Question 1. Consider an inextensible, unshearable, planar filament subject to thermal fluctuations. The filament has contour length L and is pinned at one point $x = 0$ and pulled at its end with a force F at $x = l$ (no couple is exerted on the boundaries and l is assumed to be much smaller than the persistence length). The total mechanical energy of the system is

$$\mathcal{E} = \frac{K}{2}\int_0^l \kappa^2 \,\mathrm{d}x + F(L - l),$$

where $\frac{K}{2}\int_0^l \kappa^2 \,\mathrm{d}x$ is the bending energy of a rod with curvature κ and $F(L-l)$ represents the work associated with the change in length by a force F.

(a) **[5 marks]** Show that, in the small gradient approximation, the filament can be described by its height above the x-axis $u = u(x)$ and that this energy can be written to first order as

$$\mathcal{E} = \frac{1}{2}\int_0^l \left[K(u_{xx})^2 + Fu_x^2\right] \mathrm{d}x.$$

(b) **[5 marks]** By expanding the height function as $u = \sum_{n=1}^{\infty} a_n \sin(q_n x)$ where $q_n = n\pi/l$, rewrite the energy as a function of n and a_n, then use the equipartition theorem to find $\langle a_n^2\rangle$ as a function of n, l and F.

(c) **[8 marks]** Compute the shortening of the filament due to thermal fluctuations only. To do so, give an expression for $\langle(L - l)\rangle$ in the small gradient approximation for all F (without computing explicitly the sum) and determine its value in the absence of force ($F = 0$). Similarly, give an expression for the height fluctuation $(\langle\sum a_n^2\rangle)^{1/2}$ and compute it explicitly in the absence of force.

(d) **[7 marks]** Let l_0 be the length of the filament in the absence of force as computed in the previous question and define the extension $z = l - l_0$. Compute the mechanical response of the filament for small extension $F = Cz + O(z^2)$. Give an explicit expression for C in terms of the system parameters (T, l_0, K).

Hint: you may need, and use without proof, the identities $\sum_{n=1}^{\infty} n^{-2} = \pi^2/6$ and $\sum_{n=1}^{\infty} n^{-4} = \pi^4/90$.

[B]: Book, [S]:Similar, [N]: New

Solution 1.

(a)[BS] The curvature is in small gradient approximation given by u_{xx}. The length L can be written as

$$L = \int_0^l \sqrt{1 + u_x^2}\, \mathrm{d}x \tag{1}$$

Therefore, in small gradient approximation

$$L - l = \int_0^l (\sqrt{1 + u_x^2} - 1)\, \mathrm{d}x \approx \frac{1}{2} \int_0^l u_x^2\, \mathrm{d}x. \tag{2}$$

and

$$\mathcal{E} = \frac{1}{2} \int_0^l \left(K(u_{xx})^2 + F u_x^2\right) \mathrm{d}x \tag{3}$$

(b)[BS] If $u = \sin(qx)$, we have $(u_{xx})^2 = q^4 \sin^2(qx)$, $u_x^2 = q^2 \cos^2(qx)$. Using the orthogonality of $\sin(q_n x)$ and $\cos(q_n x)$ on $[0, l]$ (and $\int_0^l \sin^2 qx = \int_0^l \cos^2 qx = l/2$), we have

$$\mathcal{E} = \frac{l}{4} \sum_{n=1}^{i} nftya_n^2 (K q_n^4 + F q_n^2) \tag{4}$$

Since the energy is quadratic and diagonal in a_n, the equipartition theorem can be stated as

$$\frac{l}{4} \langle a_n^2 \rangle (K q_n^4 + F q_n^2) = \frac{1}{2} k_B T \tag{5}$$

so that

$$\langle a_n^2 \rangle = \frac{2 k_B T}{l (K q_n^4 + F q_n^2)}. \tag{6}$$

(c) [SN] Next, consider

$$L - l = \frac{1}{2} \int_0^l u_x^2\, \mathrm{d}x = \frac{l}{4} \sum a_n^2 q_n^2 \tag{7}$$

therefore

$$\langle L - l \rangle = \frac{l}{4} \sum \langle a_n^2 \rangle q_n^2 = \frac{k_B T}{2} \sum \frac{1}{K q_n^2 + F}. \tag{8}$$

