Mathematical Mechanical Biology

Module 2: Bio-Membranes

Lecture Notes for C5.9

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Based on previous notes of Eamonn Gaffney and Alain Goriely

Contents

HEALTH WARNING:

The following lecture notes are meant as a rough guide to the lectures. They are not meant to replace the lectures. You should expect that some material in these notes will not be covered in class and that extra material will be covered during the lectures (especially longer proofs, examples, and applications). Nevertheless, I will try to follow the notation and the overall structure of the notes as much as possible.

1 Background: basic geometry of surfaces

■ **Geometry**

Here, we introduce basic notions of differential geometry for surfaces. Of particular importance are the definition of the area and length elements and the notions of mean and Gaussian curvatures. The Gauss-Bonnet theorem (given without proof) will also be important in our discussion of mechanics.

For simplicity we consider here an orientable parametrised surface Σ defined by the position vectors

$$\mathbf{x} = \mathbf{x}(\xi^1, \xi^2) \in \mathbb{R}^3, \qquad (\xi^1, \xi^2) \in M \subset \mathbb{R}^2. \tag{1}$$

We assume that $\mathbf{x}$ is at least of class C^2 and such that the tangent vectors

$$\mathbf{r}_i = \frac{\partial \mathbf{x}}{\partial \xi^i}, \quad i = 1, 2 \tag{2}$$

are linearly independent for all $(\xi^1, \xi^2) \in M$. Since Σ is orientable, we can define a normal vector (see Fig. 1)

$$\mathbf{n} = \frac{\mathbf{r}_1 \times \mathbf{r}_2}{||\mathbf{r}_1 \times \mathbf{r}_2||}, \tag{3}$$

where $||\mathbf{a}|| = \sqrt{\mathbf{a} \cdot \mathbf{a}}$. Note that by definition $\{\mathbf{r}_1, \mathbf{r}_2, \mathbf{n}\}$ forms a basis (but not necessarily orthonormal – it turns out that it is not always advantageous to use an orthonormal basis to describe surfaces).

1.1 Length and area

To identify key quantities, we first compute the area of a surface

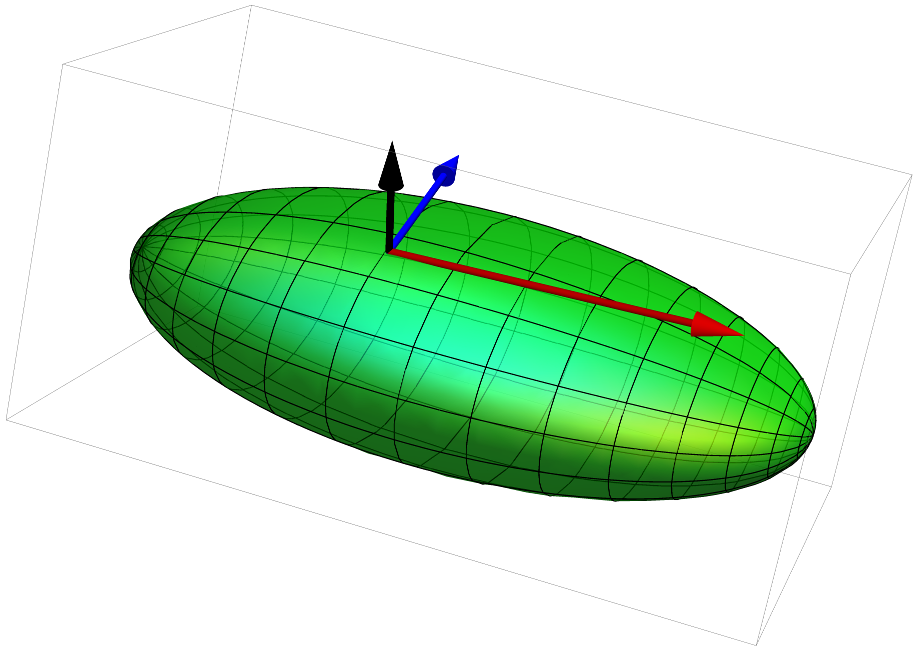

Figure 1: Tangent vectors (red and blue) on an ellipsoid parameterised by two angles (thin black line). The normal vector (in black) is simply obtained as the cross product of the two tangent vectors.

Area element

We start with

$$A = \int_{\Sigma} \mathrm{d}S \tag{4}$$

That is,

$$A = \iint_{M} \sqrt{g_{11}g_{22} - g_{12}^2}\, \mathrm{d}\xi^1 \mathrm{d}\xi^2 \tag{5}$$

where $g_{ij} = \mathbf{r}_i.\mathbf{r}_j$

Alternatively, we can write

$$A = \iint_M \sqrt{\det(G)}\ \mathrm{d}\xi^1 \mathrm{d}\xi^2 \tag{6}$$

which naturally leads to the definition of $G = (g_{ij})$, the matrix of the *metric tensor*.

Next, we compute a length element

■ Length element

We start with a curve $\mathbf{r} = \mathbf{r}(t)$ defining a path γ on Σ

$$L = \int_\gamma \mathrm{d}s \tag{7}$$

That is,

$$\mathrm{d}s^2 = g_{ij}\mathrm{d}\xi^i \mathrm{d}\xi^j \tag{8}$$

and

$$L = \int_I \sqrt{g_{ij}\dot{\xi}^i\dot{\xi}^j}\ \mathrm{d}t \tag{9}$$

Associated with the metric we have defined the *first fundamental form* $\mathrm{d}s^2 = g_{ij}\mathrm{d}\xi^i\mathrm{d}\xi^j$.

1.2 Curvatures

We are interested in defining curvatures on the surface Σ. We consider a curve C on Σ passing through a point P and parameterised by its arc length s and define $\mathbf{t}$ as the tangent vector of C at P.

We know from Module 1 that the curvature of the curve C at a point P is obtained as $|\mathbf{t}'|$. It is therefore natural to define the curvature vector

$$\mathbf{k} = \frac{d\mathbf{t}}{ds} \tag{10}$$

and decompose it into two components, the *normal curvature vector* $\mathbf{k}_n$ and the *geodesic curvature vector* $\mathbf{k}_g$

$$\mathbf{k} = \mathbf{k}_n + \mathbf{k}_g \tag{11}$$

where $\mathbf{k}_n = -k_n\mathbf{n}$ is along the normal vector[1], that is

$$k_n = -\mathbf{n}\cdot\frac{d\mathbf{t}}{ds}, \qquad k_g = ||\mathbf{k}_g|| = \left|\mathbf{t}\cdot\left(\frac{d\mathbf{t}}{ds}\times\mathbf{n}\right)\right|. \tag{12}$$

[1]Note the choice of sign designed to ensure that the normal curvature of a sphere of radius R is indeed $k_n = +1/R$ rather than $-1/R$ if we take $\mathbf{n}$ to be outer normal vector.

The *normal curvature* k_n is a property of the surface itself and gives the curvature in a planar slice spanned by the normal and tangent vector (see Fig. 1.2) whereas the *geodesic curvature* gives the curvature on the curve on the surface (it is identically zero for a geodesic curve).

