1 Viscous drag

1.1 Dimensions

All physical quantities have dimensions. In addition we have measurement units like the SI units for all these quantities.

Størrelser	dimensjoner	SI-enheter
Lengde	L	m
Tid	T	s
Masse	M	kg
Areal	L^2	m^2
Volum	L^3	m^3
Hastighet	LT^{-1}	m/s
Akselleresjon	LT^{-2}	m/s^2
Kraft	MLT^{-2}	newton
Tetthet	ML^{-3}	kg/m^3
Arbeid	ML^2T^{-2}	joule
Effekt	ML^2T^{-3}	watt
Trykk, Stress	$ML^{-1}T^{-2}$	pascal
Viskositet (kinematisk)	L^2T^{-1}	m^2/s
Viskositet (dynamisk)	$ML^{-1}T^{-1}$	pascal s

Figure 1: Physical quantities, dimensions and SI units.

1.2 Drag

Drag is the force from the fluid F_d on a body moving with velocity v.

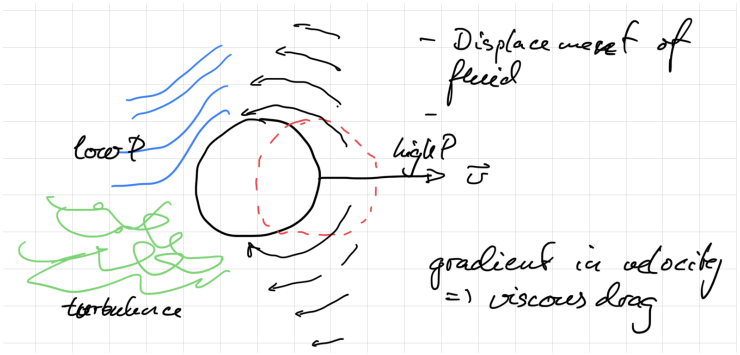


Figure 2: Drag.

What physical quantities are important?

- The drag force: F_d, $[F_d] = MLT^{-2}$
- The velocity with respct to the fluid far away: v, $[v] = LT^{-1}$
- The size of the body: r, $[r] = L$
- The fluid density: ρ, $[\rho] = ML^{-3}$
- The fluid viscosity: η, $[\mu] = ML^{-1}T^{-1}$

Viscosity. What is viscosity?

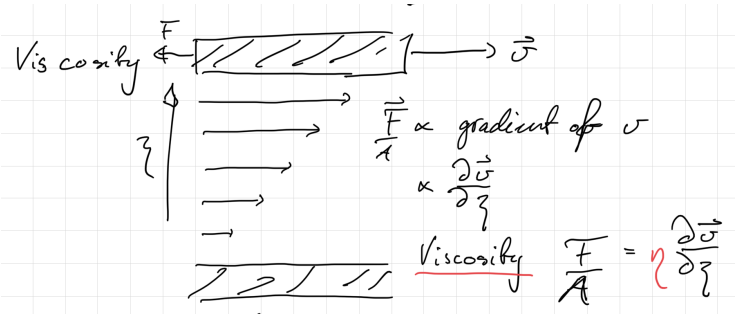


Figure 3: Viscosity.

1.3 Dimensional analysis

Buckingham's Π-theorem:

The number of independent dimensionless parameters necessary to describe a system is the number of physical quantities minus the number of independent dimensions.

In our case this gives: 5-3=2 dimensionless quantities that govern the behaviour of the system.

Let's try use the other quantities to make a dimensionless parameter with F_d and start with ρ: $[F_d/\rho] = T^{-2}L^4$. Then let's remove the dimension T: $[F_d/\rho v^2] = L^2$ and then L:

$$C_R = \frac{F_d}{\rho v^2 r^2}. \tag{1}$$

C_R is a dimensionless number that we will call the R drag coefficient

But we may also use η to remove the mass dimension from F_d:$[F_d/\eta] = L^2T^{-1}$, then we use v to remove the time: $[F_d/\eta v] = L$ and then the length:

$$C_S = \frac{F_d}{\eta v r}. \tag{2}$$

C_S is a dimensionless number that we will call the S drag coefficient. The two drag coefficients are pure numbers that depend on the shape of the body.

Now let's have a look at the ratio between the two drag forces:

$$\frac{F_{dR}}{F_{dS}} = \frac{C_R \rho v^2 r^2}{C_S \eta v r} = \frac{C_R \rho v r}{C_S \eta} \approx \frac{\rho v r}{\eta} = Re \tag{3}$$

The ratio $\frac{F_{dR}}{F_{dS}}$ is the ratio between the inertial and viscous drag forces. This is called the **Reynolds number** Re. This tells us that when $Re >> 1$ the inertial, Rayleigh, drag force F_{dR} dominates, when $Re << 1$ the viscous, Stokes, drag force F_{dS} dominates. Stokes drag for a sphere is $F_{dS} = C_s \eta v r = 6\pi\eta v r$.

