## PAPER 77

# FLUID MECHANICS OF SWIMMING ORGANISMS 

## Attempt TWO questions

There are three questions in total.
The questions carry equal weight.

You may not start to read the questions printed on the subsequent pages until instructed to do so by the Invigilator.
$1 \quad$ A slender fish of length $L$ swims at constant speed $U$ in the negative $x$ direction by means of small-amplitude undulations. The lateral displacement of the fish's centre plane is $h(x, t)$ and the added mass per unit length of the fish is $m(x)$, while its body mass per unit length is $m_{b}(x)$.
(i) Explaining the assumptions and approximations of Lighthill's elongated body theory, use it to show that the lateral force on the fish, per unit length, is

$$
F_{y}=D(m D h)
$$

where

$$
D \equiv \frac{\partial}{\partial t}+U \frac{\partial}{\partial x} .
$$

(ii) Modelling the fish body as an "active bending beam", and considering conservation of linear and angular momentum for a general transverse slice of the fish, show that the bending moment distribution, $G(x, t)$, approximately satisfies the equation

$$
\frac{\partial^{2} G}{\partial x^{2}}=m_{b} \frac{\partial^{2} h}{\partial t^{2}}-F_{y}
$$

(iii) Explain why the solution to this equation should satisfy all four boundary conditions

$$
G(0)=G(L)=G_{x}(0)=G_{x}(L)=0
$$

but that putting in a plausible-looking form for $h(x, t)$ (e.g. based on observation) does not permit all four boundary conditions to be satisfied. Explain how this apparent paradox is resolved by the recoil correction.
$2 \quad$ A spermatozoon propels itself at speed $U$ in the $-\mathbf{i}$-direction (i is a unit vector) by passing a wave along a single flagellum of length $L$. State the assumptions of resistive force theory, and show that the thrust, $T$, exerted by the flagellum on the viscous fluid in which it swims, is given by

$$
-T=\left(\kappa_{T}-\kappa_{N}\right) \int_{0}^{L}(\mathbf{w} \cdot \mathbf{t})(\mathbf{t} \cdot \mathbf{i}) d s+\kappa_{N} \int_{0}^{L}(\mathbf{w} \cdot \mathbf{i}) d s
$$

where $\kappa_{T}$ and $\kappa_{N}$ are the tangential and normal resistance coefficients, $\mathbf{t}$ is the tangential unit vector, and $-\mathbf{w}$ is the velocity of the element $d s$ of the flagellum relative to the fluid far away.

In the case of a plane wave of uniform amplitude, travelling at speed $c$ along the flagellum and at speed $V$, relative to the flagellum, in the $\mathbf{i}$-direction, show that

$$
\mathbf{w}=(U-V) \mathbf{i}+c \mathbf{t} .
$$

Hence show that

$$
T=(V-U)\left[\left(\kappa_{T}-\kappa_{N}\right) \beta L+\kappa_{N} L\right]-\kappa_{T} V L
$$

where

$$
\beta=\frac{1}{L} \int_{0}^{L}\left(\frac{\partial X}{\partial s}\right)^{2} d s
$$

and $X(s, t)$ is the Lagrangian co-ordinate in the $\mathbf{i}$-direction of a point on the flagellum.
Calculate the swimming speed $U$ when the sperm head experiences a drag force $\delta \kappa_{N} L U$.

Show that the total rate of working by the flagellum is given by $E$, where

$$
\frac{E}{\kappa_{N} L U^{2}}=\left(\frac{V}{U}-1\right)^{2}(\beta \gamma+1-\beta)-2 \gamma \frac{V}{U}\left(\frac{V}{U}-1\right)+\frac{\gamma V^{2}}{\alpha^{2} U^{2}}+\delta
$$

in which

$$
\gamma=\frac{\kappa_{T}}{\kappa_{N}} \quad \text { and } \quad \alpha=\frac{V}{c}
$$

Assuming that $\alpha^{2}=\beta$, deduce that the energy expenditure for given speed $U$ is minimised if

$$
\beta^{2}=\frac{-\gamma(\delta+1)^{2}+\sqrt{\gamma^{2}(\delta+1)^{4}+\gamma(1-\gamma)(\delta+1)^{2}\left(\delta^{2}+\gamma\right)}}{\left(\delta^{2}+\gamma\right)(1-\gamma)}
$$