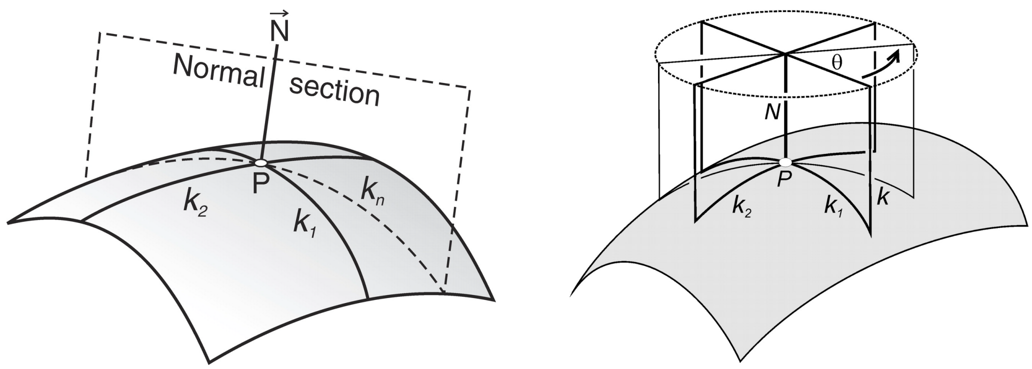

Figure 2: The normal curvature of a curve on a surface in a given direction **t** is given by the curvature of the curve obtained as the intersection of the surface with the plane spanned by **n** and **t** .

We can compute explicitly the normal curvature for a given curve.

The normal curvature

That is,

$$k_n = K_{ij}(\xi^i)'(\xi^j)' \tag{13}$$

where

$$K_{ij} = K_{ji} = -\mathbf{n} \cdot \frac{\partial \mathbf{r}_j}{\partial \xi^i} \tag{14}$$

which naturally leads to the definition of $K = (K_{ij})$, the matrix of the *extrinsic curvature tensor*. This tensor is naturally associated with the *second fundamental form* $K_{ij}\mathrm{d}\xi^i\mathrm{d}\xi^j$.

A natural question is to determine the extremal values of the normal curvature as we vary the tangent vector at P.

Principal curvatures

That is, the *principal curvatures* are the eigenvalues of the *principal curvature matrix*

$$L = G^{-1}K. \tag{15}$$

Define $\mathbf{e}_1$ and $\mathbf{e}_2$ as the orthonormal eigenvectors associated with the principal curvatures k_1 and k_2. We can write

$$\mathbf{t} = \cos\theta\ \mathbf{e}_1 + \sin\theta\ \mathbf{e}_2 \tag{16}$$

and, in general, we have (Euler's theorem 1760, see Fig. 1.2)

$$k_n = k_1 \cos^2\theta + k_2 \sin^2\theta. \tag{17}$$

The principal curvatures can be used to defined the mean curvature H and Gaussian curvature K_G as follows

$$2H = \mathrm{tr}(L) = k_1 + k_2, \tag{18}$$

$$K_G = \det(L) = k_1 k_2. \tag{19}$$

It can be shown that the Gaussian curvature is intrinsic to the surface (in the sense that it only depends on the metric and not on the normal vector). This result is contained in the Gauss' famous Theorema Egregium (remarkable theorem). Note that K_G is independent of the parameterisation but that H can change sign (depending on the choice of the normal vector).

A *minimal surface* is such that $H = 0$ identically for all points. These surfaces play a particularly important role in a number of important problems and we will indeed see that the vanishing of the mean curvature naturally arises as a condition to minimise the area.

The Gaussian curvature is particularly important in the classification of surfaces as either *elliptic* ($K_G > 0$), *hyperbolic* ($K_G < 0$), or *parabolic* ($K_G = 0$).

1.3 The Gauss-Bonnet theorem

An important result of global topology is the Gauss-Bonnet theorem (Bonnet 1848). Let Σ be a compact two-dimensional Riemannian manifold with boundary $\partial\Sigma$. Let K_G be the Gaussian

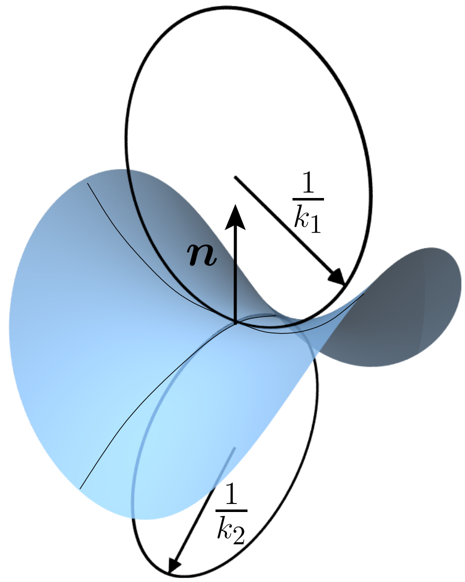

Figure 3: The principal curvatures of a surface are the maximal values of the normal curvature at a point and geometrically correspond to the inverse radius of the best fitting circles (of maximal radii).

curvature of Σ, and k_g the geodesic curvature of $\partial\Sigma$. Then

$$\int_{\Sigma} K_G \mathrm{d}S + \int_{\partial\Sigma} k_g \mathrm{d}s = 2\pi\chi(\Sigma), \tag{20}$$

where $\chi(\Sigma)$ is the Euler characteristic of Σ, a global topological property, which, for a surface of genus[2] p is given by $\chi(\Sigma) = 2 - 2p$.

Of particular interest for us is the case of a closed orientable surface for which

$$\int_{\Sigma} K_G \mathrm{d}S = 4\pi(1-p). \tag{21}$$

1.4 Examples

Examples of different minimal surfaces are given in Fig. 4. A Mathematica file that can create these graphs can be downloaded with the Lecture Notes material ("Curvature Computation.nb").

[2] In three-dimensions, the genus of an orientable surface is given by the number of handles, a sphere has genus 0, a torus or a mug has genus 1, and so on.

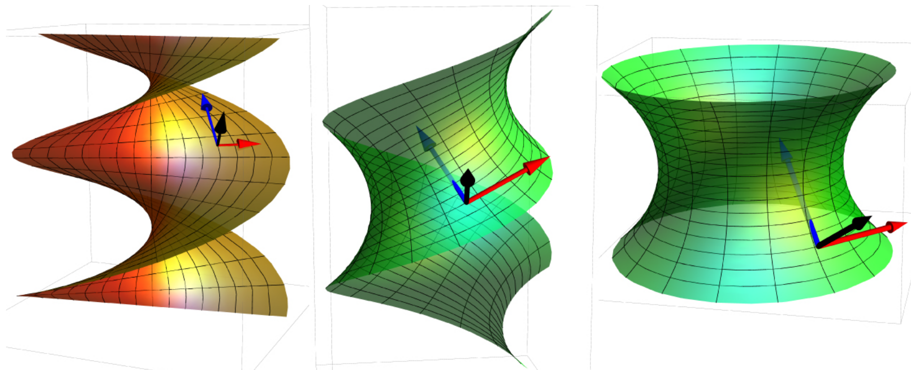

Figure 4: Different minimal surfaces. Left: the helicoid, Right: the catenoid. Middle: The helico-catenoid. Tangent vectors (red and blue). The normal vector (in black) is simply obtained as the cross product of the two tangent vectors.

2 Fluid biomembranes

Motivation

Many biological membranes are made of lipid bilayers and examples are given in MMB-Presentation, Bio-Membranes, online. Mechanically, these structures and synthetic lipid vesicles resist bending, stretching but are fluid in the plane and as such do not resist shear. In this Chapter we consider the model of Canham (1970)-Helfrich (1973)-Evans (1973) to describe the response of such membranes under pressure.