We can use $q_n = n\pi/l$ and expand this last expression for small F to obtain

$$\langle L - l \rangle = \frac{k_B T}{2} \sum_{n=1}^{\infty} \left[\frac{l^2}{K n^2 \pi^2} - F \frac{l^4}{K^2 n^4 \pi^4} \right] + O(F^2) \tag{9}$$

For $F = 0$, we use the identity $\sum_{n=1}^{\infty} n^{-2} = \pi^2/6$ to obtain

$$\langle L - l_0 \rangle = \frac{k_B T l_0^2}{12K}. \tag{10}$$

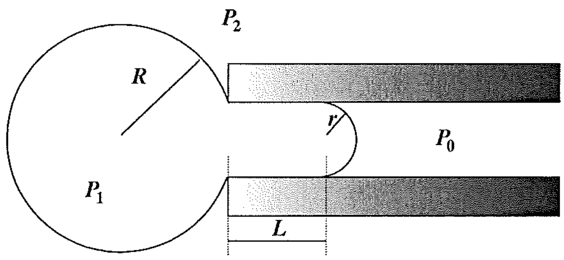
Similarly, at $F = 0$

$$\sum \langle a_n^2 \rangle = \sum \frac{2k_B T}{l_0(K q_n^4)} = \sum \frac{2k_B T l_0^3}{(K\pi^4 n^4)} = \frac{k_B T l_0^3}{45K}. \tag{11}$$

(d) [N] (Note that expansion on F should count for this section for 5pt even if they used it before. The previous question can be answered without expanding–just by setting $F = 0$). We have $L - l = L - l_0 - z$. From (9), we have

$$F = \frac{180K^2}{k_B T l_0^4} z. \tag{12}$$

Question 2. A micropipette experiment consists in sucking part of a lipid bilayer vesicle through a capillary tube by a controlled pressure $\Delta P = P_2 - P_0 > 0$ (See Figure) and measuring the length L of the vesicle in the tube. This experiment is used to measure the area compressibility modulus of the vesicle (a measure of the ability of the lipid bilayer to resist change in area).



(a) **[5 marks]** Give the general form of the Helfrich-Canham-Evans energy of a fluid bio-membrane and explain why the term involving the Gaussian curvature can be neglected in the micropipette experiment.

(b) **[5 marks]** Assuming that the unstressed shape of the bilayer is flat, compute the energy of the vesicle in the Figure by approximating the total energy as the sum of a sphere of radius R, a cylinder of length L, and a piece of a sphere of radius r and the work done by the pressure to aspirate the vesicle by a length L.

(c) **[10 marks]** Minimise this elastic energy with respect to R under the constraint that the total volume is conserved and show that the minimisation with respect to R leads to a form of the Young-Laplace equation. Since the Young-Laplace equation also applies to the vesicle in the pipette, show that the surface tension σ can be obtained as a function of ΔP, r and R only.

(d) **[5 marks]** Let A_0 be the area for $L = 0$ and $\Delta A = (A - A_0)/A_0$ the areal strain. For small areal strain, one can write $\sigma = K_a \Delta A$ where K_a is the area compressibility modulus. Express K_a in terms of all the geometric parameters and ΔP. Estimate K_a for the following values taken from an experiment on vesicles: $r = 1, R = 10, L = 10$ (all in μm) and $\Delta P = 2700$ Pa. Compare this value with the typical shear modulus of red blood cells (7μN/m) and discuss whether it is reasonable to assume area incompressibility in a fluid membrane model.

