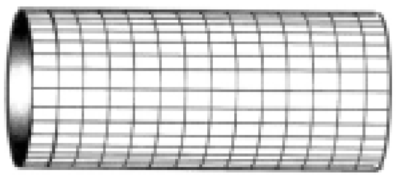
Biology 427 Biomechanics
Lecture 15. Basic fluid dynamics: defining properties of fluids.

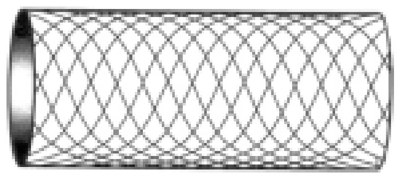
- Recap hydrostatic structures and adhesion
- Where we have been and where we are going
- The formal definition of a fluid
- Viscosity and its determinants: temperature, concentration of dissolved or suspended solutes, even shear stress (non-Newtonian characteristics)
- Coevolutionary tales: nectar feeding and malaria
- Continuity (conservation of mass)

Categorizing supportive systems

1. Tensile systems - built to resist tension only (i.e. algal stipes, fruit stems, toe-pad setae)
2. Strutted systems
   - single or branched struts (i.e. tree branches, coral)
   - articulated struts (i.e. vertebrate skeletons, insect exoskeletons)
3. Internally pressurized systems
   - hydrostats - watery-filled cavities under internal pressure (i.e. worms, plant stems)
   - muscular hydrostats - contraction of one group of muscles causes extension of another group (i.e. trunks, tentacles and tongues)

Hydrostat behavior can be controlled by tension-resisting fibers in the outer membrane





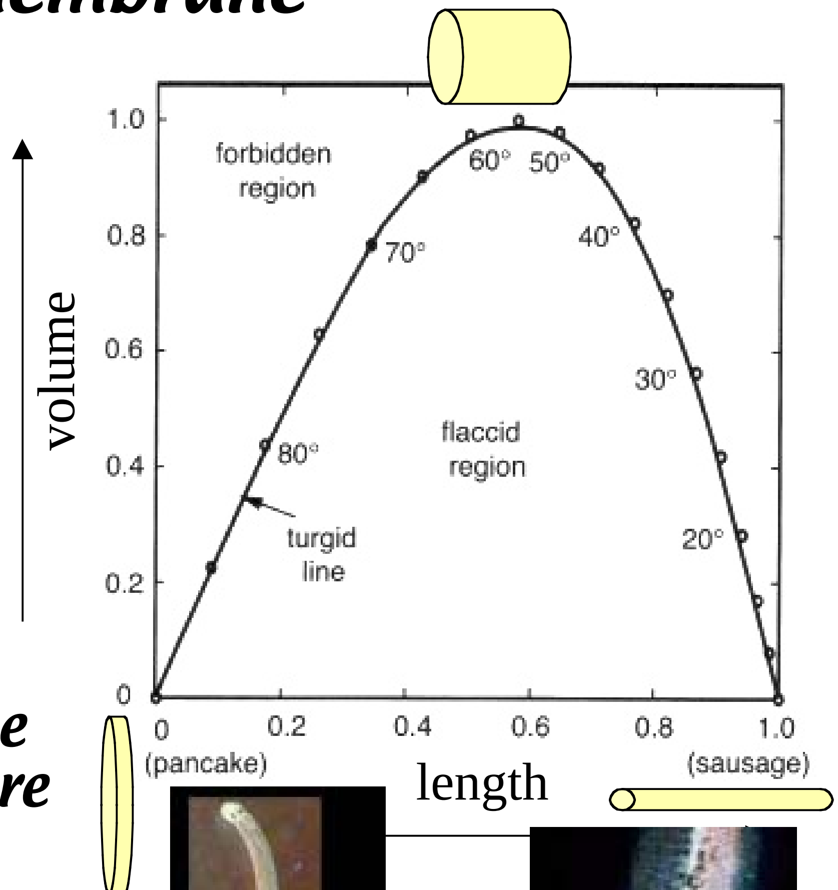
longitudinal and circumferential fibers

- *resists compression and tension, high EI*
- *low resistance to torsion*

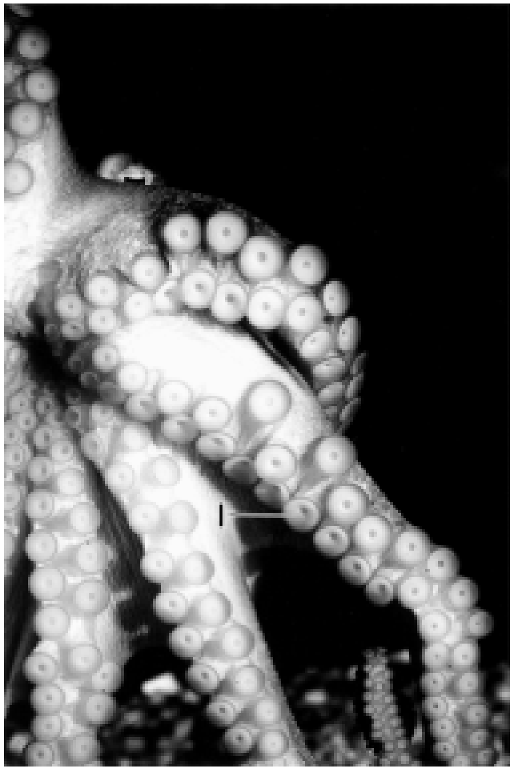
helical fibers

- *lengthens and shortens smoothly, bends more easily*
- *high resistance to torsion*
- *fiber angle determines response to increased pressure*

<55°	*55°*	*>55°*
shorter and fatter	*no shape change*	*longer and thinner*



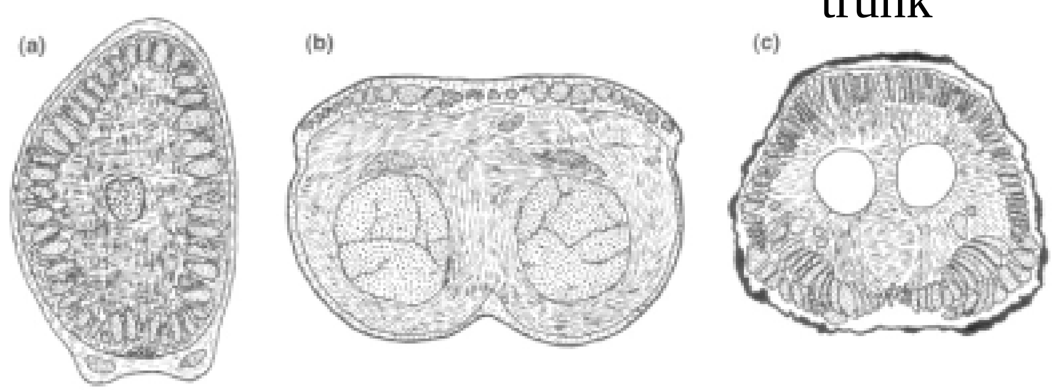
Muscular hydrostats rely on the fact that muscles themselves are incompressible



<u>Muscles wrap around each other</u>

- Contraction of one group causes extension of the other because volume cannot change

squid tentacle lizard tongue elephant trunk

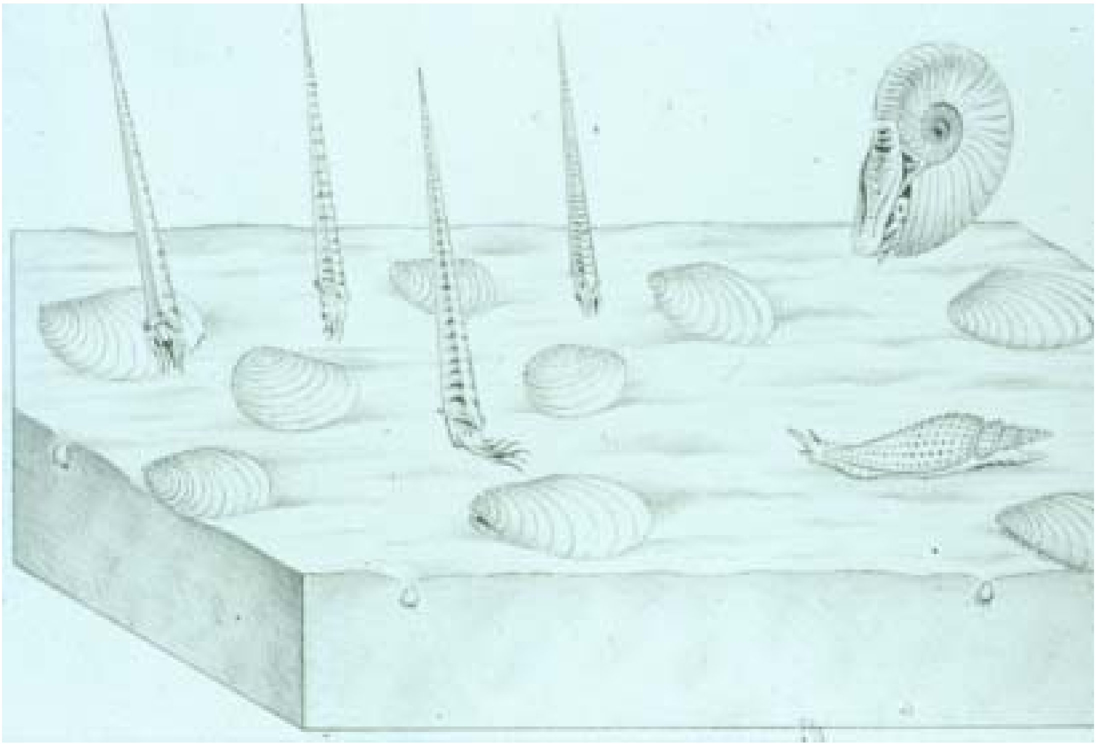


What if you don't want to go anywhere? How can you stay put just where you are?

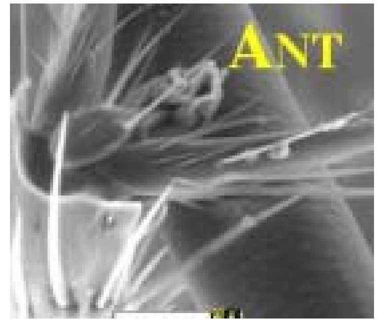
Attachments may be permanent or temporary, and must resist forces that are often quite large (i.e. gravity, wind and wave currents)

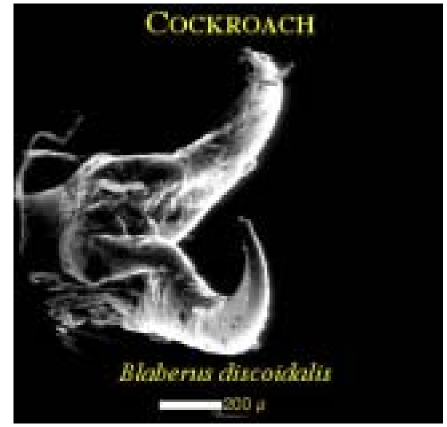
<u>Attachments may fail in:</u>

(less of a problem)	↓	compression
		shear
		tension
(more of a problem)		peel

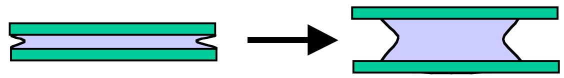


Methods of Adhesion

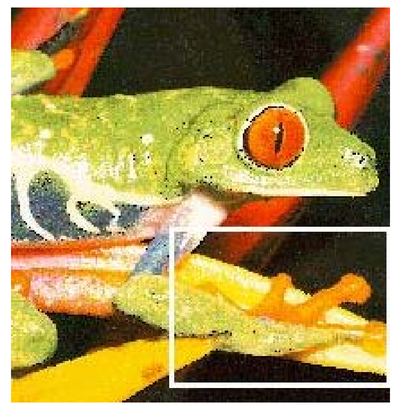


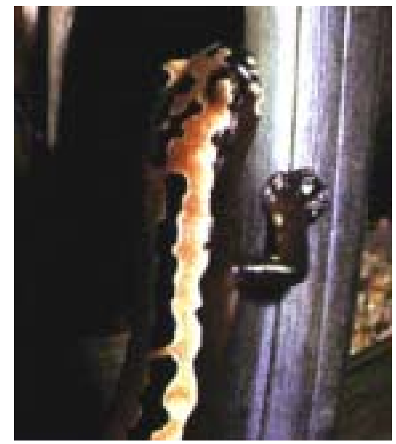


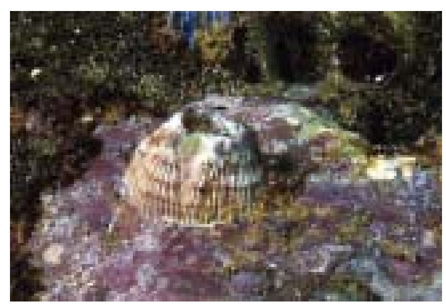
- *Interlocking devices*
- *Suction*
- *Extruded goo*
- *Capillary action*
- *Intermolecular forces*

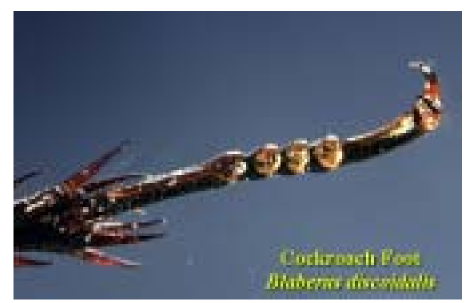


- *electrostatic attraction* - *interaction between charged ions*
- *polar interactions* - *attraction between molecules with a charge separation*
- *van der Waals forces* - *transient interactions between positive and negative portions of molecules as electrons rotate to opposite sides of orbits*





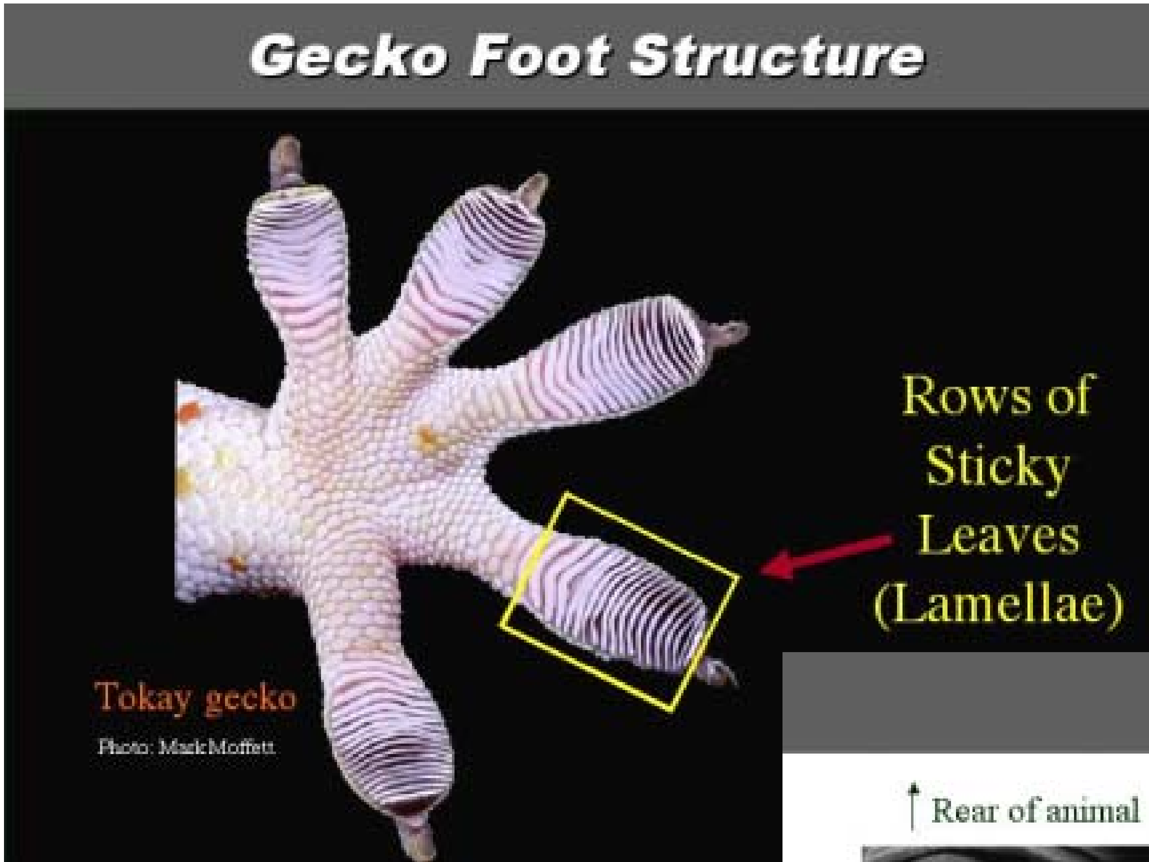


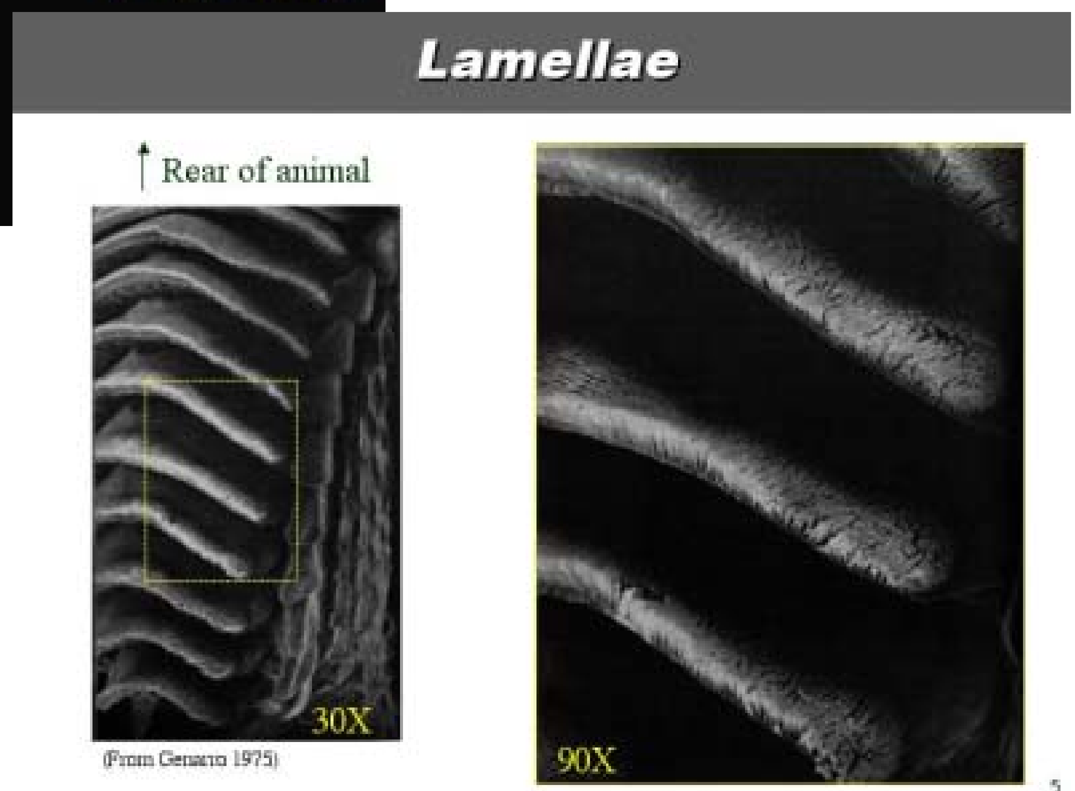


Geckos can run upside down, accelerate on polished glass, and hang from one toe.......

How do gecko feet adhere to surfaces so well?

Huge diversity of gecko feet.....


Gecko Foot Structure
Rows of Sticky Leaves (Lamellae)
Tokay gecko
Photo: Mark Moffett


Lamellae
Rear of animal
30X
90X

How do gecko feet adhere to surfaces so well?

- ***Interlocking devices*** →no hooks, can stick on perfectly smooth surface

- ***Suction***

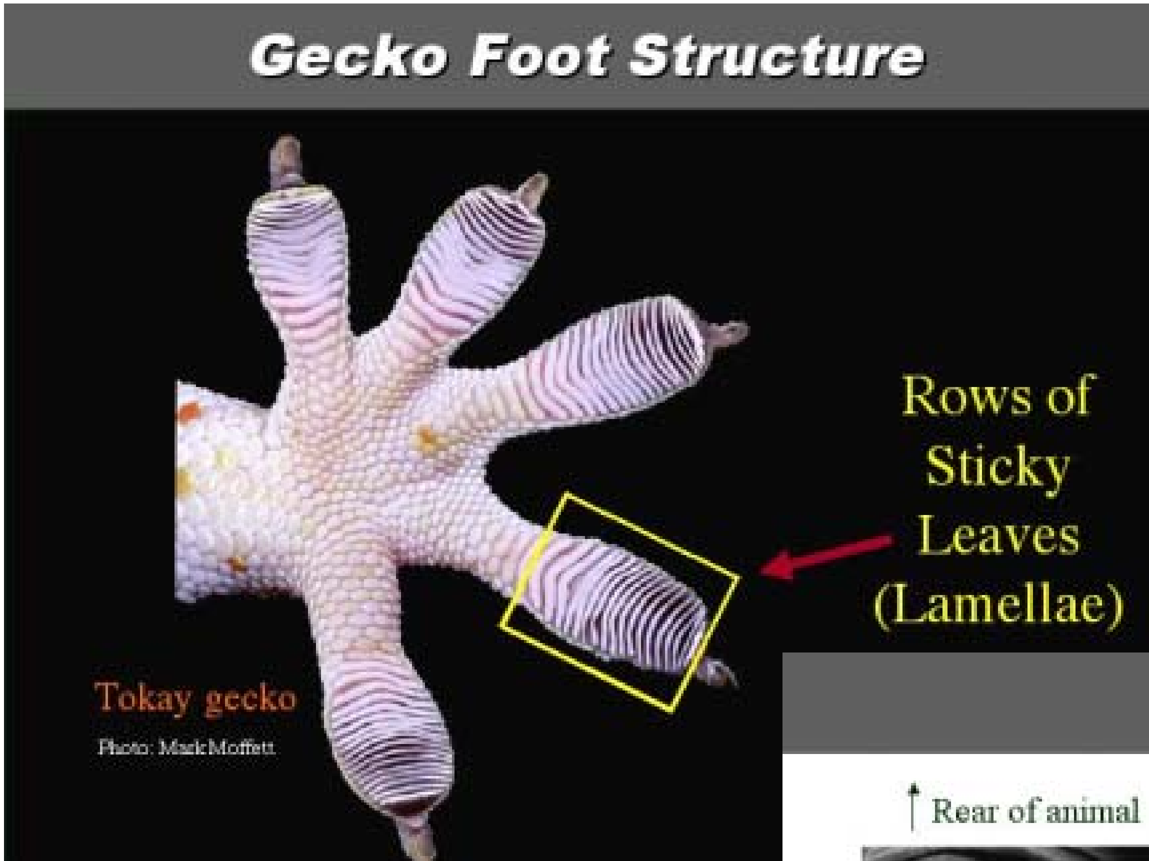
- ***Extruded goo***

- ***Capillary action***

- ***Intermolecular forces***
  - *electrostatic attraction*
  - *polar interactions*
  - *van der Waals forces*

How do gecko feet adhere to surfaces so well?

- ***Interlocking devices*** →no hooks, can stick on perfectly smooth surface
- ***Suction*** →dead geckos remain stuck to a wall in a vacuum (no pressure difference for suction to function)
- ***Extruded goo*** →no glands in feet, no footprints on surfaces
- ***Capillary action*** →toes are hydrophobic, stick equally well to hydrophobic and hydrophilic surfaces
- ***Intermolecular forces***
  - ***electrostatic attraction*** →works in ionized environment
  - ***polar interactions*** →toes hydrophobic, works on nonpolar surface
  - ***van der Waals forces*** ***!!!***


Gecko Foot Structure
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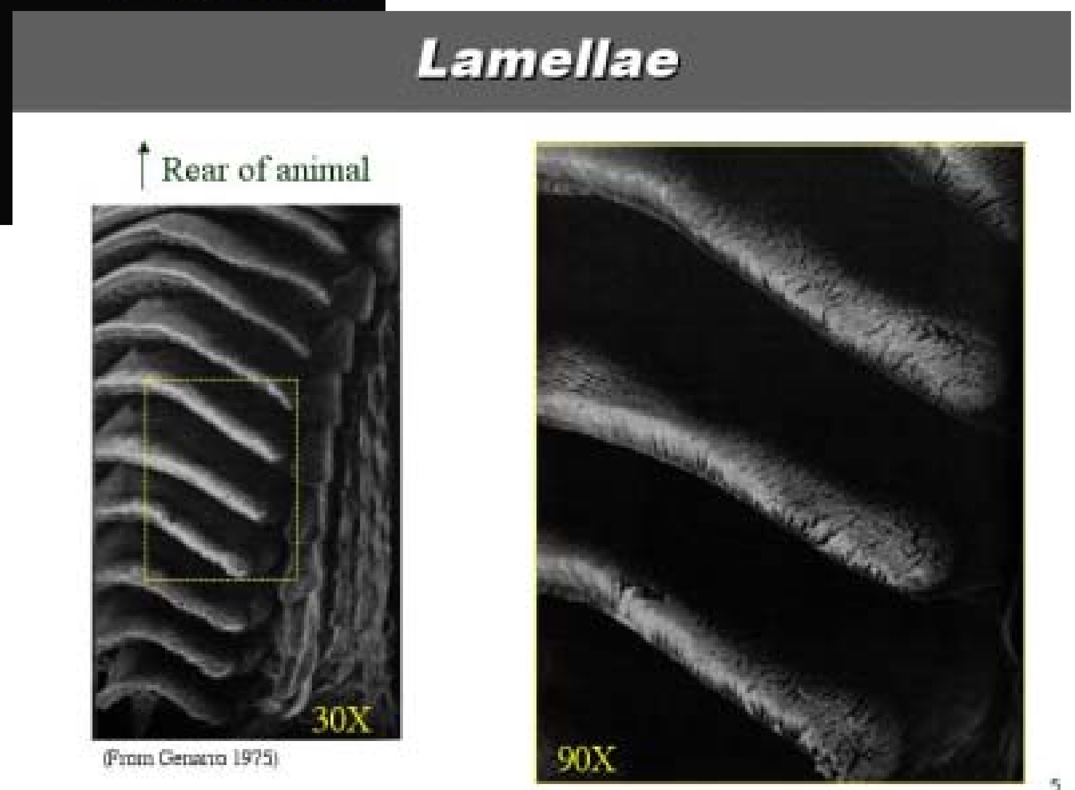
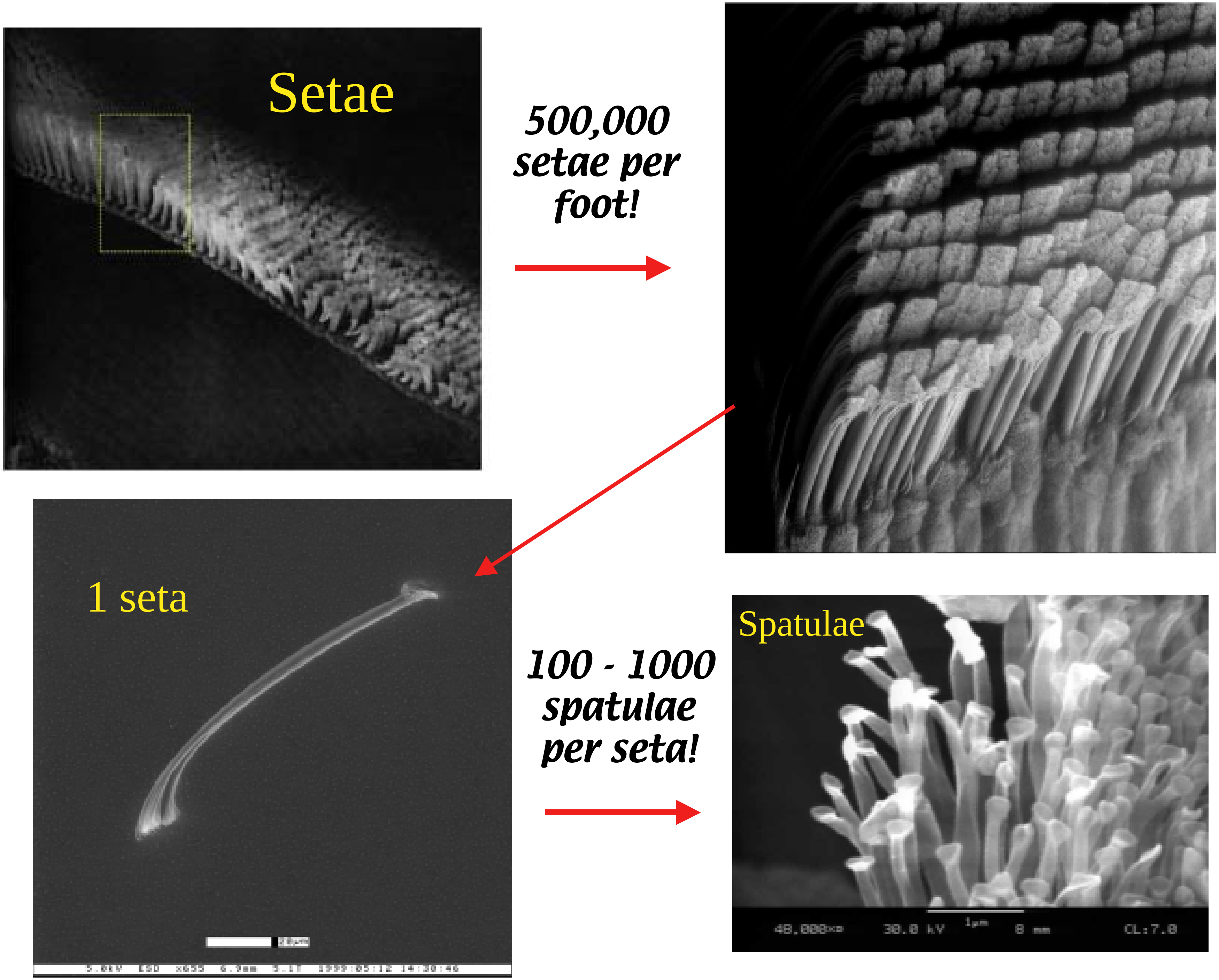
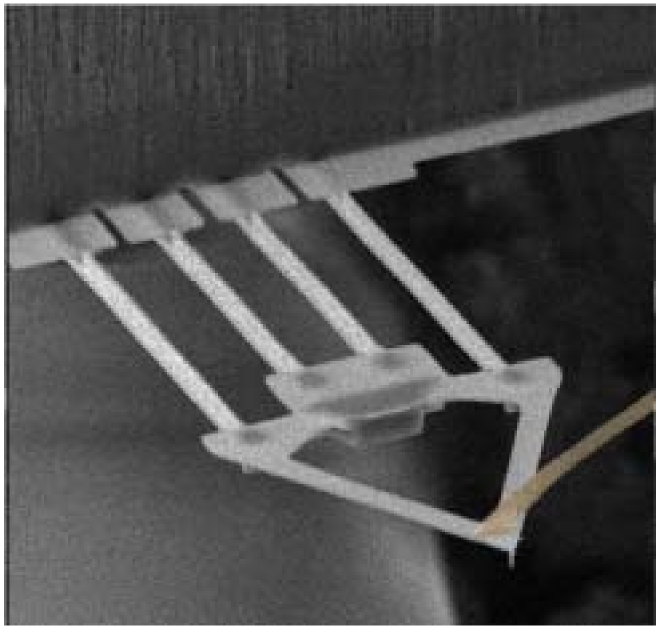
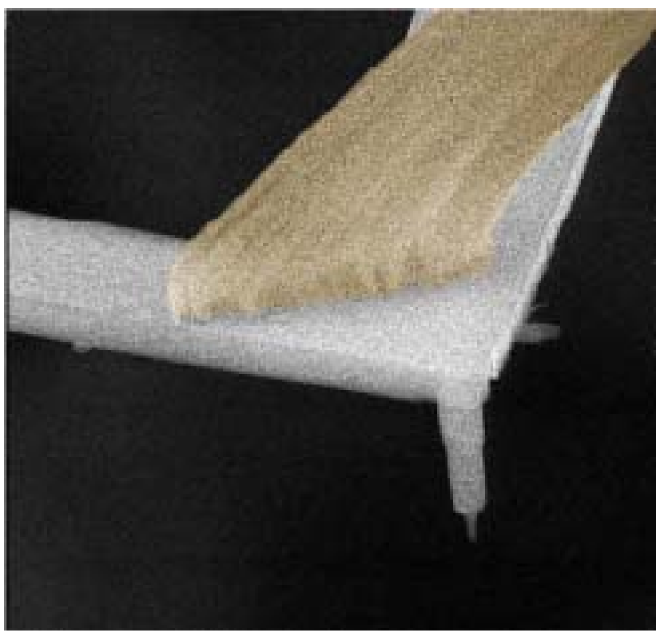

Lamellae
Rear of animal
30X
(From Genaro 1975)
90X


Setae
500,000 setae per foot!
1 seta
100 - 1000 spatulae per seta!
Spatulae
30.0 kV
8 mm
CL:7.0

How much force can one seta withstand?





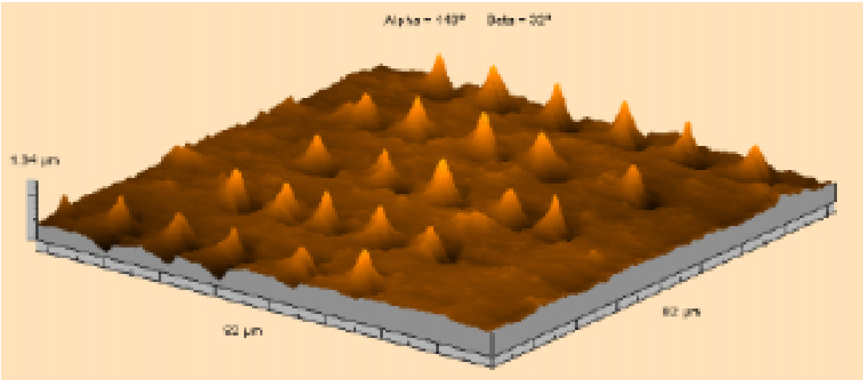
One seta (~1/10 diameter of a human hair) produces 200 μN, enough to support the weight of a large ant.

If all setae on a gecko's feet were engaged at once, they could support a 90-pound person!

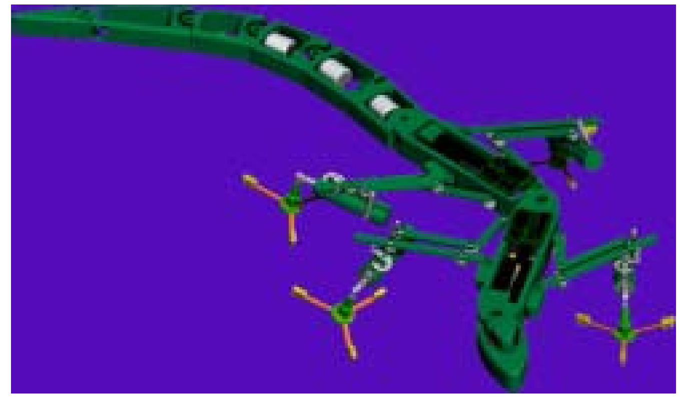
There is a large, unexplored diversity of setae found in......

- 850 species of geckos
- other species of lizards (anoles, skinks)
- some insects

Applications of artificial setae….

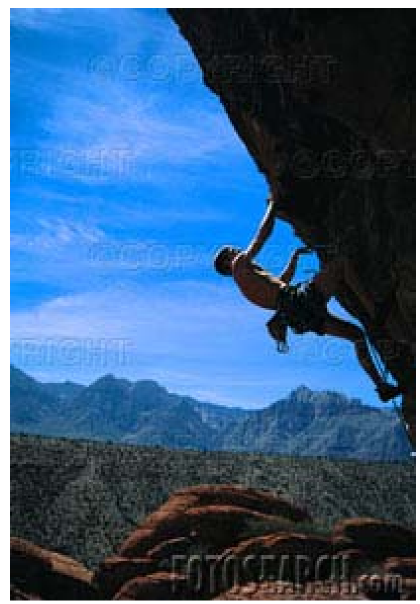


- ***climbing gecko robots** for rescue operations, planetary exploration, etc.*



***Dry, self-cleaning adhesive**:*

- *underwater use*
- *surgical sutures*
- *use in outer space*
- *moving silicon chips without scratching or residue*



Rock climbing for dummies?

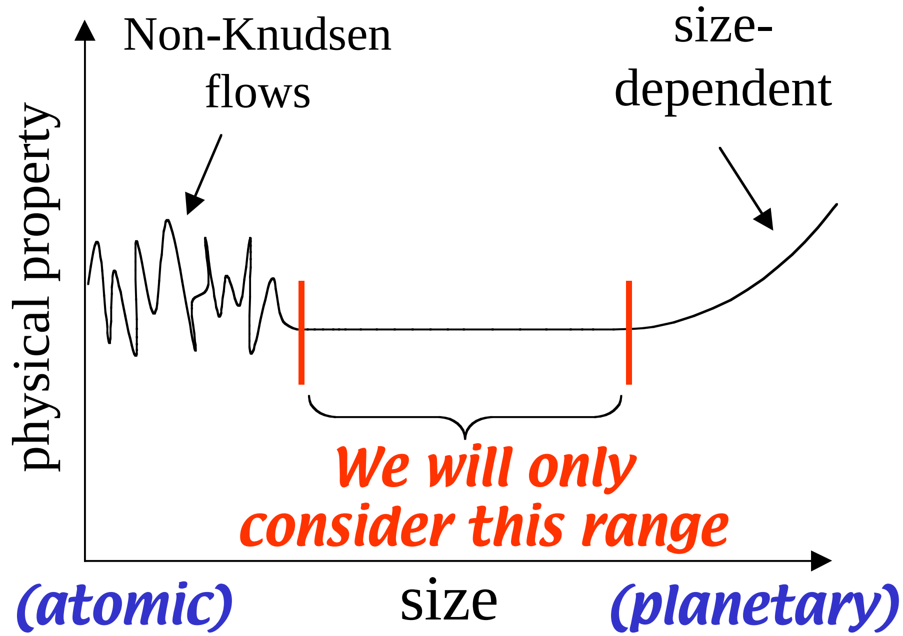
Where we have been....
Solid and structural mechanics: stress and strain distributions, movements of bodies and their parts in response to muscle forces and gravity.

Fluid dynamic issues underlie:

- *Internal flows (blood, respiratory flow, liquid food…)*
- *External flows (swimming, flying, running in air and water)*
- *Wind and water forces on sessile creatures*
- *Dispersal*
- *Transport of nutrients and heat to and from biological surfaces*

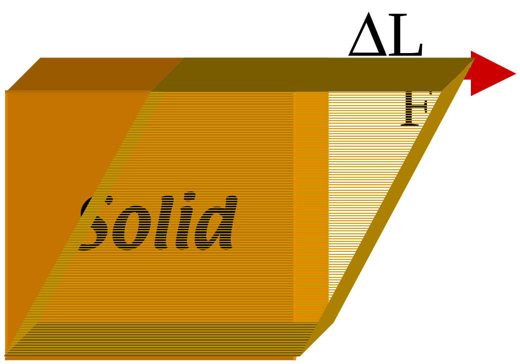
Definition: A fluid deforms continuously under an applied stress….

The CONTINUUM HYPOTHESIS will dominate our studies: density, temperature, momentum, energy ……… all vary continuously.
We can actually calculate their spatial derivatives if we have to.