2.1 The biomembrane model

We have the following assumptions:

A1. The biomembrane is thin enough with respect to its maximal radius of curvature and typical length so that it can be represented by a surface Σ.

A2. The biomembrane is shearless (offers no resistance to shear) but resists bending and stretching.

A3. The energy associated with change in bending is given by the lowest polynomial in the surface mean and Gaussian curvatures that preserve the parameterisation and the energy of stretching by the change of area.

A pedantic but important remark: A membrane is a membrane but is not a membrane, in the sense that the term membrane used in biology is the same term used by biophysicists but not the same as the term "membrane" used in mechanics. In mechanics a *membrane* is a two-dimensional structure that can resist tension but not compression or bending. A *plate* is an initially flat structure that resists bending, tension, and compression (it can be unshearable or shearable depending on the theory). A *shell* is an initially curved surface that resists bending, tension, and compression (it can be unshearable or shearable depending on the theory). We will use the term *biomembrane* or *fluid membrane* to describe a shearless structure that can resist bending and stretching.
Following the assumptions, we posit that the elastic energy of a biomembrane with surface Σ is given by

$$\mathcal{E} = \int_{\Sigma} \mathrm{d}S \left[\gamma + 2\kappa(H - H_0)^2 + \bar{\kappa} K_G\right] \tag{22}$$

where

- H and K_G are the mean and Gaussian curvatures defined in the previous section,
- γ is the surface tension (as usually found in a theory of surfactant),
- κ is the bending modulus (confusing but standard notation),
- $\bar{\kappa}$ is the saddle-splay modulus,
- H_0 is the intrinsic mean curvature of the biomembrane.

In general, one can find the shape of the surface by minimising the energy $\mathcal{E}$ with respect to all continuous deformations of a given reference shape. Typically, the system is subject to other constraints such as constant volume or constant pressure. In such cases, we can introduce the corresponding Lagrange multiplier and minimise an amended function. For instance, for constant volume $V = V_0$, the shape will be obtained by minimising

$$\mathcal{E}_P = \mathcal{E} - P(V - V_0) \tag{23}$$

subject to the condition $V = V_0$. Here P is the Lagrange multiplier (which, of course can be identified as the pressure). Similarly for the case of constant pressure, we will need to minimise

$$\mathcal{E}_V = \mathcal{E} - PV. \tag{24}$$

Note that the set of extrema of $\mathcal{E}_P$ and $\mathcal{E}_V$ are the same but their stability will be in general different.

Remember that from the Gauss-Bonnet theorem for a closed surface, we have

$$\int_\Sigma K_G \mathrm{d}S = 4\pi(1 - p). \tag{25}$$

Therefore, for a closed surface the energy contribution of the Gaussian curvature during deformation is constant (as long as the topology of the surface does not change) and can be ignored when determining the shape of the membrane.

Dimensionally, κ is an energy and γ is an energy per length squared. Therefore, we can define a typical length scale of tension versus bending given by

$$\lambda_{\mathrm{tb}} = \sqrt{\frac{\kappa}{\gamma}}. \tag{26}$$

Estimates

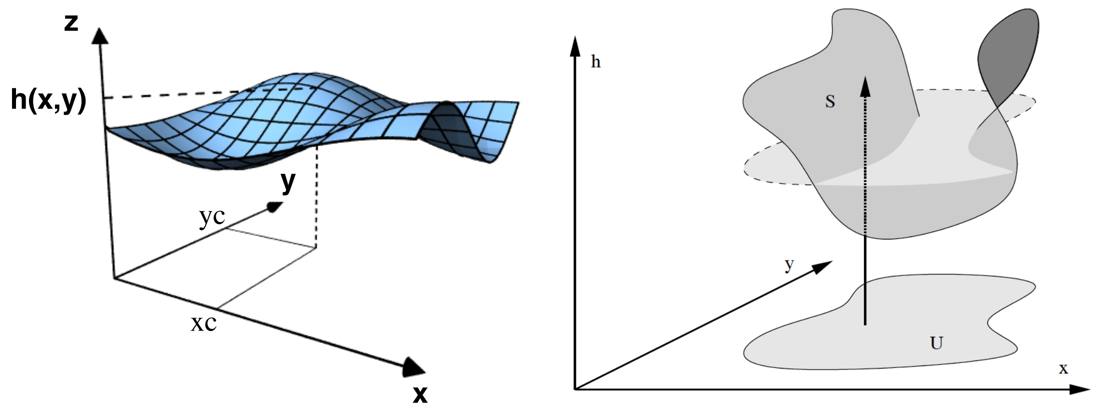

Figure 5: The height function (or Monge parameterisation) of a surface. Note that this representation is not valid if the surface curves back on itself (for instance in the case on the right).

2.2 The shape equation in the Monge representation

In order to find the shape of the surface we need to minimise the corresponding energy. This is in general a difficult task as the variations of the curvatures with respect to the deformation need to be found in general. To illustrate this process, we consider here a simpler, but important, case where the surface Σ can be represented by a height function $h = h(x, y)$ of class C^2. That is,

$$h : U \in \mathbb{R}^2 \to \mathbb{R}, \quad (\boldsymbol{\nabla} h)^2 < \infty, \tag{27}$$

where $\boldsymbol{\nabla} = \mathbf{e}_x \partial_x + \mathbf{e}_y \partial_y$. The position vector for points on the surface is simply

$$\mathbf{r} = (x, y, h(x, y)) \tag{28}$$

■ Normal and metric

We first compute the normal and metric

So that, we have for example, $\mathbf{n} = g^{-1/2} \left(-\boldsymbol{\nabla} h + \mathbf{e}_z \right), \quad g = \det(G) = 1 + (\boldsymbol{\nabla} h)^2.$

We can now compute the mean and Gaussian curvatures

■ Curvatures in Monge representation

So that, we have

$$2H = -g^{-3/2}\left[h_{xx}(1+h_y^2) + h_{yy}(1+h_x^2) - 2h_{xy}h_xh_y\right], \tag{29}$$

and

$$K_G = g^{-2}\left(h_{xx}h_{yy} - h_{xy}^2\right). \tag{30}$$

The mean curvature can also be written in a coordinate free form as

$$2H = \boldsymbol{\nabla}\cdot\left(g^{-1/2}\boldsymbol{\nabla}h\right) = -\boldsymbol{\nabla}\cdot\mathbf{n} \tag{31}$$

2.2.1 Area minimisation

Note that if $\kappa = \bar{\kappa} = H_0 = 0$ and γ is constant, the energy for the biomembrane simplifies to the well-known energy given in the theory of surface tension (in the absence of gravity)

$$\mathcal{E}_S = \gamma\int_\Sigma \mathrm{d}S. \tag{32}$$

We can now use Monge representation to obtain the condition for area minimisation

■ **Condition for area minimisation**

And we find the two equivalent local conditions for the existence of a minimal surface

$$\boldsymbol{\nabla} \cdot \mathbf{n} = 0 \iff H = 0. \tag{33}$$

Note that this condition remains valid even in the general case (where a surface cannot be represented by a height function) but only provides necessary conditions.