Sometimes we also use the viscous friction coefficient ξ that is defined as

$$\xi = \frac{F_d}{v} \tag{4}$$

The viscous friction coefficient in the Stokes regime ($Re << 1$) for a sphere is $\xi = 6\pi\eta r$.

2 Brownian motion

2.1 The childhood of statistical physics

In the beginning of the 1900s, it became increasingly clear to physicists that the "molecular-kinetic theory" (which described a statistical microscopic basis for thermodynamics) had to prevail. One of the final nails in the coffin for those who opposed it was one of Einstein's 1905 articles: "Investigations on the theory of the Brownian movement". Einstein had been made aware of microscopic observations by biologist Brown where small pollen particles in a liquid moved around randomly. Einstein used this as a basis and created a quantitative model where measurable quantities could be compared. It did not take many years before experimentalists were able to measure the different quantities independently and thus confirm Einstein's model and thereby the microscopic theory of heat that we take for granted today.

2.2 The Langevin equation: fluctuating forces and fluid friction

In 1908 Langevin published a simpler and more elegant derivation of the model of Brownian motion. Molecular motion and the equipartition principle are fundamental to the microscopic theory of heat:

The equipartition principle.
The kinetic energy of every quadratic degree of freedom of motion is $kT/2$

where k is the Boltzmann constant and T the temperature. For the translational velocity $v_x = dx/dt$ of a molecule in the x-direction the kinetic energy is

$$\frac{1}{2}m < v_x^2 >= \frac{1}{2}kT, \tag{5}$$

where $< ... >$ means the the "ensemble average" or the average over many molecules.

Viscous damping For particles that are much larger than the average distance between the liquid molecules, the liquid can be treated as a continuum and the hydrodynamic damping of the particle motion can be studied. Fluid resistance for a sphere in a viscous liquid at low Reynolds numbers is, as shown above:

$$F_d = 6\pi\eta v_x r, \tag{6}$$

where η is the shear viscosity of the fluid and r is the radius of the sphere

The Langevin equation The macroscopic particles are subject to a *rapidly varying random force* F_r due to the thermal motion of the liquid molecules and a *slowly varying damping force* F_d due to the viscosity of the liquid. Langevin combined these forces into an equation of motion for the particles:

$$m\frac{d^2x}{dt^2} = F_r - F_d = F_r - 6\pi\eta r\frac{dx}{dt}. \tag{7}$$

This type of equation of motion for systems that can be divided into a fast varying and a slow varying force is called a Langevin equation. By multiplying both sides with x and using the chain rule in differentiation, (7) can be written as

$$\frac{1}{2}m\left(\frac{d^2x^2}{dt^2} - 2v_x^2\right) = xF_r - 3\pi\eta r\frac{dx^2}{dt}. \tag{8}$$

Take the ensemble average and solve the equation If one takes the ensemble average of (8) the direct contribution from F_r disappears because $< xF_r >= 0$ because the force F_r is not correlated with itself in time or space. Equation (8) can now be written as:

$$\frac{1}{2}m\frac{d^2 < x^2 >}{dt^2} - kT = -3\pi\eta r\frac{d < x^2 >}{dt}. \tag{9}$$

This equation can be solved:

$$\frac{d < x^2 >}{dt} = \frac{kT}{3\pi\eta r} + Ce^{6\pi\eta rt/m}, \tag{10}$$

where the last term disappears when $t >> m/6\pi\eta r \sim 10^{-8}$ s. That means that if we can track the positions of many particles and calculate the mean square

displacement per unit of time, and we know the viscosity and radius of the particle, we can determine Boltzmann's constant, k. Such a determination of k and comparison with other methods of determining k was the first test of Einstein's model for Brownian motion.

3 Random walks

4 Diffusion

Then we get to the Einstein relation

$$\xi D = kT \tag{11}$$

4.1 Biological relevance

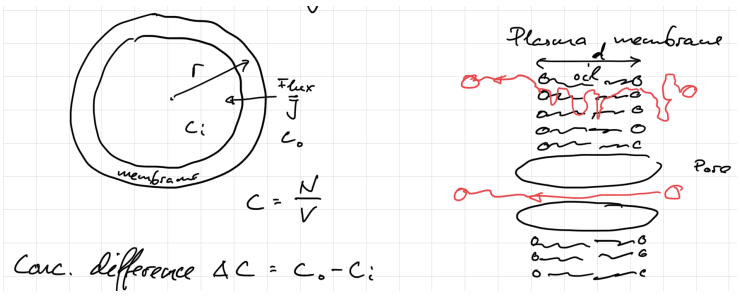


Figure 4: Permeation through a membrane.

