C5.9 - Mathematical Mechanical Biology

Sheet 3 — MT

Section A - For practice

1. 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. 1). Assume that the height only depends on x.

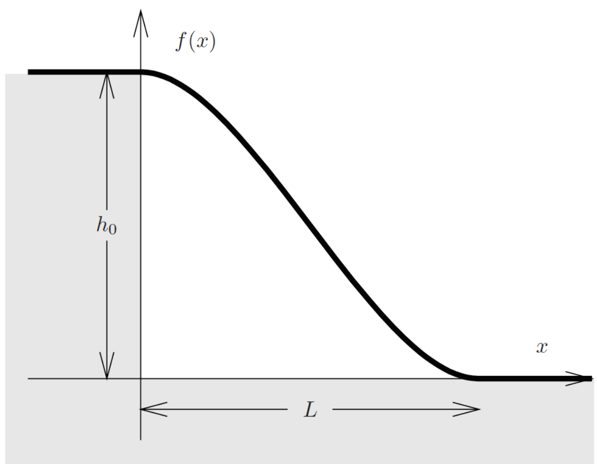


Figure 1: Find the shape of a fluid membrane attached at height h_0.

Solution: We are asked to find the shape of a membrane that is hanging over a step-edge. To do this, we work in $1D$ using the corresponding shape equation derived in lectures:

$$\frac{d^4h}{dx^4} - \frac{1}{\lambda^2}\frac{d^2h}{dx^2} = 0, \tag{1}$$

with boundary conditions given by $h(0) = h_0$, $h(L) = 0$, $h'(0) = 0$ and $h'(L) = 0$.

However, let us introduce the scaling $\hat{x} = \frac{x}{\lambda}$, so that equation (1) now becomes:

$$\frac{d^4h}{d\hat{x}^4} - \frac{d^2h}{d\hat{x}^2} = 0, \tag{2}$$

with new boundary conditions given by: $h(\hat{x} = 0) = h_0$, $h(\hat{L} = \frac{L}{\lambda}) = 0$, $h'(0) = 0$ and $h'(\hat{L}) = 0$.

The general solution of this non-dimensionalized equation is then given by:

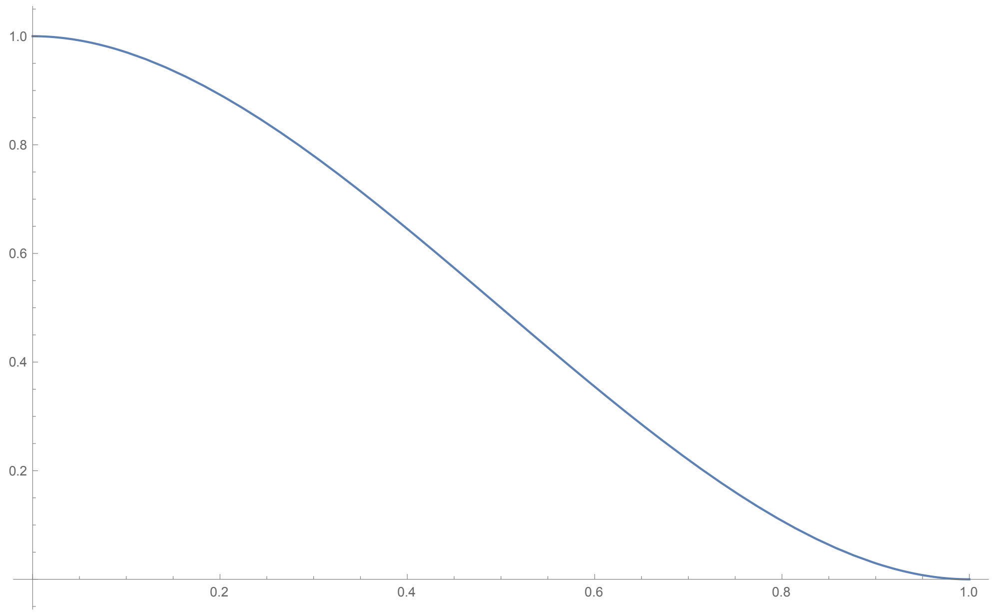
Prof. Alain Goriely: alain.goriely@maths.ox.ac.uk

$$h(\hat{x}) = A + B\hat{x} + C\sinh(\hat{x}) + D\cosh(\hat{x}), \tag{3}$$

and, by substituting the boundary conditions, we find that the resulting shape can be written in the following form (of course, this is not the only form that it could be written in):

$$h(\hat{x}) = h_0 - h_0\left[\frac{\left(\cosh\left(\hat{L}\right)-1\right)\left(\cosh(\hat{x})-1\right) - \sinh\left(\hat{L}\right)\left(\sinh(\hat{x})-\hat{x}\right)}{\left(\cosh\left(\hat{L}\right)-1\right)\left(\cosh\left(\hat{L}\right)-1\right) - \sinh\left(\hat{L}\right)\left(\sinh\left(\hat{L}\right)-\hat{L}\right)}\right], \tag{4}$$

Plotting this solution for $h_0 = 1$, $L = 1$ and $\lambda = \frac{1}{\sqrt{5}}$, we obtain the following:



We note from our definition of $\hat{x}$ that we have two length scales: L and λ. Plot the solution for various values of L and λ. What do you notice about the solution when $L \gg \lambda$? What about when $\lambda \gg L$? What sort of energy is minimized in both scenarios?