2.2.2 Small gradient approximation

We further restrict our analysis to the case of $\bar{\kappa} = H_0 = 0$ and for small gradients $|(\boldsymbol{\nabla} h)| \ll 1$.

Energy

That is, the energy now reads

$$\mathcal{E}_2 = \frac{1}{2} \iint \mathrm{d}x\mathrm{d}y \left[\kappa(\triangle h)^2 + \gamma(\boldsymbol{\nabla} h)^2 \right] . \tag{34}$$

This form of the energy is now sufficiently simple as to allow us to compute the first variation with respect to h (that is $h \to h + \delta h$). To keep track of terms on the domain boundary we need to do the variation from first principles, analogously to the derivation of the Euler-Lagrange equations

First variation of the energy

That is, we have

$$\delta \mathcal{E}_2 = \iint \mathrm{d}x\mathrm{d}y \triangle \left[\kappa(\triangle h) - \gamma h\right] \delta h + \oint \mathrm{d}s\ \mathbf{N} \cdot \left[\kappa(\triangle h) \boldsymbol{\nabla} \delta h + (\gamma \boldsymbol{\nabla} h - \kappa \boldsymbol{\nabla} \triangle h) \delta h\right]. \quad (35)$$

where $\mathbf{N}$ is the outer normal to the projected surface contour on the $x-y$ plane.

A necessary condition for minimisation is $\delta\mathcal{E}_2 = 0$. The vanishing of the area integral provides the *shape equation*

$$\triangle\left(\triangle - \lambda^{-2}\right) h = 0 \tag{36}$$

where $\lambda = \lambda_{\rm tb}$ is the typical length scale introduced in (26).

The vanishing of the line integral leads to boundary conditions for our fourth-order problem. We have two sets of conditions to satisfy.

1) For the first term in the bracket, we fix either the normal component of the contour so that

$$\mathbf{N}\cdot\boldsymbol{\nabla} h = \mathrm{Cst} \Rightarrow \mathbf{N}\cdot\boldsymbol{\nabla}\delta h = 0 \tag{37}$$

   or, we impose $\triangle h = 0$ on $\partial\Sigma$.

2) Similarly, we need to either fix h at the boundary so that $\delta h = 0$ at the boundary, or we impose

$$\mathbf{N}\cdot\boldsymbol{\nabla} h = \lambda^{-2}\mathbf{N}\cdot\boldsymbol{\nabla}\triangle h, \tag{38}$$

   for h on the boundary.

Together, this leads to four different possible sets of boundary conditions (or any combinations in different parts of the domain).

2.3 Examples

2.3.1 One-dimensional fluid membranes

As a first particular case of the shape equation (36), we consider the case where $h = h(x)$ only, that is we assume that the sheet is uniform along the y axis. In this case, we have

$$\partial_{4x} h - \lambda^{-2}\partial_{2x} h = 0, \tag{39}$$

which is exactly the form of the beam equation in module 1, where $\lambda^{-2} = F/(EI)$ plays the role of an effective tension. We conclude that in the small gradient approximation and in one dimension, a uniform elastic fluid membrane behaves as an elastic beam under tension.

2.3.2 Flicker spectroscopy

A possible method to measure the elastic parameters of the membrane is provided by measuring the spectrum of thermal undulations via light microscopy **??**. This is known as *Flicker spectroscopy*. It is typically performed on closed membranes but the analysis of a square membrane will still provide interesting information.

Consider a square membrane of size $L \times L$ with periodic boundary conditions. We expand the height of the membranes $h(\mathbf{r}) = h(x, y)$ as a double Fourier series:

$$h = \sum_{\mathbf{q}} h_{\mathbf{q}} e^{i\mathbf{q}\cdot\mathbf{r}} \quad , \qquad \mathbf{q} = \frac{2\pi}{L}\begin{pmatrix} n_x \\ n_y \end{pmatrix} \quad , \qquad n_x, n_y \in \mathbb{Z}\,. \tag{40}$$

Next, we compute the fluctuations of this membrane in thermal equilibrium.

■ **Flicker Fluctuation**

That is, we have

$$\left\langle |h_{\mathbf{q}}|^2 \right\rangle = \frac{2k_{\mathrm{b}}T}{L^2(\kappa q^4 + \sigma q^2)} \tag{41}$$

The coefficients $\left\langle |h_{\mathbf{q}}|^2 \right\rangle$ (known as the *static structure factors*) can be measured from the spectrum. Fitting it to Eq. (41) yields the bending modulus and surface tension of the membrane (see Fig. 6).

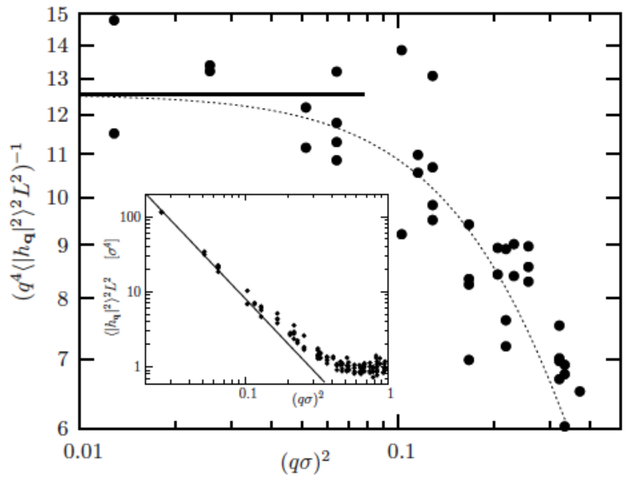

Figure 6: Flicker spectrum of a fluctuating membrane. The dashed line is a fit of the form $(k_\mathrm{B}T/\kappa + c_1(q\gamma)c_2)^{-1}$ which helps to find the asymptotic value; the inset shows the unscaled spectrum. The fit leads to $\kappa = 12.5k_\mathrm{B}T$, with an error estimated to be $\pm 1k_\mathrm{b}T$. (Figure 1 from The Journal of Chemical Physics 125(20):204905 December 2006, reproduced without permission).

3 Axisymmetric Membranes and Shells

■ Elastic membranes and shells

We consider the axisymmetric deformation of membranes and shells in linear and nonlinear elasticity. These have biological application in modelling the dformation and mechanics of red blood cells in physiological flows and also modelling filamentous growth of biological structures in the context of fungi and hyphae for instance. We start with a simple elastic membrane before considering the general case.

3.1 Elastic membranes with linear constitutive laws

We begin by considering an extensible axisymmetric elastic membrane filled with an incompressible viscous fluid under pressure *and that there is no normal shear stress*. This type of formulation has been used successfully to describe the shape of red blood cells and other biomembranes **??** and we adapt it here to include the effects of pressure induced stretch, growth and geometry dependent elastic properties of the membrane. We assume that the shape of the membrane remains axisymmetric in the deformation. Here, to derive a full set of equations, we use a method based on rational mechanics, we proceed in three steps: kinematics, mechanics, and constitutive laws.

