Life at low Reynolds Number

- Diffusion dominates transport on the μm scale of the cell
- Viscous forces dominate mechanics in the μm world
- Cells interact with water in a way that is different from our (intuitive) scale
- For example, single cells cannot swim like flipper

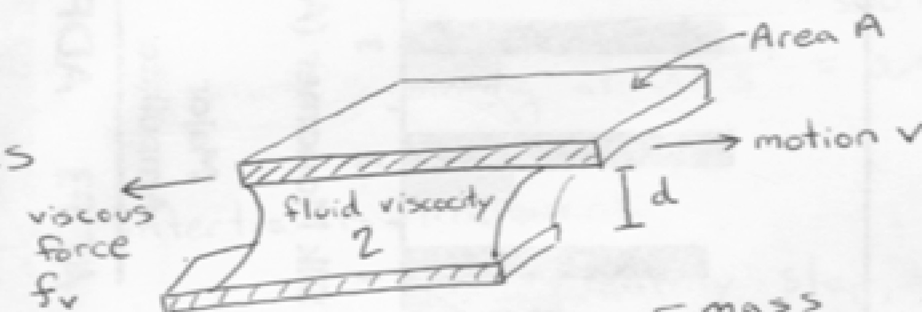
Two types of fluid flow

Laminar – dominated by $\boxed{\text{viscous}}$ forces – no mixing

Turbulent – dominated by $\boxed{\text{inertial}}$ forces – flow doesn't stop when you stop mixing / momentum keeps it going / like cream in your coffee – it immediatly swirls into a complex, turbulent pattern

Viscocity

2 plates



$$f_v = \frac{-\eta v A}{d} \qquad \eta \equiv \left[\frac{\text{mass}}{\text{length} \cdot \text{time}}\right]$$

Fluid viscocity and Inertia

- imagine a "packet" of fluid flowing around a sphere

Inertia: tendency to maintain motion

force = mass × acceleration

Dimensional analysis

Inertial term: $\frac{\overbrace{l^3 \rho}^{\text{mass}} v^2}{a}$

Viscous term: $\eta \frac{l^3 v}{a^2}$

Reynolds Number

$$Re = \frac{\text{inertial force}}{\text{viscous force}} = \frac{\frac{l^3 \rho v^2}{a}}{\frac{\eta l^3 v}{a^2}} = \frac{\rho a v}{\eta}$$

small Re → viscous forces dominate → laminar flow

large Re → ~~t~~ inertial dominates → turbulent flow

- Empirically, the transition to turbulent flow occurs around $Re \sim 1000$
- examples,

  in water ($\eta_{H_2O} = 10^{-3} \frac{kg}{m \cdot s}$)

  A 30m whale swimming @ 10 m/s $Re = \frac{(1\ g/ml)(30\ m)(10\ m/s)}{(10^{-3}\ kg/m \cdot s)}$

  $= 300{,}000{,}000$

  A 1 μm bacterium swimming at $30 \frac{\mu m}{s} = 0.00003$

- For a bacterium, intertia is irrelevant
  - if I push a bacterium, then suddenly stop, how far before it slows down?

    coasting distance ~ 0.1 Å

    coasting time $\sim 0.3\ \mu s$

  - no memory, at low Re, all movement is due to forces at that moment

Viscocity as a force

$\frac{\eta^2}{\rho}$ is a force

in water, $\frac{\eta^2}{\rho} \sim 10^{-4}$ dyne

This is the force required to tow an object (large or small) at $Re \sim 1$ (could tow a submarine)

small Re ⇒ small forces

Navier-Stokes Eqn

- for Newtonian (const ρ + μ) fluids

velocity of fluid (vector)

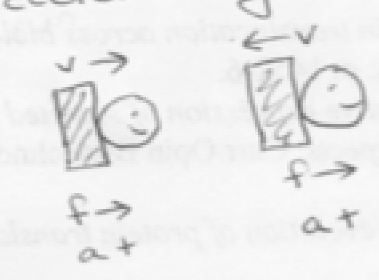
$$\underbrace{\rho \frac{\partial v}{\partial t} + \rho \nabla v}_{\text{inertial terms}} = \underbrace{\rho g}_{\text{gravitational}} - \underbrace{\nabla P}_{\text{pressure change driving flow}} + \overbrace{\mu \nabla^2 v}^{\text{viscous term}}$$

- for $Re \ll 1$, the inertial terms go to zero (and forget about gravity at the moment)

$$\mu \nabla^2 v = \nabla P$$

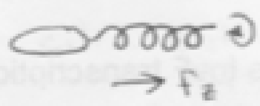
time doesn't matter: The pattern of the motion is the same, whether slow or fast, whether forward or backward in time