Prof. Alain Goriely: alain.goriely@maths.ox.ac.uk

Section B - Regular problems

2. **Cylindrical vesicles.** Consider a cylindrical vesicle of unstressed radius R_0, deformed to current radius R and length L under constant pressure P. We ignore all boundary conditions at the ends of the cylinder.

   (a) Suppose that surface tension γ is a fixed constant, and set $\kappa = 1$ without loss of generality. Compute the pressure $P = P(R)$ necessary to maintain the cylindrical shape by minimising the energy (Eqn (24) in Biomembrane typed notes) per unit length with respect to R.

   (b) Suppose instead that γ satisfies the constitutive relation

   $$\gamma = E_s \left(\frac{A}{A_0} - 1 \right),$$

   where E_s is a fixed stretching stiffness modulus, A is the current area, and A_0 is the undeformed area. Supposing that the undeformed length is L_0, minimise the energy with respect to both R and L, and thus compute the pressure P and length L as functions of R.

   In both cases, plot P as a function of R. Discuss this profile and the possibility of an instability. How does the deformed radius depend on γ?

3. **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 for Monge representation under small gradients (Eqn (36) in Biomembrane typed notes), so that it reads now

   $$\kappa \triangle^2 h - \gamma \triangle h = P. \tag{5}$$

   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.

Prof. Alain Goriely: alain.goriely@maths.ox.ac.uk

4. **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.

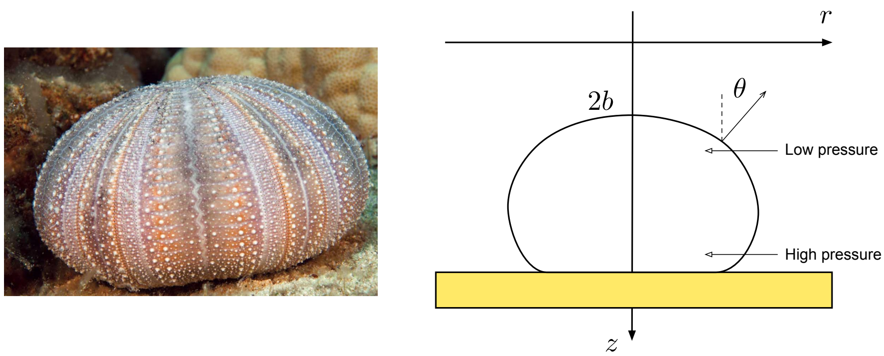


Figure 2: The shape of a sea urchin is a balance between a pressure gradient and tension.

The goal in this problem is to utilise the assumptions above within the axisymmetric shell equations to determine the shape of the urchin.

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

$$r'(s) = \cos\theta \tag{6}$$

$$z'(s) = \sin\theta \tag{7}$$

$$\theta'(s) = az - \frac{\sin\theta}{r} \tag{8}$$

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

The boundary conditions at the apex are

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

Prof. Alain Goriely: alain.goriely@maths.ox.ac.uk

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?

5. **1D growing rod under gravity.** Consider a vertical rod subject to self-weight under gravity, oriented such that $s = 0$ at the top of the rod, and $s = l(t)$ at the bottom of the rod. The rod is compressed by its own weight, but the top of the rod is free, so that the stress $\mathsf{n}_3 := \sigma = 0$ at $s = 0$. (We are using a slightly odd choice of coordinates: physically we imagine the bottom of the rod is fixed on the ground, while growth changes the location of the top of the rod; however for computational purposes it is easier to situate $S = s = 0$ at the top). Assume that it grows to reach a state of homeostatic compression ($\sigma^* < 0$), that is

$$\frac{\partial \gamma}{\partial t} = \kappa \gamma (\sigma - \sigma^*), \tag{9}$$

Find the evolution of the current length $l(t)$ as a function of time assuming that the rod is linear elastic, i.e. with constitutive law $\sigma = E(\alpha - 1)$. Obtain an expression for the total (current) length of the rod as a function of time, and show that the rod always reaches the same asymptotic length $l_\infty = -\frac{2\sigma^*}{\rho g}(1 + \frac{\sigma^*}{E})$.

Prof. Alain Goriely: alain.goriely@maths.ox.ac.uk

Section C - Optional

6. **Return of the 1D growing rod under gravity.** Replace the growth law in the previous problem by assuming that growth is confined to a region of size R at the bottom and that growth only occurs when the rod is in tension relative to the homeostatic stress, i.e. when $\sigma > \sigma^*$. This is expressed by the following law:

$$\frac{\partial\gamma}{\partial t} = \kappa\gamma(\sigma - \sigma^*)\mathrm{H}(S - (L - R))\mathrm{H}(\sigma - \sigma^*) \tag{10}$$

where H is the Heaviside function and L is the length of the rod in the evolving reference configuration. Assuming that the reference length and size of the growth region satisfy $L - R < -\sigma^*/\rho g$, obtain again an expression for the length $l(t)$ and consider the limit $t \to \infty$.