3.1.1 Kinematics

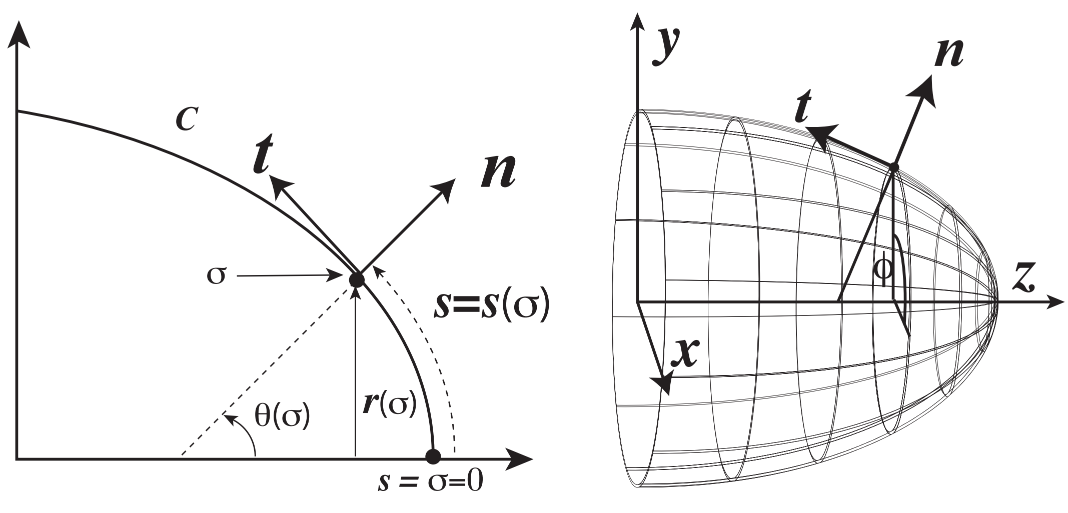

Figure 7: Basic membrane and shell geometry. A material point σ is measured by its arc-length, $s(\sigma)$ from the apex of the shell and its axial position $\mathbf{r}(\sigma)$ on a curve C, $\mathbf{n}$ and $\mathbf{t}$ denotes the normal and tangent vectors at that point. The angle $\theta(s)$ is the angle between the normal direction. The membrane is taken to be axisymmetric where φ is the azimuthal angle.

We assume that the shape of the membrane remains axisymmetric in the deformation. As shown in Figure 7, the membrane surface $\mathcal{S}$ is defined by revolving a planar curve $\mathcal{C}$ around the z-axis. The reference planar curve $\mathcal{C}$ is parameterized by a parameter σ counted from the intersection $\mathcal{O}$ of the surface with the z-axis. The shell geometry is characterized by the distance from the axis $\mathbf{r} = \mathbf{r}(\sigma)$ and the angle $\theta = \theta(\sigma)$ between the normal to $\mathcal{C}$ at σ and the z-axis. The arclength at any time $s = s(\sigma)$ is measured from $\mathcal{O}$. Before deformation or growth, the material parameter σ is chosen to be the arc length, $s = \sigma$, and the initial shell configuration is referred to as the *reference configuration.* If we consider axisymmetric deformation of the surface, we can define the *radial stretch ratio*

$$\lambda_\varphi = \frac{r}{\rho}, \tag{42}$$

at a given (material) point as the ratio between the original radius ρ at that point and the new radius r, and the *stretch ratio*

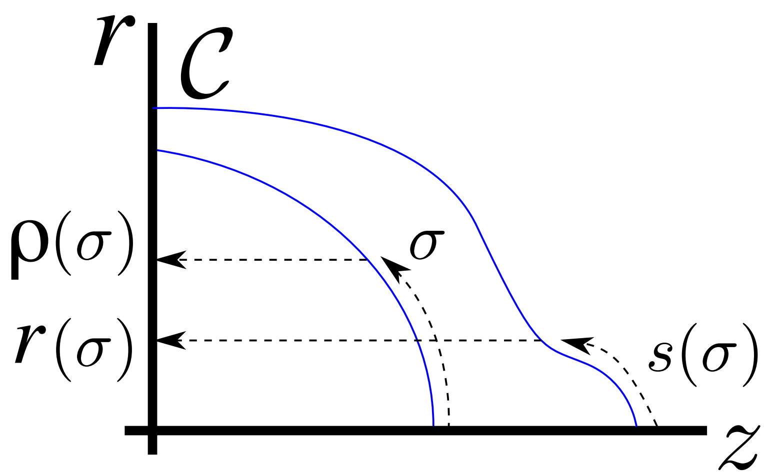

Figure 8: Definitions of stretches. We consider a reference curve before and after deformation.

$$\lambda_s = \frac{\partial s}{\partial \sigma}, \tag{43}$$

as the amount of stretching of the body coordinates with respect to arclength. These two *stretches* $(\lambda_\varphi, \lambda_s)$ completely define the deformation of an axisymmetric reference shape. The geometric variables satisfy the equations

$$\frac{dr}{ds} = \cos(\theta), \quad \frac{dz}{ds} = -\sin(\theta), \tag{44}$$

Two other important measures of the geometry of the surface are the principal curvatures which are given by

$$\kappa_s = \frac{d\theta}{ds}, \quad \kappa_\varphi = \frac{\sin\theta}{r}. \tag{45}$$

Note 1: If the we have an incompressible shell the third deformation variable, λ_3, measuring changes in the normal thickness of the shell, is simply related to λ_s and λ_φ through the incompressibility condition $\lambda_s\lambda_\varphi\lambda_3 = 1$.

Note 2: A modelling choice must be made at this point. Is the membrane, the reduction to a surface of a 3D body (as one would expect say of a rubber balloon), or is the membrane a true elastic surface (called "an elastic sheet") with no transverse structure (as one would model a lipid bilayer)? This leads to slightly different formulation of the problem. Haughton has a nice review paper on the subject **?**.

3.1.2 Mechanics

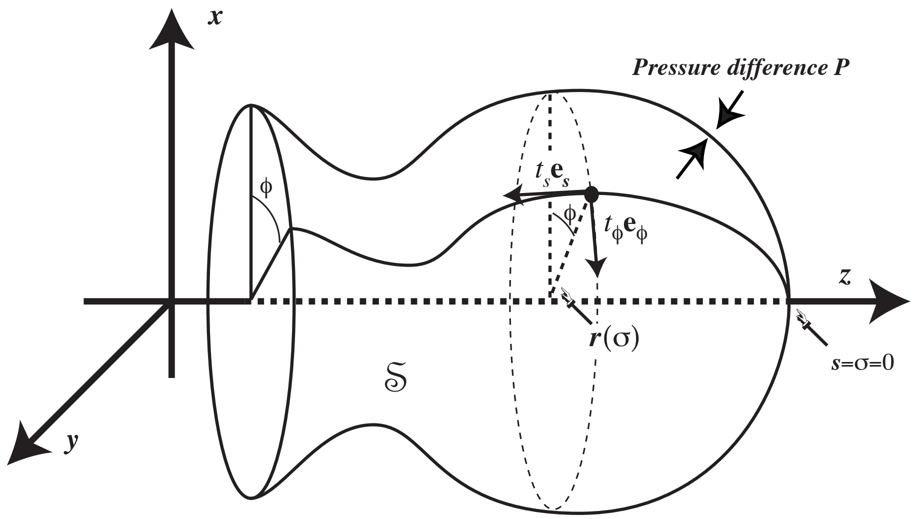

Figure 9: The surface $\mathcal{S}$ with stresses (t_s, t_φ).

We now define the stresses acting on the membrane surface: let t_s be the tension on the surface along the tangent $\mathbf{e}_s$, in the direction of increasing arclength; and let t_φ be the tension along the unit vector $\mathbf{e}_\varphi$, normal to $\mathbf{e}_s$ in a plane tangent to $\mathcal{S}$, and in the direction of increasing azimuthal angle φ (see Figure 9).

