

Reading for Lectures 34-35: PKT Chapter 12.

Hydrodynamics in the world of the Cell

Fluid flow can be very complicated, and there are large parts of it (in which turbulence plays an important role) that are poorly understood. Luckily, in at the scale of the cell, all these difficulties are absent.

General **hydrodynamic equations** for fluids couple the particle density $n(\vec{r}, t)$ or the mass density $\rho(\vec{r}, t) = mn(\vec{r}, t)$, flow velocity $\vec{v}(\vec{r}, t)$, and temperature $T(\vec{r}, t)$ fields.

And, also pressure $P(\vec{r}, t)$, but $P(n, T)$ at local equilibrium.

Changes in density and temperature produce changes in pressure.

Furthermore, changes in density and temperature modify hydrodynamic coefficients such as viscosity, which then become variable.

Simplifications:

Water and aqueous solutions are incompressible, so n and ρ do not depend on (\vec{r}, t) .

Thermal effects are usually negligible: no appreciable frictional heating, so T effectively uniform and fixed.

The Continuity Equation (particle conservation):

The particle current is $\vec{j} = n\vec{v}$ where n is the uniform particle density and \vec{v} is the local hydrodynamic flow velocity (the local average particle velocity).

The continuity equation reads $\frac{\partial n}{\partial t} = -\vec{\nabla} \cdot \vec{j}$.

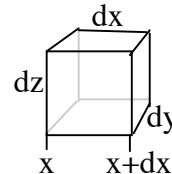
Where does this come from?

Rate at which the number of particles in the cube is increasing: $\frac{\partial n(x, y, z, t)}{\partial t} dx dy dz$

Net rate at which particles flow into cube across the yz faces:

$$\left[j_x(x, y, z, t) - j_x(x + dx, y, z, t) \right] dy dz = -\frac{\partial j_x}{\partial x} dx dy dz$$

Similar terms for the other four faces: $-\left(\frac{\partial j_y}{\partial y} + \frac{\partial j_z}{\partial z} \right) dx dy dz$



Upshot (no particles get lost): $\frac{\partial n}{\partial t} = -\left(\frac{\partial j_x}{\partial x} + \frac{\partial j_y}{\partial y} + \frac{\partial j_z}{\partial z} \right) \equiv -\vec{\nabla} \cdot \vec{j}$

Since n is spatially uniform and time-independent (incompressibility), we find

$$\frac{\partial n}{\partial t} = 0 = -\vec{\nabla} \cdot \vec{j}, \text{ so } \boxed{\vec{\nabla} \cdot \vec{v} = 0.} \text{ incompressibility condition}$$

In one dimension, this says $\frac{dv}{dx} = 0$, so the velocity is the same everywhere $v(x, t) = v(t)$.

This means that, in practice all flows are at least two dimensional, a fact which puts most calculations beyond our reach.

The Navier-Stokes Equation (momentum conservation):

For particles we have Newton's law $m\vec{a} = m \frac{\partial \vec{v}}{\partial t} = \vec{F} = -\vec{\nabla} V$ (for motion under a potential V)

or $m[\vec{v}(t + dt) - \vec{v}(t)] = \vec{F} dt$ which expresses the change of momentum due to the force \vec{F} over the interval dt .

The analog of this for a fluid element is the famous **Navier-Stokes equation**:

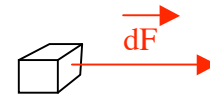
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$$\rho \frac{\partial \vec{v}}{\partial t} + \rho (\vec{v} \cdot \vec{\nabla}) \vec{v} = -\vec{\nabla} P + \eta \nabla^2 \vec{v} + \vec{f}, \quad \text{note nonlinearity; we will connect to Newton}$$

where ρ is the (uniform) mass density of the fluid, P is the pressure (variable), η is the viscosity of the fluid, and \vec{f} is any “volume force” exerted on the fluid (e.g., $\vec{f} = -\rho g \hat{z}$ for gravity). The first term on the right is the **pressure force**; the second is the **viscous force**.

