^r) \Big|_0 + \left(\nabla_\Gamma \cdot \mathcal{V} \right)^2 d\sigma^2.$$

Then use the commutator rule for the tangential divergence (Lemma D.8):

$$\int_{\Gamma} \partial_r^\circ(\nabla_{\Gamma_r} \cdot \mathcal{V}^r) \Big|_0 + \left(\nabla_\Gamma \cdot \mathcal{V} \right)^2 d\sigma^2 = \int_{\Gamma} \nabla_\Gamma \cdot (\partial_r^\circ(\mathcal{V}) \Big|_0) + \left(\nabla_\Gamma \mathcal{V} - 2 \mathcal{J}_\Gamma(\mathcal{V}) \right) : \nabla_\Gamma \mathcal{V} + \left(\nabla_\Gamma \cdot \mathcal{V} \right)^2 d\sigma^2. \quad \square$$

COROLLARY E.6 In case $\mathfrak{X}^s = x + sh\nu$, where $x \in \Gamma$ and $h : \Gamma \rightarrow \mathbb{R}^n$, we get

$$\frac{d^2}{ds^2} \left(\int_{\Gamma_s} 1 \, d\sigma^{n-1} \right) \Big|_0 = \int_{\Gamma} \nabla_\Gamma h \cdot \nabla_\Gamma h - h^2 |\mathcal{A}|^2 + h^2 H^2 \, d\sigma^{n-1}.$$

Proof. We use

$$\begin{aligned} \frac{d^2}{ds^2} \left(\int_{\Gamma_s} 1 \, d\sigma^{n-1} \right) \Big|_0 &= \int_{\Gamma} \left(\nu \otimes \nabla_\Gamma h - h \mathcal{A} \right) : \left(\nu \otimes \nabla_\Gamma h + h \mathcal{A} \right) + h^2 H^2 \, d\sigma^{n-1} \\ &= \int_{\Gamma} \nabla_\Gamma h \cdot \nabla_\Gamma h - h^2 |\mathcal{A}|^2 + h^2 H^2 \, d\sigma^{n-1}. \end{aligned} \quad \square$$

E.4 Derivative of the Willmore energy

LEMMA E.7 Let $\mathcal{G}(\Gamma_s; s \in I)$, $I \subseteq \mathbb{R}$, be a smooth orientable evolving hypersurface in \mathbb{R}^n , $n \in \mathbb{N}$. It holds,

$$\frac{d}{ds} \left(\frac{1}{2} \int_{\Gamma_s} (H^s)^2 \, d\sigma^2 \right) \Big|_0 = \int_{\Gamma} -V_\nu \Delta_\Gamma H^s - V_\nu |\nabla_\Gamma \nu_\Gamma|^2 - \frac{1}{2} V_\nu H^3 \, d\sigma^2.$$

Proof.

$$\begin{aligned}
 \frac{d}{ds} \left(\frac{1}{2} \int_{\Gamma_s} (H^s)^2 d\sigma^2(x) \right) \Big|_0 &\stackrel{(1)}{=} \int_{\Gamma} H \partial_s^\circ (H^s) \Big|_0 + \frac{1}{2} H^2 \nabla_{\Gamma} \cdot \mathcal{V} d\sigma^2 \\
 &\stackrel{(2)}{=} \int_{\Gamma} H \left(-\Delta_{\Gamma} V_v + \Delta_{\Gamma} v_{\Gamma} \cdot \mathcal{V}_{\tau} - V_v |\nabla_{\Gamma} v_{\Gamma}|^2 \right) \\
 &\quad + \frac{1}{2} H^2 \nabla_{\Gamma} \cdot \mathcal{V} d\sigma^2(x) \\
 &\stackrel{(2)}{=} \int_{\Gamma} H \left(-\Delta_{\Gamma} V_v + \left(\nabla_{\Gamma} H - v_{\Gamma} \nabla_{\Gamma} v_{\Gamma} : \nabla_{\Gamma} v_{\Gamma} \right) \cdot \mathcal{V}_{\tau} \right. \\
 &\quad \left. - V_v |\nabla_{\Gamma} v_{\Gamma}|^2 \right) \\
 &\quad + \frac{1}{2} H^2 \nabla_{\Gamma} \cdot \left(V_v v_{\Gamma} + \mathcal{V}_{\tau} \right) d\sigma^2(x) \\
 &\stackrel{(3)}{=} \int_{\Gamma} -V_v \Delta_{\Gamma} H - V_v |\nabla_{\Gamma} v_{\Gamma}|^2 + \frac{1}{2} V_v H^3 d\sigma^2.
 \end{aligned}$$

(1): Theorem D.1 (2): see Elliott *et al.* (2017) (3): Corollary D.6 (4): integration by parts

□