The equations for mechanical equilibrium for a surface of revolution in the normal and tangential direction results from the balance of force and moments acting on a surface element.

Mechanical force balance

That is, we have,

$$P = \kappa_s t_s + \kappa_\varphi t_\varphi, \tag{46}$$

$$\frac{\partial (r t_s)}{\partial s} - t_\varphi \frac{\partial r}{\partial s} + r f = 0, \tag{47}$$

where P is the pressure difference across the membrane, and f is the shear stress on the membrane.

This last term could be taken to represent the drag forces exerted by the surrounding medium on the membrane. Appropriate modeling of this effect is nontrivial. For now, this term will be set to zero in our analysis.

We proceed to consider moments.

■ **Mechanical moment balance**

Hence

$$\frac{\partial}{\partial s}(rm_s) - m_\varphi \cos\theta = 0. \tag{48}$$

Note: The two equations (46, 47) can be written in terms of r and θ by using the geometric relation $\mathbf{e}_s = \cos\theta \mathbf{e}_r + \sin\theta \mathbf{e}_z$, and $\partial\theta/\partial s = \kappa_s$, and take the form

$$t_s \frac{\partial\theta}{\partial s} + \frac{\sin\theta}{r} t_\varphi = P, \tag{49}$$

$$\frac{\partial t_s}{\partial s} = \frac{\cos\theta}{r}(t_\varphi - t_s). \tag{50}$$

In the case of constant pressure P we can verify that there is an integral of equations (49, 50), *i.e.* a function of the variables constant along the curve $\mathcal{C}$, given by:

$$C = r^2 \left(2t_s\kappa_\varphi - P\right). \tag{51}$$

In particular, for all solutions $(r(\sigma), \theta(\sigma))$ crossing the z-axis, we have $C = 0$ and $P = 2t_s\kappa_\varphi$.

3.1.3 Constitutive laws

From the general theory of elasticity for isotropic incompressible material, the tensions in the directions of the stretches are given by

$$t_i = \lambda_i \frac{\partial W}{\partial \lambda_i} - p, \qquad i = s, \varphi, 3. \tag{52}$$

Here p is a Lagrange multiplier for incompressibility. A 3D membrane relationship is derived by using the membrane assumption, that states $t_3 = 0$, to eliminate p, whilst λ_3 is eliminated as incompressibility gives $\lambda_3\lambda_2\lambda_\phi = 1$.

Regardless of the general model of material properties, one can generally write the constitutive relationships in the form

$$t_s = Af_s(\lambda_s, \lambda_\varphi). \tag{53}$$
$$t_\varphi = Af_\varphi(\lambda_s, \lambda_\varphi), \tag{54}$$

Moments. Finally, we need to specify a constitutive relationship for the bending moments. The bending moments are assumed to be isotropic and proportional to the change in the surface's mean curvature, *i.e.*

$$m_\varphi = m_s = B(\kappa_s + \kappa_\varphi - K_0), \tag{55}$$

where K_0 is the sum of membrane curvtaures in the absence of bending moments and B is the bending modulus [E. A. Evans and R. Skalak. Mechanics and thermodynamics of biomembranes. CRC Press, Inc, Boca Raton, Florida, 1980].

Combining this with equation (48) immediately implies

$$\kappa_s + \kappa_\varphi = K_1,$$

where K_1 is a constant.

In summary To find the membrane shape, that is $r,\ z$, with constant pressure the complete system of membrane equations can be written as the closed system

$$\frac{ds}{d\sigma} = \lambda_s, \tag{56}$$
$$\frac{dz}{d\sigma} = -\lambda_s \sin(\theta), \tag{57}$$
$$\frac{dr}{d\sigma} = \lambda_s \cos(\theta), \tag{58}$$
$$\frac{d\theta}{d\sigma} = \lambda_s \kappa_s = \lambda_s \left(K_1 - \frac{\sin\theta}{r} \right), \tag{59}$$
$$\frac{dt_s}{d\sigma} = \lambda_s A \left[\frac{\cos\theta}{r} (f_\varphi - f_s) \right]. \tag{60}$$
$$P = Af_s \left(K_1 - \frac{\sin\theta}{r} \right) + Af_\phi \cdot \frac{\sin\theta}{r} \tag{61}$$

with $f_s = f_s(\lambda_s, \frac{r}{\rho}),\ f_\varphi = f_\varphi(\lambda_s, \frac{r}{\rho})$, with initial profile $z = z_0(\sigma),\ r = \rho(\sigma)$, from which initial curvatures and thus K_1 can be found.

Note 1: computationally, we have a system of 5 differential equations and one algebraic equation for the variables $\{s, z, r, \theta, t_s, \lambda_s\}$. It can usually easily be solved numerically for given boundary conditions. Some care may be needed to find the correct boundary condition at $\sigma = 0$. This can sometimes be determined asymptotically for simple configurations (see Exercises).

Note 2: If volume rather than pressure is kept constant, then the pressure becomes a Lagrange multiplier that enforces the volume constraint. Starting from a guess pressure, one can iterate the computation by computing the solution for each pressure under a volume constraint).

Note 3: In the case of a surface incompressibility (typical for bilayers), one needs to modify the strain energy density with the constraint, the associated new "surface pressure" will then need to be determined as part of the unknowns. This is a possible way to relate this theory to the fluid membranes section above.

3.1.3.1 Variable moduli. A deformation of the membrane can follow from either an increase in pressure or a softening of the walls. The softening can easily be taken into account by using a material dependent elastic function $A = A(\sigma)$. A general form of $p = P/A$ can be taken as

$$p = \frac{P}{2}\left[1 - \tanh(\frac{\sigma - \sigma_1}{\alpha})\right] + \beta, \tag{62}$$

where P is the internal pressure and the parameters σ_1 and α describe the length of the extension zone. Since $\lim_{\sigma\to\infty} p = \beta$, the parameter β describes the effective pressure in distal regions. Close to the deformation tip ($\sigma = 0$), the walls are soft and the elastic coefficient minimal. In the distal regions, the walls are set and the elastic coefficient A is, comparatively, very large, so that the effective pressure is small (equal to β). Note that a decreased modulus or increased pressure (or *vice versa*) are, at the mechanical level, indistinguishable, trivial mathematically, highly non-trivial biologically.

3.1.4 Inflation of a spherical membrane

It is of interest to consider the inflation of a spherical membrane.

■ The spherical membrane

We start with a shell of initial radius A_0 and deform it to a new shell of radius a and we define $\lambda = a/A_0$.

3.2 Nonlinear elastic shells

We now briefly discuss axisymmetric shells, that is, elastic objects that can be represented by a surface, support bending, and have a non-flat unstressed shape. At the level of kinematics, there is no difference in the geometric description of the deformations. Therefore, we move directly to mechanics.