Permeation through a membrane. Flux (flow rate per unit area): $J_i = \frac{1}{A}\frac{\Delta N_i}{\Delta t}$

How does c_i change with time? (c_0 is const.)

$$\frac{\partial c_i}{\partial t} = -\frac{\partial \Delta c}{\partial t} = \frac{1}{V}\frac{\partial N_i}{\partial t} = \frac{3}{r}J_i \tag{12}$$

because $A = 4\pi r^2$, $V = \frac{4}{3}\pi r^3$, $V/A = r/3$. The permeability P is defined $J = P\Delta c$. We can enter this into the above equation and solve:

$$-\frac{\partial \Delta c}{t} = \frac{3}{r}P\Delta c \tag{13}$$

$$\int_{\Delta c_0}^{\Delta c}\frac{\Delta c}{\Delta c} = -\frac{3P}{r}\int_0^t \partial t \tag{14}$$

$$\ln \Delta c - \ln \Delta c_0 = -\frac{3P}{t} \tag{15}$$

$$\frac{\Delta c}{\Delta c_0} = e^{-t/\tau}, \qquad \tau = \frac{r}{3P}. \tag{16}$$

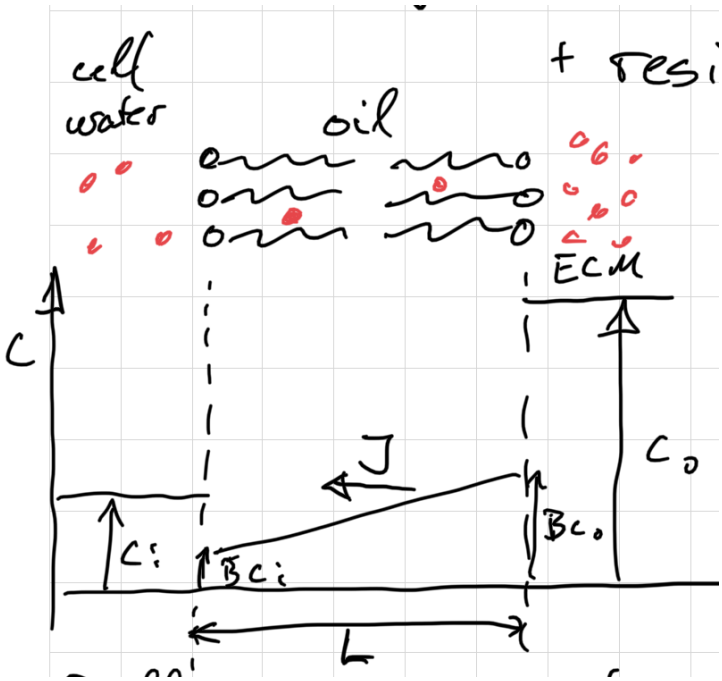


Figure 5: Diffusion through membrane with low partition coefficient.

The permeation is diffusion through the membrane and resistance to entry/exit. The partition coefficient B is

$$B = \frac{\text{solubility in oil}}{\text{solubility in water}} \tag{17}$$

Diffusion in membrane is

$$J = -D\frac{dc}{dt} = -\frac{DB\Delta c}{L} = P\Delta c \quad \Rightarrow \quad P = \frac{DB}{L} \tag{18}$$

Some numbers:

- Partition coefficient of water in lipid bilayer membrane: $B = 4.2 \cdot 10^{-5}$ (A Finkelstein, J. Gen. Phys. **68**, 127 (1976))
- Thickness of cell membrane: $L = 7.5 - 10$ nm. (B10NUMB3R5)
- This gives a permeability of $P = 10^{-9}4 \cdot 10^{-5}/10^{-8}$ m/s≈ 4 μm/s.
- And a time constant of permeation of water into a cell with radius 10 μm: $\tau = r/(3P) \approx 1$ s. That's pretty fast!
- Partition coefficient of monovalent ions: $B \approx 10^{-60}$. That's why cells need ion channels.

Oxygen diffusion limit on microbial metabolism. See Nelson 4.6.2 p.138.