(*Note: In a typical experiment one cannot measure the change of radius R as a function of L. It is therefore a reasonable approximation* *to assume that the surface area of the original sphere is equal to the sum of the area of the current sphere and the small hemispherical cap.)*

Solutions

(a)[B] The elastic energy of a fluid biomembrane with surface Σ is given by

$$\mathcal{E} = \int_\Sigma \mathrm{d}S \left[\sigma + 2\kappa(H - H_0)^2 + \bar{\kappa} K_G\right] \tag{13}$$

where

- H and K_G are the mean and Gaussian curvatures,
- σ is the surface tension,
- κ is the bending modulus,
- $\bar{\kappa}$ is the saddle-splay modulus,
- H_0 is the intrinsic mean curvature of the biomembrane.

In our case $H_0 = 0$ (the unstressed shape of bilayer is flat) and we can ignore the contribution of K_G the Gaussian curvatures since in our experiment there is no change of topology and the surface is closed. Therefore, according to Gauss-Bonnet theorem the contribution to the elastic energy is constant.

(b)[BS] We have $\mathcal{E}_{\text{tot}} = \mathcal{E}_{\text{bend}} + \mathcal{E}_{\text{stretch}} + \mathcal{W}$, where

$$\mathcal{E}_{\text{bend}} = \kappa\left(4\pi + 2\pi\frac{L}{r} + 2\pi\right) \tag{14}$$

$$\mathcal{E}_{\text{stretch}} = \sigma\left(4\pi R^2 + 2\pi L r + 2\pi r^2\right) \tag{15}$$

$$\mathcal{W} = -(P_1 - P_0)\left(\pi L r^2 + \frac{2}{3}\pi r^3\right) \tag{16}$$

(c)[SN] The functional is $\mathcal{E} = \mathcal{E}_{\text{tot}} - pV$ where p is a Lagrange multiplier and V is the total volume

$$V = \frac{4}{3}\pi R^3 + \pi L r^2 + \frac{2}{3}\pi r^3. \tag{17}$$

The first variation of $\mathcal{E}$ with respect to R leads to

$$-4\pi R(pR - 2\sigma) = 0 \tag{18}$$

That is,

$$p = 2\frac{\sigma}{R} = P_1 - P_2. \tag{19}$$

This is the Young-Laplace equation with parameter p, a pressure, that can be identified with $P_1 - P_2$. The law also applies to the small hemisphere in with case

$$P_1 - P_0 = 2\frac{\sigma}{r}. \tag{20}$$

Assuming σ is constant on the vesicle, we have

$$\sigma = \frac{(P_0 - P_2)\, r.R}{2(r-R)} \tag{21}$$

(d)[N] The change in areal strain is

$$\Delta A = \frac{Lr}{2R^2} \tag{22}$$

Therefore

$$K_a = \frac{(P_0 - P_2)\, R^3}{L(r-R)}. \tag{23}$$

The choice of the value leads to $K_a = 0.03\text{N/m}$ which is 4×10^4 times greater than the shear rigidity. Hence it is reasonable to approximate the vesicle as an area incompressible object in most experiments.

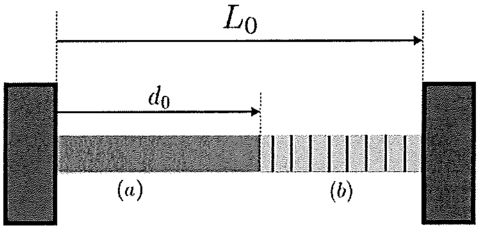
Question 3. Consider a rod of initial length L_0 at time $t = 0$. The rod is constrained between two walls and is not subject to body loads. It can only deform along its axis through stretch or growth (see Figure). The rod is parameterised by $S_0 \in [0, L_0]$ but has two domains referred to as (a) and (b): the rod in the interval (b) is a passive structure (it does not grow), whereas the rod in the interval (a) grows. The the growth law for the entire rod is

$$\frac{\partial \gamma}{\partial t} = \begin{cases} k\gamma(\sigma - \sigma^\star) & \text{if } S_0 \in [0, d_0), \\ 0 & \text{if } S_0 \in [d_0, L_0], \end{cases} \qquad \gamma(S_0, t = 0) = 1, \tag{24}$$