But, when the spatial scale of the problem (L) is of the order of the mean free path of the fluid molecules (λ), we have a problem.
Knudsen number = λ/L. This underlies many subcellular problems and remains rather unresolved

Definition: A fluid deforms continuously under an applied stress….



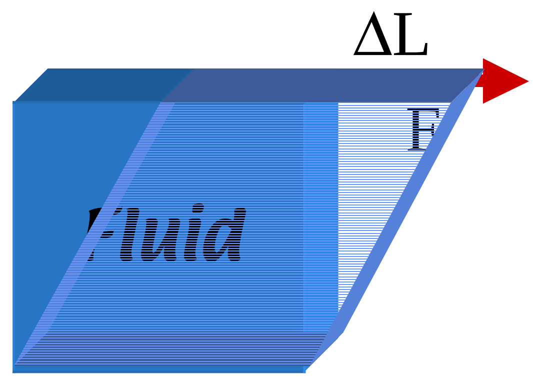
$F \sim \Delta L$

stiffness

$\sigma \sim \varepsilon$

$\sigma = E\varepsilon$

spring

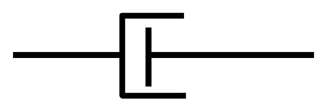


$F \sim \Delta L/\Delta t \sim dL/dt$

$\tau \sim d\varepsilon/dt$

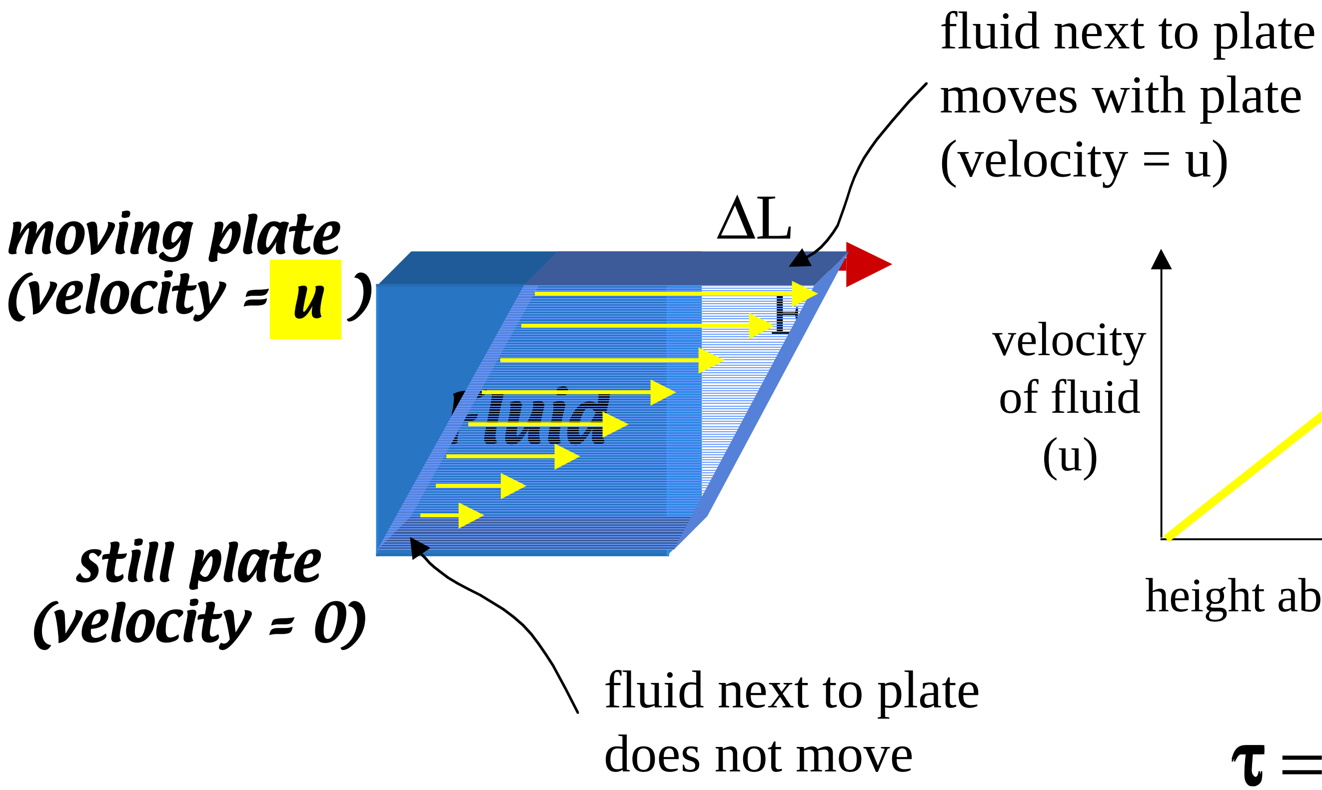
dynamic viscosity

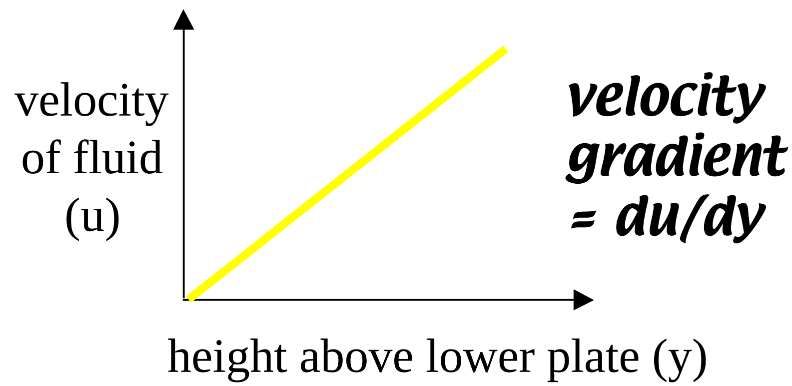
$\tau = \mu \, d\varepsilon/dt$



dashpot

The no-slip condition: Fluid velocity is zero immediately adjacent to a solid surface (fluid sticks to surface)





$$\tau = \mu \, d\varepsilon/dt$$

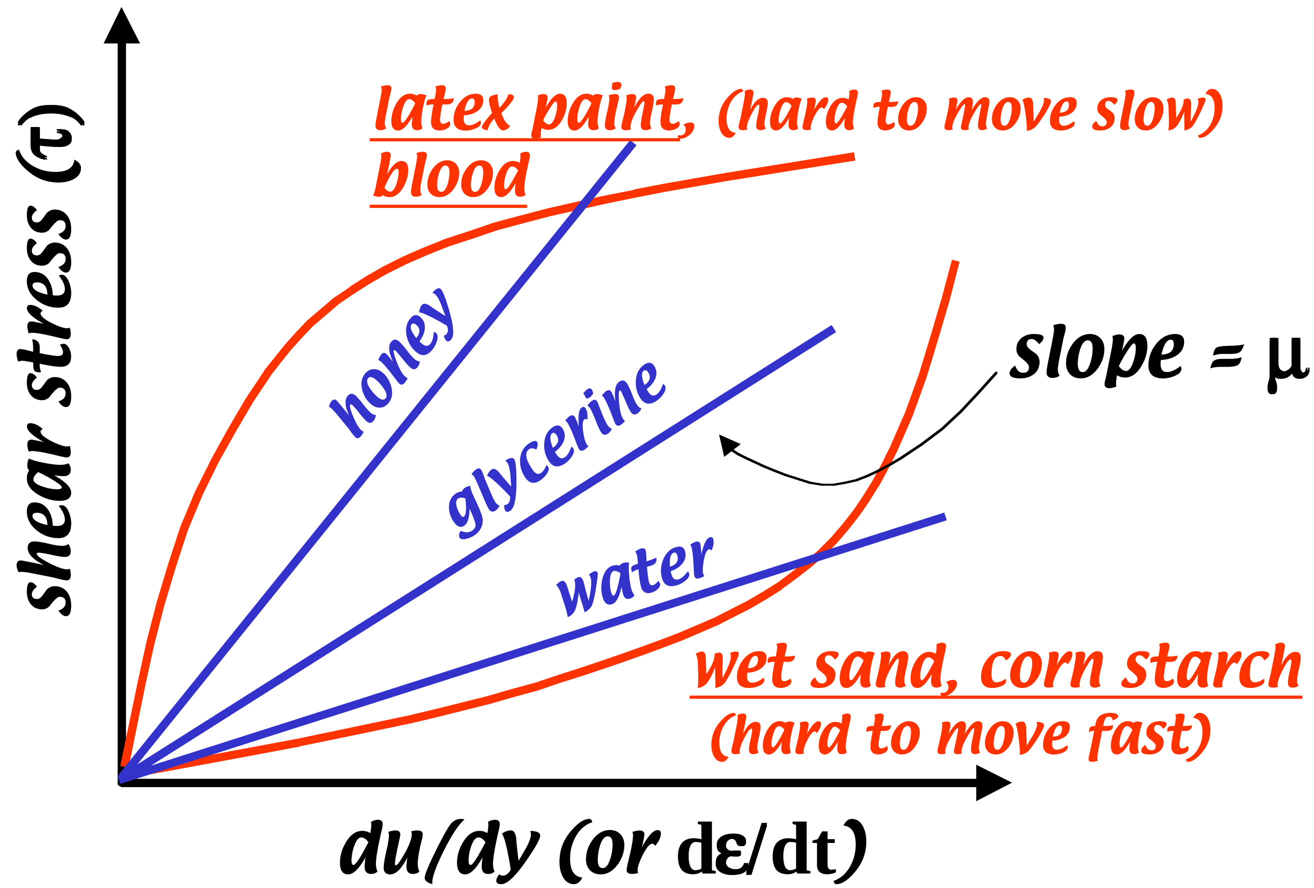
$$du/dy = d\varepsilon/dt$$

Newton's Law of Viscosity → $\tau = \mu \, du/dy$

Newtonian fluids....... *non-Newtonian fluids*

shear stress is directly proportional to strain rate

viscosity is independent of strain rate



dynamic viscosity (μ)
measure of resistance to shear

$$\tau = \mu \, d\varepsilon/dt$$

$$\tau = \mu \, du/dy$$

Dynamic vs. kinematic viscosity in biologically relevant fluids

dynamic viscosity **(μ)**

measure of resistance to shear

kinematic viscosity **ν = μ/ρ**

ratio of dynamic viscosity to density
--> measure of how readily momentum diffuses through fluid

	dynamic viscosity, μ (Pa s)	density, ρ (kg/m³)	kinematic viscosity, ν (m²/s)
air	18.1×10^{-6}	1.20	15.00×10^{-6}
water	1.00×10^{-3}	1.00×10^{3}	1.00×10^{-6}
seawater	1.07×10^{-3}	1.02×10^{3}	1.05×10^{-6}

* all at 20 ° C

Determinants of dynamic viscosity (μ):

Temperature ... there is a huge latitudinal gradient in ocean water temperatures

6 - 26° C along the west coast

2 - 32 ° C along the east coast

viscosity of water at 0 = 0.0018 kg/ m s
at 20 = 0.001 kg/ms
at 40 = 0.0006 kg/m s

almost 1/2 viscosity with 20 ° rise in temperature

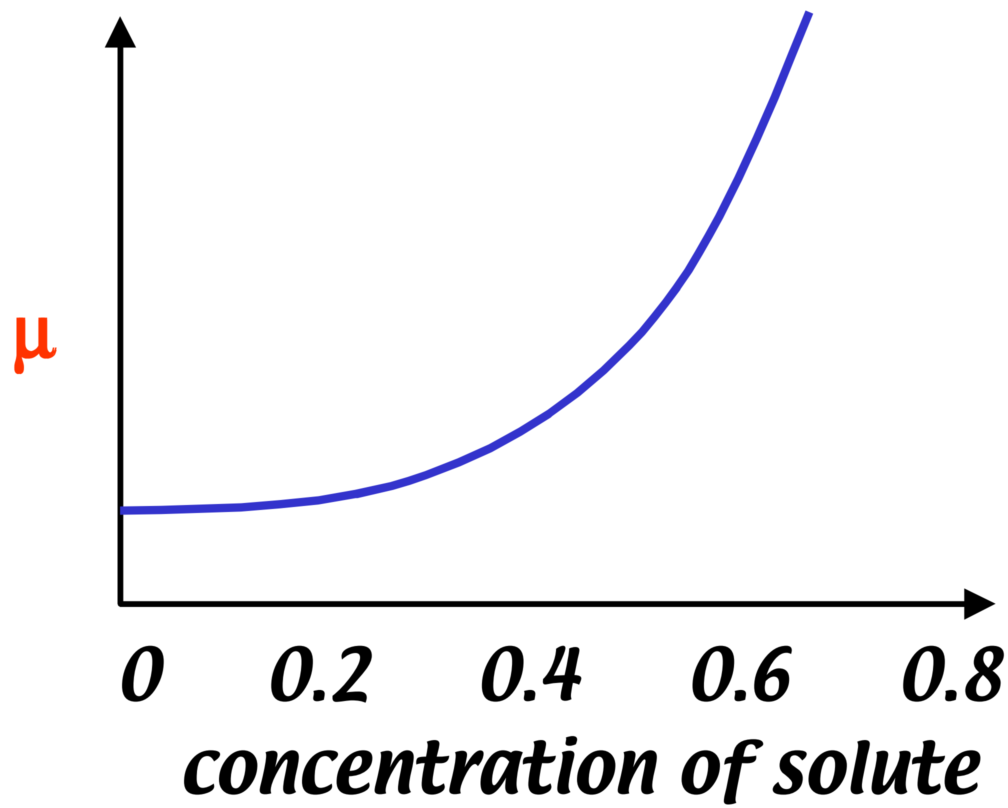
viscosity of air at 0 = 0.0017 g/ m s
at 20 = 0.0018 g/ms
at 40 = 0.0019 g/m s

* viscosity declines with temperature in fluids (heat disrupts order of fluids and allows flow)

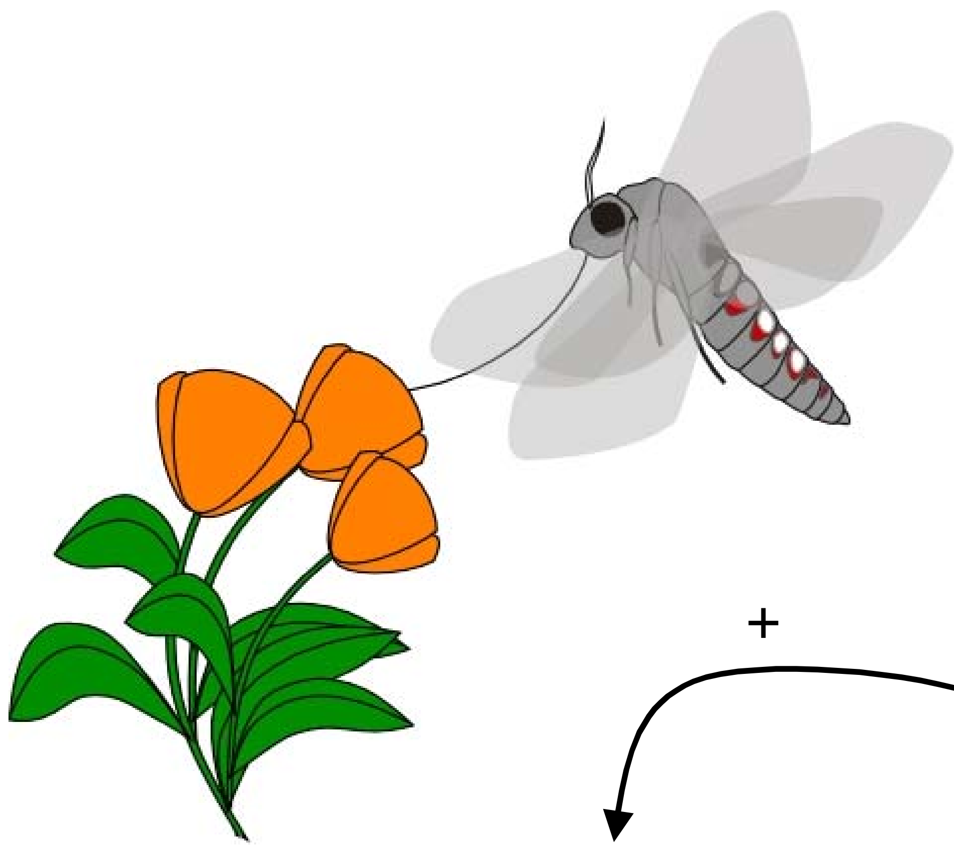
* viscosity increases with temperature in gases (heat increases molecular collisions)

Determinants of dynamic viscosity (μ):

Concentration of dissolved or suspended solutes …
Viscosity increases exponentially with concentration

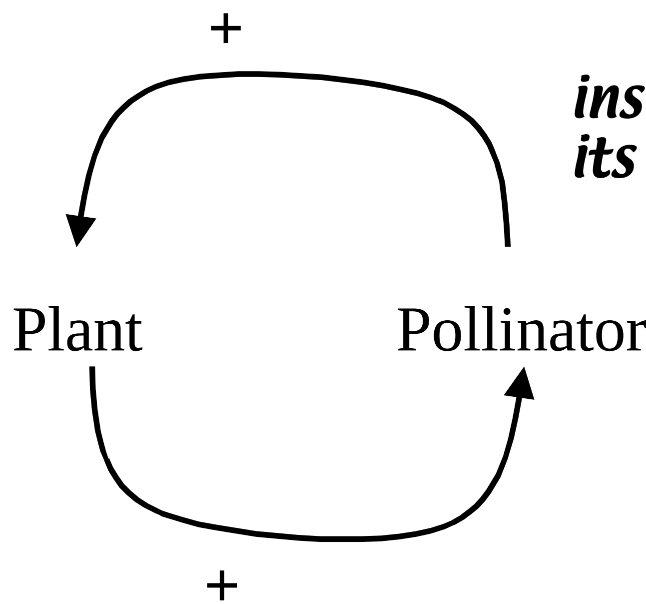


Coevolutionary tales of solute concentration and viscosity……



Nectar feeding and insect-pollinated plants

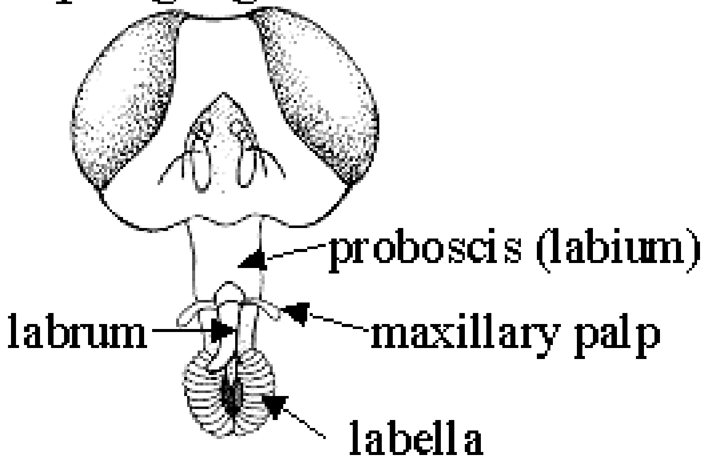
insect wants to maximize its sugar uptake rate



plant wants insect to visit it

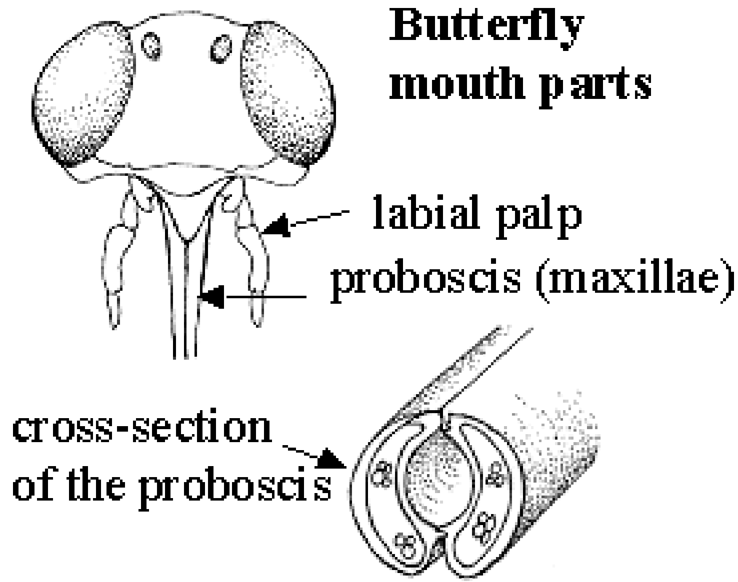

Butterfly and moth pollinated flowers generally produce dilute nectars (~20% sucrose by weight).
Bee and fly pollinated flowers often produce more concentrated nectars (~30-40% sucrose by weight)

House fly
sponging mouth

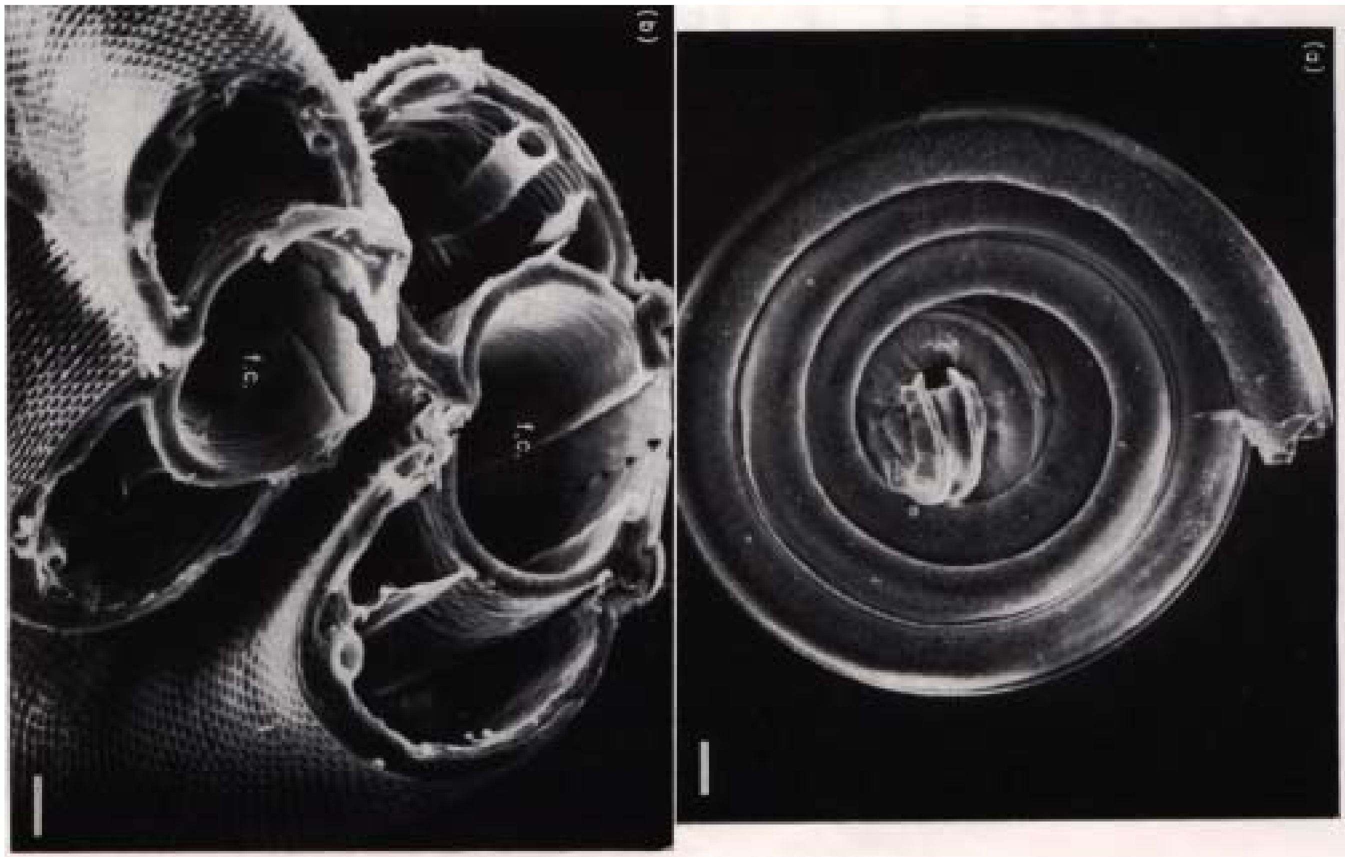


Honeybee
modified hairy tongue to lap up nectar

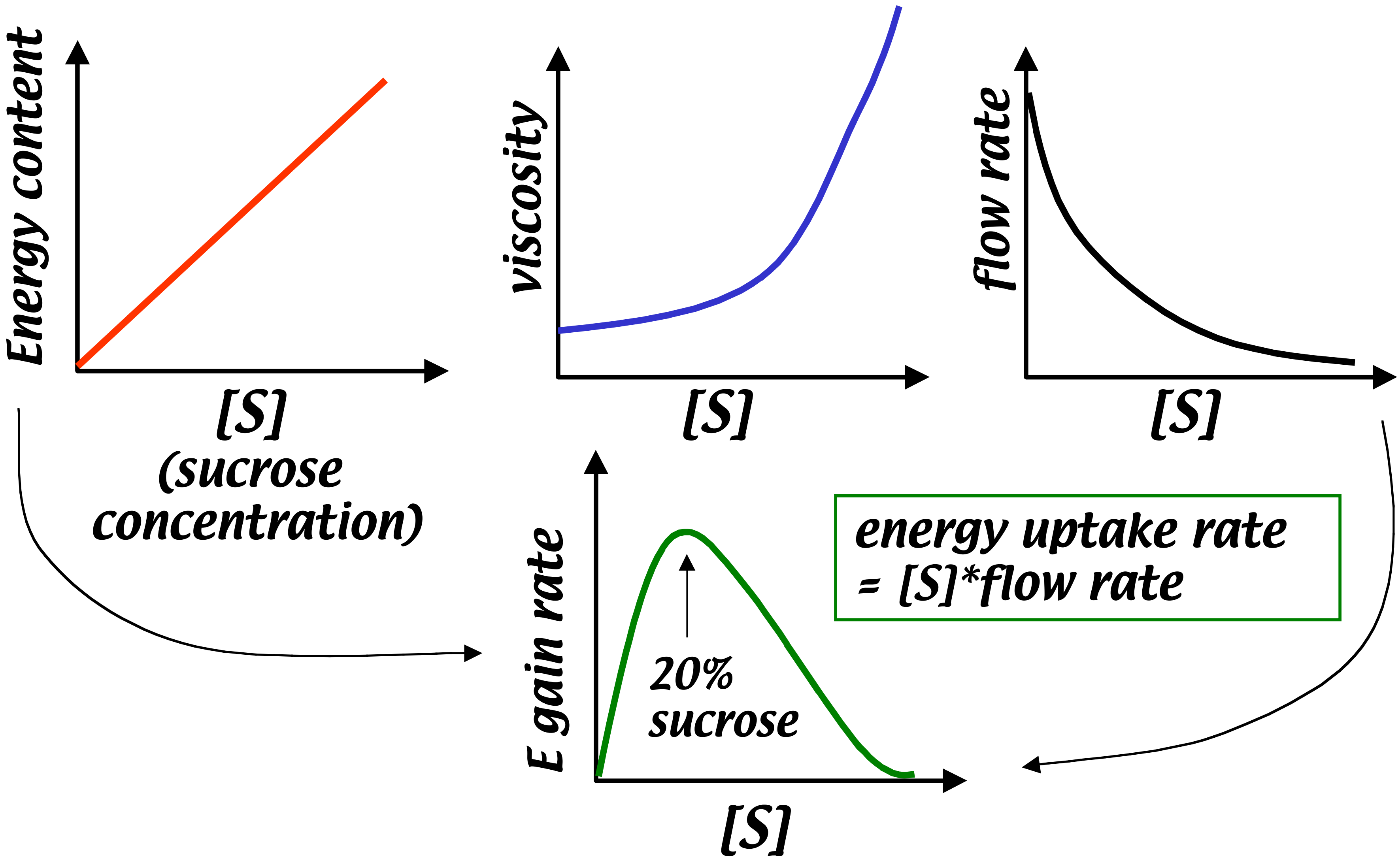
Butterfly mouth parts



Butterfly proboscis unwinds and inflates to suck up nectar

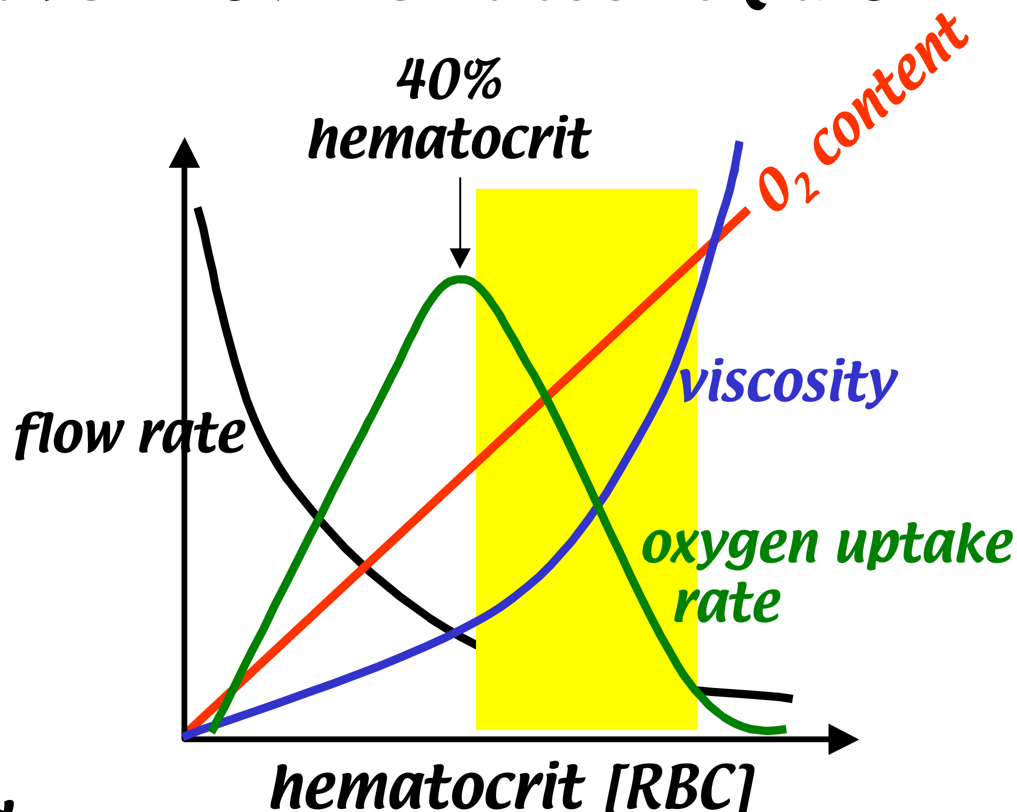


Why are nectars in moth and butterfly-pollinated flowers dilute?



Blood is also a viscous fluid with suspended red blood cells

If red blood cells carry oxygen and more oxygen is good, why do we only have ~40% hematocrit (RBC concentration)?



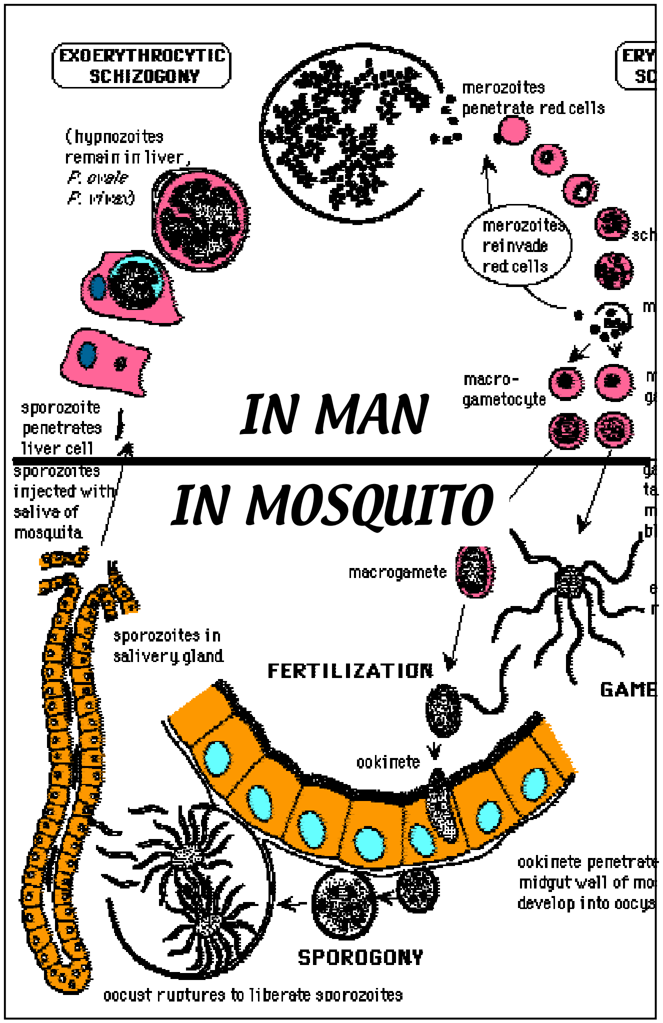
Blood doping - athletes stockpile their own RBCs and re-infuse into bloodstream before a competition

* increasing hematocrit over 40% leads to a dramatic increase in blood viscosity!

Coevolutionary tales of solute concentration and viscosity……

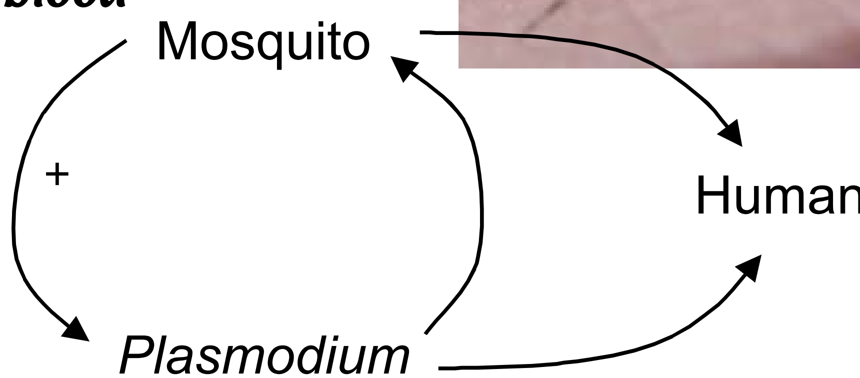
Mosquitoes and *Plasmodium* parasite

Plasmodium life cycle:



Plasmodium parasite (protozoan) causes malaria in humans, and is transmitted by mosquito vector

mosquito wants to maximize protein uptake rate from blood

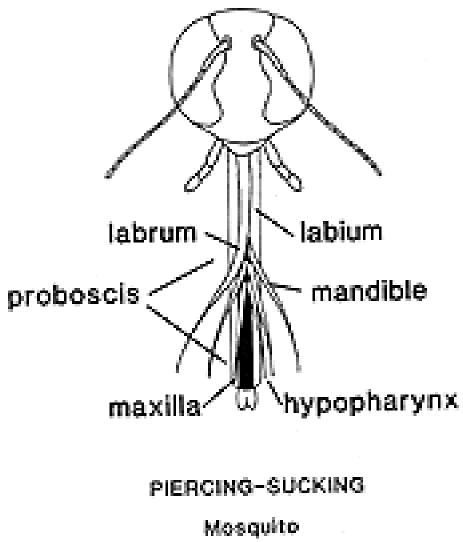


Plasmodium needs to be transported within mosquito to complete its lifecycle and find new human hosts

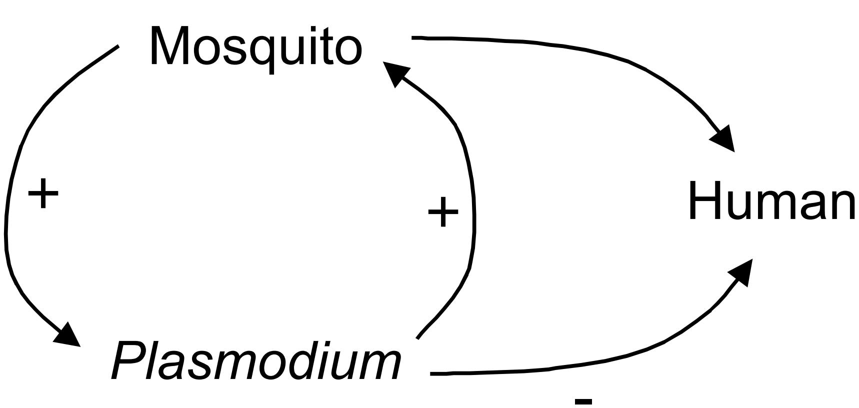
Coevolutionary tales of solute concentration and viscosity……

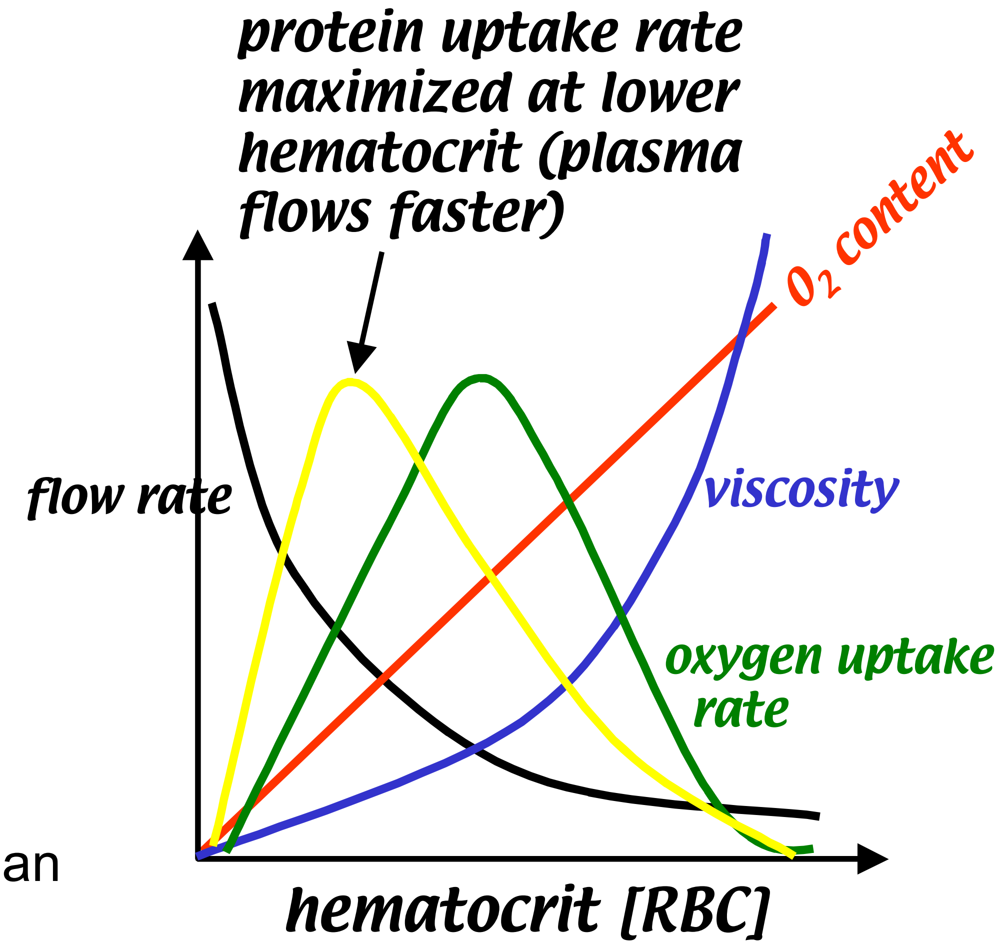
Mosquitoes and *Plasmodium* parasite

Malaria lowers hematocrit [RBC] in humans

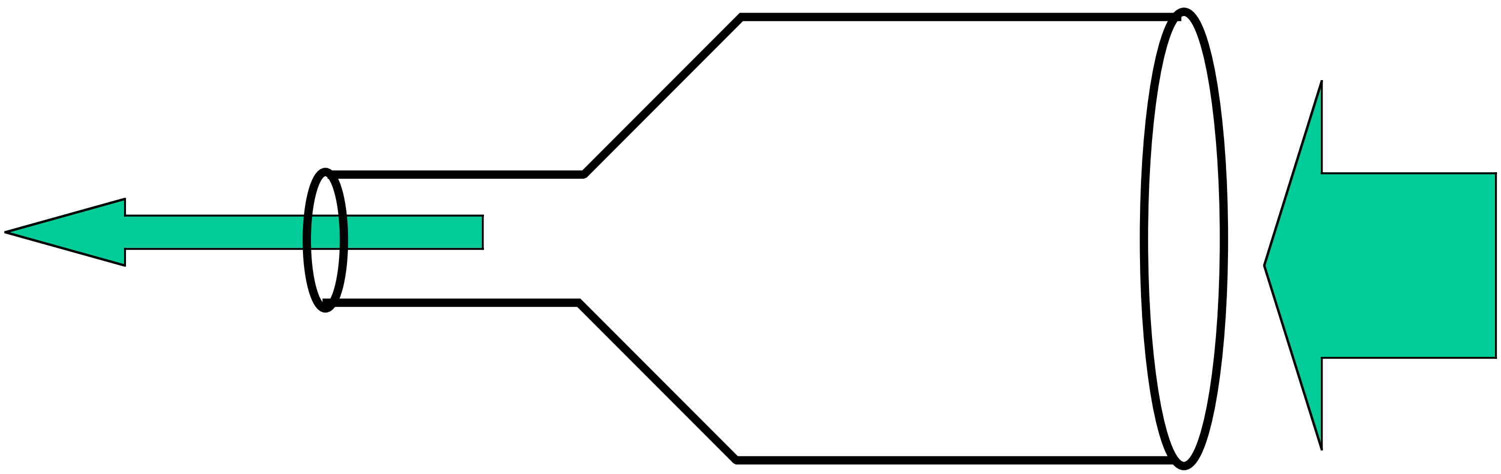


Mosquitoes have piercing-sucking mouthparts





Continuity: what goes in must come out (mass may not appear or disapear)



$Volume_{out}/time$

$u_{out}\,A_{out}$

$Volume_{in}/time$

$u_{in}\,A_{in}$ $(m/s * m^2)$

$$\Sigma\, u_{in} A_{in} = \Sigma\, u_{out} A_{out}$$

Biology 427 Biomechanics
Lecture 16. Bernoulli's principle and applications

- Properties of gases vs. liquids, pressure, and buoyancy
- Recap definition of a fluid and Newton's law of viscosity.
- Conservation of mass and continuity
- Conservation of energy and Bernoulli's principle
- Conservation of momentum

States of matter

SOLID

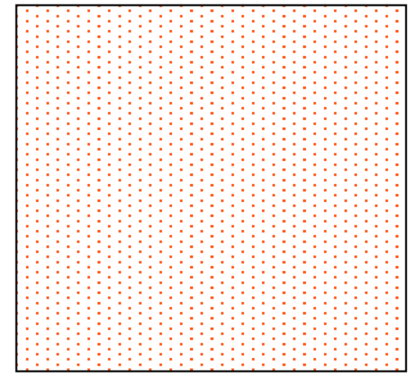
resists compression, tension, and shear

has size and shape

LIQUID

resists compression and tension (cohesion of water allows root to tip flow in plants)

has size but no shape



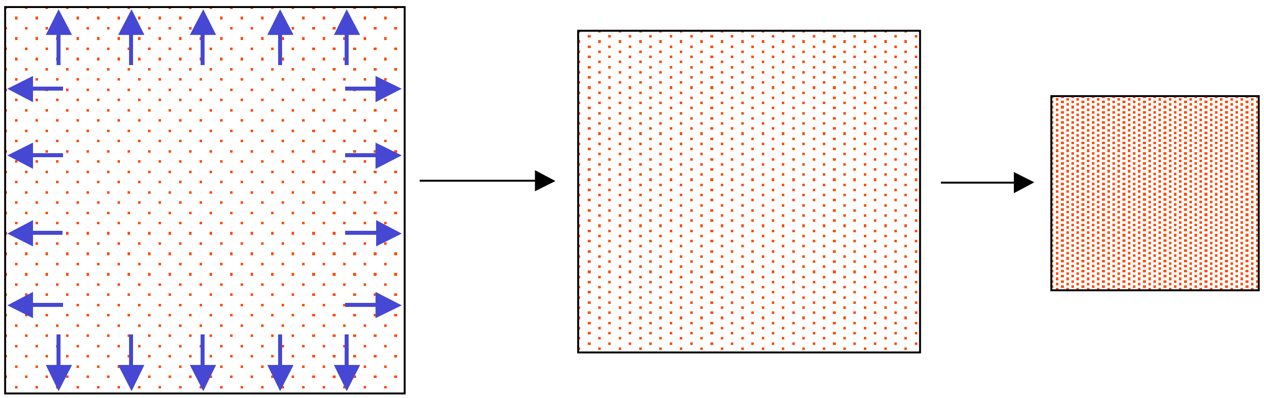
GAS

resists compression (can be done, but takes work)

- gases rarely compress much in biological systems
- has no size or shape

How do liquids and gases behave differently in biological systems?