Like Newton’s law, this equation expresses (local) momentum conservation. I will now derive it for you: **I want you to have a feeling for where this complicated and important equation comes from. You are not responsible for the derivation; you are responsible for the “ideas.”**

Focus attention on a small volume element of fluid (dr) moving with the local velocity $\vec{v}(\vec{r}, t)$.



We apply Newton’s law to this element $dm(\vec{v}(t + dt) - \vec{v}(t)) = d\vec{F} dt$. $(dr) = da dr = dx dy dz$

$\rho(dr)[\vec{v}(\vec{r} + \vec{v} dt, t + dt) - \vec{v}(\vec{r}, t)] = d\vec{F} dt$, since the material packet which started at (\vec{r}, t) has now moved on to $(\vec{r} + \vec{v} dt, t + dt)$. **Note that $d\vec{F}$ will have to be proportional to (dr) .**

But, $\vec{v}(\vec{r} + \vec{v} dt, t + dt) = \vec{v}(\vec{r}, t) + dt \frac{\partial \vec{v}}{\partial t} + (\vec{v} dt \cdot \vec{\nabla}) \vec{v} = \vec{v}(\vec{r}, t) + dt \left[\frac{\partial \vec{v}}{\partial t} + (\vec{v} \cdot \vec{\nabla}) \vec{v} \right]$, so

$$\rho(dr) \left[\frac{\partial \vec{v}}{\partial t} + (\vec{v} \cdot \vec{\nabla}) \vec{v} \right] = d\vec{F}$$

Now, let’s deal with the forces:

1. Volumes forces:

Force $d\vec{F} = \vec{f}(dr)$ on fluid element, e.g., gravity exerts $\vec{f}(dr) = -dm g \hat{z} = -\rho(dr) g \hat{z}$, so $\vec{f}_{grav} = -\rho g \hat{z}$.

2. Pressure:

Note that, if the pressure is constant, there will be no net force on (dr) .

If the pressure is changing, then it will exert a force in the direction **opposite** to the gradient of P which is just $d\vec{F}_P = -(P(r + dr) - P(r)) \hat{r} da = -\vec{\nabla} P (dr)$, where \hat{r} is a unit vector along $\vec{\nabla} P$.

Clearly, this gives the pressure term.

3. Viscosity:

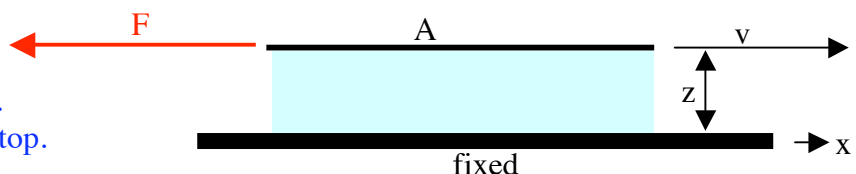
Viscosity is the property of a fluid whereby, as the fluid is “sheared,” each layer exerts a force on its neighbors proportional to the velocity gradient in the direction perpendicular to the flow.

Bottom plate fixed.

Top plate has area A and moves with v to the right.

Fluid has $v=0$ at bottom; v at top.

Fluid is in uniform “shear.”



\vec{F} is the drag force on top plate; force of plate on fluid is $-\vec{F}$.

Warning, this formula only applies in planar geometry shown $F_x = \eta A \frac{v_x}{d} \rightarrow \eta A \frac{dv_x}{dz}$.

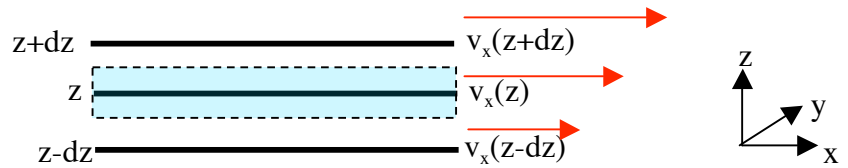
Any fluid obeying this law of friction is called a “**Newtonian fluid.**”

NOT all biological fluids are Newtonian, although many are nearly Newtonian.

The principle cause of non-Newtonian behavior is deformable solute macromolecules, 34.3
 which deform in shear flow. This deformation has an elastic part (storage of elastic PE) and a
 dissipative part (loss of energy to frictional heating).