3.2.1 Mechanics

The mechanical equilibrium, including bending moments can be obtained by balancing linear and angular momenta on a small surface element. Long and tedious force and couple balances via a complex body diagram that are better done in the privacy of one's office lead to a system of three equations

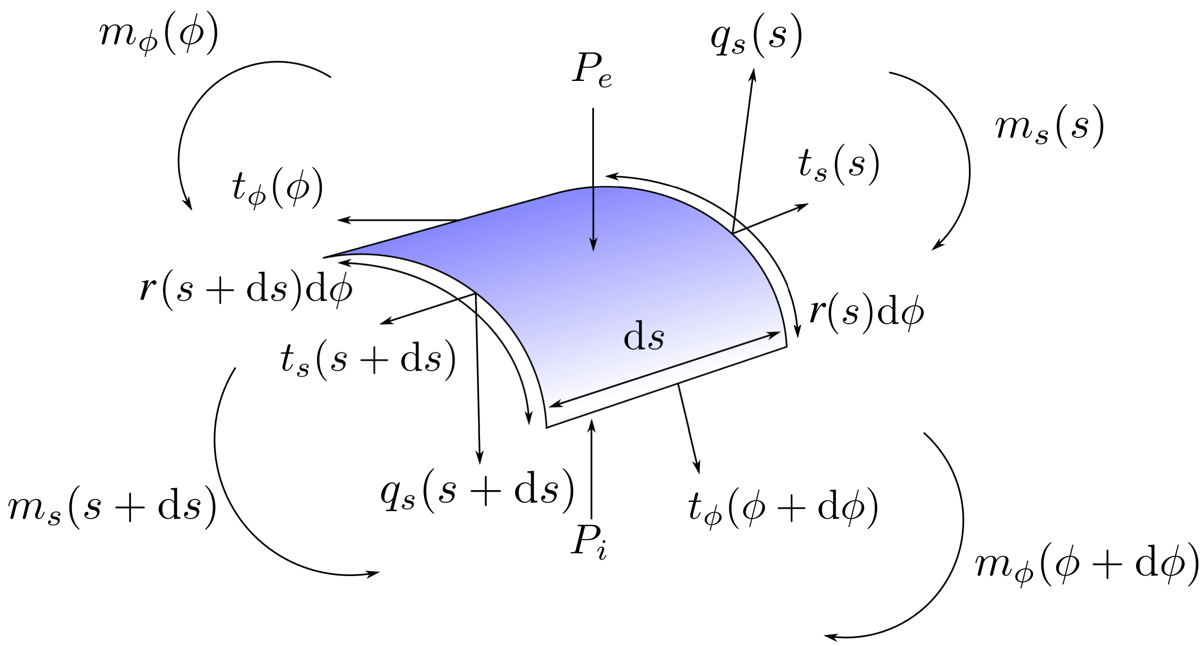

Figure 10: A rather complex balance of forces and moments acting on a surface element, where the difference in the normal stress across the membrane is q_n, which has a pressure contribution, but may have other contributions as well, as detailed further in the text.

$$\frac{d(rq_s)}{ds} = rq_n - r\left(\kappa_s t_s + \kappa_\varphi t_\varphi\right), \tag{63}$$

$$\frac{d(rt_s)}{ds} = t_\varphi \cos\theta + r\kappa_s q_s, \tag{64}$$

$$\frac{d(rm_s)}{ds} = m_\varphi \cos\theta + rq_s, \tag{65}$$

where t_s and t_φ are, respectively, the meridional and azimuthal stresses; m_s and m_φ are the bending moments; and q_s is the shear stress normal to the surface.

In equation (63), which represents the balance of normal stresses, q_n represents the total *normal* stress exerted on the shell. If the problem is pressure driven then $q_n = \Delta P$, namely the pressure difference across the shell; and if it is a combination of pressure and cytoskeletal action, represented by some function τ_n, then $q_n = \Delta P + \tau_n$.

Note: If the normal forces acting on the shell are due to, say, cytoskeletal action represented by some function τ_n, then $q_n = \tau_n$; and if the total normal forces are a combination of both of these effects, $q_n = \Delta P + \tau_n$.

In Equation (64), which represents the balance of tangential stresses, τ_s is the external tangential shear stress acting on the shell and will be used here to represent the friction between the deformed shell and its environment.

3.2.2 Constitutive relationship

For the stresses t_s, t_φ, we use the same relationships as for the case of membranes. Finally, we need to specify a constitutive relationship for the bending moments. Similarly for the moments we use as previously

$$m_\varphi = m_s = B(\kappa_s + \kappa_\varphi - K_0), \tag{66}$$

where B is the bending modulus and K_0 is the sum of membrane curvatures in the absence of bending moments.

3.2.3 The shell equations

The geometric and mechanical equations can be combined to give a closed system. It is convenient to express all the derivatives in terms of the material coordinate, σ, leading to

$$\frac{dz}{d\sigma} = -\lambda_s \sin(\theta), \tag{67}$$

$$\frac{dr}{d\sigma} = \lambda_s \cos(\theta), \tag{68}$$

$$\frac{d\theta}{d\sigma} = \lambda_s \kappa_s, \tag{69}$$

$$\frac{d\kappa_s}{d\sigma} = \lambda_s \left[\frac{\cos\theta}{r} \left(\frac{\sin\theta}{r} - \kappa_s \right) + \frac{q_s}{B} \right] \tag{70}$$

$$\frac{dt_s}{ds} = \lambda_s A \left[\frac{\cos\theta}{r} (f_\varphi - f_s) + \kappa_s \frac{q_s}{A} \right], \tag{71}$$

$$\frac{dq_s}{d\sigma} = \lambda_s A \left[\frac{q_n}{A} - \kappa_s f_s - \frac{\sin\theta}{r} f_\varphi - \frac{q_s}{A} \frac{\cos\theta}{r} \right], \tag{72}$$

where (70) is obtained from (65) using the constitutive relation (66) and equation (45) is used to express κ_φ in terms of r and θ. In equations (71) and (72) t_s and t_φ are expressed in terms of λ_s and λ_φ through the scaled constitutive relations (53,54), and equation (71) is converted into a differential equation for λ_s by eliminating λ_φ through the relation $\lambda_\varphi = r/\rho$.

The six ordinary differential equations (67-72) together with the relationships (53,54) and $\lambda_\varphi = r/\rho$ form a closed system for the variables $(z, r, \theta, \kappa_s, \lambda_s, q_s)$ that can be solved for given initial profile $\rho(\sigma)$, elastic parameters A, B, prescribed normal and tangential stresses q_n and τ_n, and appropriate boundary conditions.

When bending moments can be neglected the shell no longer supports an out-of-plane shear force, *i.e.* $q_s = 0$ and equation (72) reduces to

$$\frac{q_n}{A} = \kappa_s f_s + \kappa_\varphi f_\varphi, \tag{73}$$

which is just a generalized form of the Young-Laplace law as seen before. The system of shell equations then simplifies to the membrane equations from the previous section.

$$\frac{ds}{d\sigma} = \lambda_s, \tag{74}$$

$$\frac{dz}{d\sigma} = -\lambda_s \sin(\theta), \tag{75}$$

$$\frac{dr}{d\sigma} = \lambda_s \cos(\theta), \tag{76}$$

$$\frac{d\theta}{d\sigma} = \lambda_s \kappa_s = \lambda_s \left(K_1 - \frac{\sin\theta}{r} \right) \tag{77}$$

$$\frac{dt_s}{d\sigma} = \lambda_s A \left[\frac{\cos\theta}{r} (f_\varphi - f_s) \right]. \tag{78}$$

4 Problems

1) **Area and length invariance.** Show that the definitions of area (Eq. (6)) and length (Eq. (9)) are invariant under a change of parameterisation.