✓Gases can be compressed



pressure = force/area

chamber filled with gas molecules

lower volume = higher pressure

Unlike stress, pressure acts in all directions, perpendicular to surfaces

•pressure and volume inversely proportional in gases

Ideal Gas Law

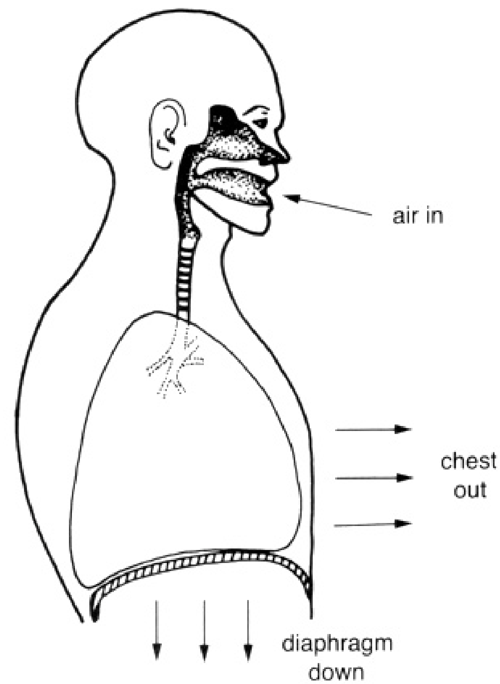
$$PV = nRT$$

P   1/V

assume constant if no change in temperature

Fluids want to move from areas of high pressure to areas of low pressure

Breathing



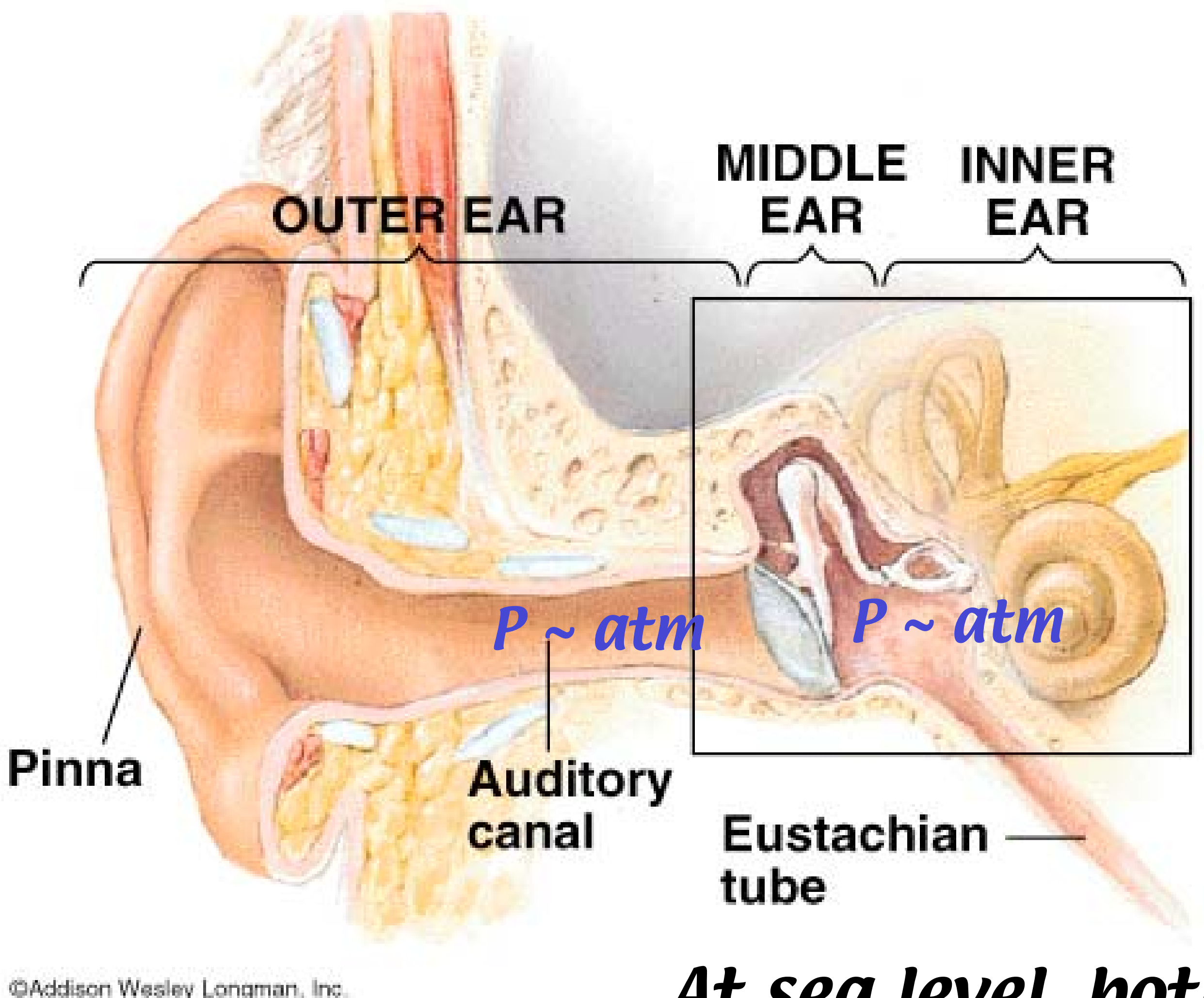
diaphragm drops and chest expands

volume of lungs ≠, pressure

Air outside (P = 101,000 Pa) wants to flow into lower pressure lungs (P = 90,000 Pa)

P 1/V

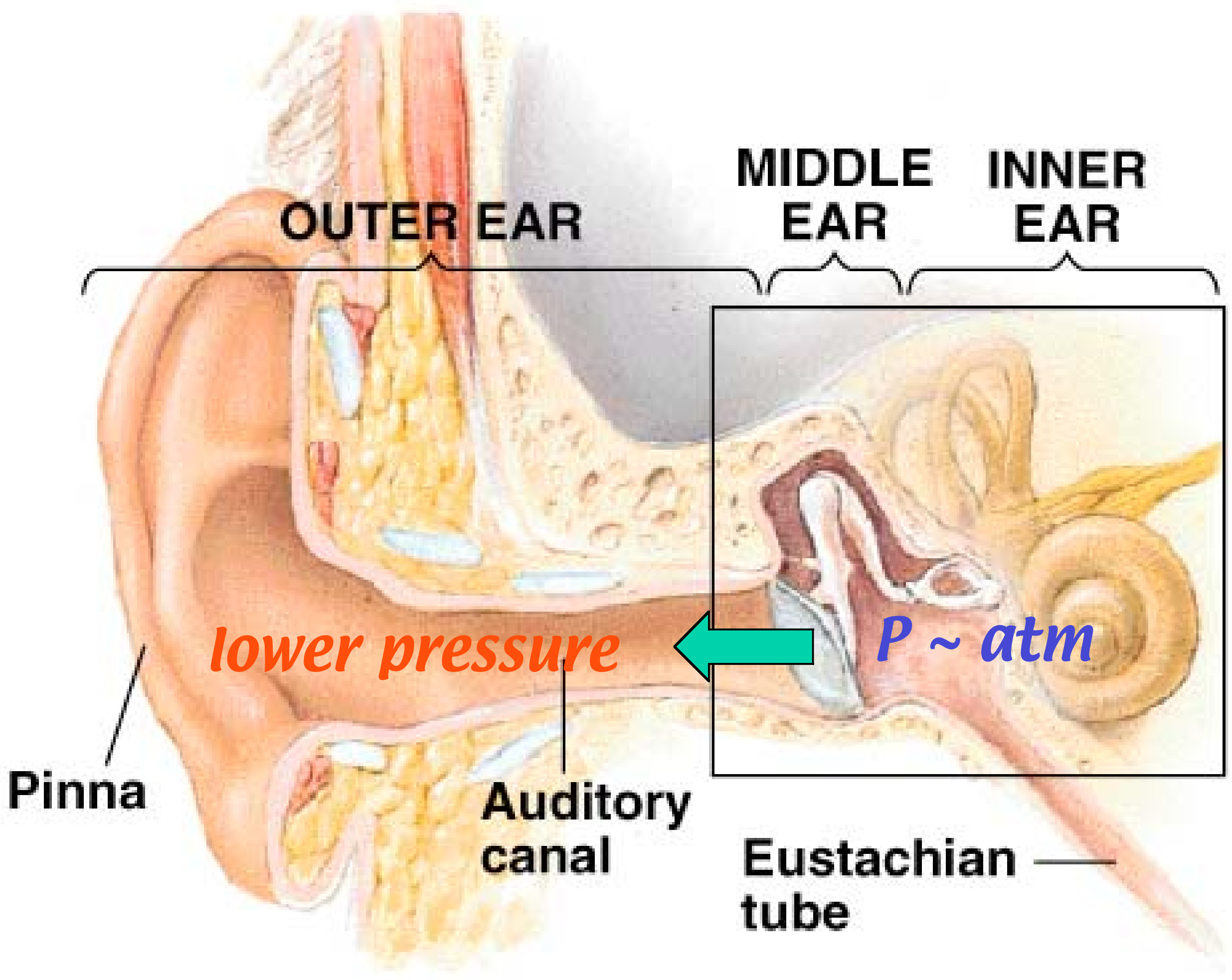
Flying in airplanes and scuba diving....



Eustachian tube is a (relatively) sealed air cavity inside the ear

At sea level, both the outside air and the Eustachian tube are at ~ atmospheric pressure

Flying in airplanes and scuba diving….



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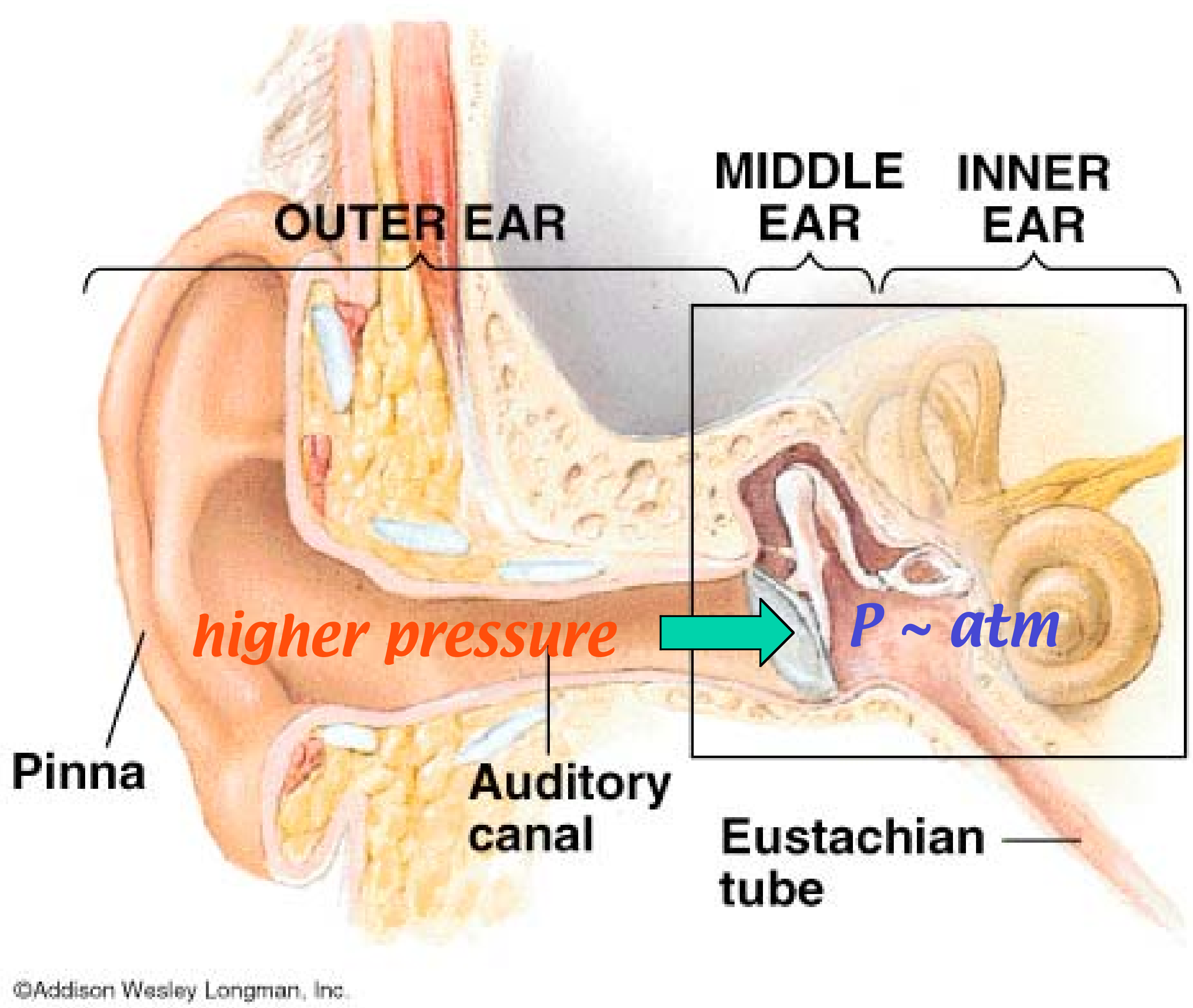
Lower pressure at higher altitudes - eardrums are pulled (pushed) out

P 1/V

Flying in airplanes and scuba diving....

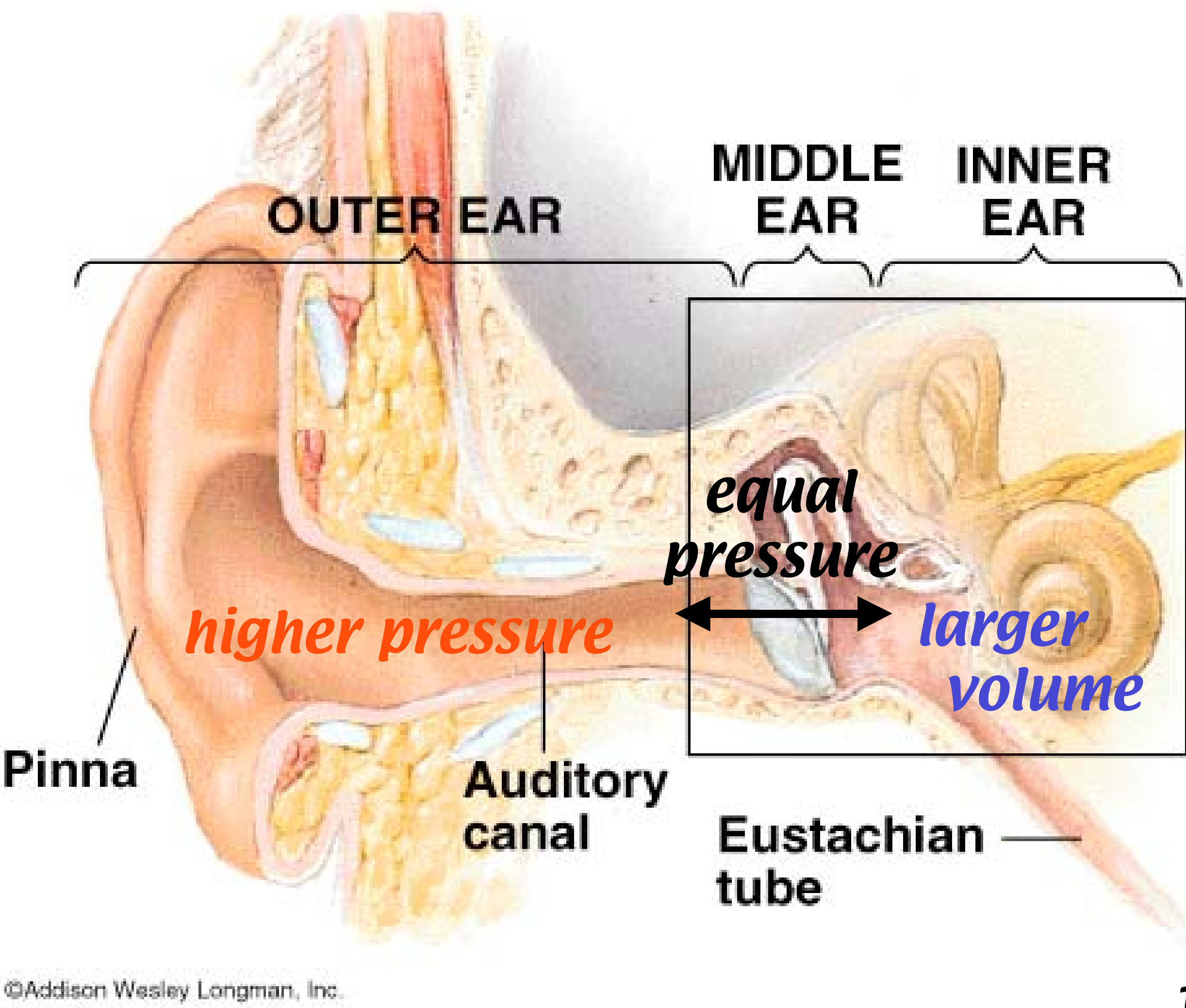


As you descend in depth underwater, pressure outside ears increases (much more quickly than in air!)

Eardrums are pushed inward (P ≠, V)

P 1/V

Flying in airplanes and scuba diving….



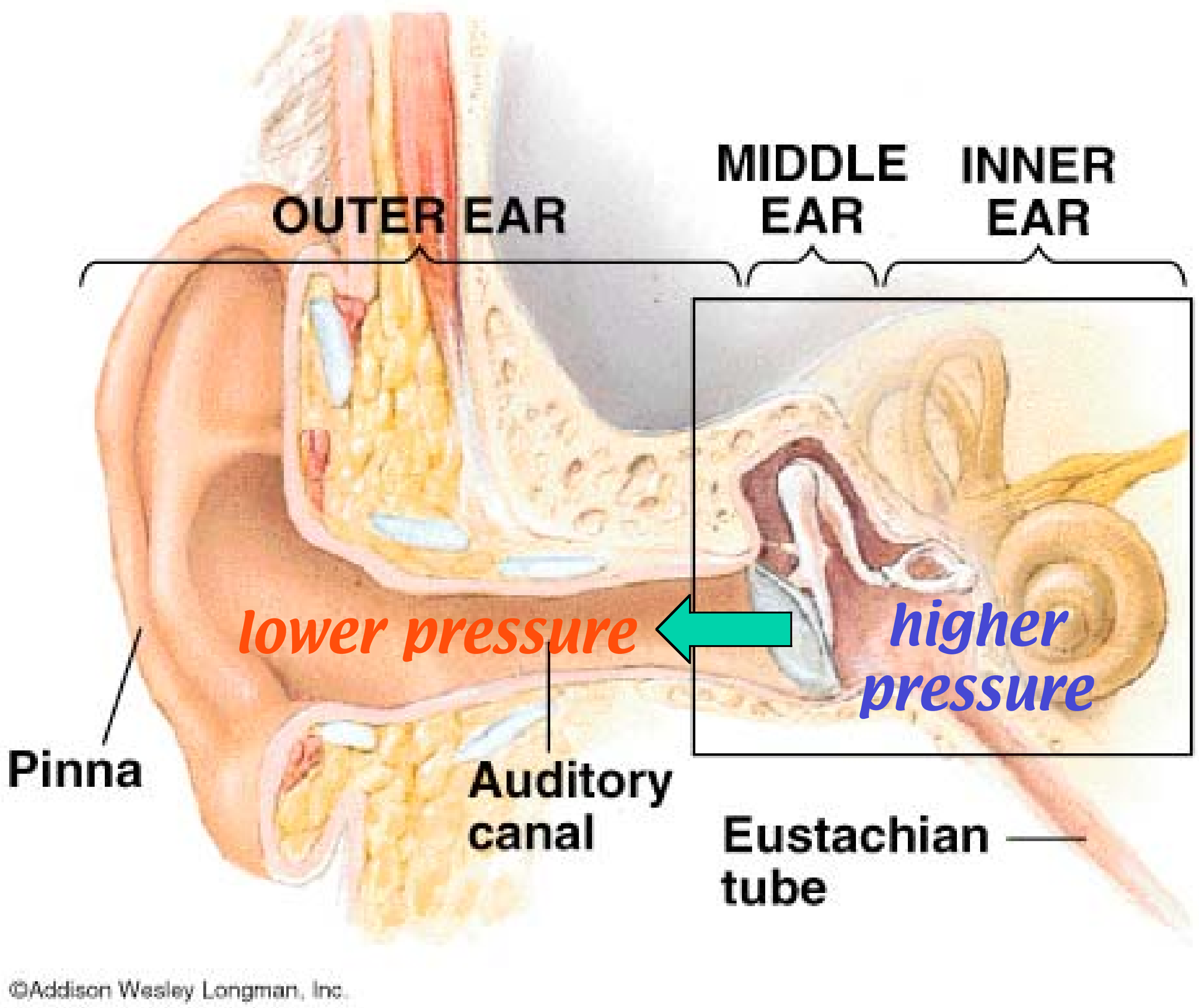
As you descend in depth underwater, pressure outside ears increases (much more quickly than in air!)

Eardrums are pushed inward (P ≠, V)

Have to equalize pressure in ears (expand Eustachian tube) while descending (V ≠, P)

P 1/V

Flying in airplanes and scuba diving….



As you ascend, pressure outside decreases

Eardrums are pushed outward

Must ascend slowly to allow air to escape from Eustachian tube

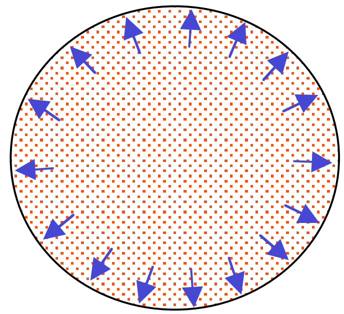
P   1/V

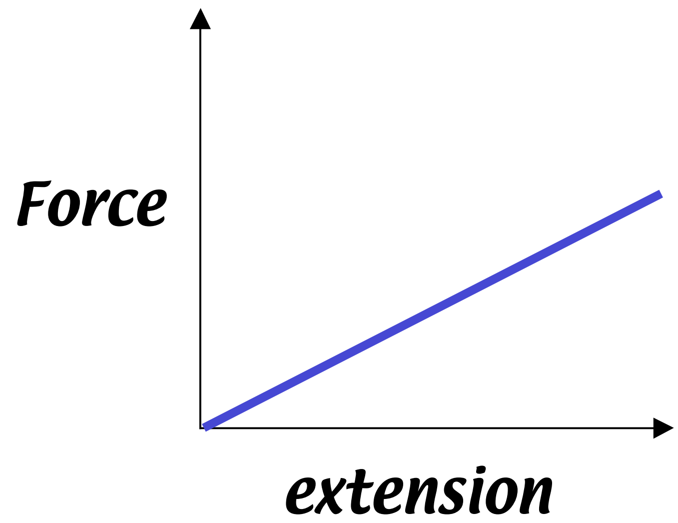
Pressure and tension in flexible walls

LaPlace's Law

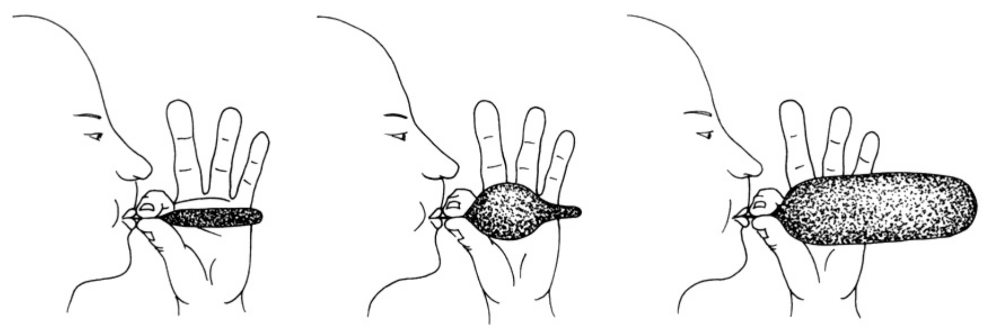
T = Pr

tension in wall = pressure difference* radius of curvature





- This means that for a given pressure difference, a flexible membrane will extend more where the radius is bigger (i.e. where it has already expanded!)



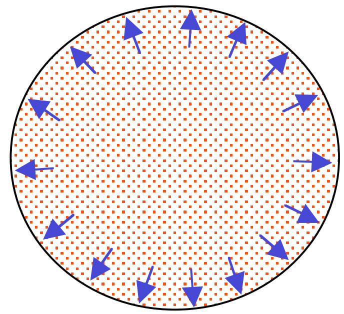
Balloons extend in one part to the point of almost bursting, then expansion extends lengthwise

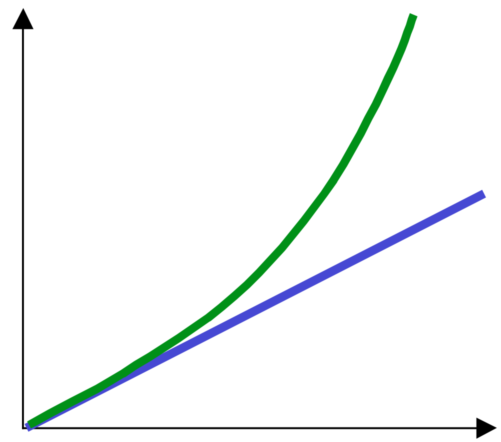
Pressure and tension in flexible walls

LaPlace's Law

$T = Pr$

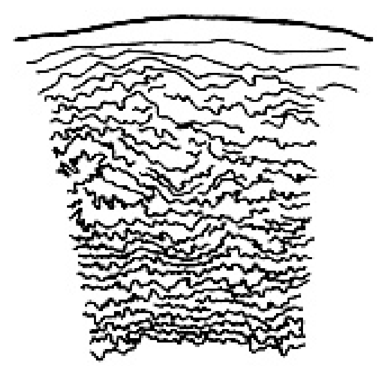
tension in wall = pressure difference* radius of curvature

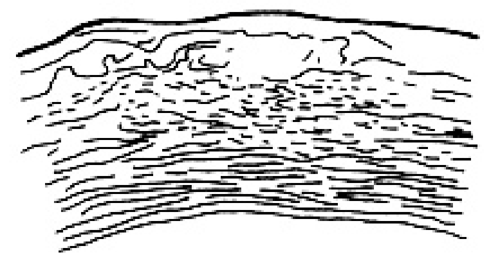




Why don't our arteries expand in a local spot until they burst (aneurysm)?

Arteries have kinked collagen fibers that initially unwind under tension, then become much stiffer to applied force





How do liquids and gases behave differently in biological systems?

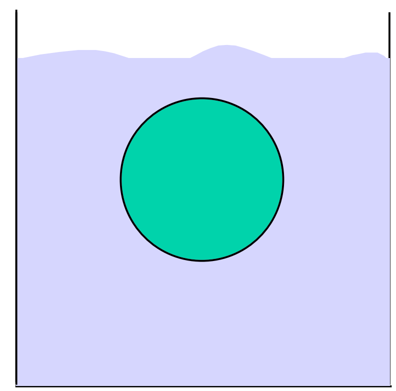
✓ **Buoyancy** is generally only a consideration in liquids

If less dense than displaced fluid, object feels upward force (positively buoyant)

If more dense than displaced fluid, object feels downward force (negatively buoyant)

If more same density as displaced fluid, object feels no net force (neutrally buoyant)

A submerged object displaces a volume of fluid



$$F = mg = (\quad - \quad _0)Vg$$

where $_0$ = density of medium

and = density of object

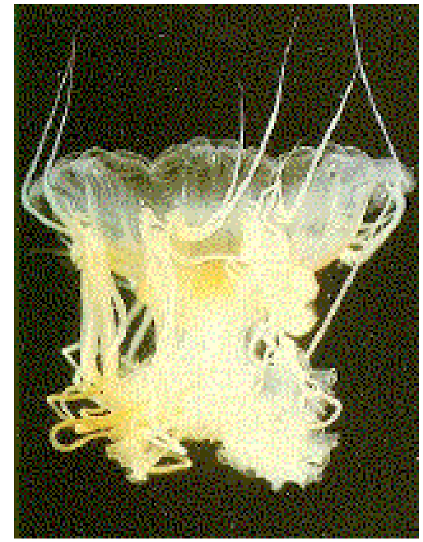
Most biological materials are denser than fresh water

water = 1000 kg/m^3
seawater = 1000 kg/m^3
fat = 940 kg/m^3, but
bone = 1700 kg/m^3 - 2500 kg/m^3

How do aquatic creatures stay afloat?