Solution: Here we consider the growth law:

$$\frac{\partial\gamma}{\partial t} = \kappa\gamma\left(\sigma - \sigma^\star\right) H\left(S - (L - R)\right) H\left(\sigma - \sigma^\star\right), \tag{11}$$

which confines growth to a region, R, at the bottom of the rod and also imposes that growth only acts when the stress exceeds the homeostatic stress (i.e. when the rod is in tension relative to the homeostatic compressive stress $\sigma^* < 0$). Furthermore, the homeostatic stress and the region of size R satisfy the inequality $L - R < \frac{-\sigma^\star}{\rho g}$, where L is the reference length of the growing rod.

As before, we work out the stress that acts on the rod under gravity:

$$\frac{\partial\sigma}{\partial S} = -\rho g \implies \sigma = -\rho g S, \tag{12}$$

with the same boundary condition of $\sigma = 0$ at $S = 0$, and use the relationship between S, γ and S_0:

$$\gamma = \frac{\partial S}{\partial S_0} \implies S = \int_0^{S_0} \gamma dS_0, \tag{13}$$

and thus the reference length is

$$L = \int_0^{L_0} \gamma dS_0, \tag{14}$$

L_0 being the fixed initial length.

Differentiating with respect to time and using the new growth law, we find:

Prof. Alain Goriely: alain.goriely@maths.ox.ac.uk

$$\frac{\partial L}{\partial t} = -\kappa \int_0^L \left(\rho g S - \rho g S^\star\right) H\left(S - (L-R)\right) H\left(\sigma - \sigma^\star\right) dS, \tag{15}$$

where $S^\star$ is the S coordinate associated with $\sigma^\star$.

We now consider the Heaviside functions, keeping in mind that the stress σ is a monotonically decreasing function of S, which simply relates the fact that lower points of the rod are always more compressed than higher points due to having more weight above them. Thus $\sigma > \sigma^*$ only for $S < S^*$, and so the rod can only grow in the region $S \in [0, S^*]$. But also, the growing region is restricted to the bottom, $S \in [L-R, L]$. Therefore, if there is no overlap between the two then no growth occurs. However, we are given that $L - R < -\sigma^*/\rho g = S^*$, so there is in fact a growing region, and the integral simplifies to

$$\frac{\partial L}{\partial t} = -\kappa\rho g \int_{L-R}^{S^\star} \left(S - S^\star\right) dS. \tag{16}$$

Integrating, we find:

$$\frac{\partial L}{\partial t} = \kappa\rho g \left[\frac{(L-R)^2}{2} - S^\star (L-R) + \frac{(S^\star)^2}{2}\right] = \frac{\kappa\rho g}{2}\left(L - R - S^\star\right)^2. \tag{17}$$

We can now solve this equation as a separable differential equation:

$$\int_{L_0}^{L} \frac{dL}{\left(L - R - S^\star\right)^2} = \frac{\kappa\rho g}{2}\int_0^t dt, \tag{18}$$

which gives:

$$-\frac{1}{(L - R - S^\star)} + \frac{1}{(L_0 - R - S^\star)} = \frac{\kappa\rho g}{2} t. \tag{19}$$

Solving for L, we obtain:

$$L(t) = \frac{1 + (R + S^\star)\left(\frac{1}{L_0 - R - S^\star} - \frac{\kappa\rho g}{2} t\right)}{\frac{1}{L_0 - R - S^\star} - \frac{\kappa\rho g}{2} t}. \tag{20}$$

Lastly, we can obtain an expression for the current length $l(t)$ (following both growth and loading) by integrating

$$\alpha = \frac{ds}{dS}$$

from $S = 0$ to $L(t)$ and using the constitutive relation

$$\sigma = E(\alpha - 1).$$

We get

$$l(t) = \int_0^{L(t)} \alpha \, dS = \int_0^L 1 - \frac{\rho g S}{E} dS, \tag{21}$$

which gives the relation:

$$l = L - \frac{\rho g L^2}{2E}, \tag{22}$$

in a similar manner as in the previous question.

The full expression for the current length is quite messy:

$$l = \frac{1 + (R + S^\star)\left(\frac{1}{L_0 - R - S^\star} - \frac{\kappa \rho g}{2} t\right)}{\frac{1}{L_0 - R - S^\star} - \frac{\kappa \rho g}{2} t} - \frac{\rho g}{2E}\left(\frac{1 + (R + S^\star)\left(\frac{1}{L_0 - R - S^\star} - \frac{\kappa \rho g}{2} t\right)}{\frac{1}{L_0 - R - S^\star} - \frac{\kappa \rho g}{2} t}\right)^2, \tag{23}$$

however, considering the limit of $t \to \infty$, we find that:

$$l_\infty \sim (R + S^\star) - \frac{\rho g}{2E}(R + S^\star)^2 = R - \frac{\sigma^\star}{\rho g} - \frac{\rho g}{2E}\left(R - \frac{\sigma^\star}{\rho g}\right)^2. \tag{24}$$