where k is the growth rate, $\gamma = \gamma(S_0, t)$ is the growth stretch and $\sigma^\star < 0$ is a constant homeostatic stress. Defining $\sigma = \sigma(S_0, t)$ to be the stress and $\alpha = \alpha(S_0, t)$ the elastic stretch, the elastic response of the rod is

$$\sigma = \begin{cases} E_a(\alpha - 1) & \text{if } S_0 \in [0, d_0) \\ E_b(\alpha - 1) & \text{if } S_0 \in [d_0, L_0] \end{cases} \tag{25}$$

where $E_{a,b}$ are the extensional moduli of the rod.



(a) **[10 marks]** Assuming that growth is slow so that the system is in mechanical equilibrium at all time, obtain an equation for the dynamic of γ which only involves γ and the constants of the problem (L_0, d_0, E_a, E_b, k).

(b) **[10 marks]** Assuming $|\sigma^\star| < E_a$, show that this equation has two stationary states γ_1 and $\gamma_2 > \gamma_1$ and compute the length of the two intervals (a) and (b) for these two solutions.

(c) **[5 marks]** Show that as $t \to \infty$, $\gamma(t) \to \gamma_2$, and that $\sigma(t) \to \sigma^*$.

Solutions

(a)[BS] (Similar as the two problems in the problem sheet on growth under gravity) The mechanical equilibrium satisfies $\partial_{S_0}\sigma = 0$ hence σ is uniform and so is α and γ in each interval. We define α_i and γ_i to be the growth and elastic stretches in interval $i = a, b$ (obviously $\gamma_b = 1$), we also define $A = d_0 = L_{0a}$ and $B = L_0 - d_0 = L_{0b}$ and we have

$$\sigma = E_a(\alpha_a - 1) = E_b(\alpha_b - 1). \tag{26}$$

The current length of each interval is $l_i = \alpha_i\gamma_i L_{0i}$ and since the length does not change we have

$$L_0 = l_a + l_b = \alpha_a\gamma_a A + \alpha_b B. \tag{27}$$

The solution of the system (26-27) is

$$\alpha_a = \frac{BE_a + AE_b}{BE_a + \gamma_a AE_b} \tag{28}$$

$$\alpha_b = \frac{BE_a + AE_a + A\gamma_a(Eb - Ea)}{BE_a + \gamma_a AE_b} \tag{29}$$

so that the equation for γ_a is

$$\partial_t\gamma_a = k\gamma_a\left[\frac{AE_aE_b(1-\gamma_a)}{BE_a + \gamma_a AE_b} - \sigma^*\right] \tag{30}$$

(b) [SN] The stationary states are $\gamma_1 = 0$ (with length $l_a = 0, L_b = L_0$) and

$$\gamma_2 = \frac{E_a}{AE_b}\frac{AE_b - B\sigma^*}{E_a + \sigma^*}. \tag{31}$$

Note that since $\sigma^* < 0$ and $|\sigma^*| < E_a$, we have $\gamma_2 > 0$. We compute the length using (27) to find

$$l_a = A\alpha_a\gamma_2 = A - B\frac{\sigma^*}{E_b} = d_0 - (L_0 - d_0)\frac{\sigma^*}{E_b} \tag{32}$$

and

$$l_b = B(1 + \frac{\sigma^*}{E_b}) = (L_0 - d_0)(1 + \frac{\sigma^*}{E_b}). \tag{33}$$

(c)[N] It can be shown (graphically or by inequalities) that $\partial_t\gamma > 0$ for $\gamma_1 < \gamma < \gamma_2$ and $\partial_t\gamma < 0$ for $\gamma > \gamma_2$ and therefore conclude that $\gamma(t) \to \gamma_2$ as $t \to \infty$. Obviously, $\sigma \to \sigma^*$ but it is nice to check it.