Carry large reservoirs of fats and oils

Avoid dense materials



Carry air-filled chambers

If incompressible chamber (i.e. chambered nautilus, cuttlefish), don't need to worry about compression at depth

With flexible chambers such as swim bladders, need to infuse and release air as change depth

States of matter

SOLID

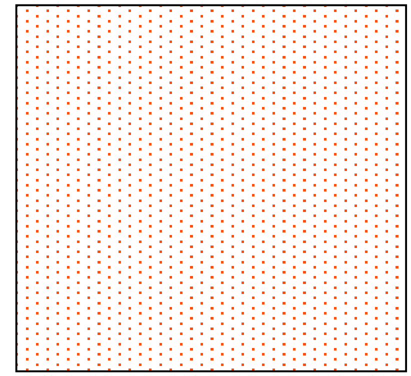
resists compression, tension, and shear

has size and shape

LIQUID

resists compression and tension (cohesion in plants)

has size but no shape



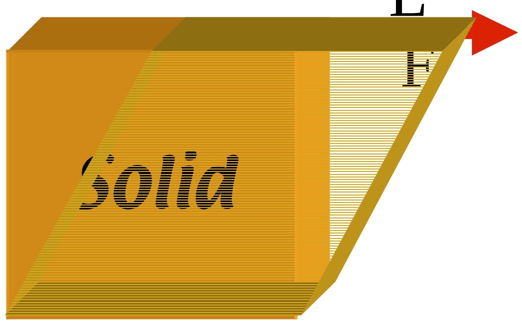
GAS

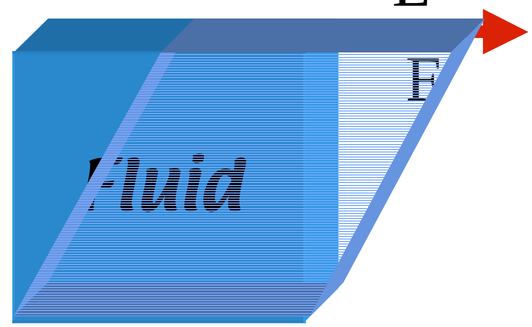
resists compression (can be done, but takes work)

- gases rarely compress much in biological systems
- has no size or shape

Despite differences, liquids and gases share many common behaviors - we will lump them as “fluids”

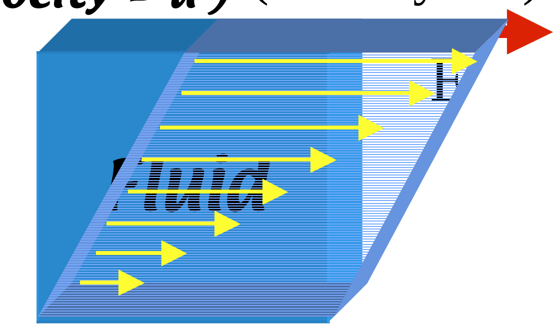
Definition: A fluid deforms continuously under an applied stress….





moving plate (velocity = u)

fluid next to plate moves with plate (velocity = u)



still plate (velocity = 0)

fluid next to plate does not move

F ~ L

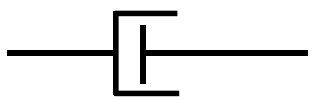
F ~ L/ t ~ dL/dt

d / dt

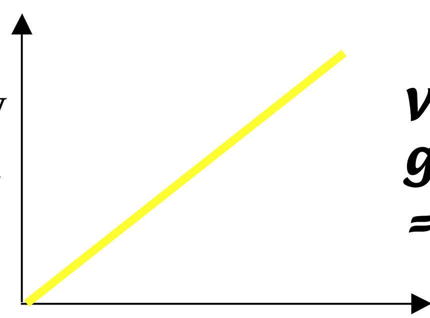
=

= d / dt

spring



dashpot



velocity gradient = du/dy

du/dy = d /dt

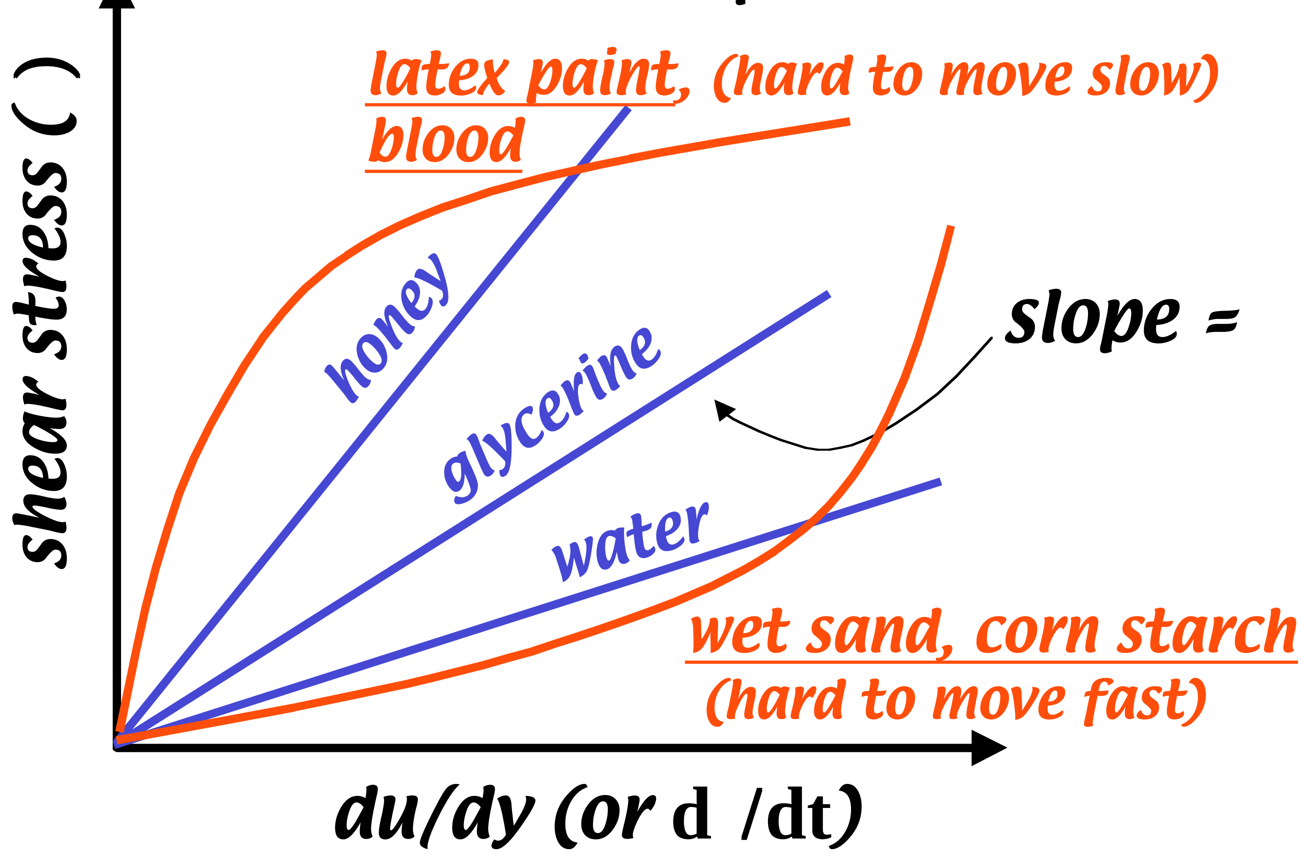
= du/dy ← **Newton's Law of Viscosity**

Newtonian fluids.......

non-Newtonian fluids

depends on strain rate!

shear stress is directly proportional to strain rate



viscosity is independent of strain rate

dynamic viscosity ( )

measure of resistance to shear

= d /dt

= du/dy

Dynamic vs. kinematic viscosity in biologically relevant fluids

***dynamic viscosity* ( )**

measure of resistance to shear

***kinematic viscosity* = /**

ratio of dynamic viscosity to density
--> measure of how readily momentum diffuses through fluid

	dynamic viscosity, (Pa s)	density, (kg/m^3)	kinematic viscosity, (m^2/s)
air	18.1×10^{-6}	1.20	15.00×10^{-6}
water	1.00×10^{-3}	$1.00 \times \mathbf{10^{3}}$	1.00×10^{-6}
seawater	$1.07 \times \mathbf{10^{-3}}$	$1.02 \times \mathbf{10^{3}}$	1.05×10^{-6}

* all at 20 ∞C

Determinants of dynamic viscosity ( ):

Temperature ... there is a huge latitudinal gradient in ocean water temperatures

6 - 26∞C along the west coast

2 - 32 ∞C along the east coast

viscosity of water

at 0 = 0.0018 kg/ m s

at 20 = 0.001 kg/ms

at 40 = 0.0006 kg/m s

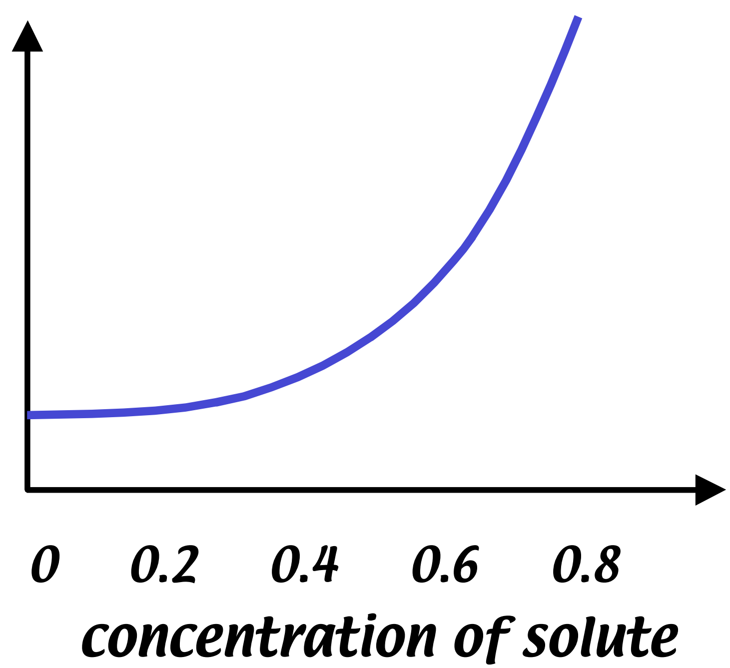
viscosity of air

at 0 = 0.0017 g/ m s

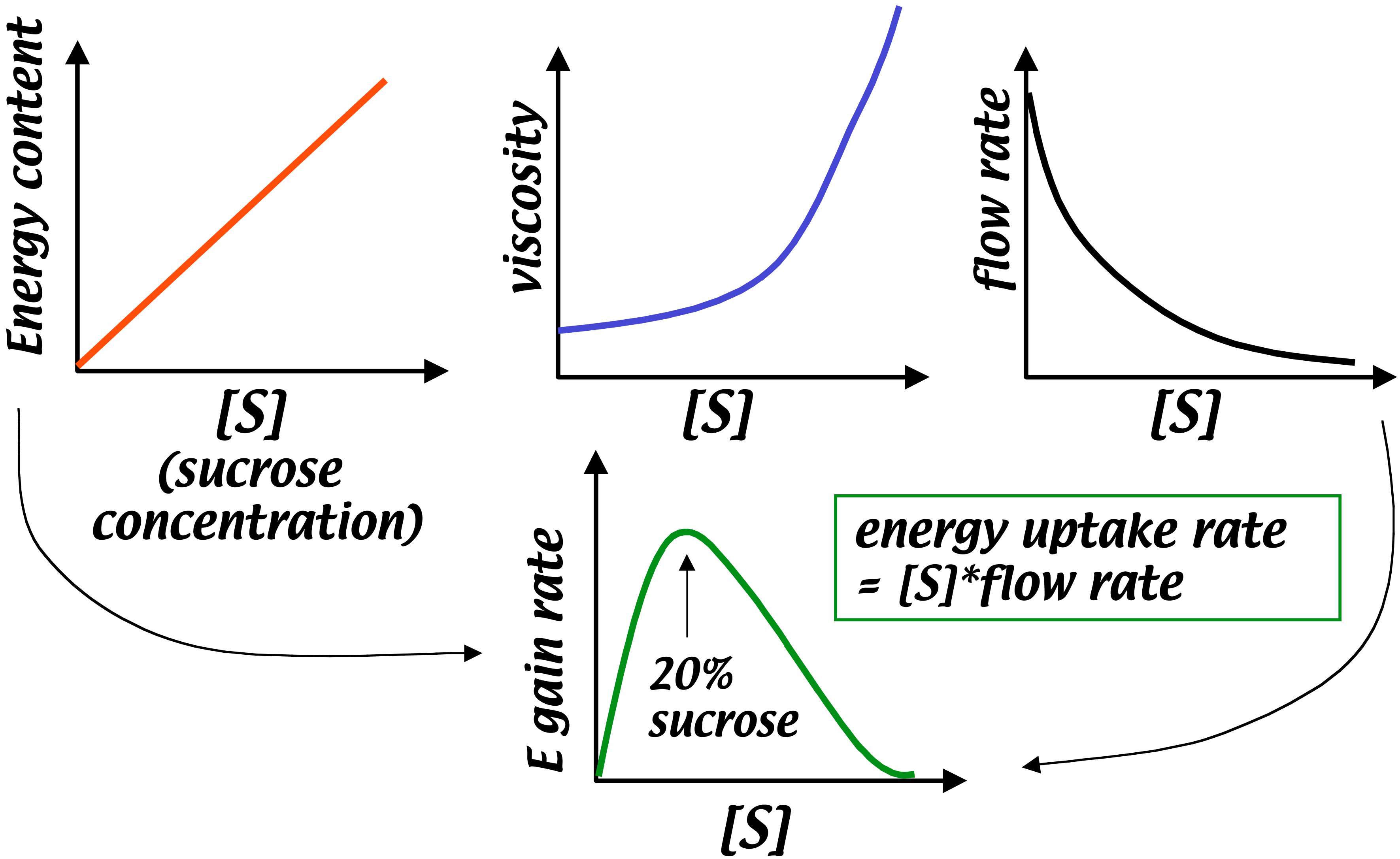
at 20 = 0.0018 g/ms

at 40 = 0.0019 g/m s

Concentration of dissolved or suspended solutes ... Viscosity increases exponentially with concentration



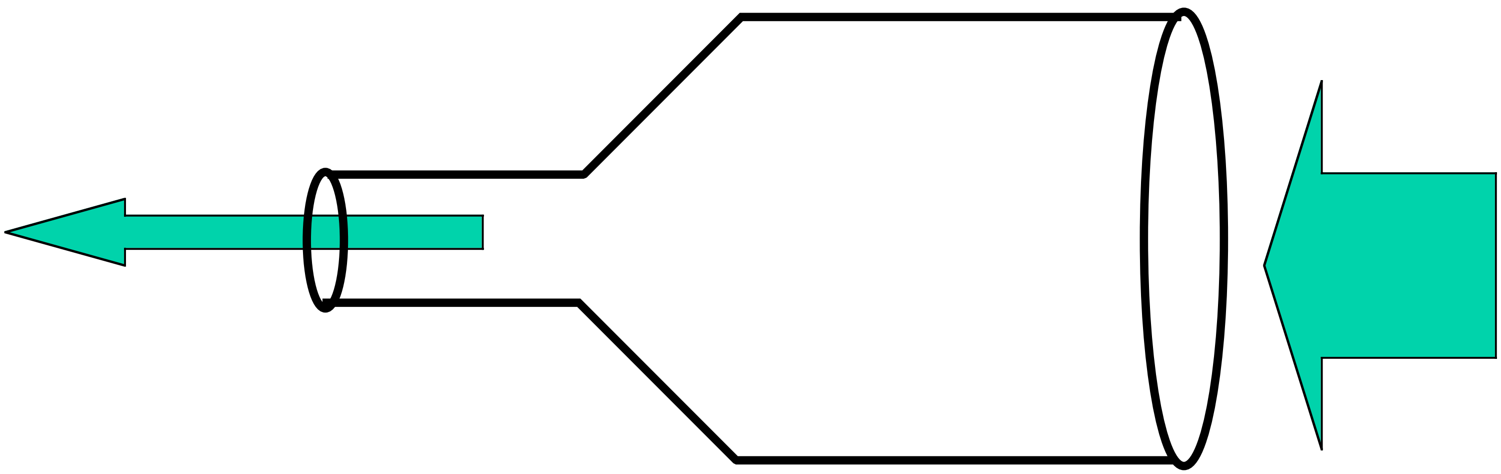
Nectars in moth and butterfly-pollinated flowers are produced at concentrations that maximize pollinators' energy uptake rate



Continuity (Conservation of mass)

What goes in must come out

(mass may not appear or disapear)



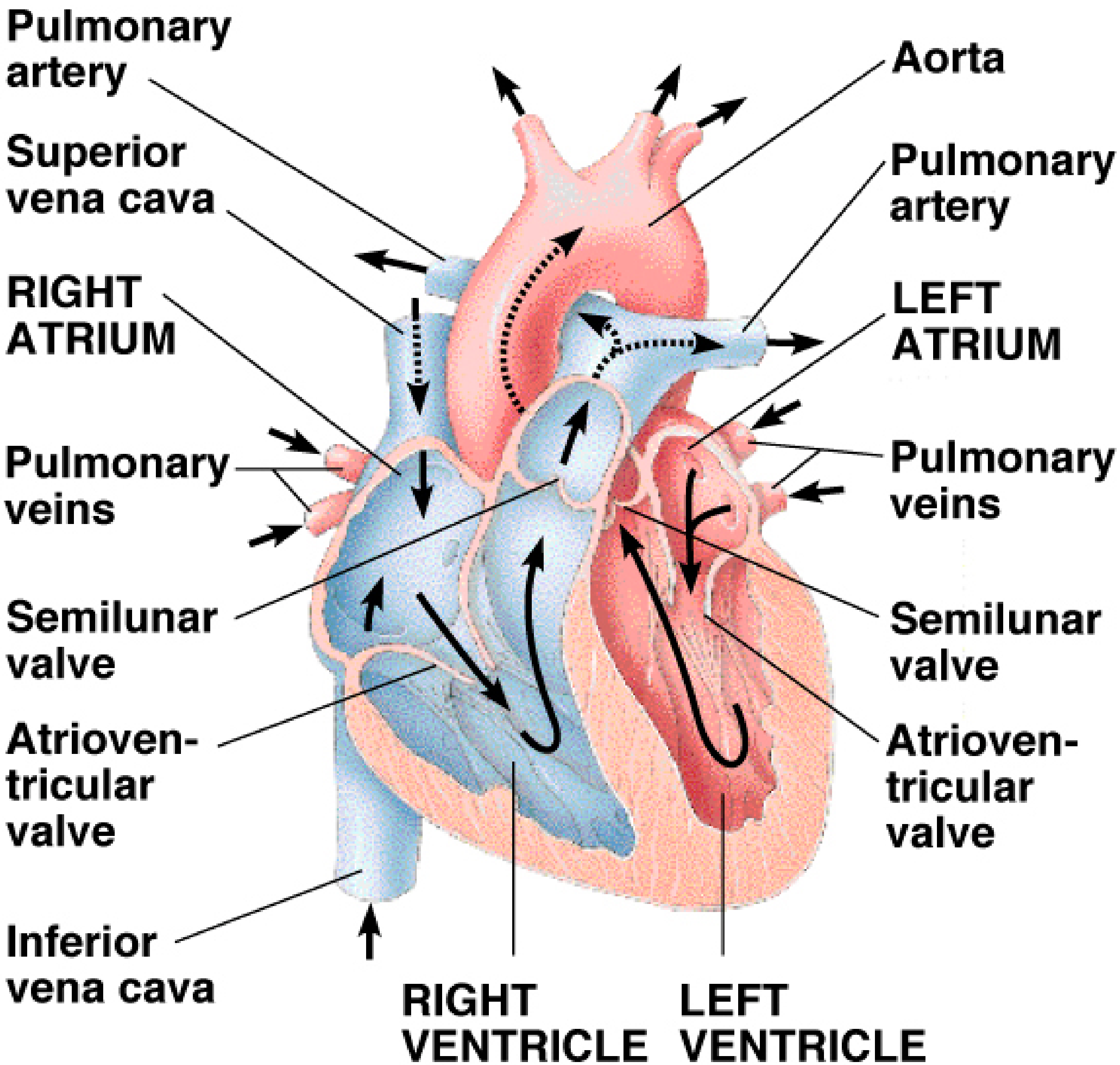
Volume$_{out}$/time

$u_{out}\ A_{out}$

Volume$_{in}$/time

$u_{in}\ A_{in}$

$$u_{in} A_{in} = u_{out} A_{out}$$



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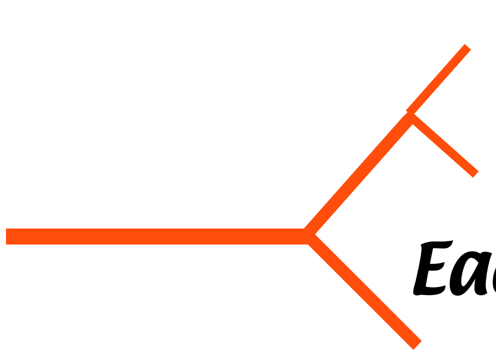
How many capillaries (N) ?

Aorta Area 1 cm^2

Aorta velocity 10 cm/s



Capillary velocity = 0.1 cm/s

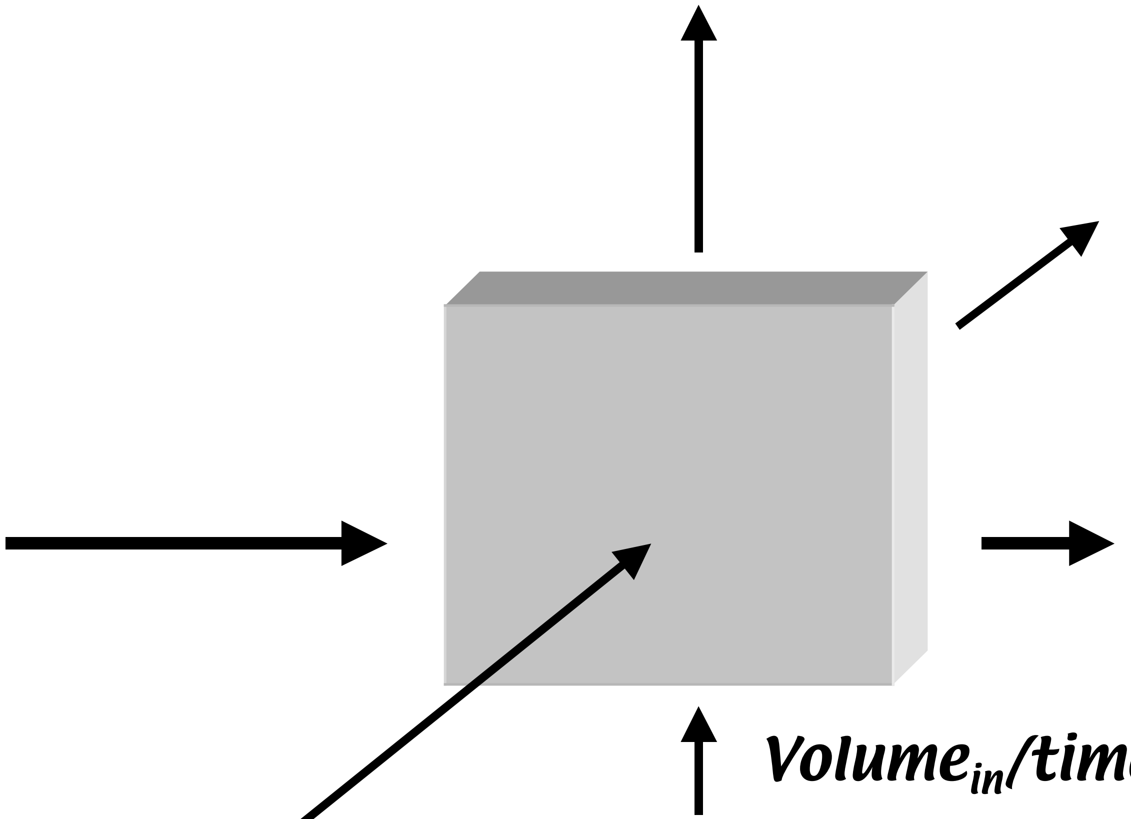
Each capillary has 5 m diameter

$$u_{in} A_{in} = u_{out} A_{out}$$

$$u_{aorta} A_{aorta} = N\, u_{cap} A_{cap}$$

$$N = u_{aorta} A_{aorta} / (u_{cap} A_{cap})$$

Continuity applies at every point in space!



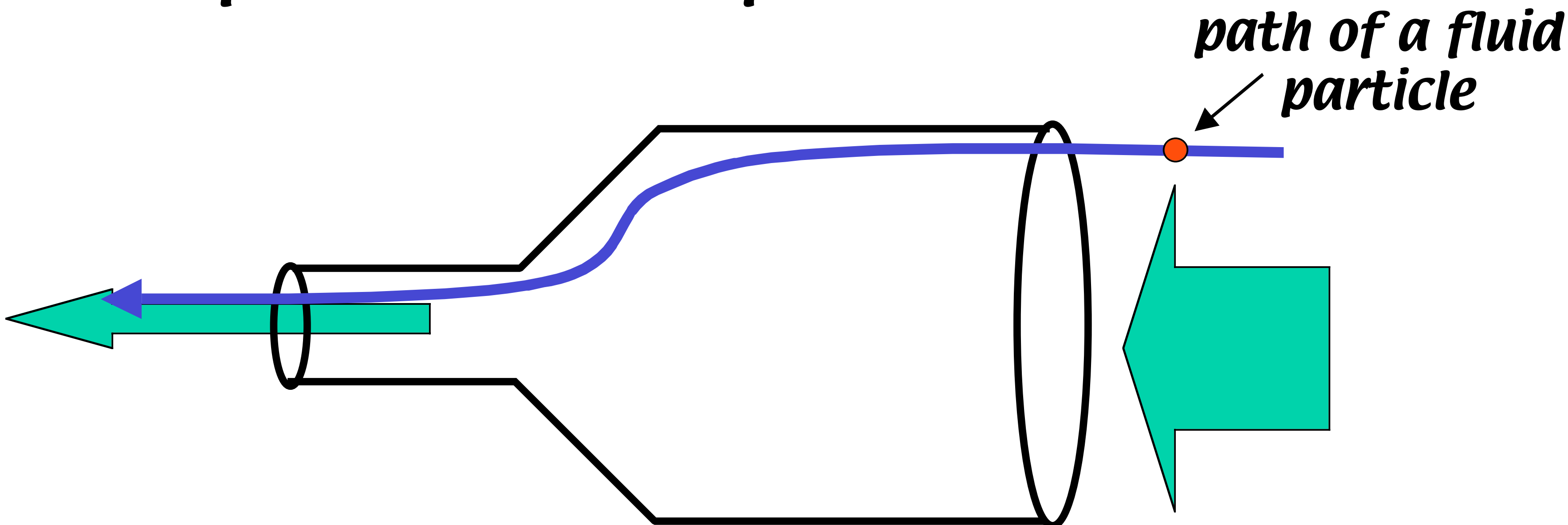
$$Volume_{in}/time = Volume_{out}/time$$

$$u_{in} A_{in} = u_{out} A_{out}$$

$$\partial u/\partial x + \partial v/\partial y + \partial w/\partial z = 0$$

x velocity gradient
(change in velocity in x direction)
(x $velocity_{in}$/x $velocity_{out}$)

Conservation of Energy: what is the relationship between fluid motion and pressure?



Like mass, energy cannot appear or disappear unaccountably -- it is conserved. We will follow this along a streamline.

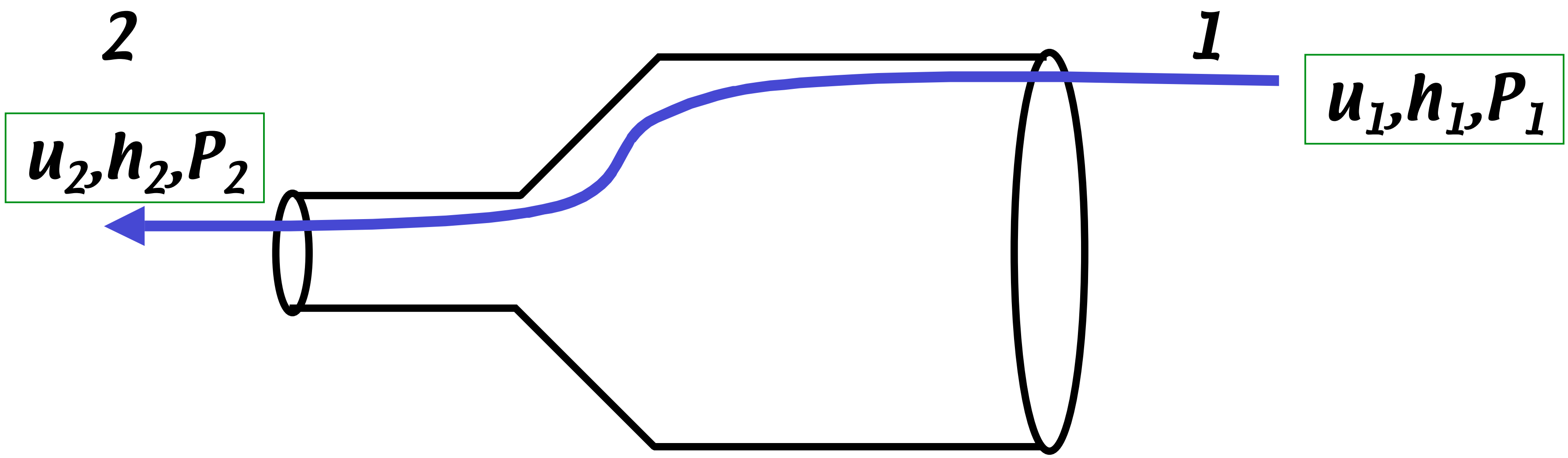
3 assumptions:

► flow is steady (no change in velocity <u>at a fixed point in space</u> - i.e. no pulsing)

► fluid is incompressible (= constant)

► flow is "inviscid" (= 0) ☆ **ignoring viscosity and no-slip condition!**

Conservation of Energy: what is the relationship between fluid motion and pressure?

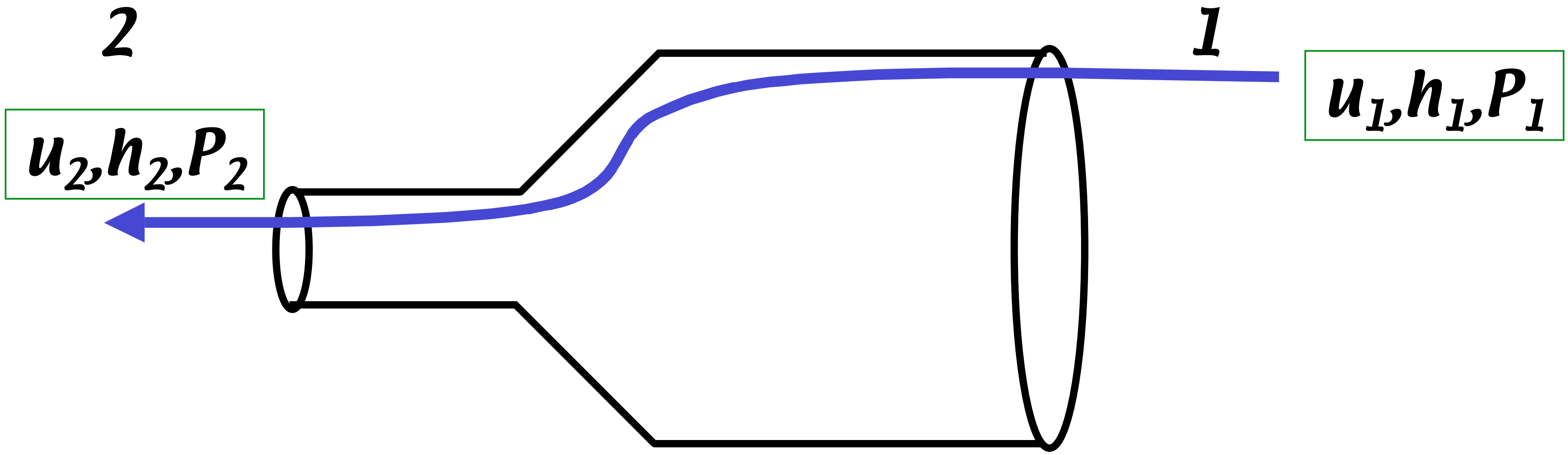


Along a stream line we consider three forms of energy

Potential energy (PE $= m\, g\, h$)
Kinetic energy (KE $= m\, u^2/2$)
Mechanical work (W $= F\, d =$
[P Area] d = P V = P m/)

Along a streamline PE + KE + W = constant

Conservation of Energy: what is the relationship between fluid motion and pressure?



Along a stream line we consider three forms of energy **per unit mass of fluid**

Potential energy (PE = g h)

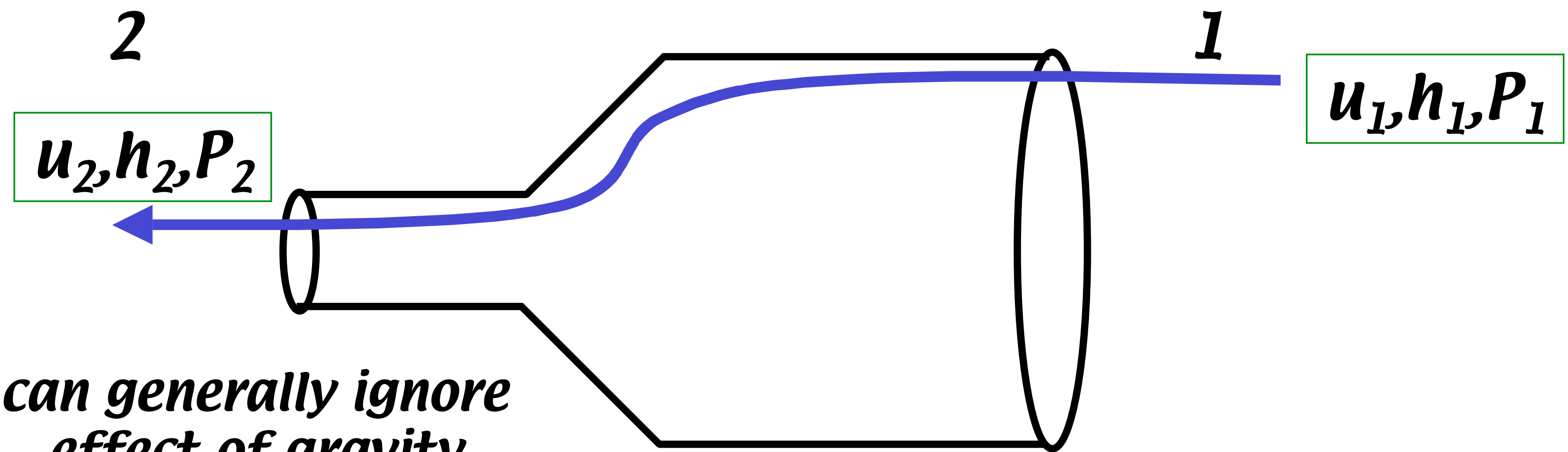
Kinetic energy (KE = $u^2/2$)

Mechanical work (W = F d/m =

[P Area] d/m = P V/m = P /)

Along a streamline gh + $u^2/2$ + P / = constant

Conservation of Energy: what is the relationship between fluid motion and pressure?



can generally ignore effect of gravity

$$gh_2 + u_2^2/2 + P_2/ \quad = gh_1 + u_1^2/2 + P_1/$$

$$g(h_2 - h_1) + (u_2^2 - u_1^2)/2 + (P_2 - P_1)/ \quad = 0$$

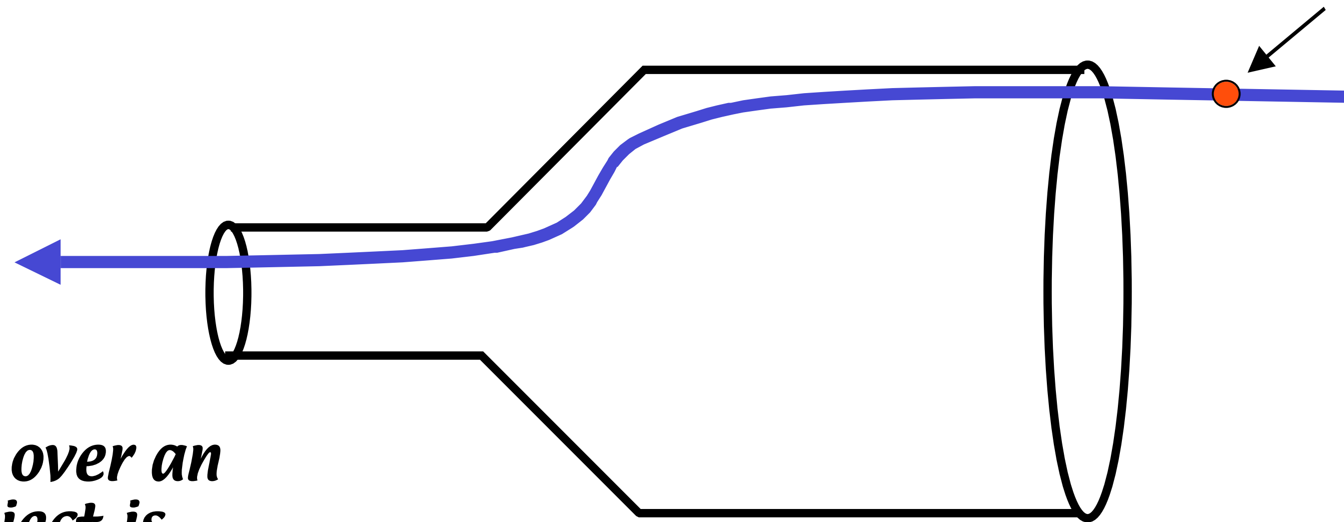
$$(u_2^2 - u_1^2)/2 + (P_2 - P_1)/ \quad = 0$$

Bernoulli's Principle

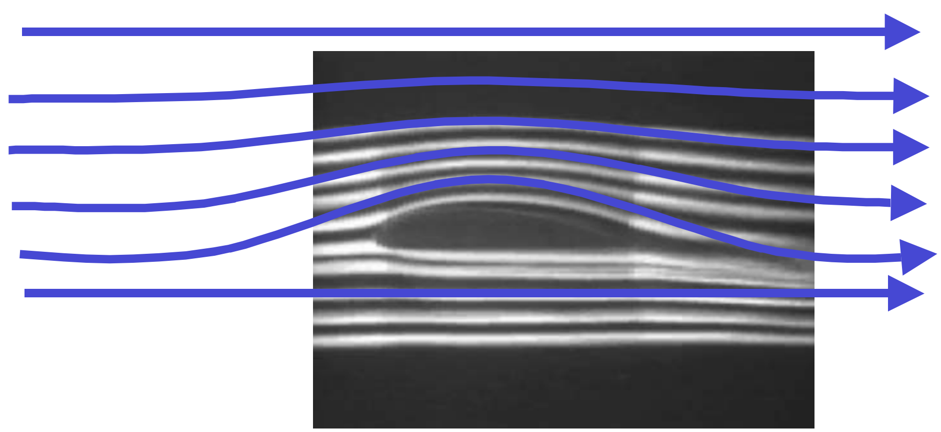
Along a streamline $\quad gh + u^2/2 + P/ \quad = \text{constant}$

Conservation of Energy: what is the relationship between fluid motion and pressure?

path of a fluid particle



flow over an object is constricted just like flow through a tube

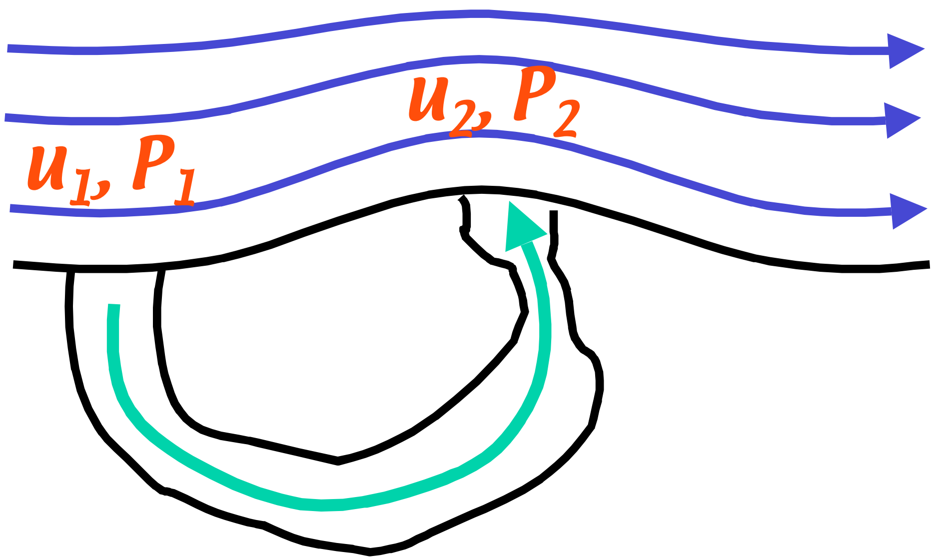


Energy is conserved along a streamline in open flow too

$$(P_2 - P_1)/\quad = (u_1^2 - u_2^2)/2$$

Conservation of Energy: what is the relationship between fluid motion and pressure?

Prairie dogs live in two-sided burrows up to 15 m and 3 m under the ground



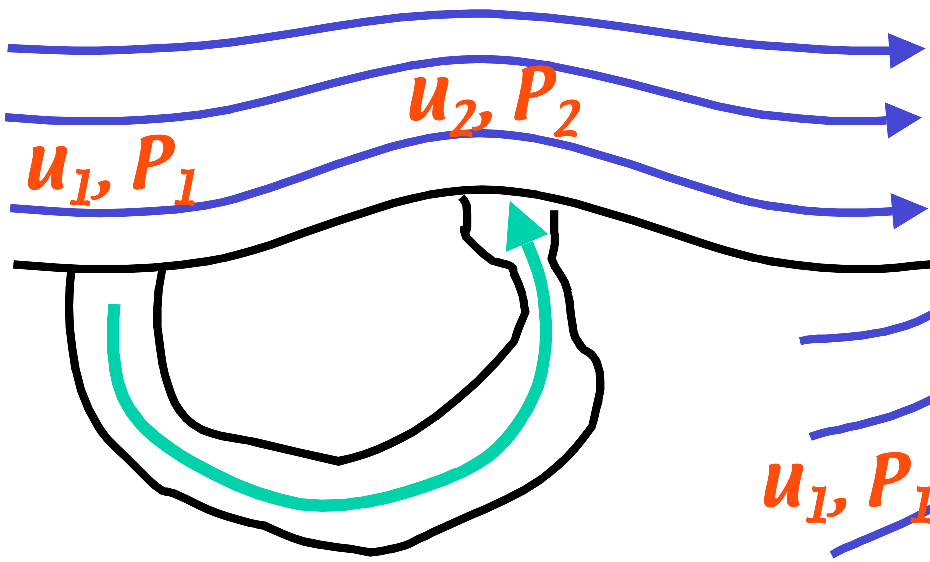
$u_2 > u_1$, so $P_2 < P_1$

1 mile/hr wind can ventilate burrow completely every 10 minutes!