- Other time-reversible processes
  - ballistics ⇒ the solution of the trajectory ~~rt~~ is the same both in the forward and reverse of time
  - accelerating and deaccelerating in car



- Because low Re is time reversible, swimming by reciprical motion doesn't get you anywhere
  - applying a force to a fluid generates a motion that can be canceled completely by applying the time reversed force
  - no net progress is made; all particles return to their original position

- Bacteria swim using flagella

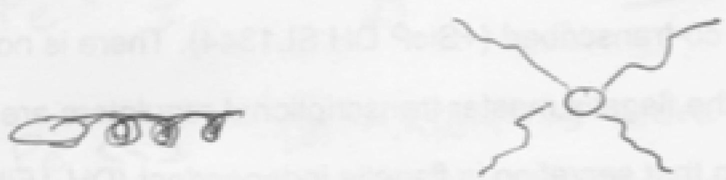


corkscrew motion

is periodic, but not reciprical

if you sum forces over the flagellum spiral, you are left with a z-component (no x or y components) to the force

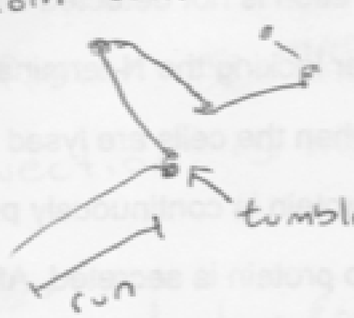
- E. coli has multiple flagella



'run'

'tumble' (randomly pick new direction)

A biased random walk



Moving & Stirring

- Can a bacterium get more food by swimming?
- Can a cilia enhance its food uptake by sweeping fluid across its surface?

$\tau_m \simeq \frac{d}{v}$ ← distance, ← speed   timescale that fluid is replaced

$\tau_D \simeq \frac{d^2}{D}$ timescale that diffusion will move a particle a distance

Peclet Number

$Pe = \frac{\tau_D}{\tau_m} = \frac{vd}{D}$

convection: internal movements of currents within fluids

advection: mass transfer due to convection

$Pe \ll 1$ Diffusion is more rapid than convection

$Pe \gg 1$ Convection is more rapid

Diffusion is more rapid at short distances

Convection is more rapid at long distances

- A bacterium is $d \simeq 1\mu m$ long so $v > 1000 \frac{\mu m}{s}$ to enhance food intake beyond diffusion (they only swim $\sim 30 \frac{\mu m}{s}$)
- bacteria do not move like a grazing cow (but they do move to greener pastures)
- Can bacteria move fast enough to outrun diffusion?

$\frac{vd}{D} > 1 \Rightarrow d > \frac{D}{v}$

$\frac{D}{v} = 30 \mu m$

So E. coli must 'run' at least $30 \mu m$ to outrun diffusion (that's what they do)

~~convection~~ advection-Diffusion Eqn

$$\frac{\partial c}{\partial t} + \underbrace{\vec{v}}_{\text{fluid velocity}}\vec{\nabla} c = D\nabla^2 c$$

only when $Pe \sim 1$

$Pe \gg 1 \quad D\nabla^2 c \to 0$

$Pe \ll 1 \quad \vec{v}\vec{\nabla} c \to 0$

Fairly rare that both terms are required in a physical system volvocne green algae ⇒ body is spherical shell

bottleneck radius beyond which diffusion cannot meet metabolic demand

convection of coordinated beating of surface flagella

$I_d = 4\pi D R C_0$ inward $\frac{\text{molecules}}{\text{sec}}$ due to diffusion

R: cell radius

$I_m = 4\pi R^2 \beta$

β: time-dependent nutrient demand rate per unit area (2D sheet of cells)

$I_d = I_m$ at the critical area

$$R_c = \frac{D C_0}{\beta}$$

considering O_2,

$$R_c = \frac{(2\times10^{-5}\ \frac{cm^2}{s})(10^{17}\ \frac{1}{cm^3})}{(10^{17}\ \frac{1}{cm^2 s})} = 50\text{-}200\ \mu m$$

advection?

~~convection-diffusion Eqn~~

$$\cancel{\frac{\partial c}{\partial t} + \vec{u}\cdot\vec{\nabla} c = D\nabla^2 c}$$

$\vec{u}$: fluid velocity

Transport due to the collective beating of flagella eliminates the diffusion-only inhibition of growth and facilitates the transition to enlargement and multicellularity