- Oxygen is consumed by microbe
- Transport of oxygen from outside
  - Lakes, ocean: turbulent flow
  - ECM, ponds: diffusion
- Assume instant uptake at microbial surface

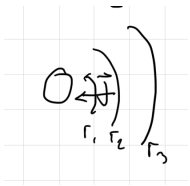


Figure 6: The same current flows through spheres of all radii.

$$J(r) = \frac{I}{4\pi r^2} = -D\frac{dc}{dr} \tag{19}$$

$$-\frac{I}{4\pi r^2}\frac{dr}{r} = dc \tag{20}$$

$$-\frac{I}{4\pi r^2}\left.\frac{1}{r}\right|_{r_0}^{\infty} = c|_0^{c\infty} \tag{21}$$

$$-\frac{I}{4\pi r^2}\left(-\frac{1}{r_0}\right) = c_\infty \tag{22}$$

$$I = 4\pi D c_\infty r_0 \tag{23}$$

This is the maximum rate at which O_2 can be consumed by any bacterium whatsoever.

So the maximum O_2 diffusion rate scales linearly with radius r of the microbe. How does the consumption rate scale with size of the organism? A first guess would be $I \propto r^3$, but it turns out there is an empirical relationship called Kleiber's law that has been shown to be valid all the way down to microbe size: $I \propto M^{0.75}$, where M is the mass of the organism. So since $M \propto r^3$ the scaling is $I \propto r^{9/4} = r^{2.25}$. (T.E. Riedel, W.M. Berelson, K.H. Nealson, S.E. Finkel, Applied and Environ. Microbiol. **79**, 4921 (2013))

Plotting the scaling of consumption and transport rate with microbe size one finds that there must be an upper limit to the size $r_{\max}$ of a microbe that does noot swim or lives in a turbulent world.

Ions at membranes, a first look.

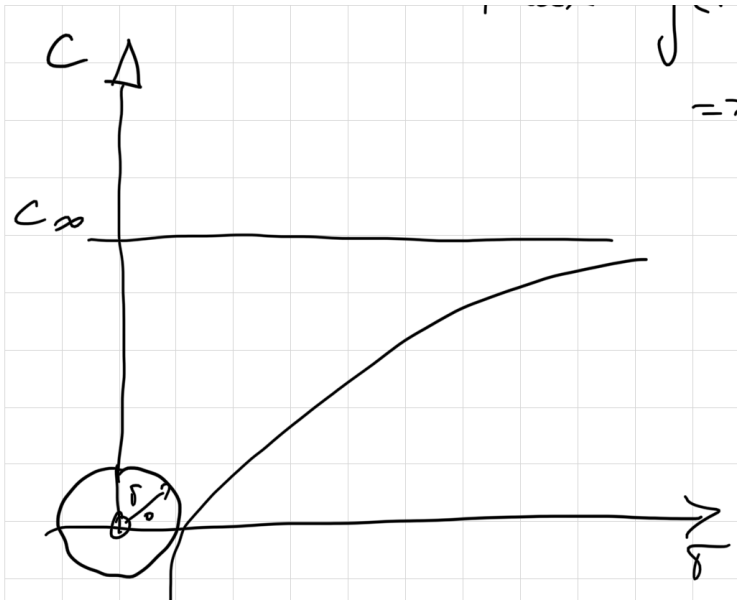


Figure 7: Concentration distribution around a consuming bacteria.

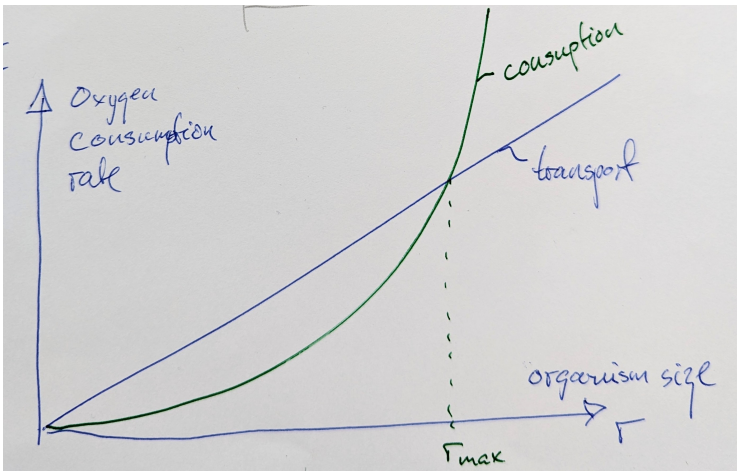


Figure 8: Scaling of consumption and transport rate with bacteria size.

5 Life at low Reynolds number