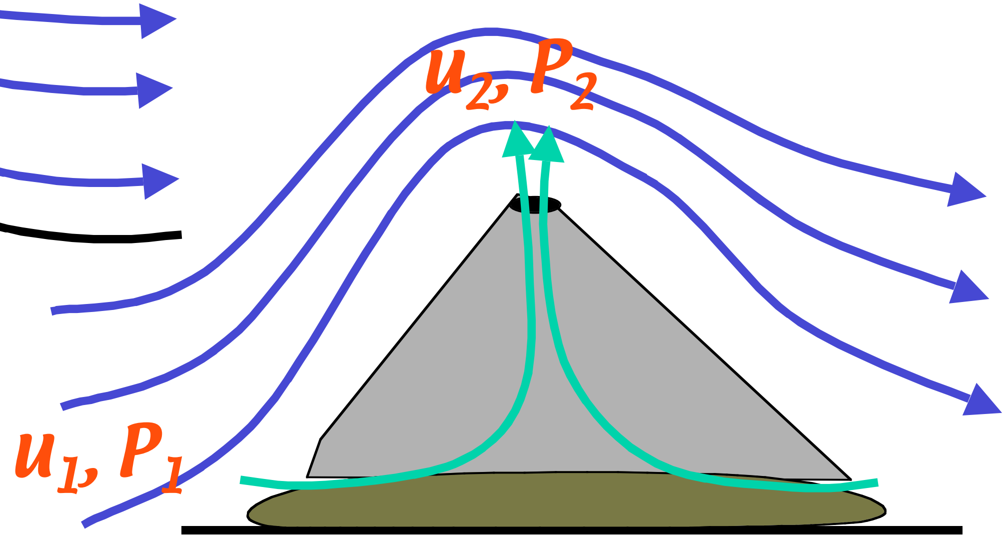
Based on this size, prairie dogs should asphyxiate in their burrows if they just rely on oxygen diffusion --> they need some mechanism of ventilation

$$(P_2 - P_1) / \quad = (u_1^2 - u_2^2)/2$$

Conservation of Energy: what is the relationship between fluid motion and pressure?



sponges,
termite mounds,
teepees.........



keyhole limpet

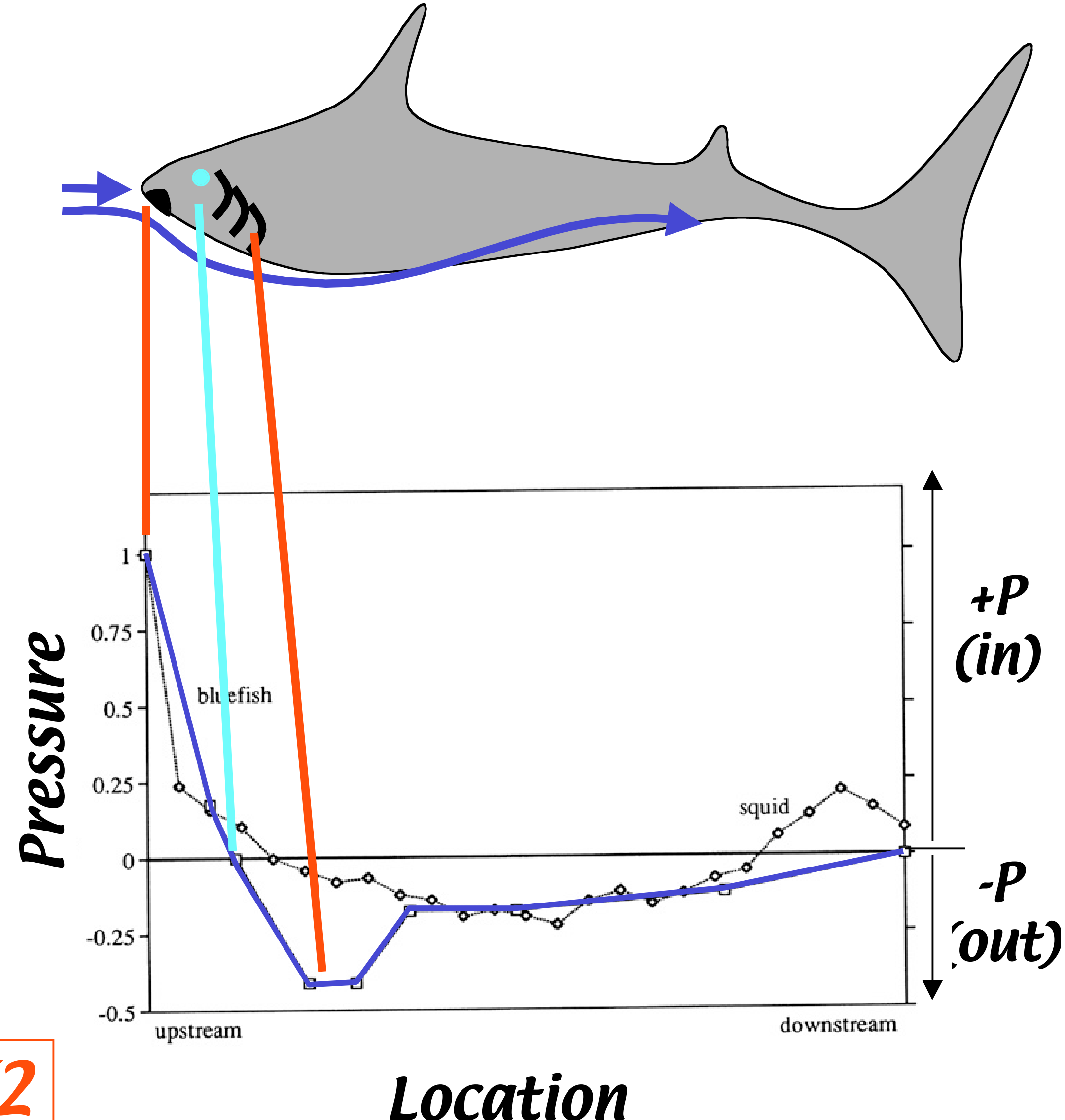
$$(P_2 - P_1) / \quad = (u_1^2 - u_2^2)/2$$

Conservation of Energy: what is the relationship between fluid motion and pressure?

Ram ventilation

(sharks, tuna, mackerel)

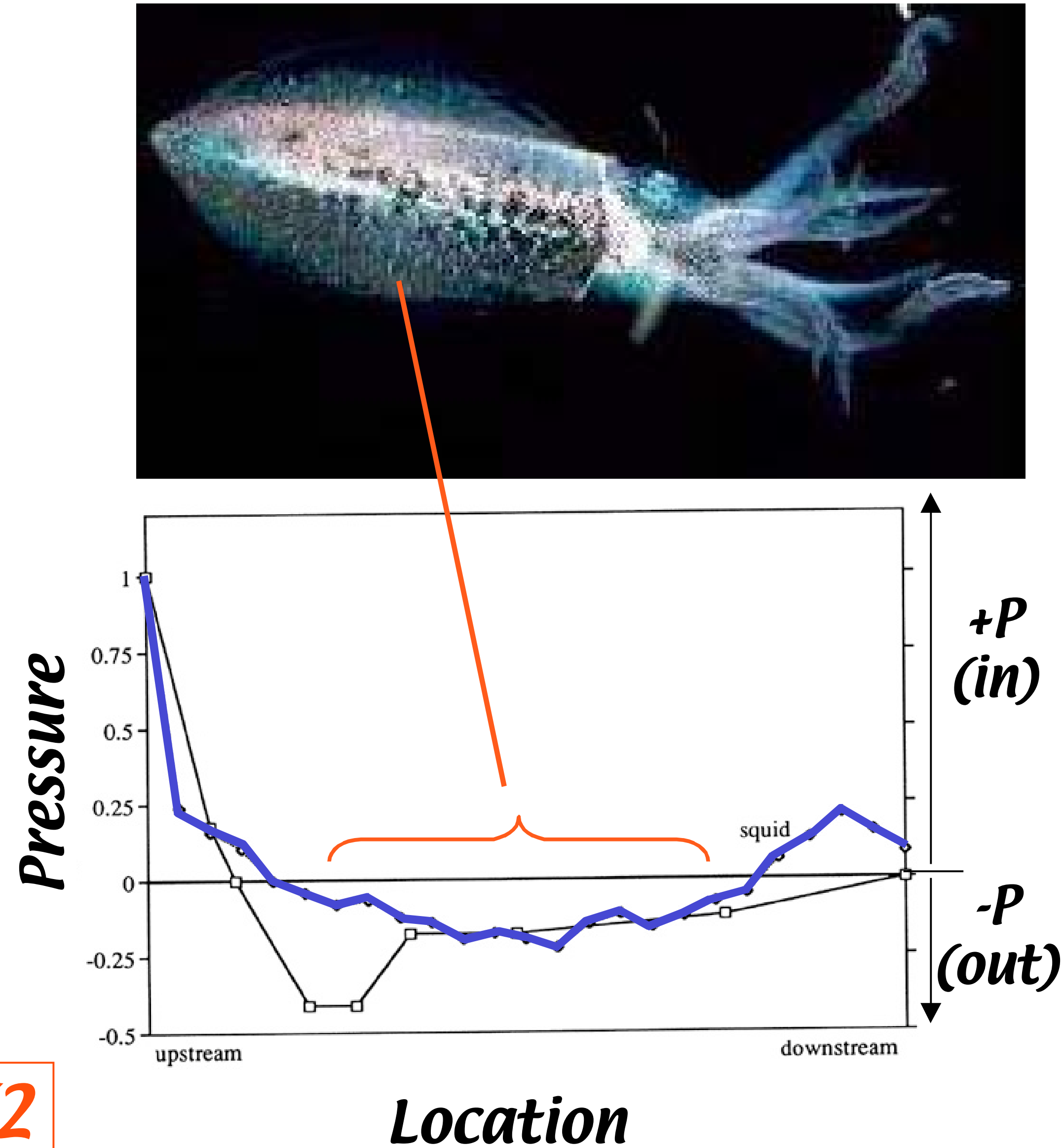
- ▶ventilate gills by pressure difference
- ▶ must swim constantly to breathe!



$(P_2 - P_1) / \quad = (u_1^2 - u_2^2)/2$

Conservation of Energy: what is the relationship between fluid motion and pressure?

▶ Negative pressure on squid mantle helps mantle expand and refill passively



Ram ventilation

(sharks, tuna, mackerel)

▶ ventilate gills by pressure difference

▶ must swim constantly to breathe!

$$(P_2 - P_1) / \quad = (u_1^2 - u_2^2)/2$$

Conserved quantities:

✓Mass

✓Energy

►Momentum is also conserved

Momentum = mu ← velocity has magnitude <u>and</u> direction

Momentum = lSu

Conservation of mass: V_{out}/time = V_{in}/time

$A_{out}u_{out} = A_{in}u_{in}$

Water nozzle reduces A_{out}, so u_{out} increases

But mass (volume) out is same as mass in, so there must be some velocity backwards to balance velocity out of nozzle

►hose kicks back to conserve momentum

Conserved quantities: ▸**Momentum** is also conserved

✓Mass

✓Energy

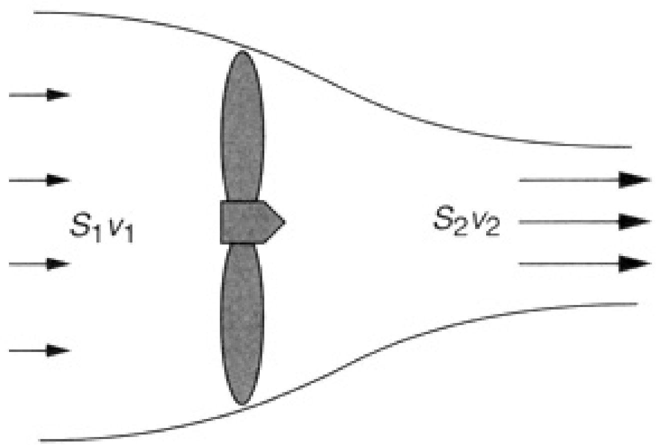
Momentum = mu ← velocity has magnitude and direction

Momentum = lSu

Conservation of mass: V_{out}/time = V_{in}/time

$A_{out}u_{out} = A_{in}u_{in}$

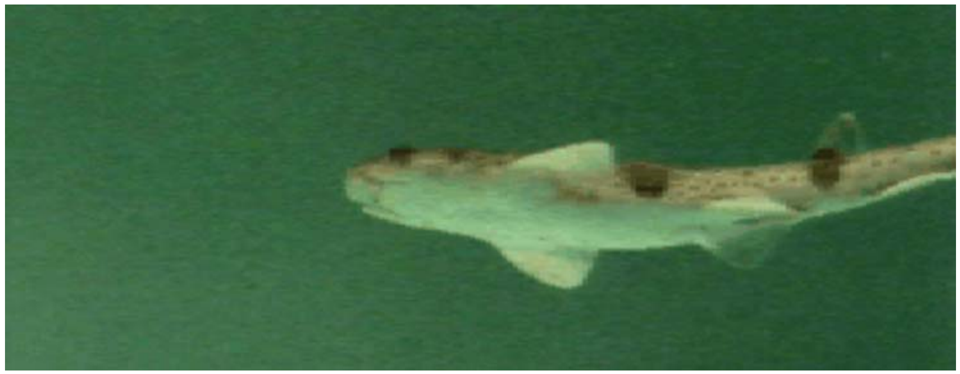
Fan or propeller reduces area and increases velocity of airstream



$mass_{out} = mass_{in}$, so backward velocity must balance forward velocity to conserve momentum

▸ backwards momentum from propeller moves boat forward

How does momentum change relate to motion through fluids?



$$F = ma = m(u/t) = (mu)/t = \text{change in momentum}$$

$$F = (Slu)/t = Sv^2$$

fish swims forward by imparting rearward momentum to the water

(muscle forces produce change in momentum of water)

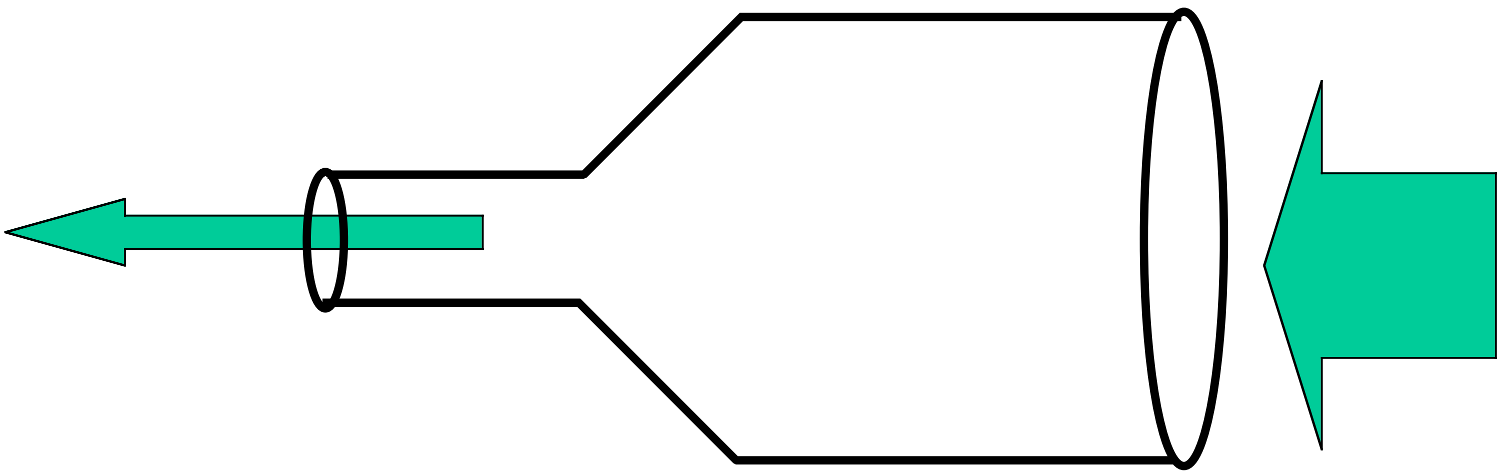
Biology 427 Biomechanics
Lecture 17. Drag and the Reynolds number.

- Recap conservation of mass and energy
- Conservation of momentum
- D'Alembert's Paradox and the missing energy
- The Reynolds number measures the relative importance of viscous and inertial stresses
- A wake is a separate issue
- Reynolds number and the function of hairy little appendages

Continuity (Conservation of mass)

What goes in must come out

(mass may not appear or disapear)



Volume$_{out}$/time

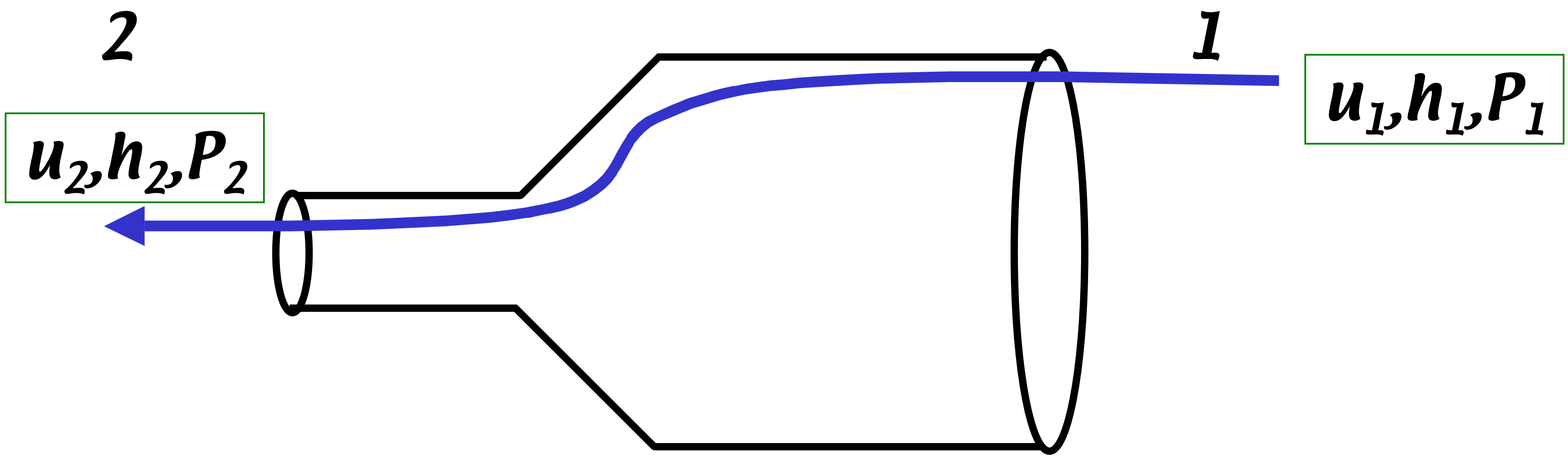
$u_{out} A_{out}$

Volume$_{in}$/time

$u_{in} A_{in}$

$$\Sigma u_{in} A_{in} = \Sigma u_{out} A_{out}$$

Conservation of Energy: what is the relationship between fluid motion and pressure?



Along a stream line we consider three forms of energy **per unit mass of fluid**

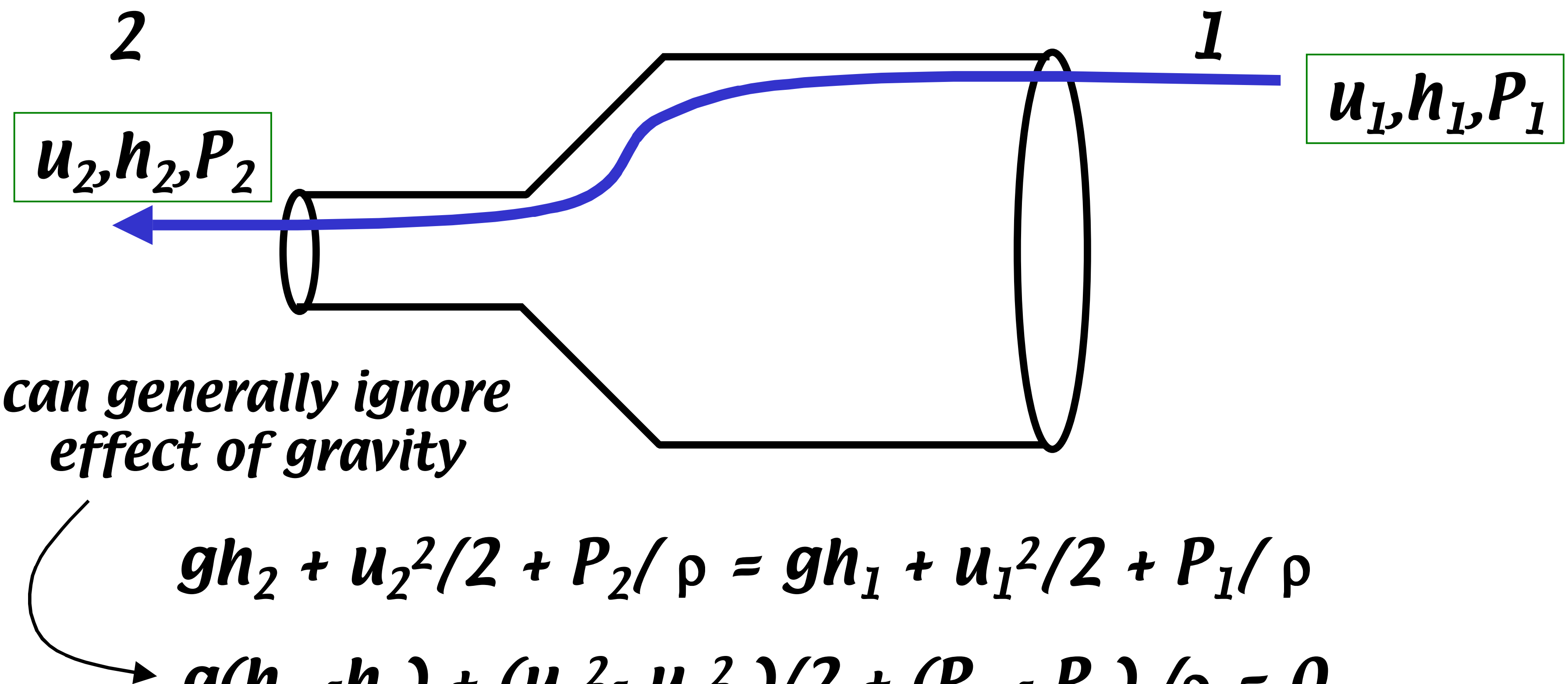
Potential energy (PE = $g\,h$)

Kinetic energy (KE = $u^2/2$)

Mechanical work ($W = F\,d/m$ = [P Area] $d/m = P\,V/m = P\,/\,\rho$)

Along a streamline $gh + u^2/2 + P\,/\,\rho$ = constant

Conservation of Energy: what is the relationship between fluid motion and pressure?



$$gh_2 + u_2^2/2 + P_2/\rho = gh_1 + u_1^2/2 + P_1/\rho$$

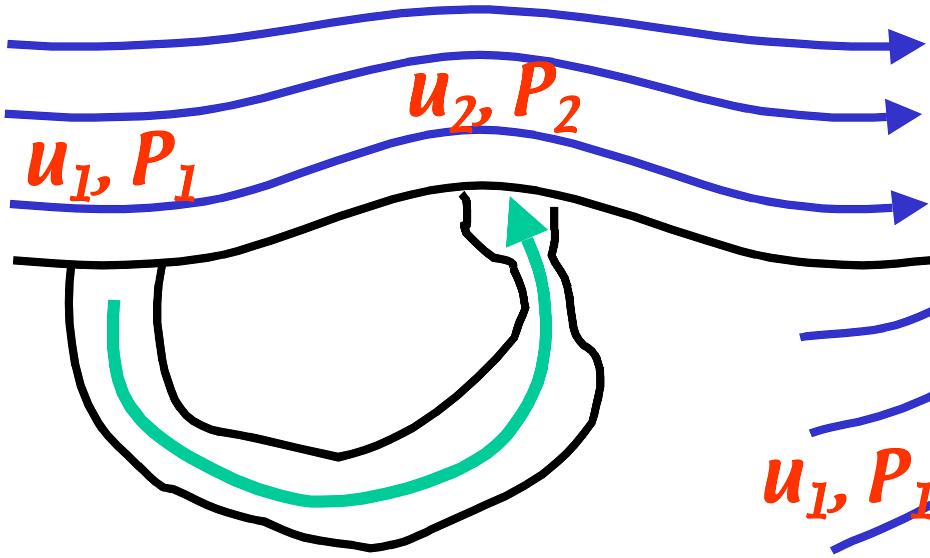
$$g(h_2 - h_1) + (u_2^2 - u_1^2)/2 + (P_2 - P_1)/\rho = 0$$

$$(u_2^2 - u_1^2)/2 + (P_2 - P_1)/\rho = 0$$

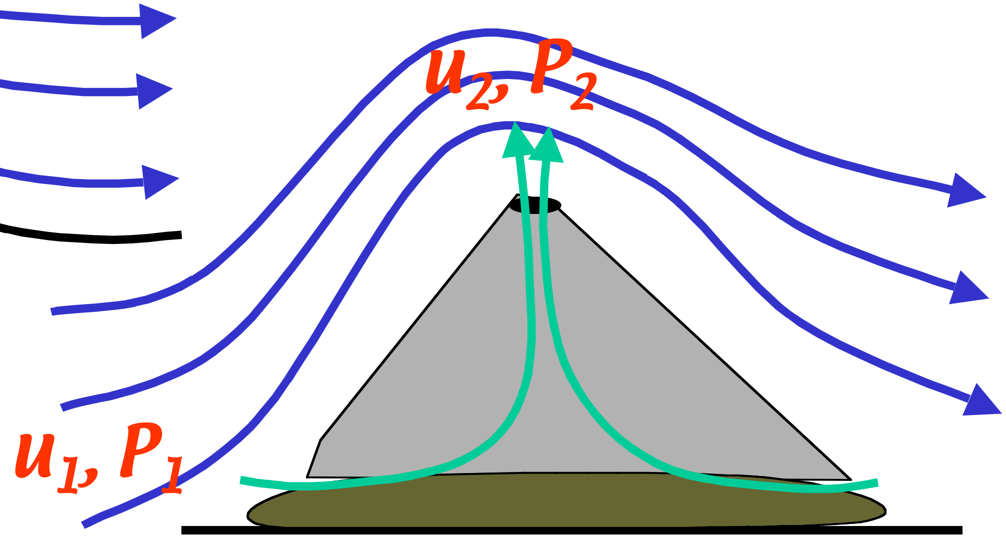
Bernoulli's Principle

Along a streamline $gh + u^2/2 + P/\rho = \text{constant}$

Conservation of Energy: what is the relationship between fluid motion and pressure?

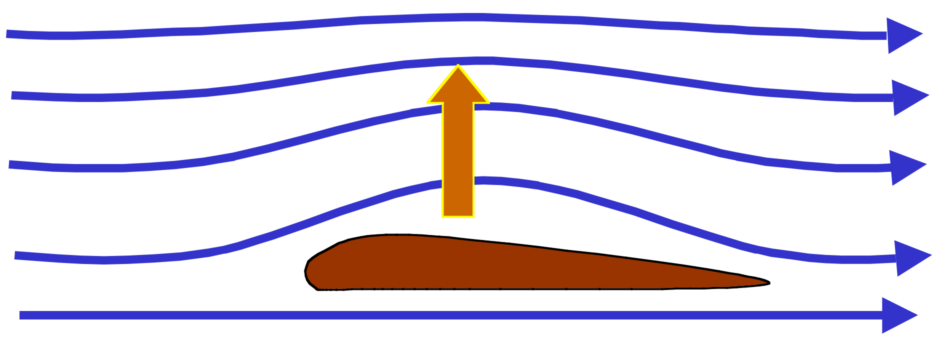


prairie dog burrow



keyhole limpet

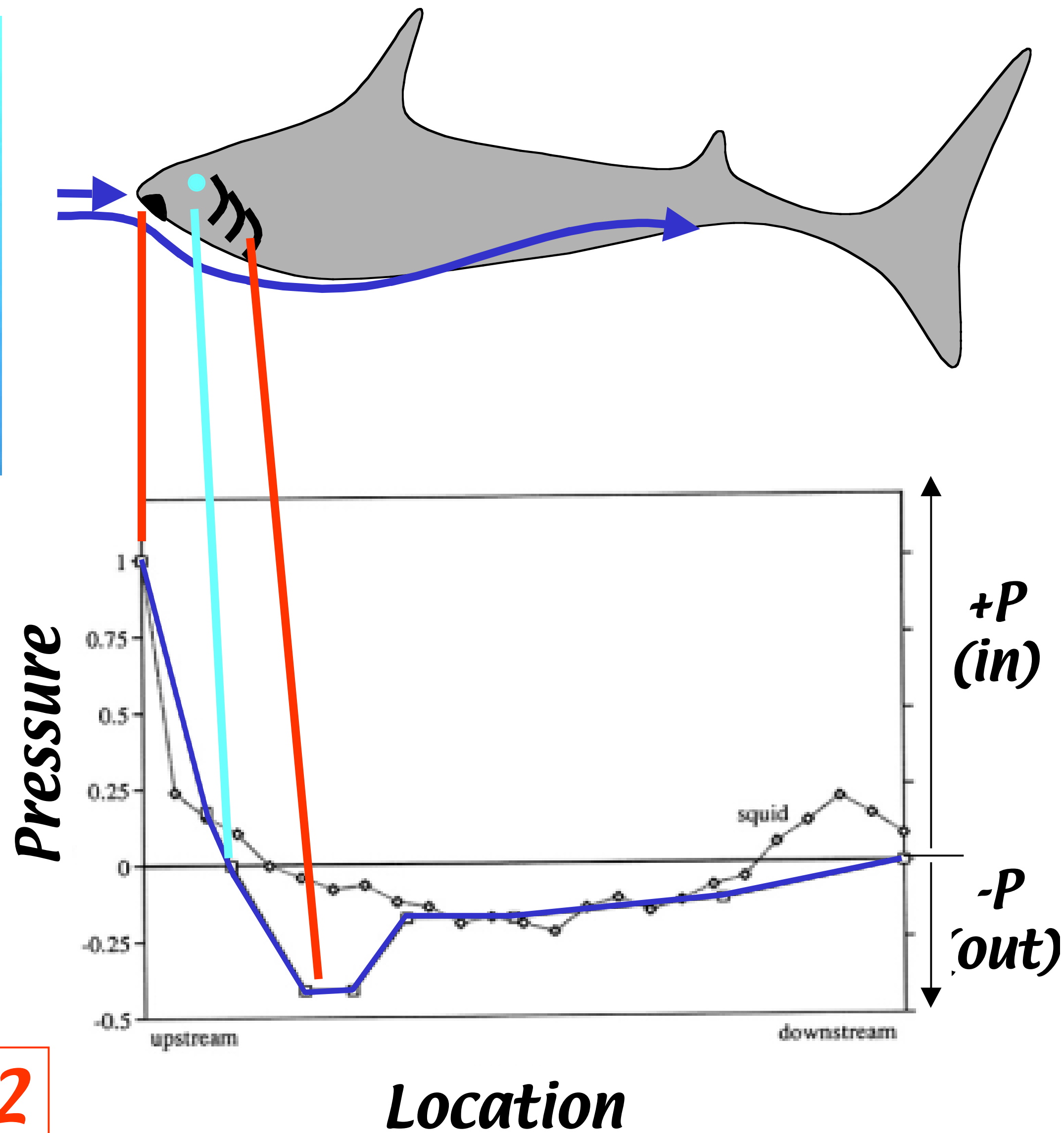
Induced flow provides passive ventilation



$$(P_2 - P_1)/\rho = (u_1^2 - u_2^2)/2$$

also in sponges, termite mounds, teepees........

Conservation of Energy: what is the relationship between fluid motion and pressure?



Ram ventilation

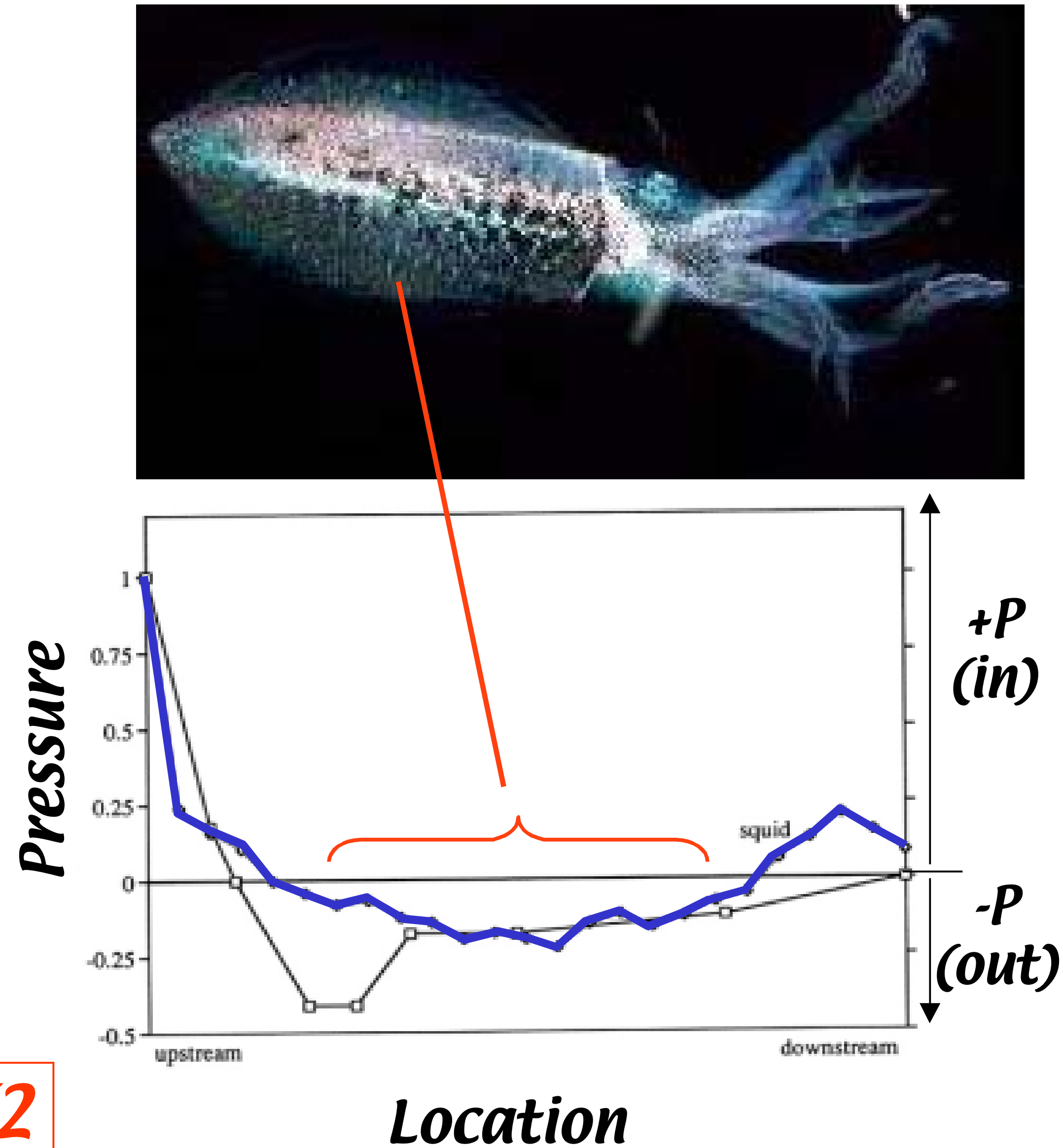
(sharks, tuna, mackerel)

- ▸ventilate gills by pressure difference
- ▸ must swim constantly to breathe!

$$(P_2 - P_1)/\rho = (u_1^2 - u_2^2)/2$$

Conservation of Energy: what is the relationship between fluid motion and pressure?

▸ *Negative pressure on squid mantle helps mantle expand and refill passively*



Ram ventilation

(sharks, tuna, mackerel)

▸ *ventilate gills by pressure difference*

▸ *must swim constantly to breathe!*

$$(P_2 - P_1)/\rho = (u_1^2 - u_2^2)/2$$

Conserved quantities:

✓Mass

✓Energy

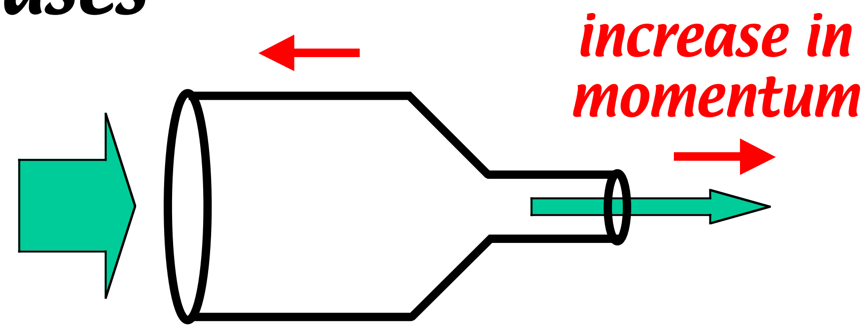
►Momentum is also conserved

Momentum = mu ← velocity has magnitude and direction

Conservation of mass: V_{out}/time = V_{in}/time

$A_{out}u_{out} = A_{in}u_{in}$

Water nozzle reduces A_{out}, so u_{out} increases



Mass (volume) out is the same as mass in, so there is an increase in forward momentum

►hose kicks back to conserve momentum

Conserved quantities:

✓ Mass

✓ Energy

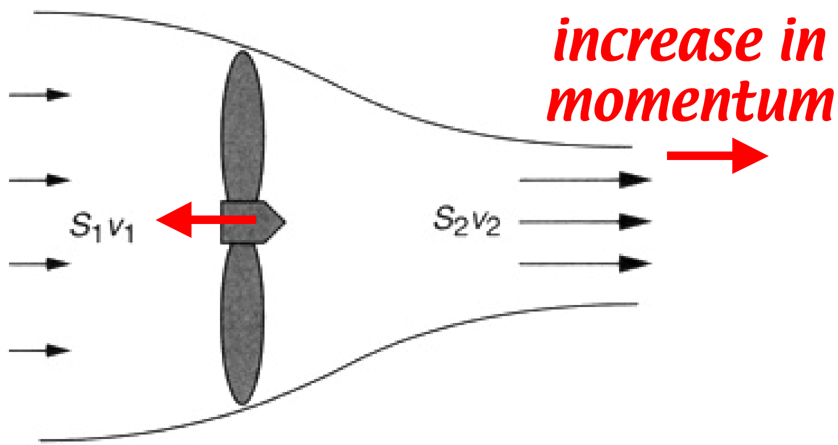
► **Momentum** is also conserved

Momentum = mu ← velocity has magnitude and direction

Conservation of mass: $V_{out}/time = V_{in}/time$

$A_{out}u_{out} = A_{in}u_{in}$

Fan or propeller reduces area and increases velocity of airstream



$mass_{out} = mass_{in}$
backward momentum on fan must balance forward momentum of fluid

► backwards momentum from propeller moves boat forward

How does momentum change relate to motion through fluids?

change in momentum = (mu)/t = m(u/t) = ma = F

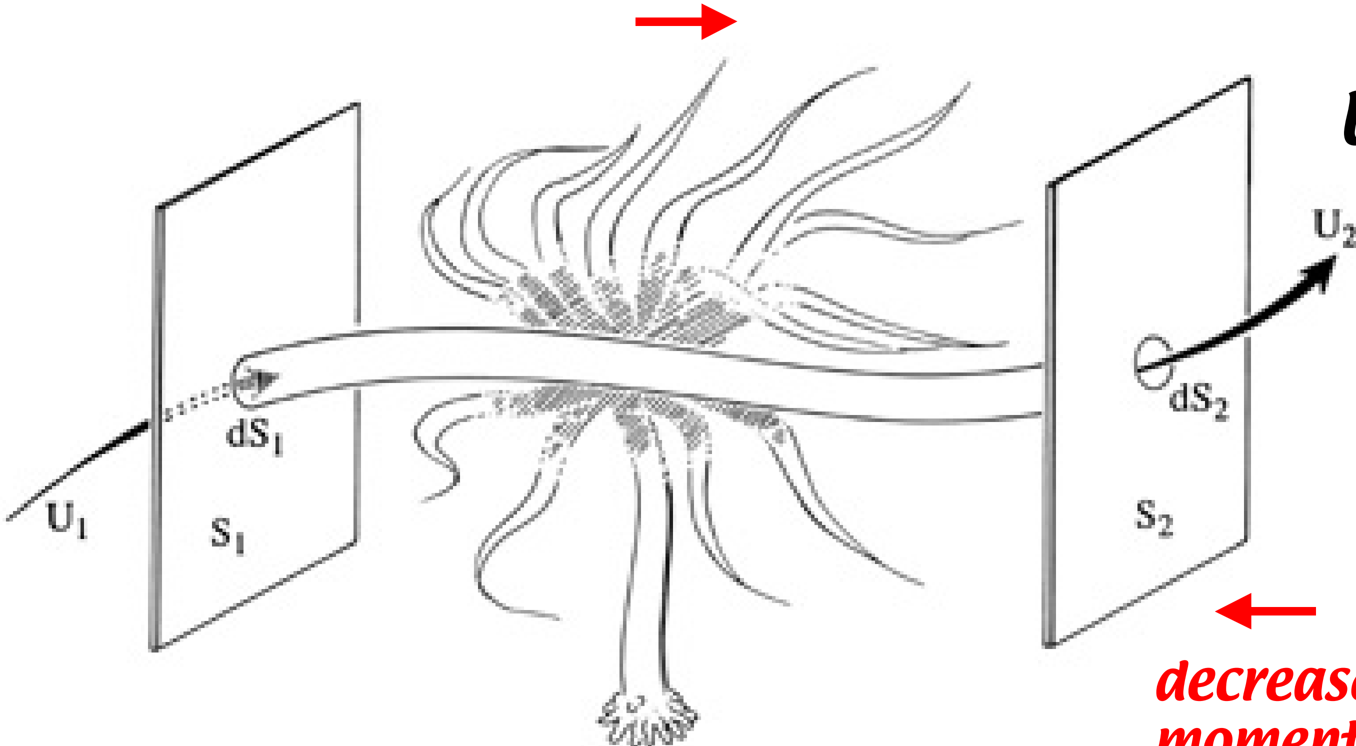
$$F = (\rho Slu)/t = \rho Su^2$$

fish swims forward by imparting rearward momentum to the water

(muscle forces produce change in momentum of water which moves fish forward)

How is momentum conserved when moving fluid passes by an object?