Thus, in the standard geometry and assuming that the velocity is in the x direction and the shear in the z direction:

$$F = \eta A \frac{\Delta v}{\Delta z}.$$



We compute force on area dA of middle (blue) layer due to its shear relative to what's above and below:

$$d\vec{F}_{upper} = \eta dA \frac{dv_x(z + dz/2)}{dz} \hat{x}$$

$$d\vec{F}_{lower} = -\eta dA \frac{dv_x(z - dz/2)}{dz} \hat{x}$$

But, $dA = dx dy$, so

$$d\vec{F}_{visc} = \eta dx dy \left[\frac{dv_x(z + dz/2)}{dz} - \frac{dv_x(z - dz/2)}{dz} \right] \hat{x} = \eta (dz) \frac{\partial^2 v_x}{\partial z^2} \hat{x}$$

Taking account of other variations (and using $\vec{\nabla} \cdot \vec{v} = 0$) gives the full viscous term.

Note that the viscous term looks “diffusive” with an effective diffusion constant $D_{eff} \equiv \frac{\eta}{\rho}$,

sometimes called the kinematic viscosity. This is not an accident. What the viscosity term describes is momentum diffusion, which takes place when there is a gradient of the momentum density.

Our starting point for hydrodynamics are two equations:

Continuity equation:

$$\vec{\nabla} \cdot \vec{v} = 0$$

Navier-Stokes equation:

$$\rho \frac{\partial \vec{v}}{\partial t} + \rho (\vec{v} \cdot \vec{\nabla}) \vec{v} = -\vec{\nabla} P + \eta \nabla^2 \vec{v} + \vec{f}$$

Four equations for the four fields $\vec{v}(\vec{r}, t), P(\vec{r}, t)$. Since there is no time derivative of P , we can think of P as an “auxiliary” field whose variation is completely determined by the velocity field and the boundary conditions.

Of course, these equations contain ordinary hydrostatics:

Let $\vec{v}=0$ everywhere.

$\vec{f} = -\rho g \hat{z} = \nabla P$, from which it follows that P varies only in the z direction and

$\frac{dP}{dz} = -\rho g \Rightarrow P = P_0 - \rho g z$. The integration constant P_0 is set by boundary conditions, e.g., at top or bottom.

Removal of the gravitational term:

As long as the force term is constant, as it is in gravity, it plays no essential role and can be removed.

Suppose I have a solution $\vec{v}(\vec{r}, t)$ of Navier-Stokes with $g=0$. This will give some $P_0(\vec{r}, t)$.

Now, form $P_1(\vec{r}, t) = P_0(\vec{r}, t) - \rho g z$.

Claim: The *same* velocity field plus the new pressure field solves the Navier-Stokes equation with gravity.

Proof: $\vec{\nabla} P_1(\vec{r}, t) = \vec{\nabla} P_0(\vec{r}, t) - \rho g \hat{z}$

$$\rho \frac{\partial \vec{v}}{\partial t} + \rho (\vec{v} \cdot \vec{\nabla}) \vec{v} = -\vec{\nabla} P_1 + \eta \nabla^2 \vec{v} - \rho g \hat{z} = -\vec{\nabla} P_0 + \eta \nabla^2 \vec{v} \quad \text{QED}$$

Comment: A little care on boundary conditions is required.

Thus, in what follows, I will set $g=0$ with no loss of generality.

These equations are not easy to solve.

I will talk about three topics:

1. Pipe flow (Hagen-Poiseuille law) (flow in blood vessels)
2. Drag on a sphere moving through a fluid (Stokes drag and sedimentation)

These are examples of steady-state flow. No time dependence.

Comment: Solving for steady state flow is like solving a statics problem in mechanics. Mechanical equilibrium may be stable, unstable, or neutral. You must check this to find out whether you are likely to see the static configuration. Same thing here: As we will discuss, there are situations for which you never see steady-state flow, since it is unstable to turbulent flow, which is intrinsically time-dependent. Although such turbulent instability is common at the macroscopic level, it is generally absent for cellular problems.

3. What's special about hydrodynamics at the cellular level?