3 (i) Certain phototactic micro-organisms respond to light as if they experience a light-torque

$$
\mathbf{G}_{L}=\mathbf{p} \wedge \mathbf{L}
$$

where $\mathbf{p}$ is the unit vector in the direction of a cell's swimming and $\mathbf{L}$ is the light intensity vector which is directed towards the light source. The cells are spherical and in an ambient flow with vorticity $\boldsymbol{\omega}$ a cell experiences a viscous torque

$$
\mathbf{G}_{V}=\alpha\left(\frac{1}{2} \boldsymbol{\omega}-\boldsymbol{\Omega}\right)
$$

where $\boldsymbol{\Omega}$ is the cell's angular velocity and $\alpha$ is a constant. Show that, in the absence of random swimming, a balance of torques gives the following expression for the rate of change of $\mathbf{p}$ :

$$
\begin{equation*}
\dot{\mathbf{p}}=\frac{1}{2} \boldsymbol{\omega} \wedge \mathbf{p}+\frac{\mathbf{L}}{\alpha} \cdot[\underline{\mathbf{I}}-\mathbf{p p}], \tag{1}
\end{equation*}
$$

where $\underline{\mathbf{I}}$ is the identity tensor.
When there is random swimming, the probability density function for swimming direction, $f(\mathbf{p})$, satisfies a Fokker-Planck equation. For the case in which $\mathbf{L}=L \mathbf{e}_{x}$ and $\boldsymbol{\omega}=\omega \mathbf{e}_{y}$ (where $\mathbf{e}_{x}, \mathbf{e}_{y}$ are unit vectors in the direction of Cartesian $x$ and $y$ axes), this equation reduces to

$$
\begin{aligned}
\nabla^{2} f & \equiv \frac{1}{\sin \theta} \frac{\partial}{\partial \theta}\left(\sin \theta \frac{\partial f}{\partial \theta}\right)+\frac{1}{\sin ^{2} \theta} \frac{\partial^{2} f}{\partial \phi^{2}} \\
& =-\lambda\left(\sin \theta \frac{\partial f}{\partial \theta}+2 \cos \theta f\right)-\epsilon\left(\sin \phi \frac{\partial f}{\partial \theta}+\cot \theta \cos \phi \frac{\partial f}{\partial \phi}\right)
\end{aligned}
$$

where

$$
\lambda=\frac{L}{\alpha D_{r}}, \quad \epsilon=\frac{\omega}{2 D_{r}}
$$

and $\theta, \phi$ are spherical coordinates with $\theta=0$ along the $\mathbf{e}_{x}$ axis and $\theta=\pi / 2, \phi=0$ along the $\mathbf{e}_{y}$ axis.

For small $\epsilon$, show that

$$
f=\eta e^{\lambda \cos \theta}+\epsilon f^{(1)}(\theta, \phi)+O\left(\epsilon^{2}\right),
$$

where

$$
\eta=\frac{\lambda}{4 \pi \sinh \lambda} \quad \text { and } \quad f^{(1)}=\eta \sin \phi g(\theta)
$$

for some function $g(\theta)$ [do not attempt to calculate $g(\theta)$ ].
Defining the average of a quantity $q$ as

$$
<q>\equiv \int_{0}^{2 \pi} \int_{0}^{\pi} q f(\theta, \phi) \sin \theta d \theta d \phi
$$

show that

$$
<\mathbf{p}>=K_{0} \mathbf{e}_{x}+\epsilon K_{1} \mathbf{e}_{z}+O\left(\epsilon^{2}\right)
$$

for constants $K_{0}, K_{1}$ that depend on $\lambda$ [no need to evaluate them explicitly].
(ii) A dilute suspension of these micro-organisms occupies a long vertical channel $-a<x<a$, closed at the ends $z= \pm L$, where $L / a \gg 1$; the $z$-axis is vertically upwards. The average cell concentration is $n_{0}$ cells per unit volume; the cells are slightly denser than the water in which they are suspended. The light-intensity vector is directed horizontally in the $+x$ direction. The cell conservation equation, mass conservation and momentum equations for the suspension are

$$
\begin{aligned}
\frac{\partial n}{\partial t} & =-\nabla \cdot\left[n\left(\mathbf{u}+V_{s}<\mathbf{p}>\right)-\underline{\mathbf{D}} \cdot \nabla n\right] \\
\nabla \cdot \mathbf{u} & =0, \quad \rho\left[\frac{\partial \mathbf{u}}{\partial t}+(\mathbf{u} \cdot \nabla) \mathbf{u}\right]=-\nabla p_{e}-g^{\prime} n \mathbf{e}_{z}+\mu \nabla^{2} \mathbf{u}
\end{aligned}
$$

where $V_{s}$ is the cell swimming speed, assumed constant. Explain all the terms in these equations and any approximations that have been made in their derivation.

Assuming that the fluid velocity vector $\mathbf{u}=(0,0, w)$ is directed entirely vertically, except in small regions near $z= \pm L$ which can be neglected, show that a solution of the equations and relevant boundary conditions exists in which both $n$ and $w$ are functions of $x$ alone. You may assume that $\underline{\mathbf{D}}=D \underline{\mathbf{I}}$ and that $\epsilon$ remains small. Find this solution in the form

$$
\begin{aligned}
n & =n_{1} e^{\beta x} \\
w & =\frac{g^{\prime} n_{1}}{\mu \beta^{2}} e^{\beta x}+\frac{G}{2 \mu} x^{2}+A x+B
\end{aligned}
$$

where the constants $\beta, n, G, A, B$ should be determined. Explain the physical meaning of $G$. Sketch the velocity profile $w(x)$ in the case in which $\beta a \gg 1$.