Force on object = Drag



$U_2 < U_1$

decrease in momentum

change in momentum = (mu)/t = m(u/t) = ma = F

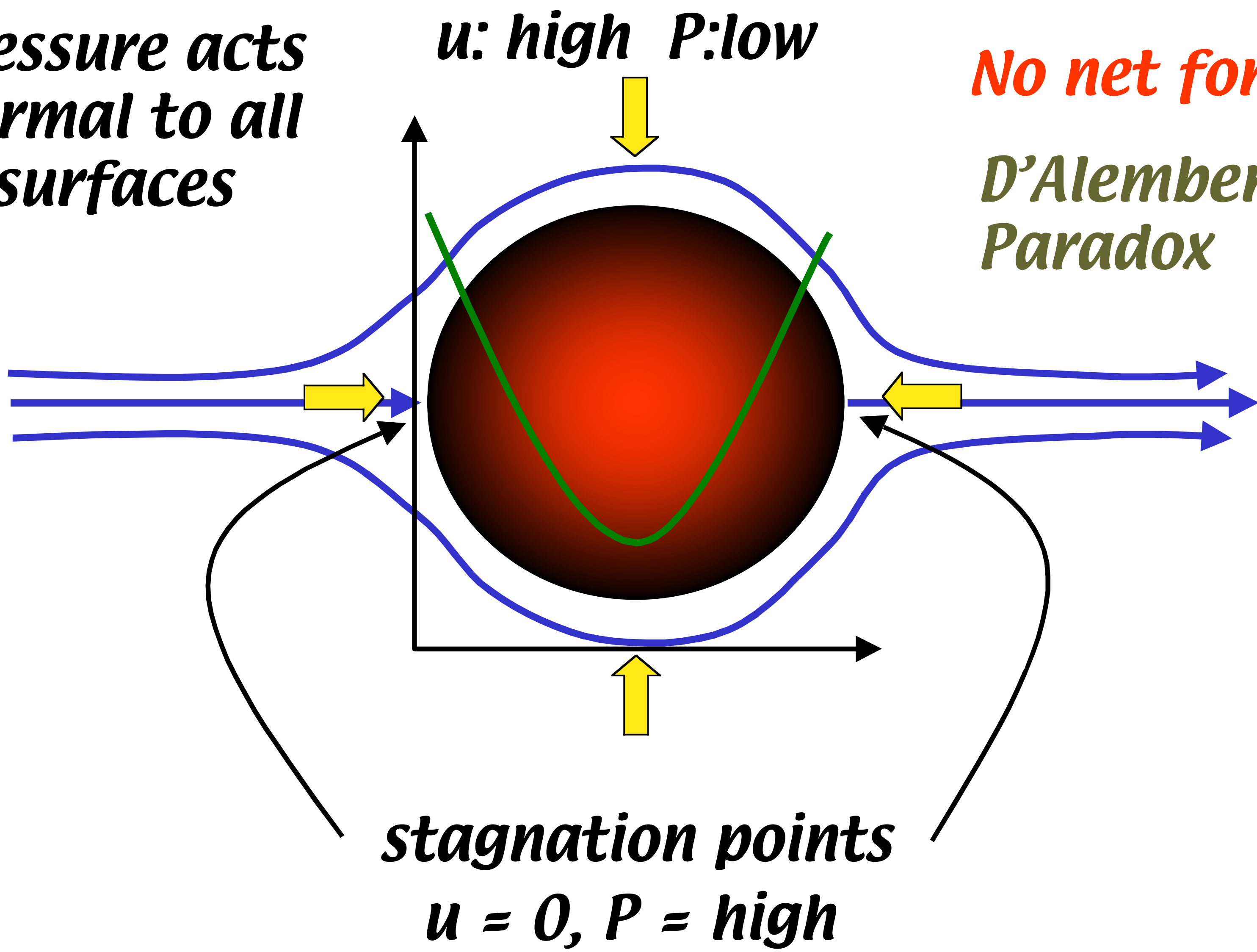
How is energy conserved when moving fluid passes by an object?

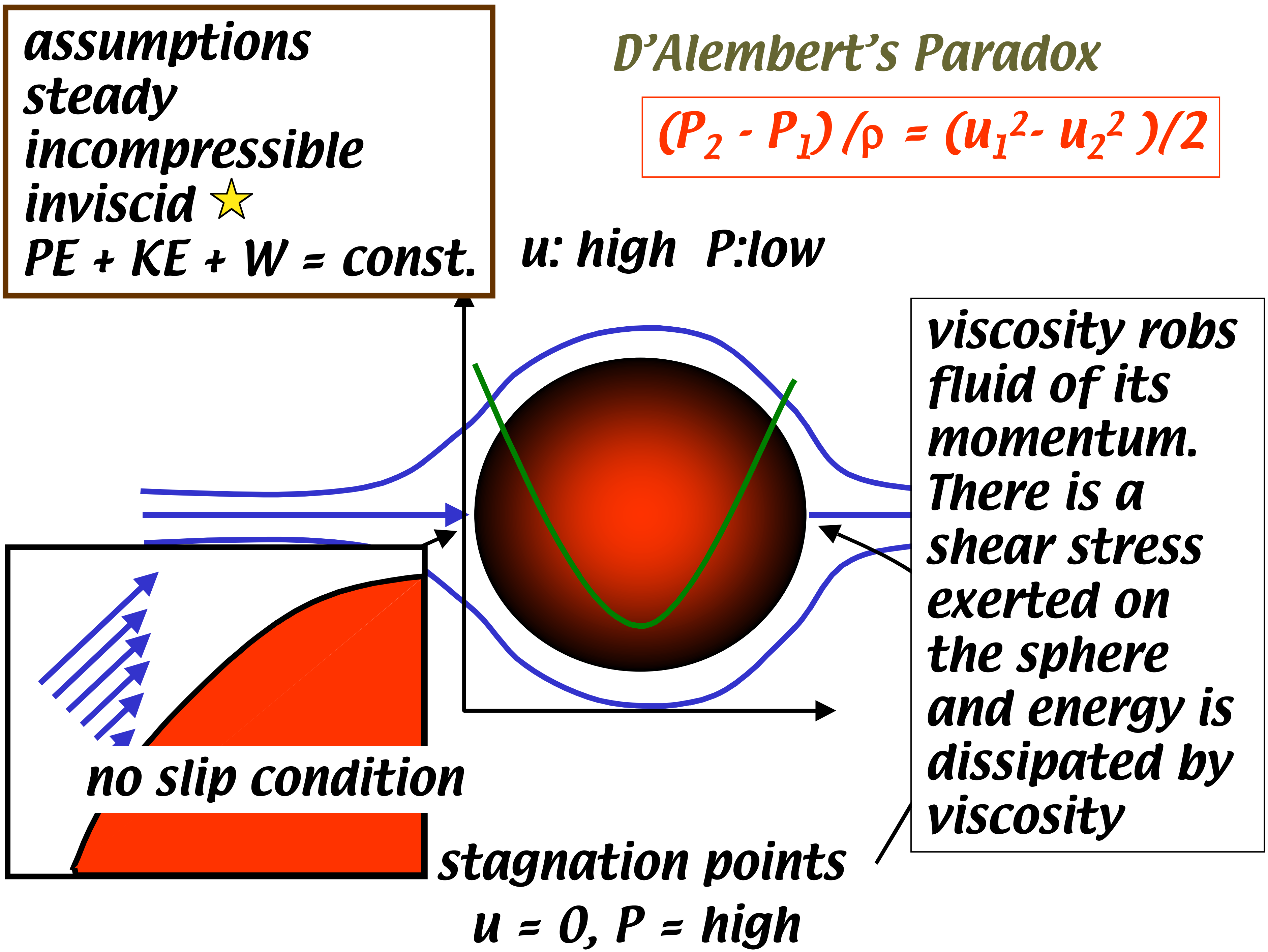
$$(P_2 - P_1)/\rho = (u_1^2 - u_2^2)/2$$

pressure acts normal to all surfaces

No net force?

D'Alembert's Paradox





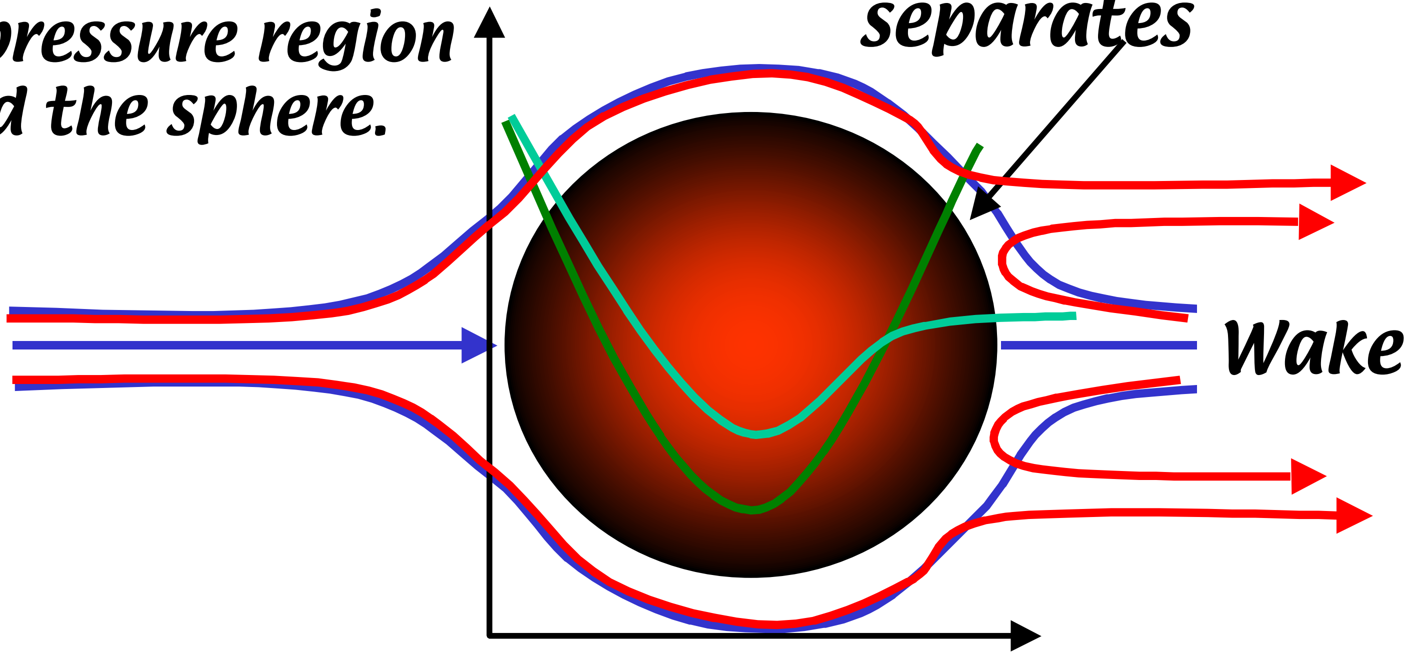
assumptions
steady
incompressible
inviscid
PE + KE + W = const.
D'Alembert's Paradox
(P2 - P1) /ρ = (u1²- u2²)/2
u: high P:low
viscosity robs fluid of its momentum. There is a shear stress exerted on the sphere and energy is dissipated by viscosity
no slip condition
stagnation points
u = 0, P = high

PE + KE + W + Ediss = const

$(P_2 - P_1)/\rho = (u_1^2 - u_2^2)/2$

because of viscosity, velocity cannot increase enough to penetrate the high pressure region behind the sphere.

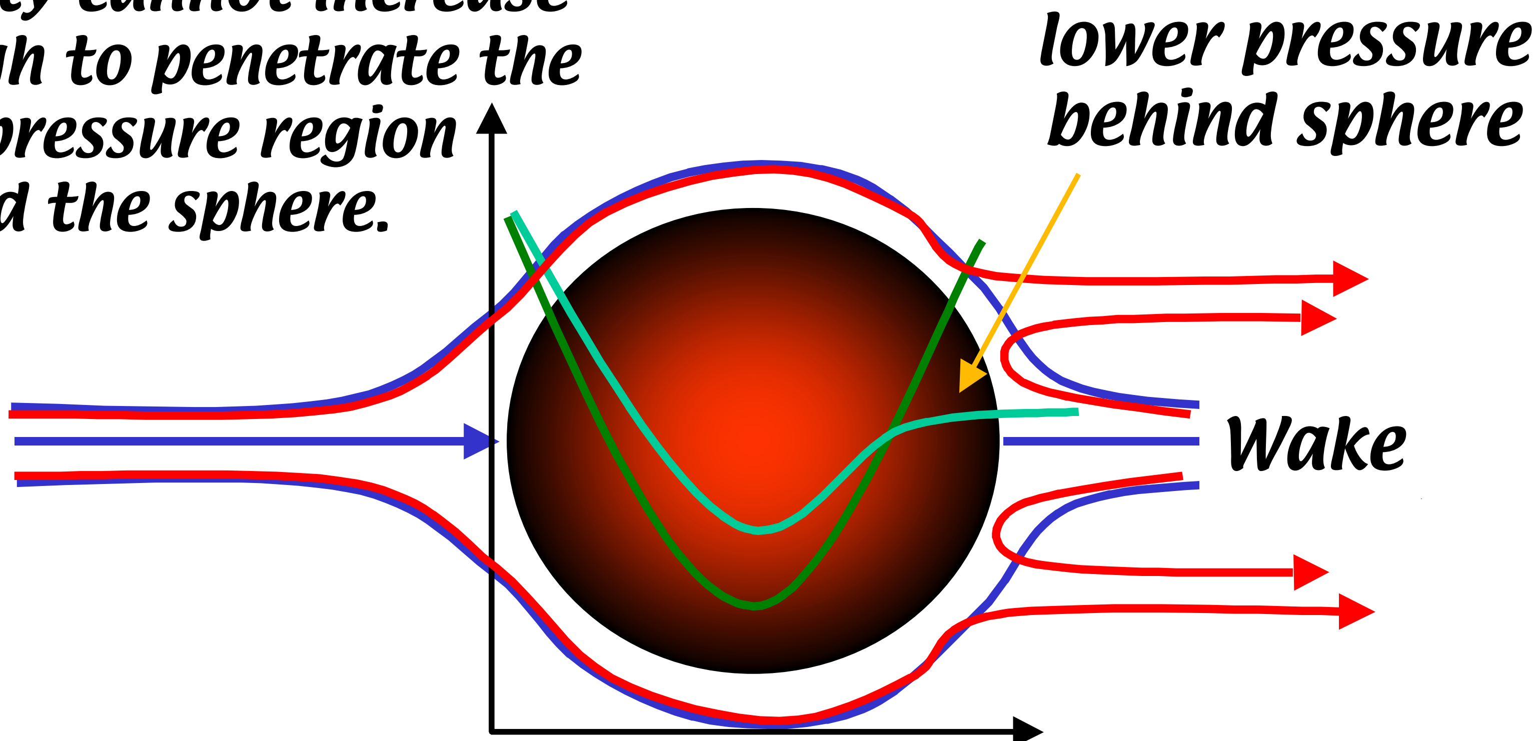
new stagnation point where the flow separates



PE + KE + W + Ediss = const

$(P_2 - P_1)/\rho = (u_1^2 - u_2^2)/2$

because of viscosity, velocity cannot increase enough to penetrate the high pressure region behind the sphere.



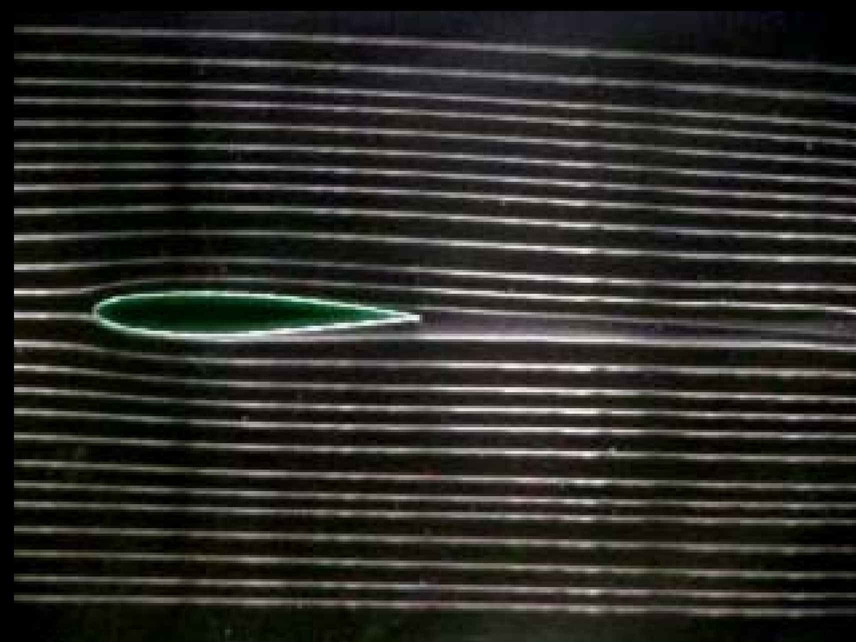
There are two mechanisms leading to drag force:

- ▸ the fore-aft asymmetry in pressure : pressure drag
- ▸ shear stress on the sphere : friction drag

The total drag is a composite of these and depends on size and shape of the body

An object with a large amount of surface area perpendicular to the flow experiences large pressure drag

An object with a large amount of surface area parallel to the flow experiences large friction drag



How can we quantify the relative contributions of pressure stress and shear stress to total drag?

Pressure stress: $P \sim \rho u^2$

$$(P_2 - P_1)/\rho = (u_1^2 - u_2^2)/2$$

How can we quantify the relative contributions of pressure stress and shear stress to total drag?

$$\frac{\text{Pressure stress: } P \sim \rho\, u^2}{\text{Shear stress: } \tau \sim \mu\, u/L} = Re = \frac{\rho\, u\, L}{\mu}$$

Reynolds number measures the relative importance of inertial (pressure) and viscous (friction) stresses

Inertial effects : fluid particles want to keep moving as they have been moving (resist acceleration or deceleration)

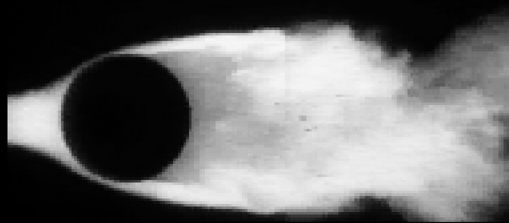
Viscous effects : fluid particles want to stay together (resist shear and formation of velocity gradients)

Re is a non-dimensional measure:

$$Re = \frac{\rho\, u\, L}{\mu} \quad \left[\frac{m}{L^3}\ \frac{L}{t}\ \frac{L}{}\ \ \underbrace{\frac{t^2\, L^2}{m\ \ L}\ \frac{}{t}}_{\mu\ (Pa*s)} \right]$$

The Reynolds number measures the relative importance of inertial and viscous stresses in determining the pattern of flow.

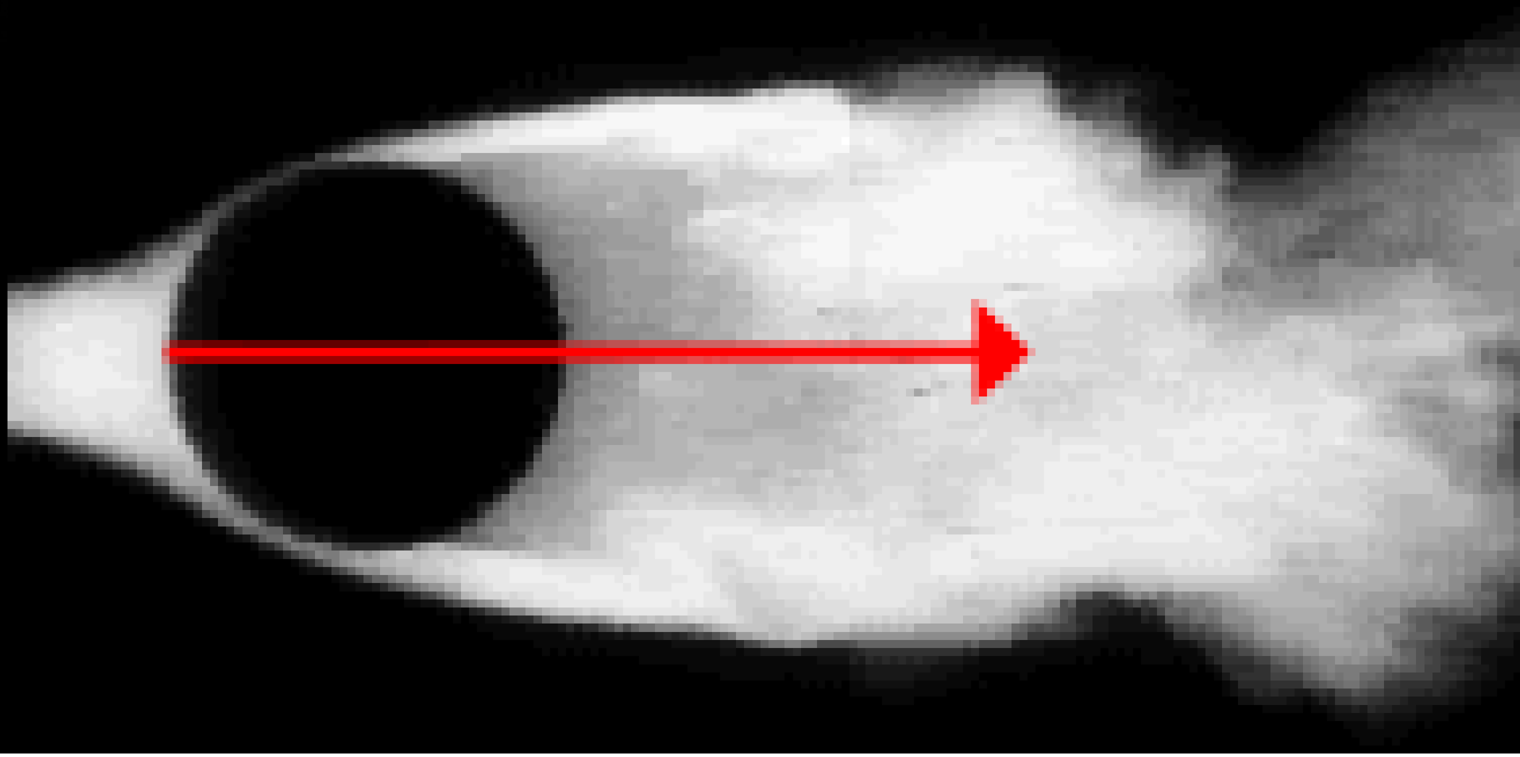
Conservation of Re implies identical flow patterns!



$$Re = \frac{\rho\, u\, L}{\mu}$$

$L\uparrow \rightarrow \rho$ or $u\downarrow$

$L\uparrow \rightarrow \mu\uparrow$



Reynolds scaling allows us to study flows and forces that are otherwise difficult to measure (i.e. too small, too fast.....)

<u>Hawkmoth</u> (Manduca sexta)
25 wingbeats per second
▸hard to visualize fluid flow around flapping wings

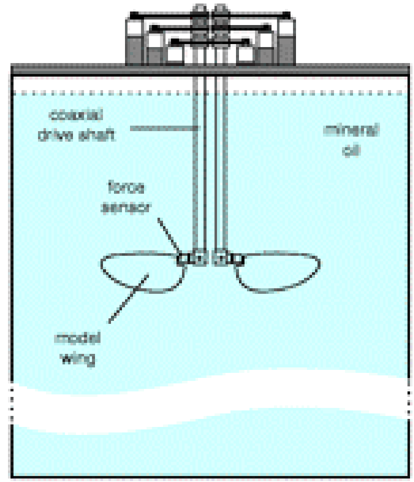
$$Re = \frac{\rho \, u \, L}{\mu}$$

Ellington et al. built a Reynolds-scaled hawkmoth robot
▸robot was much bigger, so velocity of wings could be slower
▸smoke could be released over slowly-beating wings to visualize flow patterns

Reynolds scaling allows us to study flows and forces that are otherwise difficult to measure (i.e. too small, too fast.....)

Fruitfly (Drosophila)
200-300 wingbeats per second!

$$Re = \frac{\rho \, u \, L}{\mu}$$

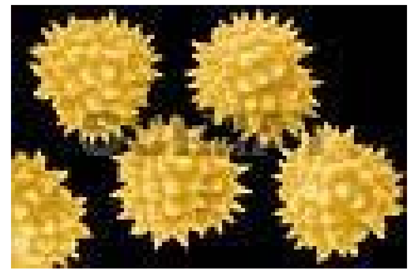


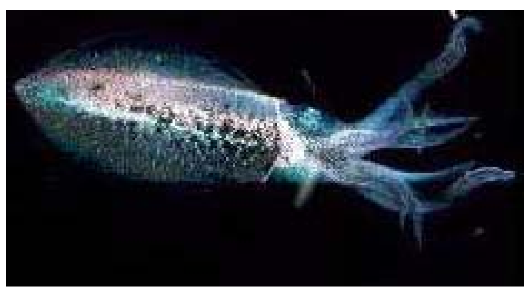
Dickinson et al. built "robofly" - large robotic wings that flap slowly in a vat of mineral oil

- *Can measure forces with force sensors and visualize flow with suspended bubbles*

How much does Reynolds number vary in moving organisms? *>15 orders of magnitude!*

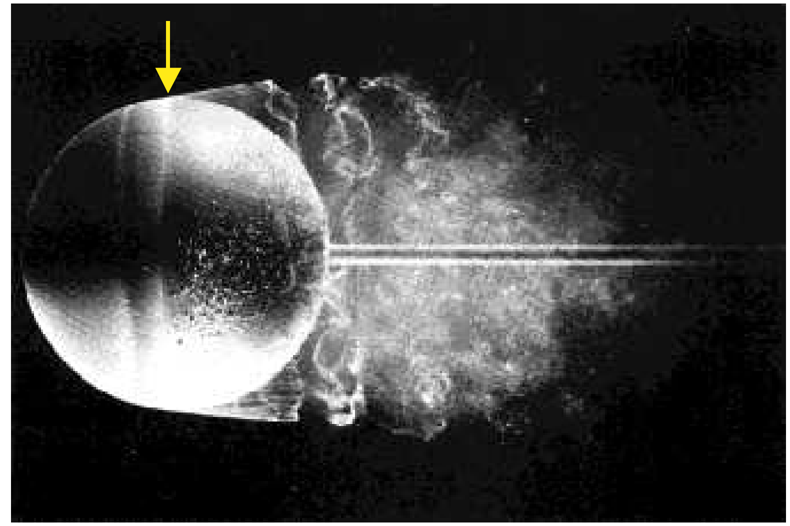
Organism	Reynolds Number
swimming bacterium	0.000001
falling pollen grain or swimming sperm	0.01
fruit fly flying	100
small bird flying	100,000
fast jetting squid	1,000,000
swimming large whale	200,000,000





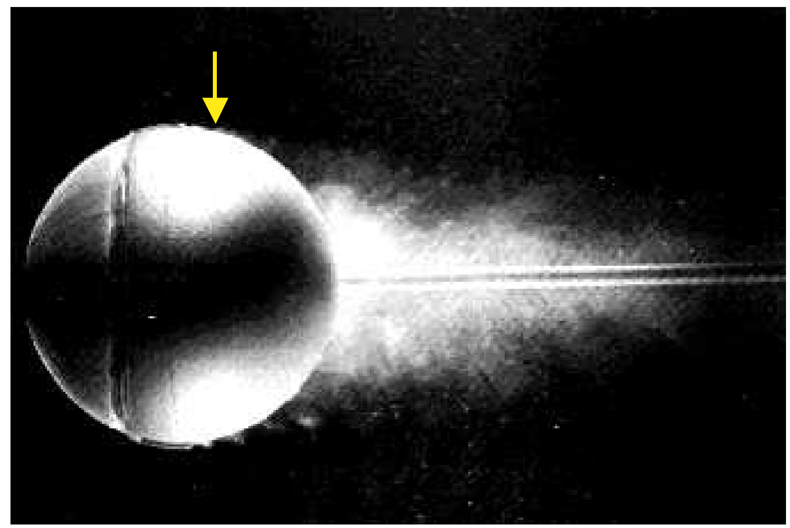
How does fluid flow change with increasing Reynolds number?

lower u
(lower Re)



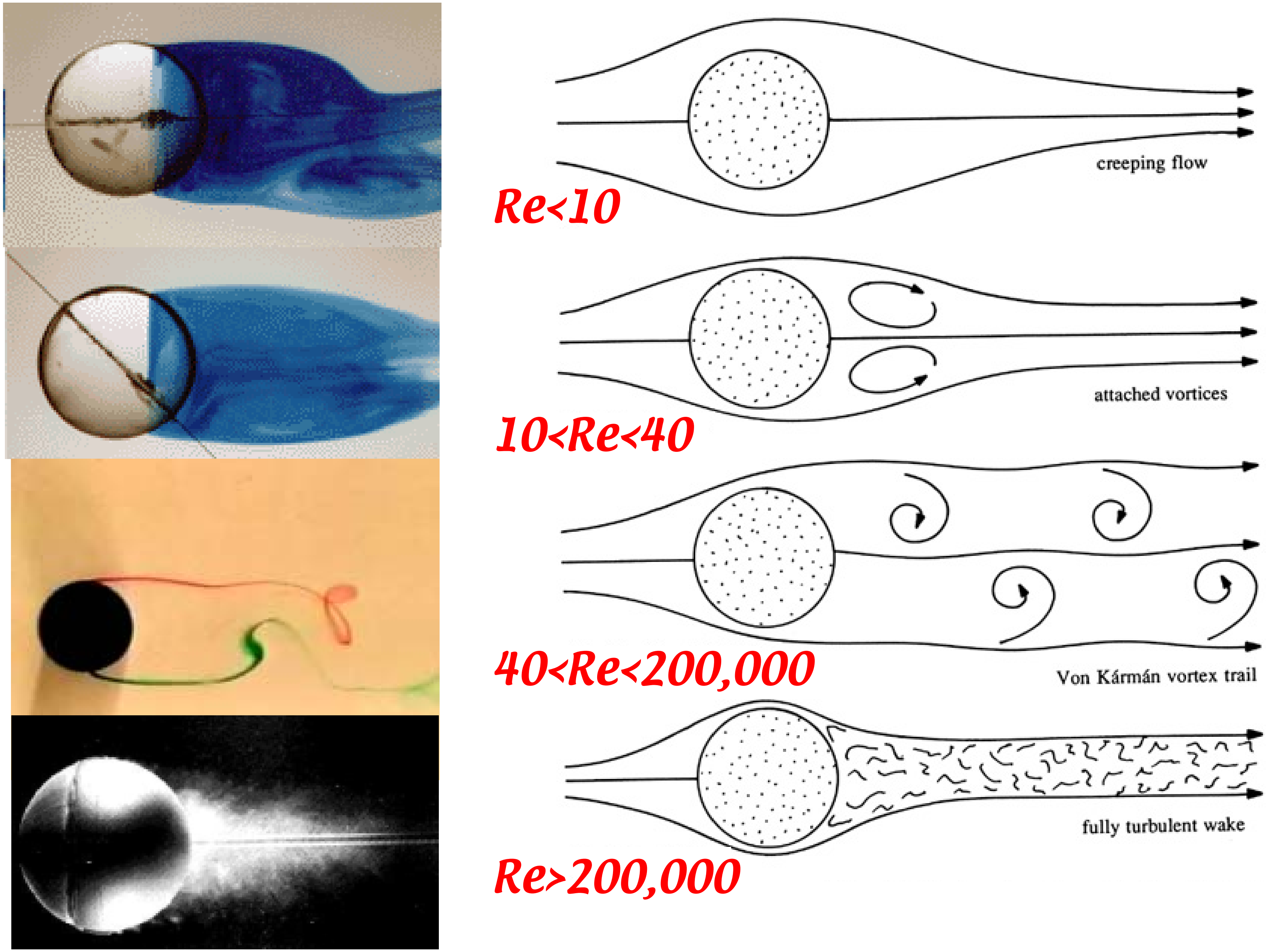
Point of fluid separation from a sphere depends on Reynolds number

higher u
(higher Re)

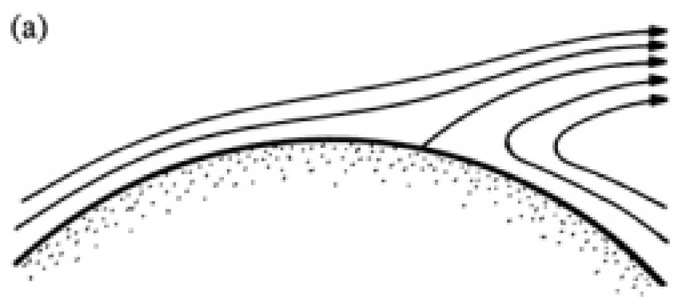


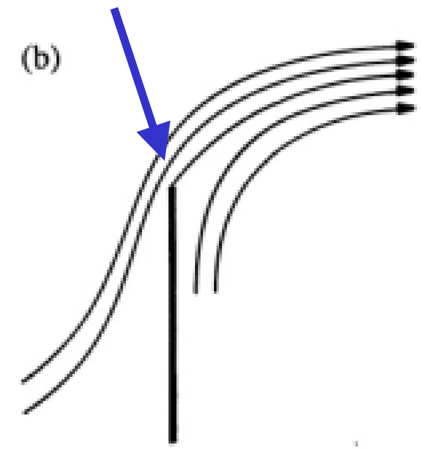
$$\frac{\text{Pressure stress: } P \sim \rho\, u^2}{\text{Shear stress: } \tau \sim \mu\, u/L} = Re = \frac{\rho\, u\, L}{\mu}$$

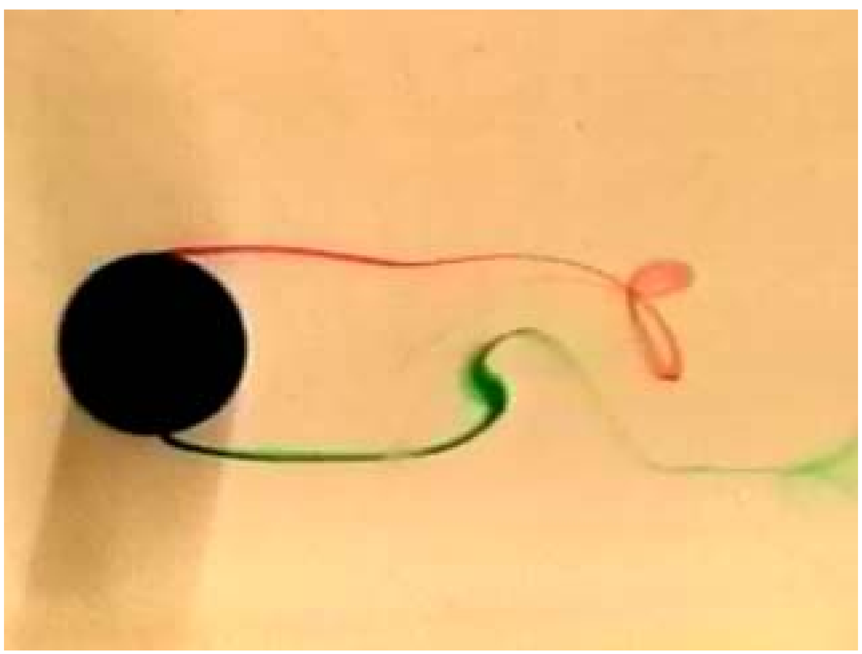
How does fluid flow around a sphere change with increasing Reynolds number?

