UNIVERSITY OF CAMBRIDGE

MATHEMATICAL TRIPOS Part III

Thursday, 2 June, 2022 1:30 pm to 4:30 pm

PAPER 355

BIOLOGICAL PHYSICS AND FLUID DYNAMICS

Before you begin please read these instructions carefully

Candidates have THREE HOURS to complete the written examination.

Attempt **ALL** questions.
There are **THREE** questions in total.

STATIONERY REQUIREMENTS
Cover sheet
Treasury tag
Script paper
Rough paper

SPECIAL REQUIREMENTS
None

You may not start to read the questions printed on the subsequent pages until instructed to do so by the Invigilator.

1

A recently discovered multicellular microorganism exists in the form of a linear chain of cells that can exhibit two distinct conformations of opposite curvature, with transitions between the two triggered by light. A model for the energy of the filament of length L is

$$E = \frac{1}{2} A \int_0^L ds \, (\kappa - \kappa_0)^2 \, ,$$

where κ is the curvature and $\kappa_0 = \pm H_0$ in the light $(+)$ and dark $(-)$.

(a) Working with the energy E in the Monge representation up to quadratic order in a height function $h(x,t)$ for $x \in [0, L]$ describing the filament shape, find the linear equation of motion for h and boundary conditions that result from the Stokesian force balance

$$\zeta \frac{\partial \mathbf{r}}{\partial t} = -\frac{\delta E}{\delta \mathbf{r}}.$$

Use the available constants to nondimensionalise the resulting PDE in a natural way.

(b) Suppose a filament has been kept in the dark for $t < 0$ sufficiently long that it reaches its equilibrium shape. Find that shape. At $t = 0$ the light is turned on. Using the dark-adapted shape as the initial condition, find the subsequent shape evolution using a suitable set of basis functions constructed from the biharmonic operator. Awkward projection integrals need not be evaluated analytically.

(c) Confirm that the shape evolution computed in (b) satisfies appropriate constraints on the net force and torque on the filament.

2

A bacterium swims in a viscous fluid by rotating a rigid flagellar filament relative to its cell body. The centerline of the helical filament has radius R, total length L and the helix is aligned with the cell body. Hydrodynamic interactions between the cell body and the helical filament are neglected. Locomotion (both translation and rotation) is assumed to take place only along the axis z of the helix.

(a) The hydrodynamics of the helical filament is described using resistive-force theory for slender filaments (we denote the drag coefficients $c_{\|}$ and $c_{\perp}$). Explain briefly the form of the drag law embodied in resistive force theory.

(b) The linear relationship between the hydrodynamic force $\tilde{F}\mathbf{e}_z$ and torque $\tilde{T}\mathbf{e}_z$ experienced by the helix and the translation velocity $\tilde{U}\mathbf{e}_z$ and angular velocity $\tilde{\Omega}\mathbf{e}_z$ of the helix is of the form

$$\begin{pmatrix} \tilde{F} \\ \tilde{T} \end{pmatrix}_{\text{helix}} = -\begin{pmatrix} A & B \\ B & D \end{pmatrix} \begin{pmatrix} \tilde{U} \\ \tilde{\Omega} \end{pmatrix}_{\text{helix}}, \qquad (\dagger)$$

with $A = (c_{\|} \cos^2\theta + c_{\perp} \sin^2\theta)L$ and $D = (c_{\|} \sin^2\theta + c_{\perp} \cos^2\theta)R^2L$, where θ denotes the angle between the z axis and the local tangent to the filament centreline. Compute the value of B.

(c) We now consider the combined "cell + helix" system where the filament and cell body undergo relative rotation and translate with identical velocity $U\mathbf{e}_z$. The cell body rotates with angular velocity $\Omega\mathbf{e}_z$ and the helical filament with angular velocity $(\Omega + \omega)\mathbf{e}_z$ in the laboratory frame of reference (so ω is the magnitude of the relative rotation). We write for the cell body $F_{\text{body}} = -A_0 U_{\text{body}}$ and $T_{\text{body}} = -D_0 \Omega_{\text{body}}$. Assuming the whole cell to be force and torque-free, compute the swimming speed U of the bacterium and the body rotation rate Ω as a function of A, B, D, A_0, D_0.

(d) Compute the value of the torque N applied by the bacterial motor (equal to the hydrodynamic torque exerted by the helical filament on the fluid).

(e) We define the efficiency ϵ as the ratio between the useful swimming power $(A_0 U^2)$ and the power output of the motor $(N\omega)$. Compute ϵ. Assuming $B^2 \ll AD$ and $D \ll D_0$ for common bacteria, find a simplified expression for ϵ. Use a scaling in the cell body size by λ (i.e. so that $A_0 \to \lambda A_0$) in order to derive the maximum value of ϵ over all possible cell body sizes.

3

A spherical lipid vesicle of equilibrium radius R has membrane bending modulus k_c and surface tension σ_0, and is in equilibrium at temperature T.

(a) Using a planar calculation with large-scale cutoff R and a molecular cutoff a, calculate to quadratic order in shape deformations the fractional excess area $\alpha(\sigma_0) = (A - A_{\rm proj})/A$ of the membrane that is contained in thermal fluctuations, where A is the total membrane area and $A_{\rm proj} = 4\pi R^2$ is the projected area of the membrane.

(b) A thin cylindrical tether of length L and radius r is now slowly pulled out from the vesicle by a force F, and the system remains in thermal equilibrium. In the process, the membrane tension increases to σ. If the tension remains in the regime $\sigma \ll \pi^2 k_c/a^2$, show that the change in the fractional area $\Delta\alpha = \alpha(\sigma_0) - \alpha(\sigma)$ contained in the vesicle membrane fluctuations can be approximated by

$$\Delta\alpha = \frac{k_B T}{8\pi k_c} \ln\left(\frac{\pi^2 k_c/A + \sigma}{\pi^2 k_c/A + \sigma_0}\right).$$

(c) Assume that the change in area found in (b) is taken up completely by the tether, on which fluctuations are negligible. A suitable total energy for the system is the sum of the bending energy in the tether, the energy arising from the entropic elasticity, and the work done by the force F,

$$E = \frac{1}{2} k_c \int_{\rm tether} dS (2H)^2 + A\frac{k_B T \sigma}{8\pi k_c} - FL,$$

where H is the mean curvature, and one may assume $A = 4\pi R^2$ to leading order. Setting $\sigma_0 = 0$ for simplicity, minimise E with respect to both L and r, and find the force-extension relationship for the tether. Using heuristic arguments, compare this result to the case of a thether extracted from a reservoir at fixed tension σ.

END OF PAPER