2) **Eigenvalues of L.** The matrices G and K associated with the first and second fundamental form are symmetric. However, the combination $L = G^{-1}K$ is not necessarily symmetric. Prove that, nevertheless, the eigenvalues of L are real and that eigenvectors with distinct eigenvalues are orthogonal with respect to the inner product $<\mathbf{a}, \mathbf{b}>= \mathbf{a}^T G\mathbf{b}$.

3) **Euler's theorem.** Prove Euler's theorem given in Eq. (17). For simplicity you may restrict to the case of a surface for which the matrices K and G are diagonal.

4) **Monkey-saddle.** Draw and compute all the curvatures (principal, mean, Gaussian) for the monkey-saddle defined by $z = x^3 - 3xy^2$. Show that every point has negative Gaussian curvature, except the origin.

5) **Slightly deformed sphere.** Compute the mean and Gaussian curvatures of a slightly deformed sphere. That is, find to order $\mathcal{O}(\epsilon)$, the curvatures of

$$\mathbf{x}(\theta, \phi) = R(1 + \epsilon h(\theta, \phi)) \left[\cos(\phi)\sin(\theta), \sin(\phi)\sin(\theta), \cos(\theta)\right] \tag{79}$$

and show that they can be expressed as

$$H = \frac{\mathrm{tr}(L)}{2} = \frac{1}{R}\left(1 - \frac{\epsilon}{2}\Delta(\theta, \phi)\right) + \mathcal{O}(\epsilon^2) \tag{80}$$

$$K = \det(L) = \frac{1}{R^2}\left(1 - \epsilon\Delta(\theta, \phi)\right) + \mathcal{O}(\epsilon^2). \tag{81}$$

where

$$\Delta = 2h + \frac{1}{\sin^2\theta}\partial_{\phi\phi}h + \cot\theta\ \partial_\theta h + \partial_{\theta\theta}h. \tag{82}$$

6) **Volume/pressure constraint.** Show that the addition of the constraint of fixed volume or fixed pressure adds a constant P term to the shape equation (36), so that it reads now

$$\triangle\left(\triangle - \lambda^{-2}\right)h = P. \tag{83}$$

Hint: you may want to rewrite the volume integral $\int \mathrm{d}V$ as $1/3 \int \boldsymbol{\nabla}\cdot\mathbf{r}\ \mathrm{d}V$ for $\mathbf{r} = (x, y, z)$ so that you can use the divergence theorem to transform it into a surface integral.

7) **Membrane on step.** Compute the shape of a membrane that smoothly covers a step-edge of height h_0 and touches the lower level a distance L away (see Fig. 11). Assume that the height only depends on x.

8) **Cylindrical vesicles.** Consider a family of cylindrical vesicles of unstressed radius R_0, current radius R, and length L under constant pressure P. Ignoring all boundary conditions at the face of the cylinder, compute the pressure $P = P(R)$ and surface tension $\gamma = \gamma(R)$ necessary to maintain this cylindrical shape by minimising the energy (24) with respect to both R and L (assume $\kappa = 1$ without loss of generality). Plot P as a function of R and find the maximal value of the pressure and the radius at which it occurs. Discuss this profile and the possibility of an instability.

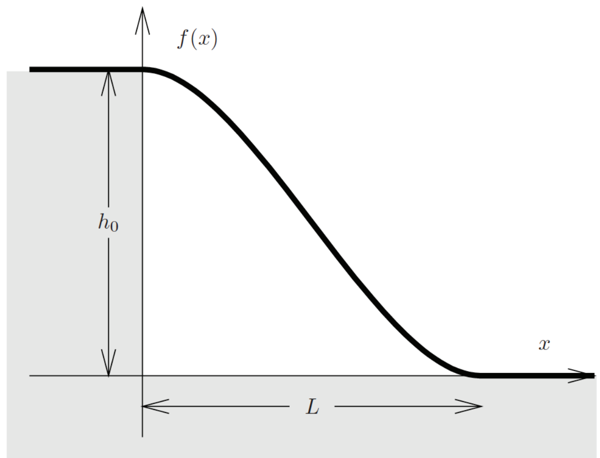

Figure 11: Find the shape of a fluid membrane attached at height h_0.

9) **Sea urchin.** The shape of a sea urchin is understood to be the result of a mechanical balance between a pressure gradient and surface tension. Here we consider a simple model for the basic shape of a sea urchin, treated as an axisymmetric elastic membrane. The model is based on two assumptions:

- The pressure difference across the membrane, P, increases linearly with depth.
- The tensions t_s and t_ϕ are equal.

The first assumption models an internal gravitational pressure gradient: due to the weight of the fluid within the body cavity the pressure is highest at the base and lowest at the top of the urchin. We define the z-axis to be flipped from the notes, so that pressure increases with increasing z (see the figure); thus this assumption is expressed as $P = \rho g z$. The second assumption is a biological adaptation to maximise strength of the shell, and is achieved by a complex process of growth of membrane plates that we need not explicitly model here.

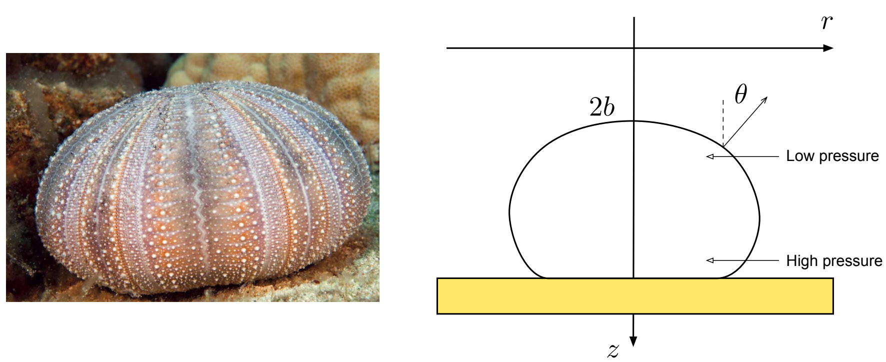

Figure 12: The shape of a sea urchin is a balance between a pressure gradient and tension.

The goal in this problem is to utilise the assumptions above within the shell equations (56)-(61) to determine the shape of the urchin.

First, show that the urchin shape is determined by the system of only 3 equations

$$r'(s) = \cos\theta \tag{84}$$

$$z'(s) = \sin\theta \tag{85}$$

$$\theta'(s) = az - \frac{\sin\theta}{r} \tag{86}$$

where a is a control parameter to be defined, and s is the *current* arclength.

The boundary conditions at the apex are

$$\theta(0) = 0,\ r(0) = 0,\ z(0) = 2b,$$

where $b > 0$ is a parameter used to fix a non-zero pressure at the apex. These boundary conditions create a removable singularity since θ' is undefined at $s = 0$. Consider a first order expansion of the boundary conditions around $s = 0$ to obtain well-defined conditions at $s = \epsilon$ for given $\epsilon \ll 1$.

Set $b = 1$, and integrate the system numerically from $s = 0$ to $s = L$, where L is such that $\theta(L) = \pi$, which models the condition that the urchin meets the interface it rests on (the sea floor, e.g.) with a fixed angle of π.

Showing how the shape changes with a produces what is called a *morphospace*. Create such a morphospace for a few values of a. Does the shape change match your intuition when connecting to the physical interpretation of a?