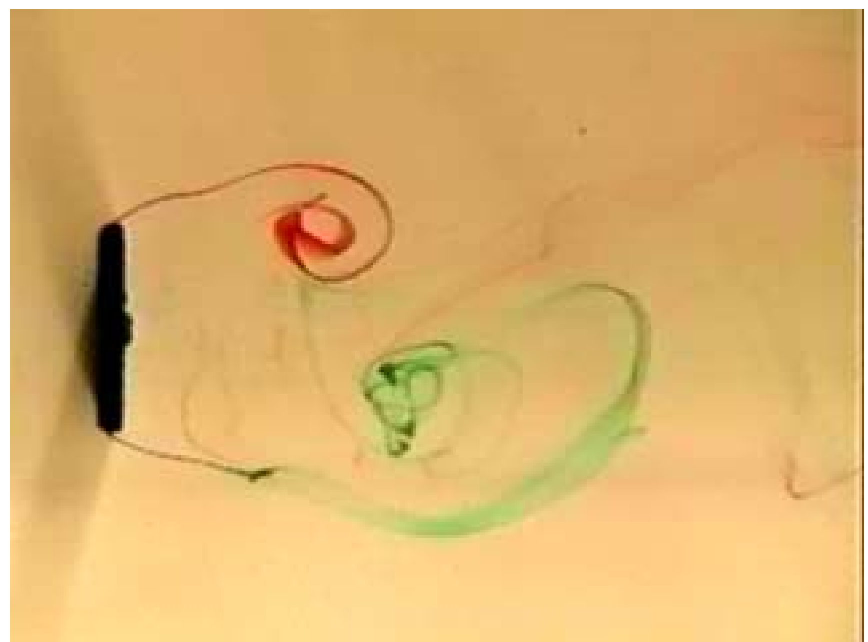


Flow always separates at sharp edges, so drag on a vertical plate is less sensitive to Reynolds number

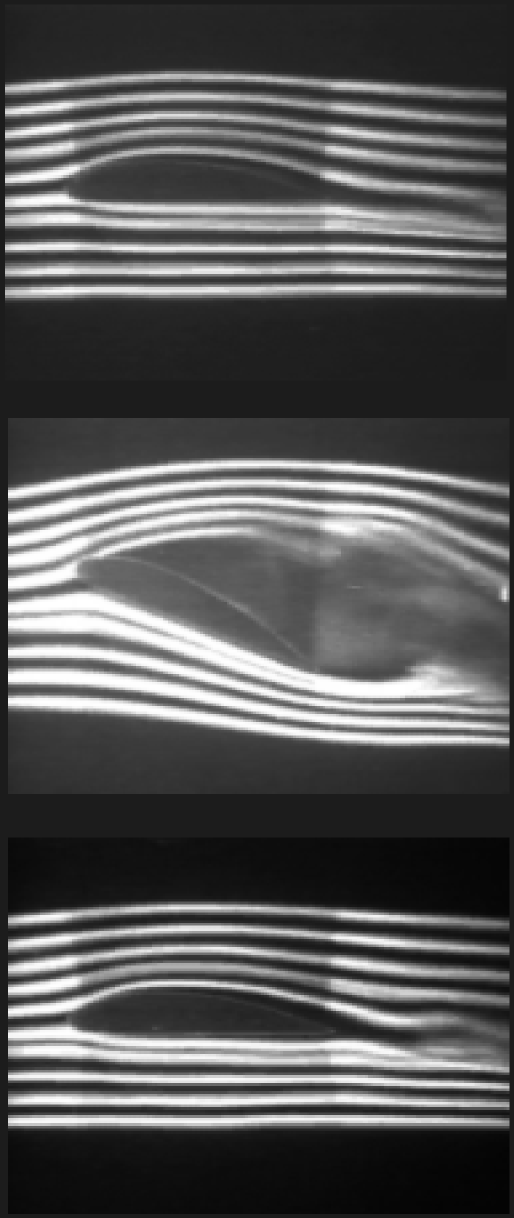








Orientation of an object to flow can also affect the separation point and pressure drag

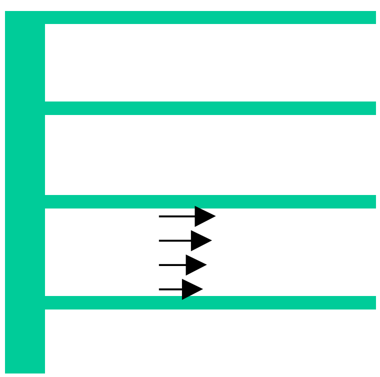


Paddles or brushes? How does Reynolds number affect the functioning of hairy little appendages?

$$Re = \frac{\rho\, u\, L}{\mu}$$

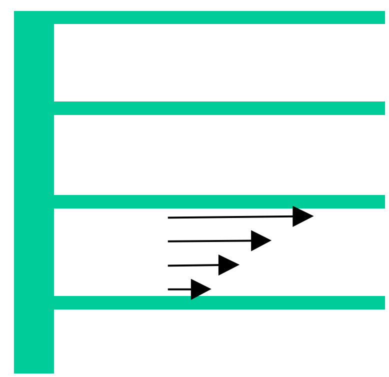
Copepods and other tiny creatures can move their appendages slowly to swim (paddles) or quickly to fish for food (brushes)

When viscous effects dominate, fluid will resist forming sharp velocity gradients and much of the fluid will remain stagnant



PADDLE

When inertial effects dominate, fluid will form sharp velocity gradients and will tend to continue moving in the same direction



BRUSH

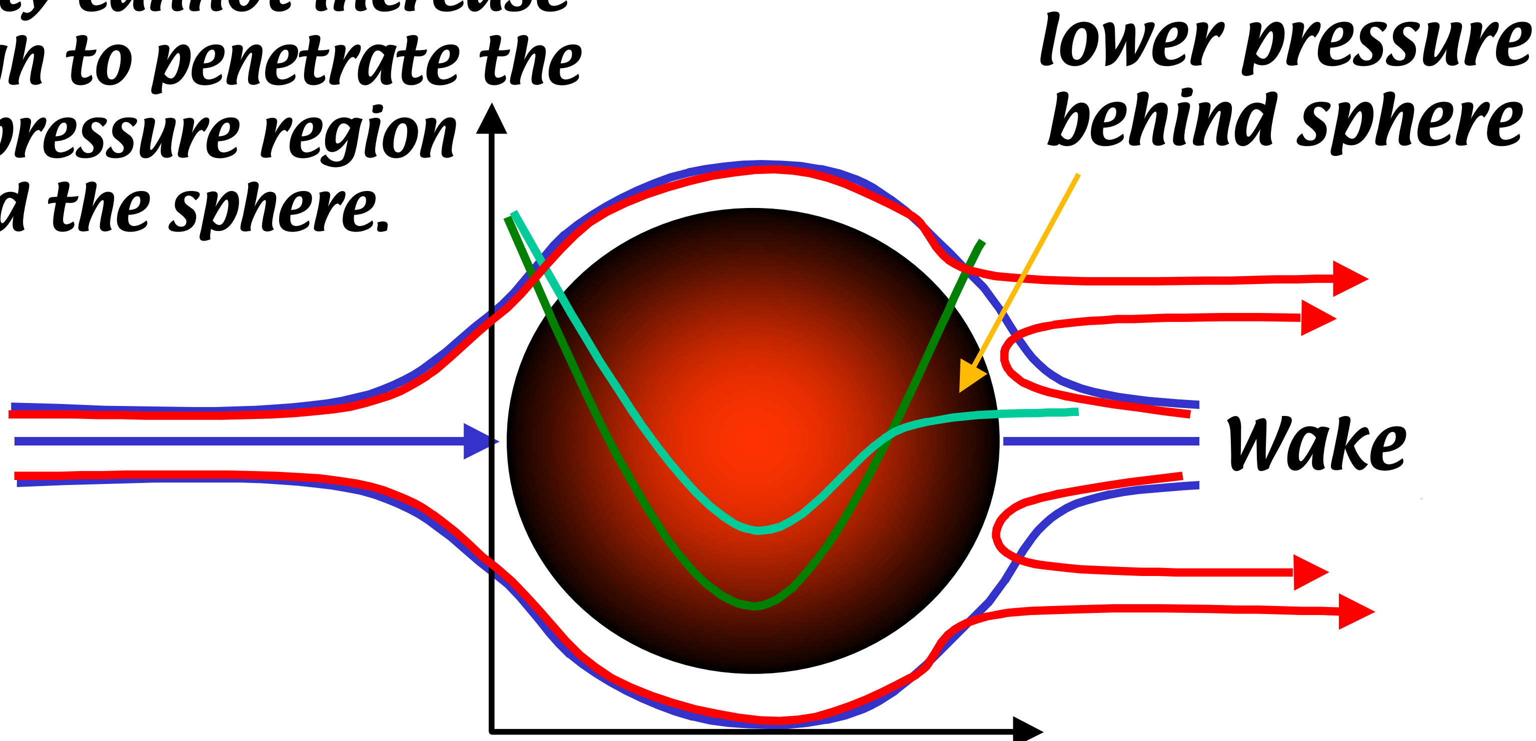
Biology 427 Biomechanics   Winter 2004
Lecture 18.   Shape and drag

- Recap sources of drag and the Reynolds number
- Drag force and its coefficient
- How size, shape, and the Reynolds number determine drag
- Mechanisms of drag reduction in animals and athletes
- Sometimes drag is a good thing

$PE + KE + W + Ediss = const$

$(P_2 - P_1)/\rho = (u_1^2 - u_2^2)/2$

because of viscosity, velocity cannot increase enough to penetrate the high pressure region behind the sphere.



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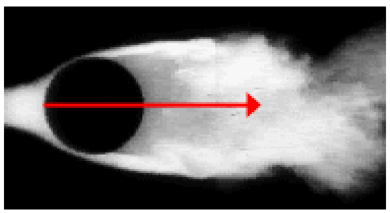
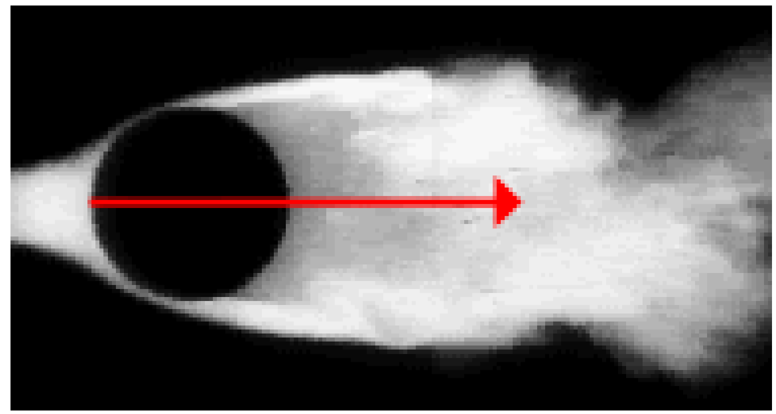


$$Re = \frac{\rho u L}{\mu}$$

$L\uparrow \rightarrow \rho$ or $u\downarrow$

$L\uparrow \rightarrow \mu\uparrow$



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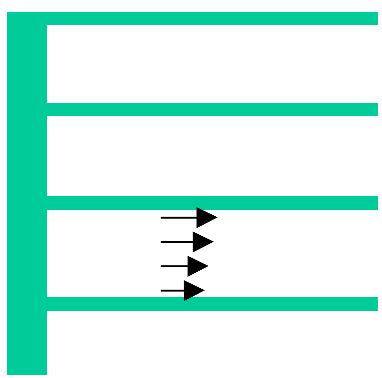
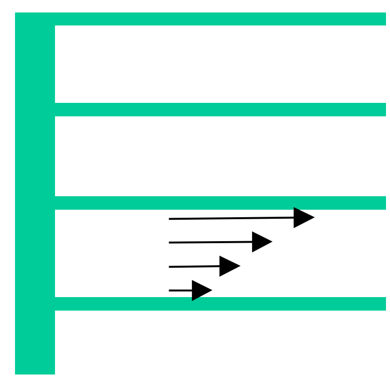


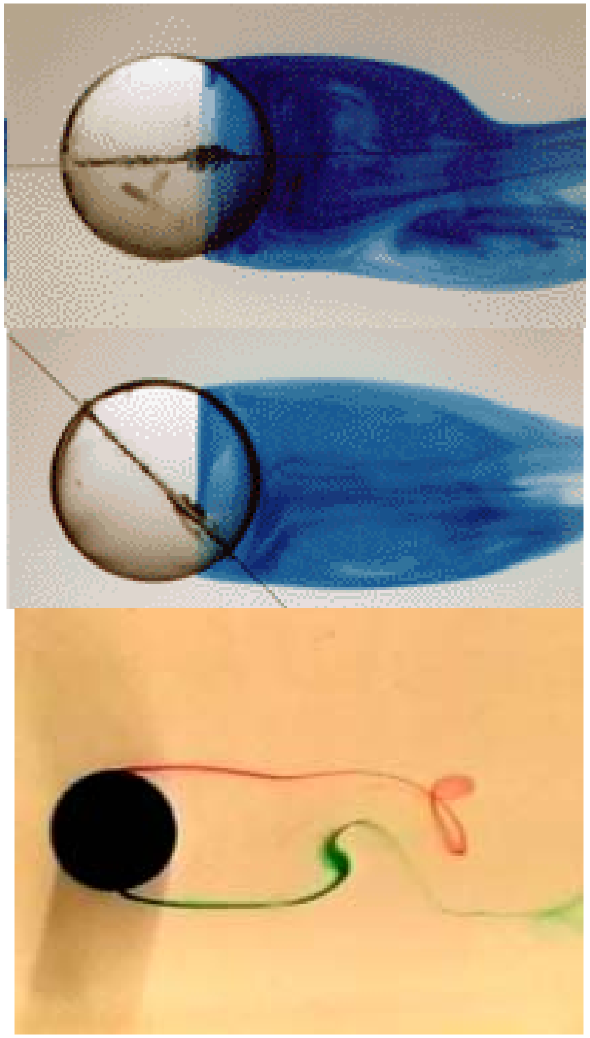
PADDLE

When inertial effects dominate, fluid will form sharp velocity gradients and will tend to continue moving in the same direction



BRUSH

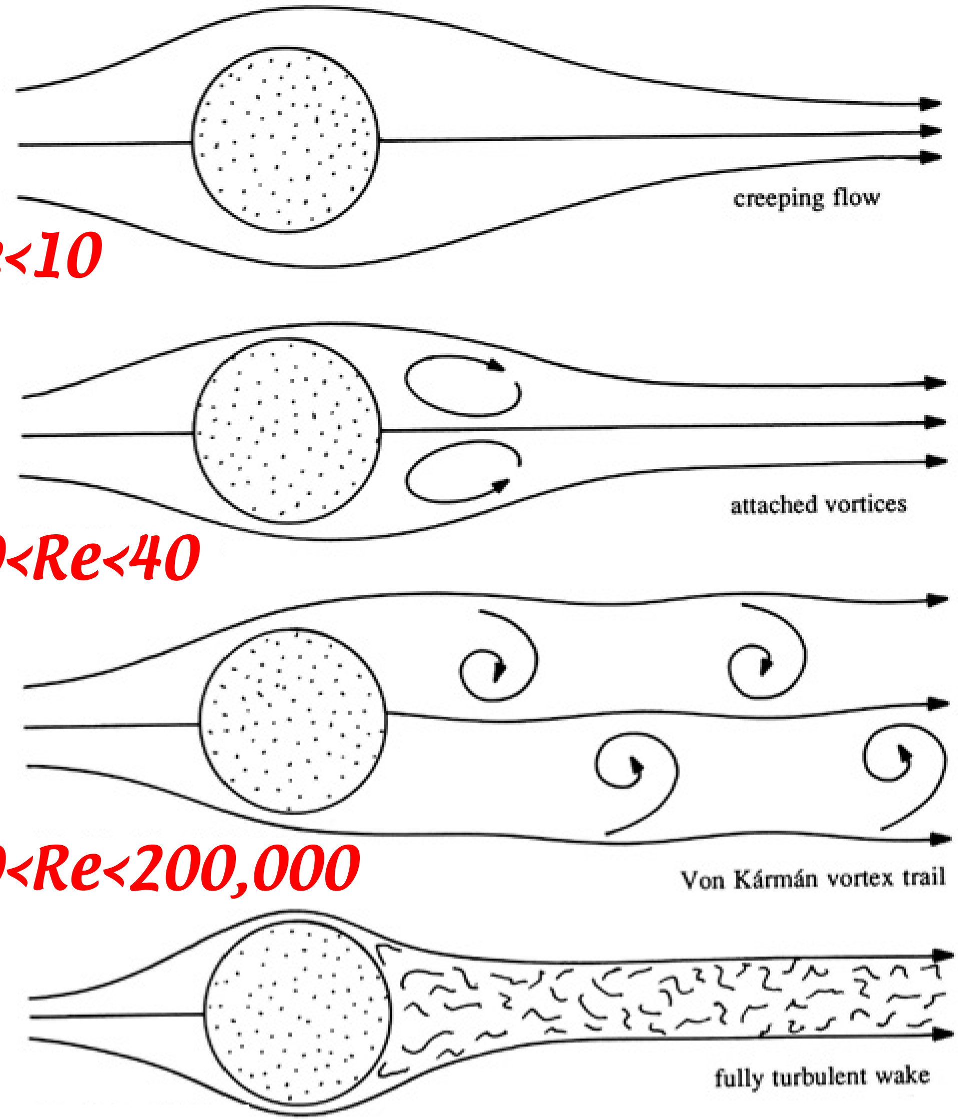
How does fluid flow around a sphere change with increasing Reynolds number?



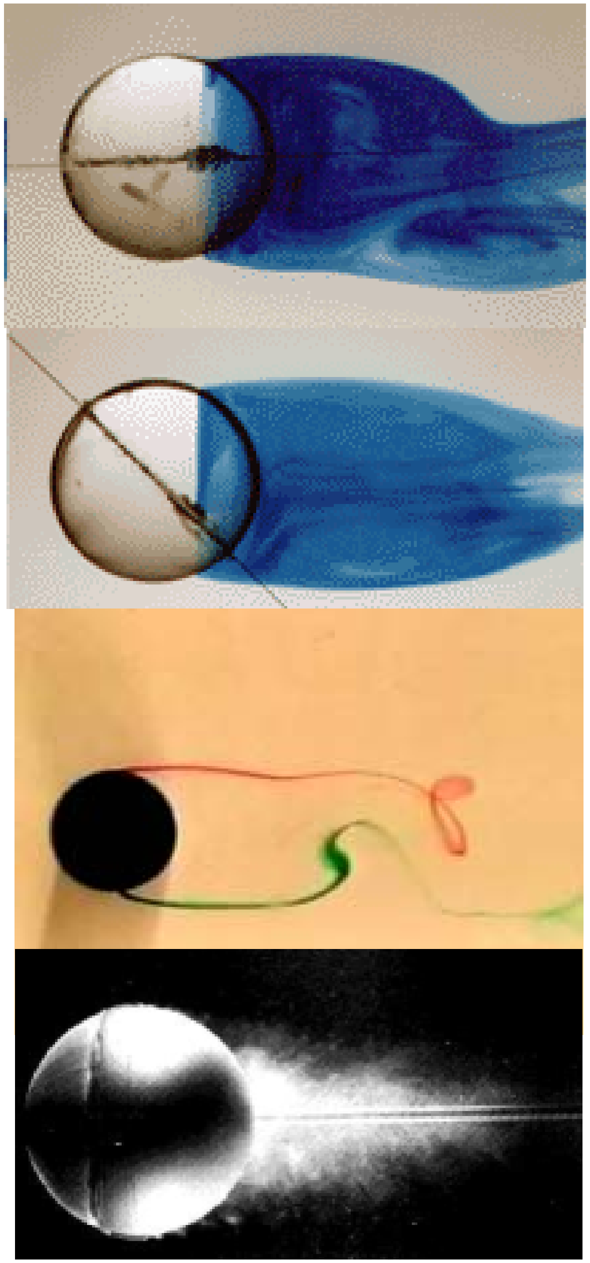
Re<10

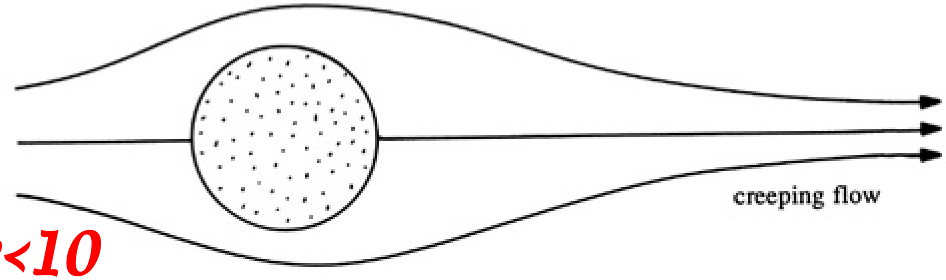
10<Re<40

40<Re<200,000

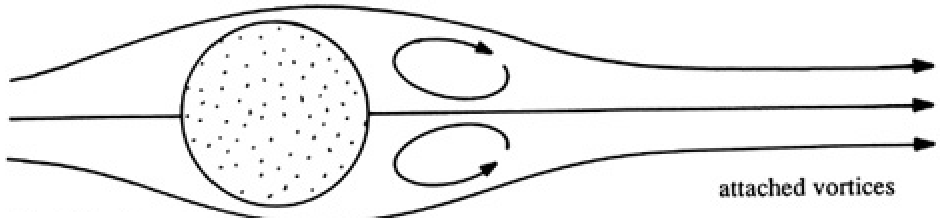


How does fluid flow around a sphere change with increasing Reynolds number?

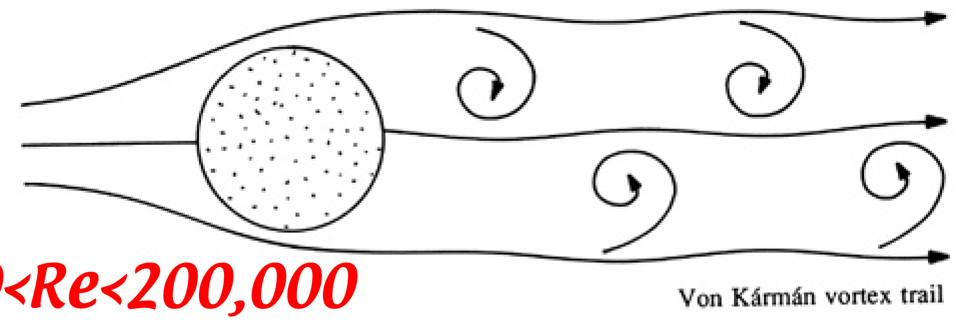




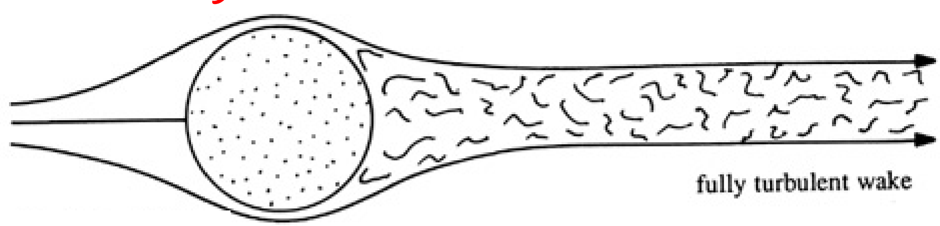
Re<10



10<Re<40

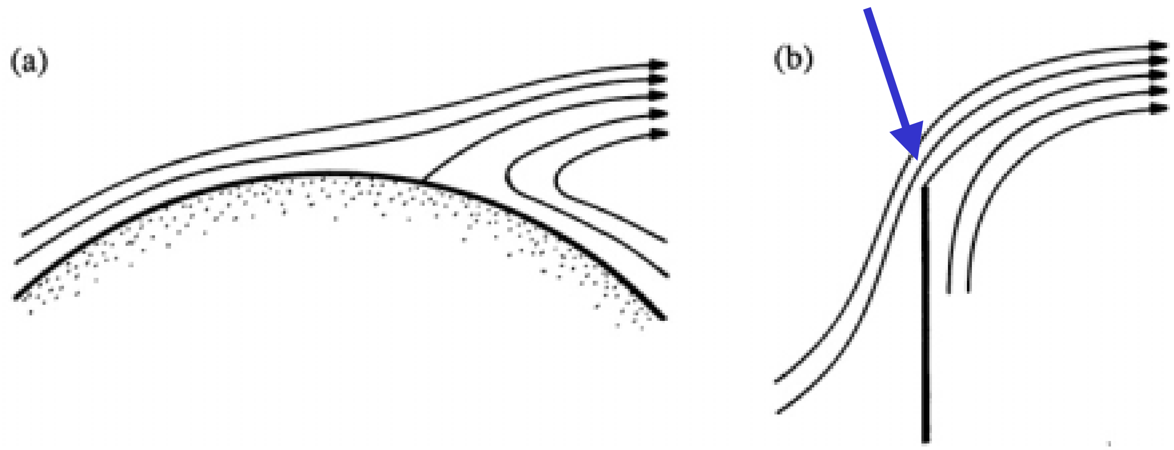


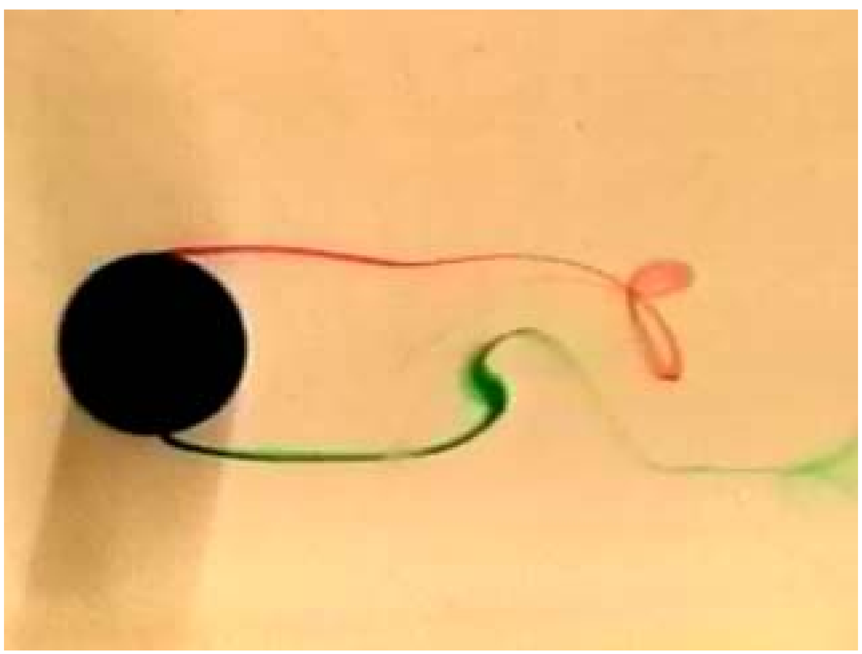
40<Re<200,000

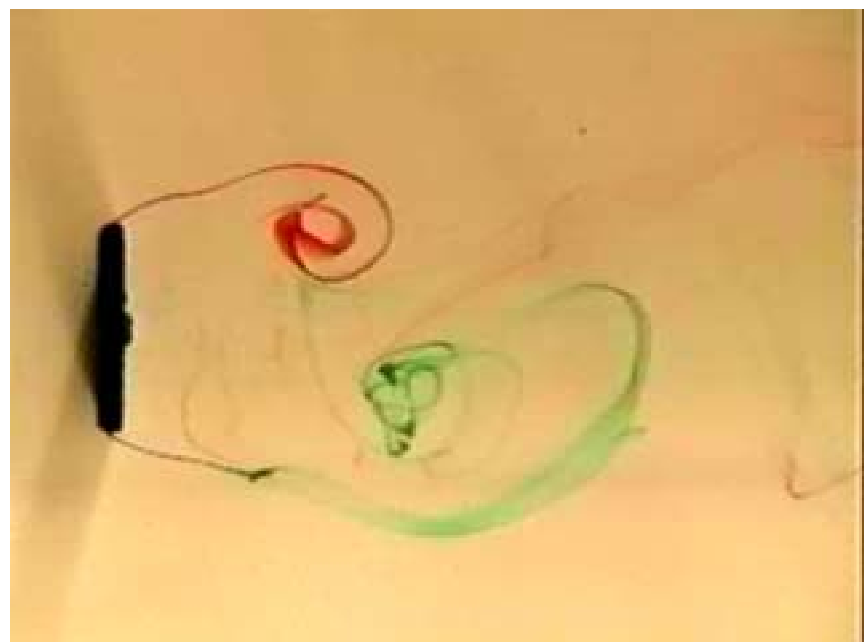


Re>200,000

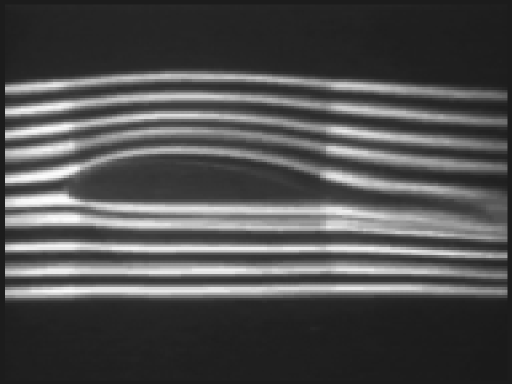
Flow always separates at sharp edges, so drag on a vertical plate is less sensitive to Reynolds number

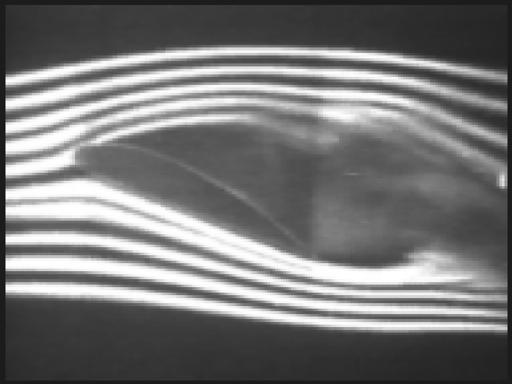


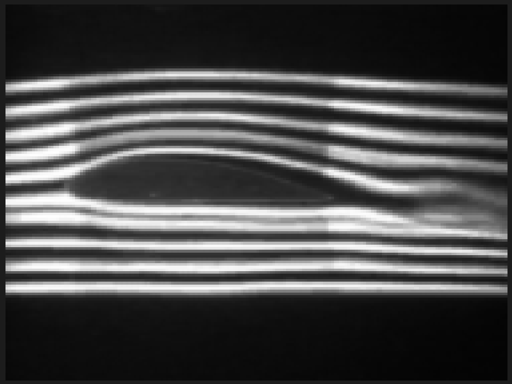




Orientation of an object to flow can also affect the separation point and pressure drag

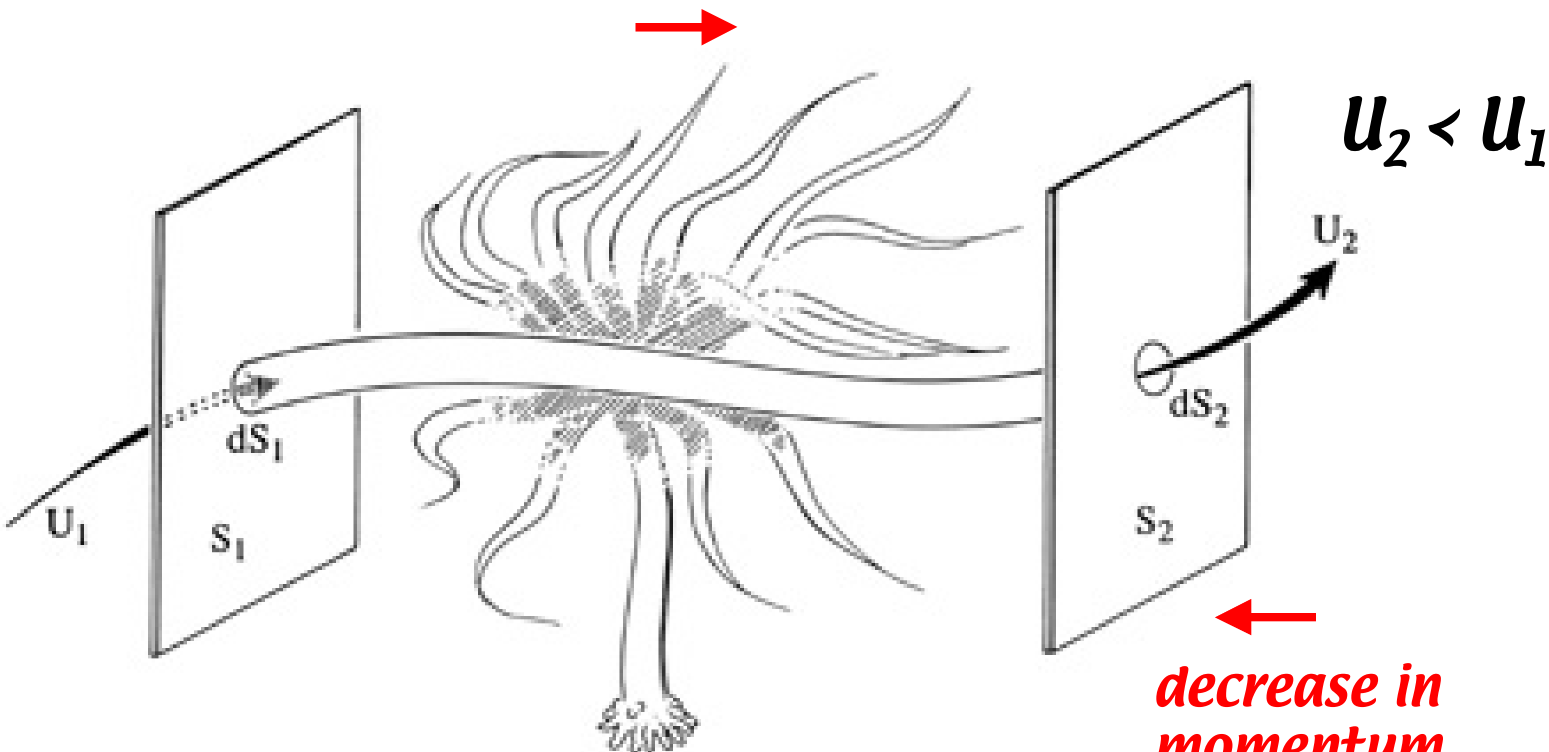






Organisms moving through a fluid, as well as sessile organisms surrounded by moving fluid experience a drag force parallel to fluid flow

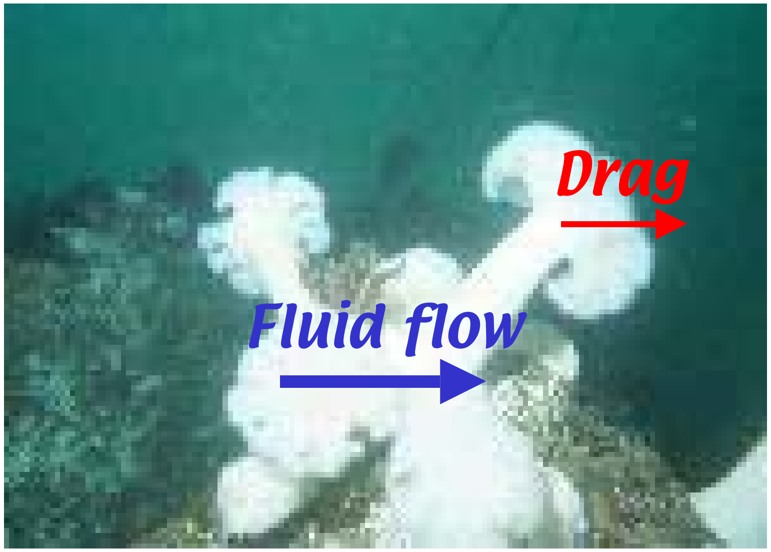
Force on object = Drag



change in momentum = (mu)/t = m(u/t) = ma = F

Why is drag reduction important in biology?

1. *Sessile creatures* - ***reducing drag mitigates the forces leading to breakage/dislodgement***



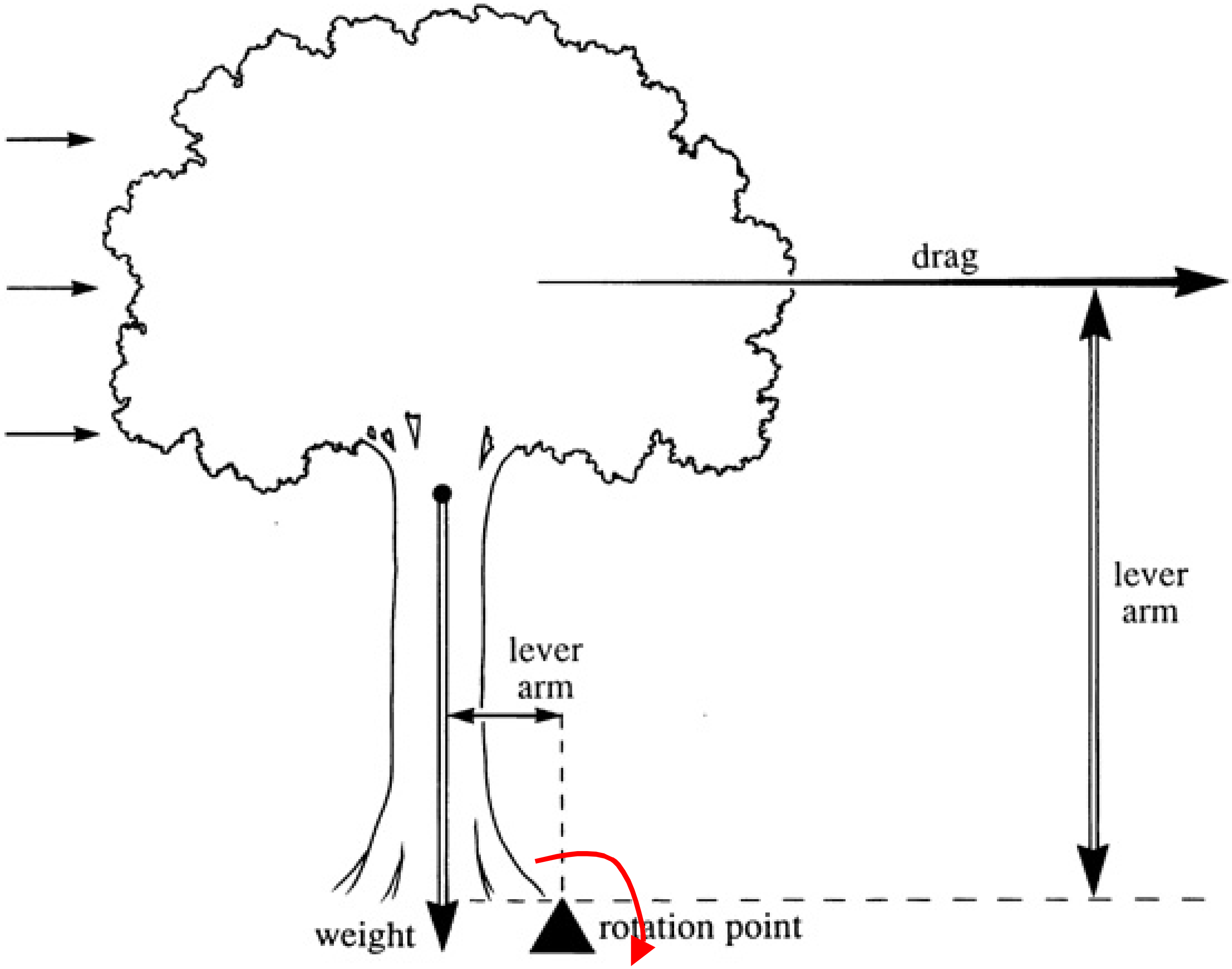
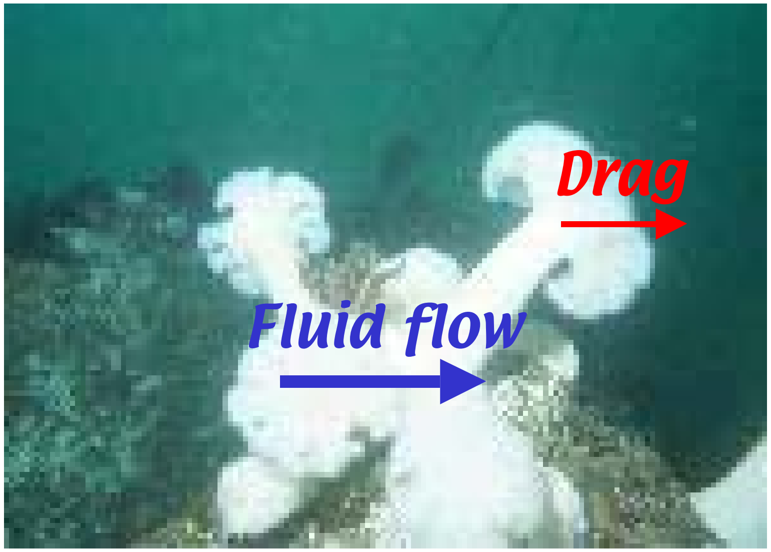


FIGURE 6.8. The principal forces with their lines of action and lever arms caused by a wind blowing on a stiff tree such as a large oak.

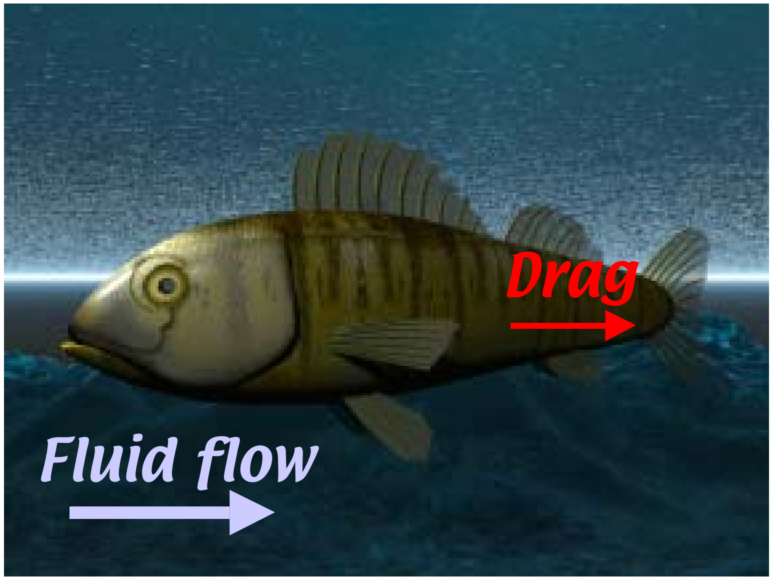
Why is drag reduction important in biology?

1. *Sessile creatures* -
   reducing drag mitigates the forces leading to breakage/dislodgement



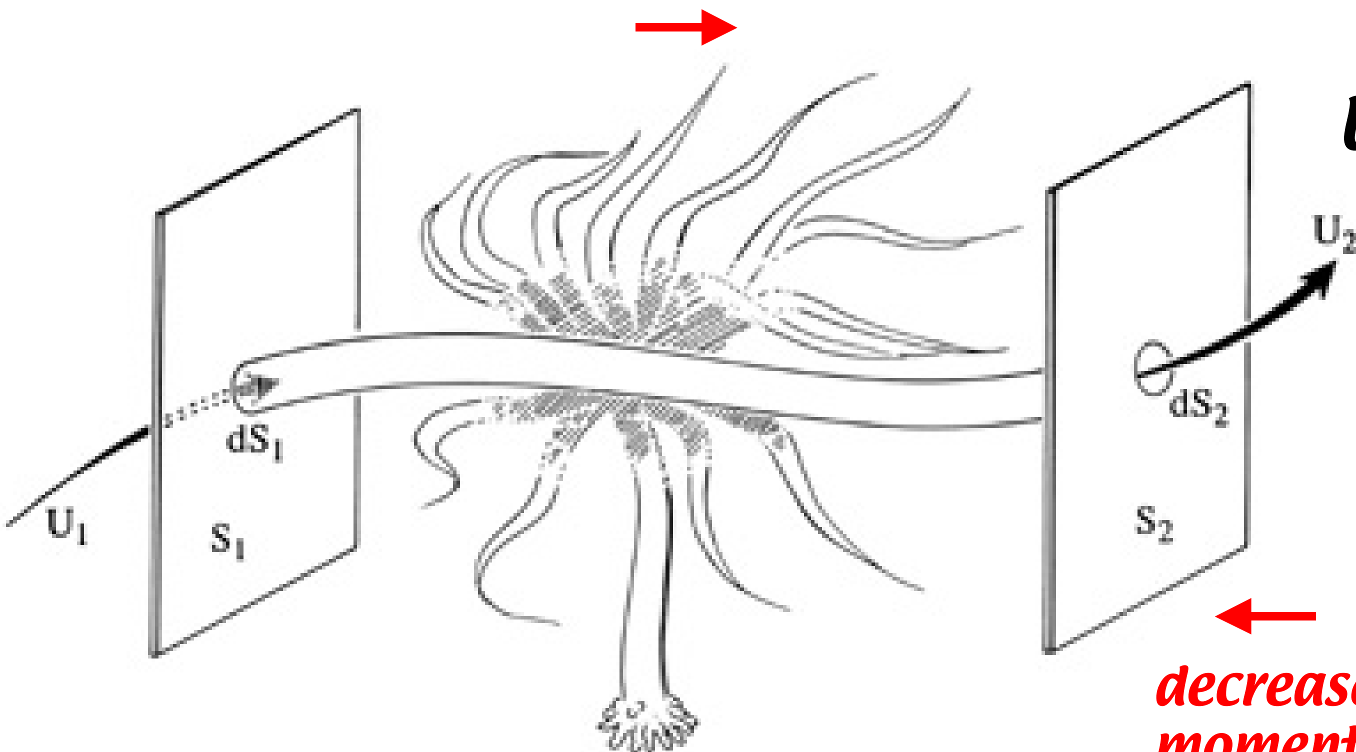
2. *Mobile creatures* -
   reducing drag reduces power expended to overcome drag forces

Power = Force x Velocity



How can we quantify the drag force?

Force on object = Drag



$U_2 < U_1$

decrease in momentum

F = change in momentum

can directly measure loss of momentum in fluid

$F = ma$ $D \propto (\rho S l u)/t \propto \rho S u^2$

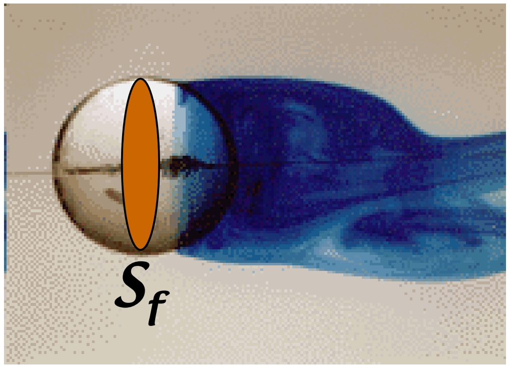
How can we quantify the drag force?

drag force $D \sim \rho S u^2$

drag coefficient → $D = C_d \rho S u^2/2$ ← projected surface area

size

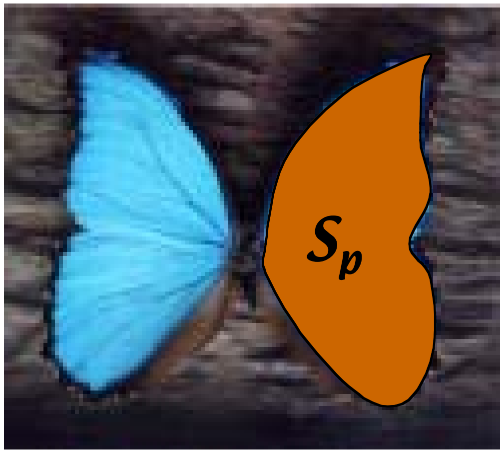
shape, Re, surface features.....



S_f = frontal surface area (perpendicular to flow)

$$Re = \frac{\rho u L}{\mu}$$

Pressure stress: Shear stress



S_w = wetted surface area (entire surface area)

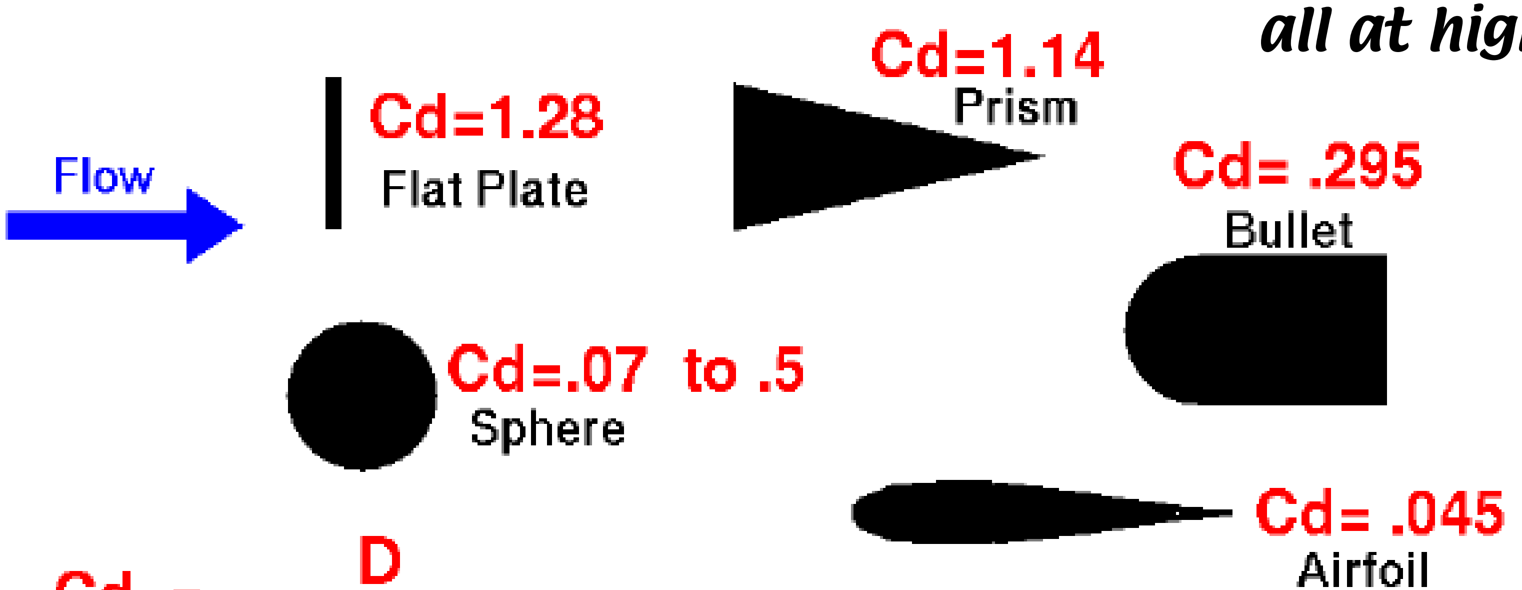
S_p = planform area (area of wing when viewed from above)

Glenn Research Center

Shape Effects on Drag

The shape of an object has a very great effect on the amount of drag.

all at high Re



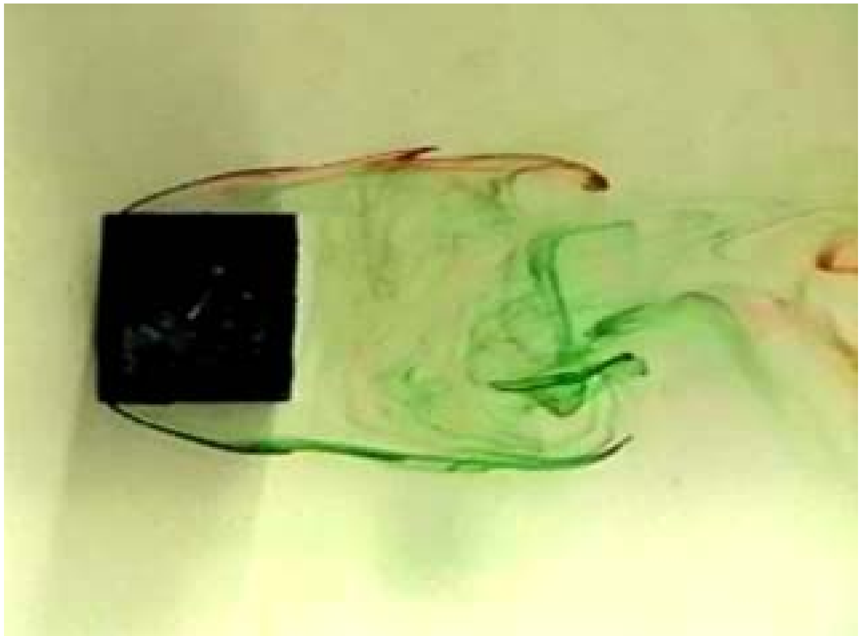
$$Cd = \frac{D}{r\ A\ V^2/2}$$

A = frontal area

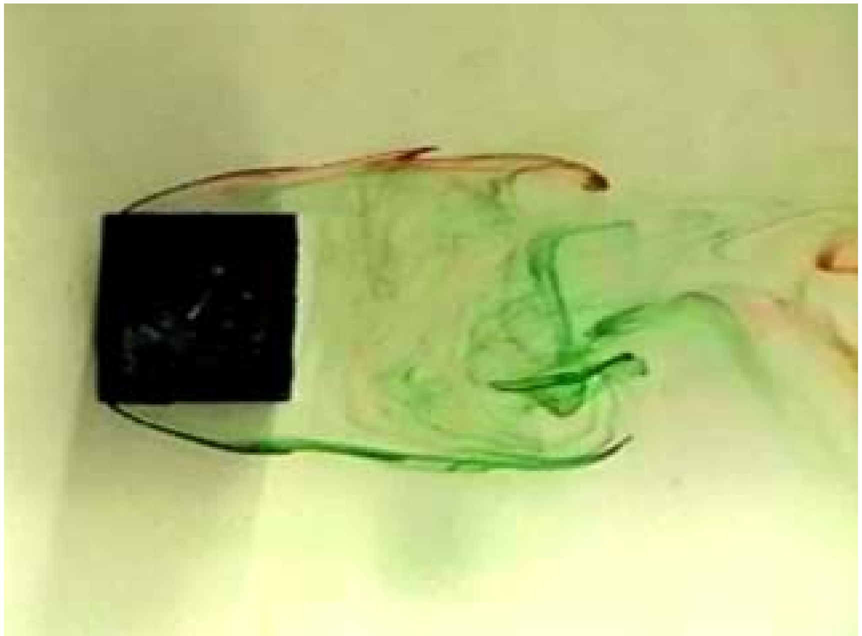
All objects have the same frontal area.

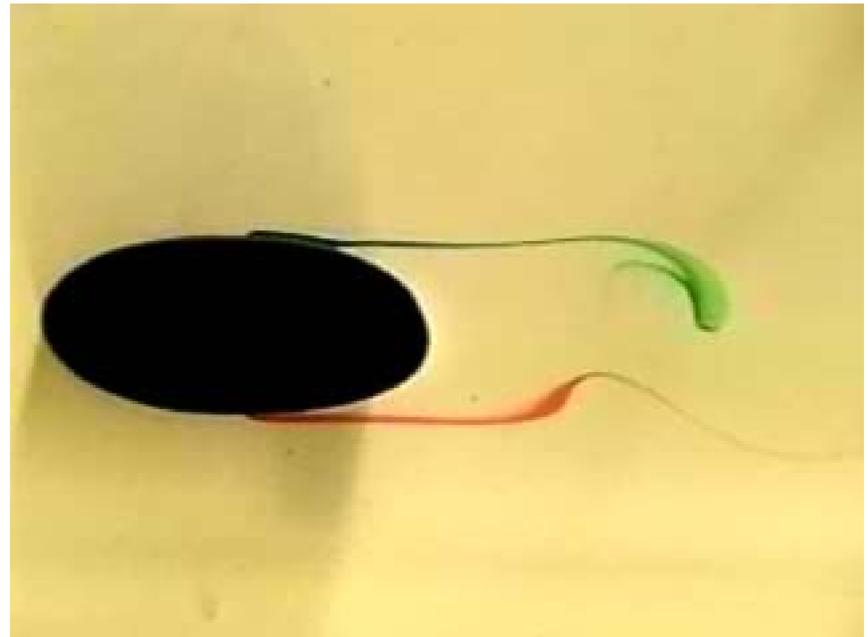
Drag force is >25X larger on plate than on airfoil!

Streamlined shapes reduce flow separation and pressure drag

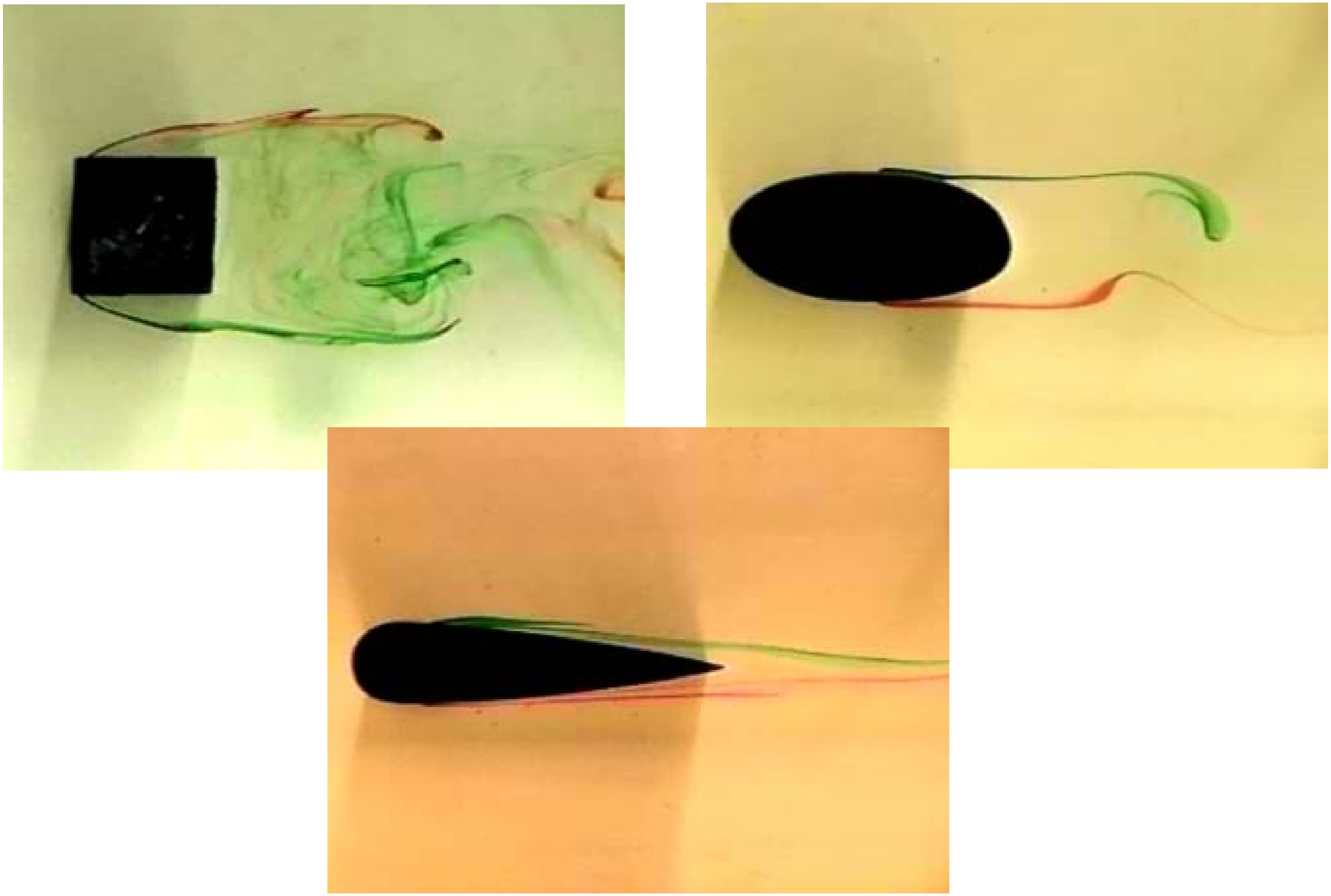


Streamlined shapes reduce flow separation and pressure drag





Streamlined shapes reduce flow separation and pressure drag



Many swimming organisms are streamlined in the direction of flow

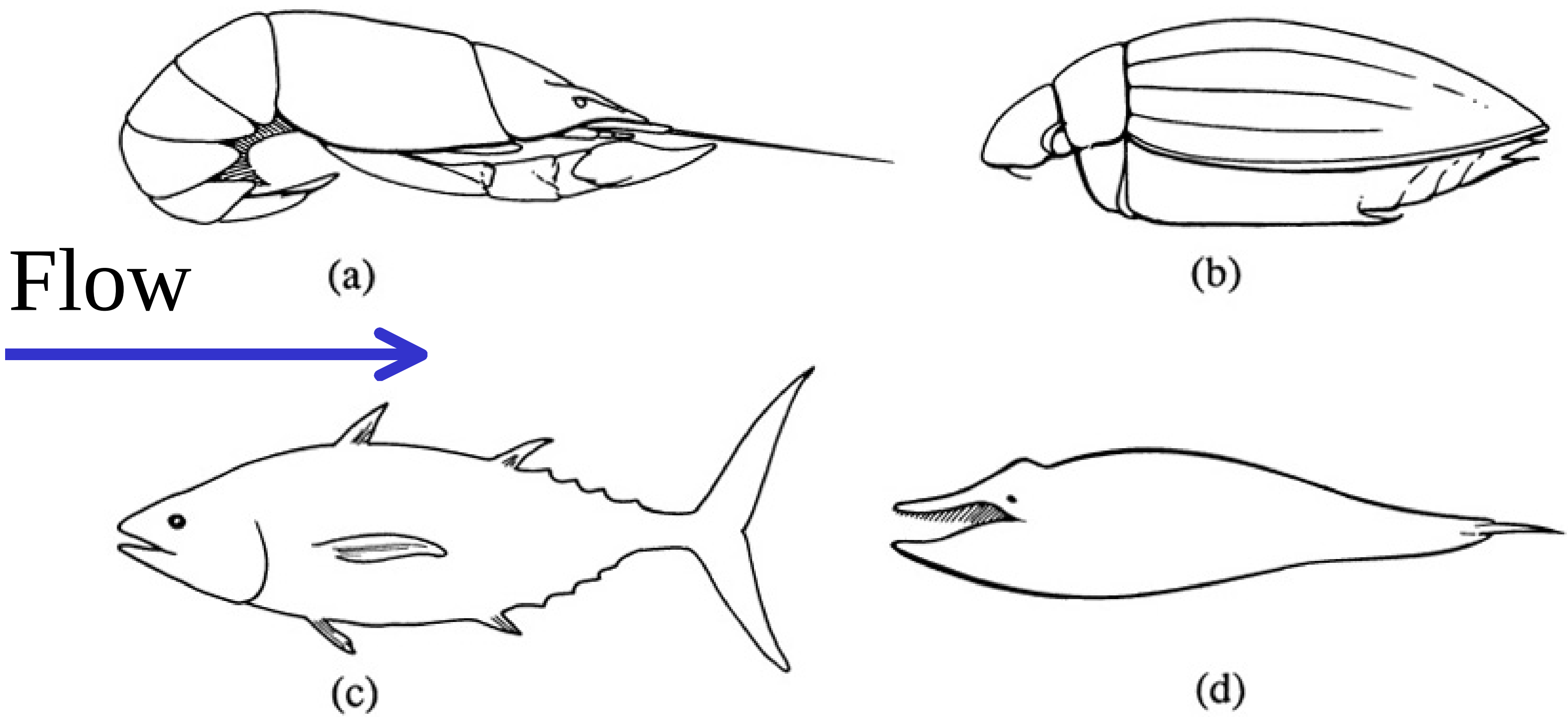


FIGURE 7.3. Streamlined organisms in a flow that goes from left to right: (a) a crayfish going rearward in a rapid escape; (b) a large aquatic beetle; (c) a pelagic fish such as a tuna; and (d) a baleen whale.

Increased fineness ratio (length:width) reduces drag

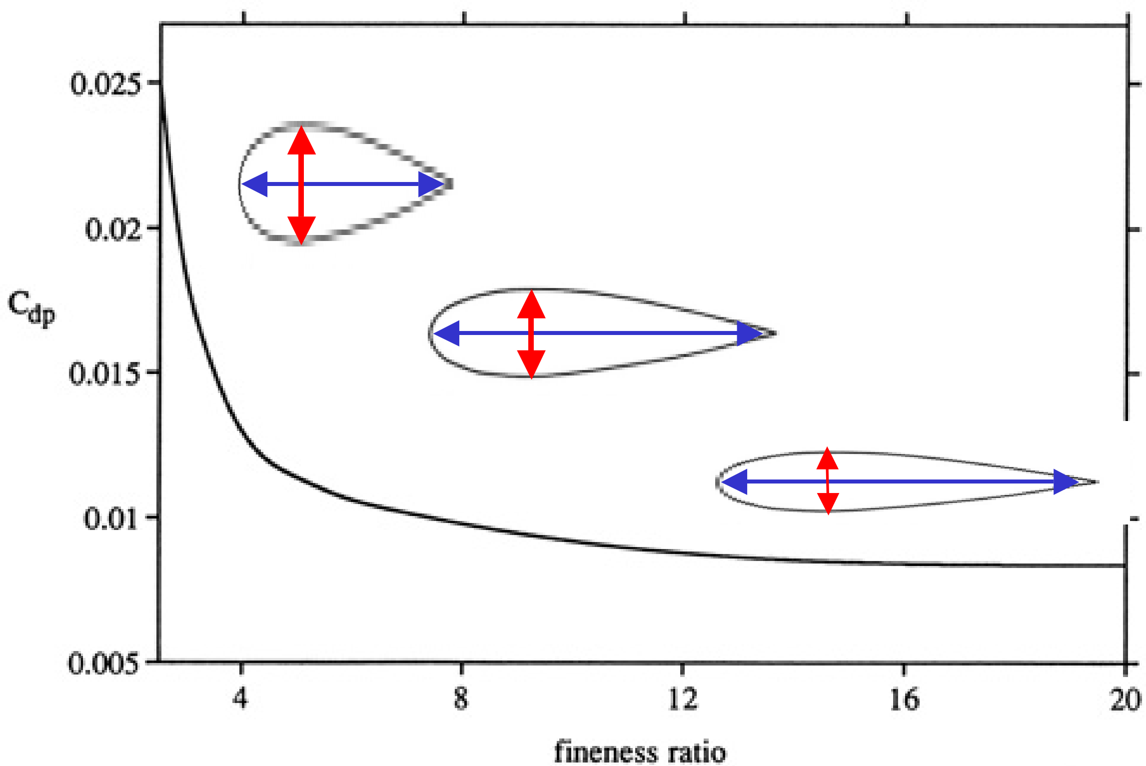
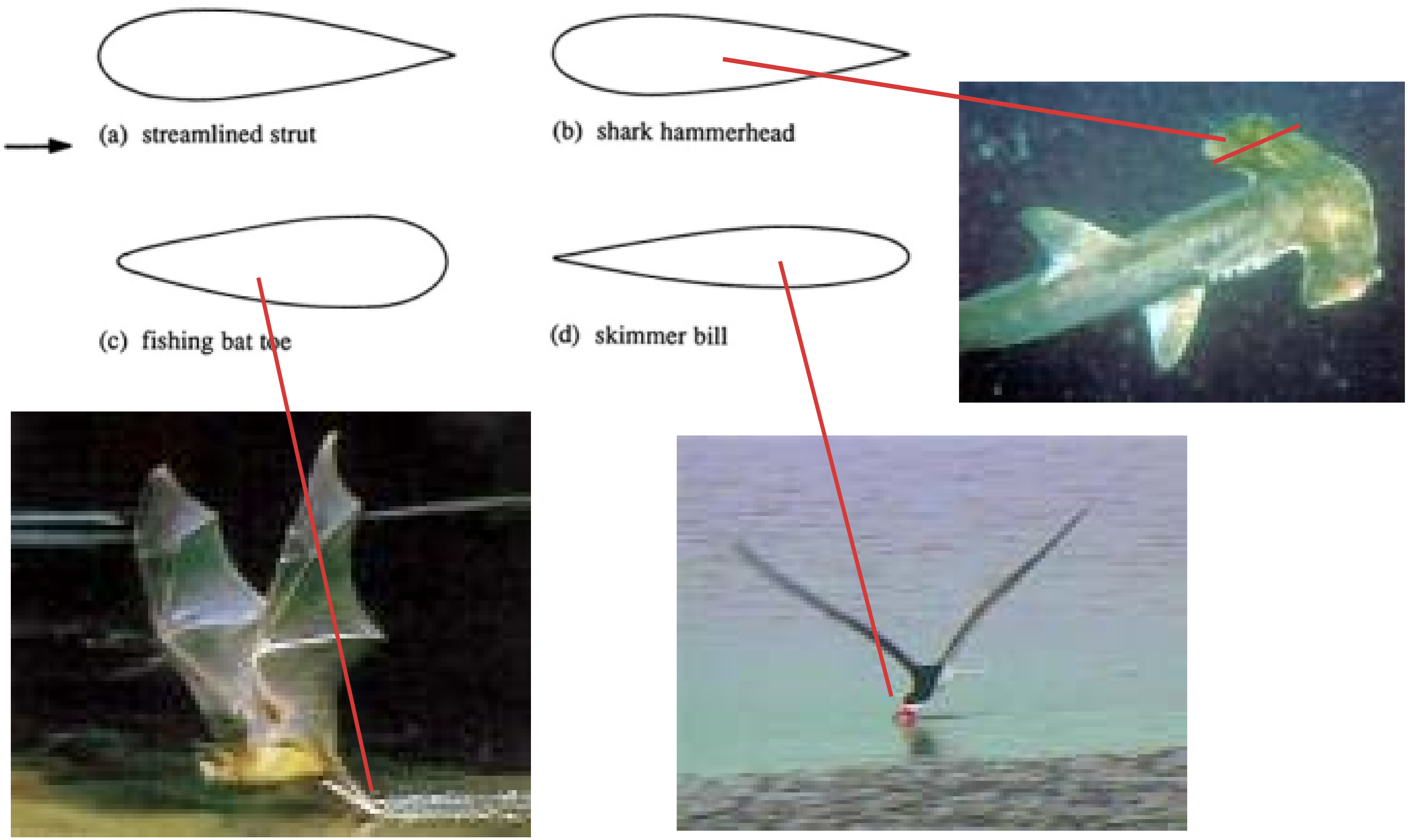
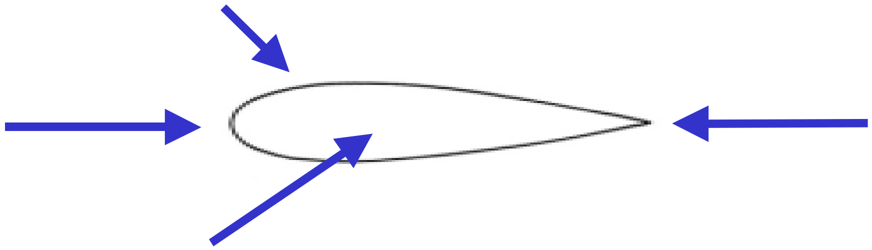


FIGURE 6.2. The variation of drag coefficient, based on plan form area, with fineness ratio (recall 5.7) for an airfoil section at a Reynolds number of 600,000. As an exercise, the reader might try to visualize such a graph with a drag coefficient based on frontal area.

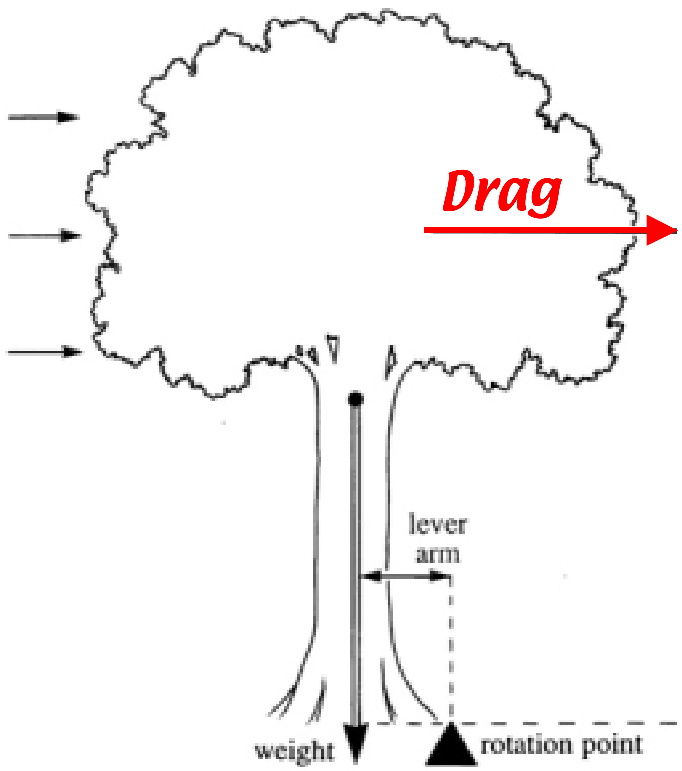
Even individual parts of organisms are often streamlined

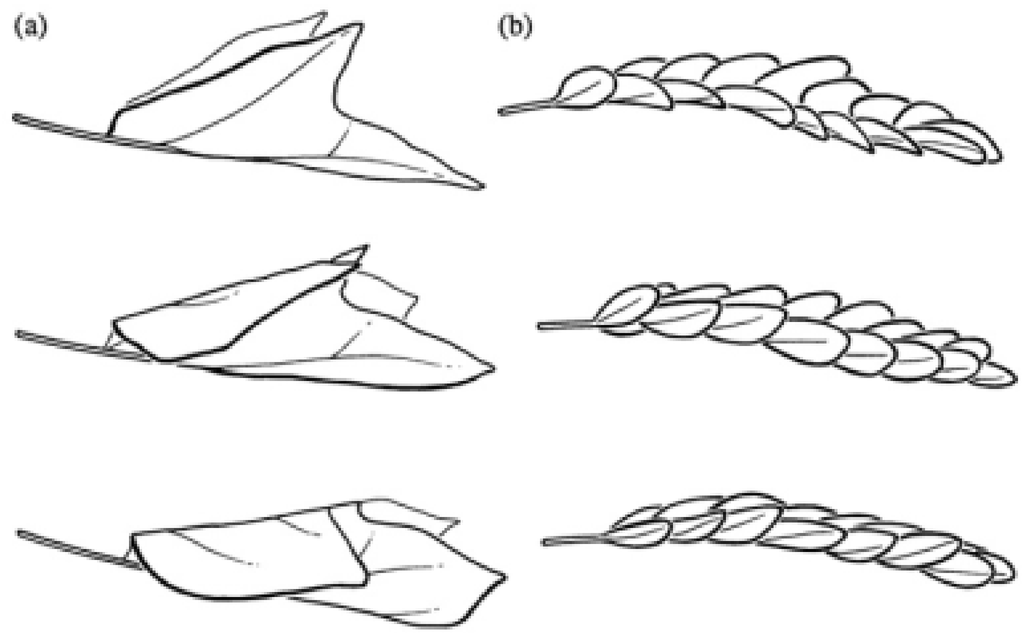


But what if flow direction is not predictable?



Exposed leaf area is reduced passively as wind velocity increases





* triangular petioles allow leaves to twist into the direction of wind

Some sessile creatures can reduce drag via adaptive shape change and reconfiguration

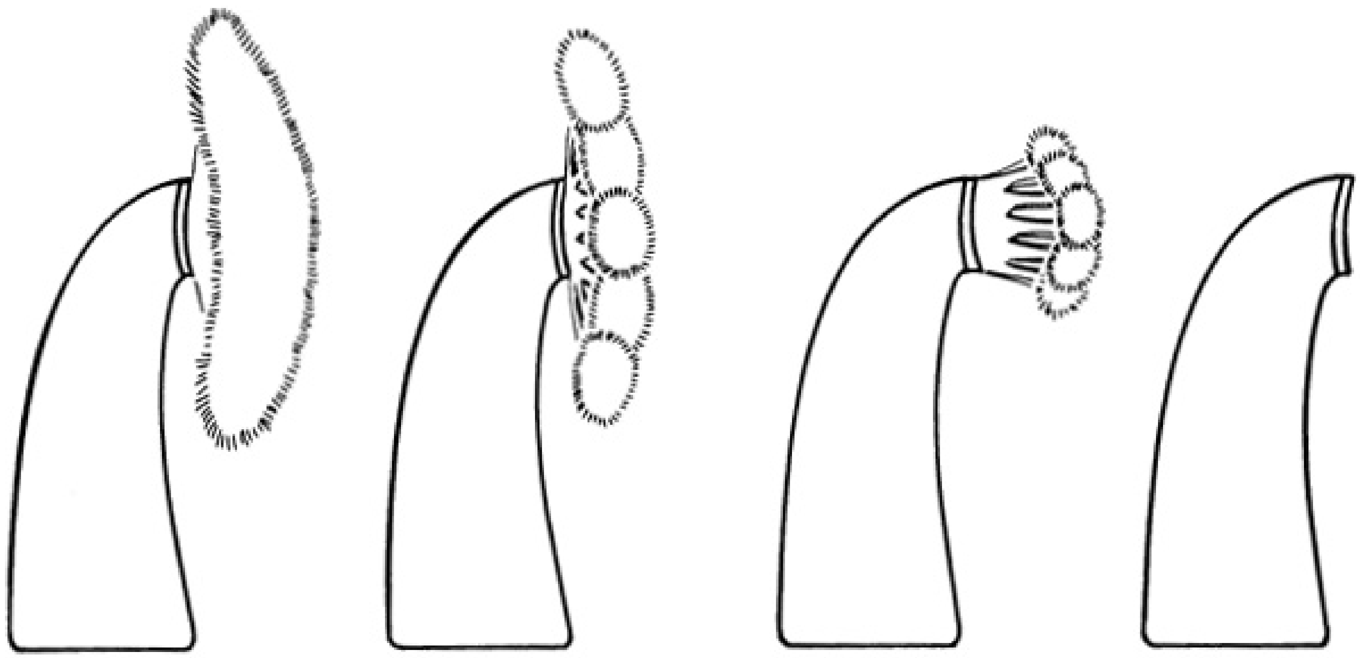
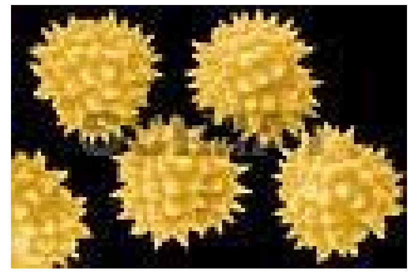


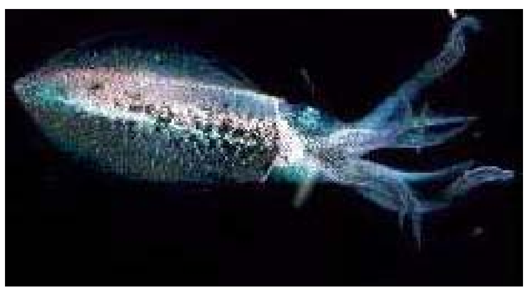
FIGURE 6.6. Successive changes in the appearance of a large sea anemone, *Metridium*, as current increases. Drag coefficients (based on original frontal area) are 0.9, 0.4, 0.3, and 0.2.

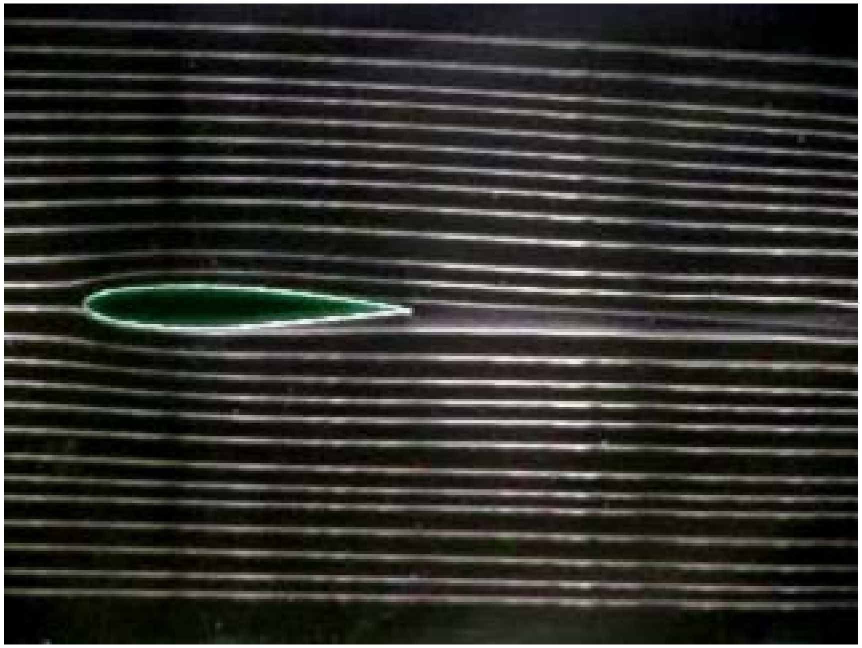
From Koehl, 1977

Does streamlining make sense at all Reynolds Numbers?

Organism	Reynolds Number
swimming bacterium	0.000001
falling pollen grain or swimming sperm	0.01
fruit fly flying	100
small bird flying	100,000
fast jetting squid	1,000,000
swimming large whale	200,000,000

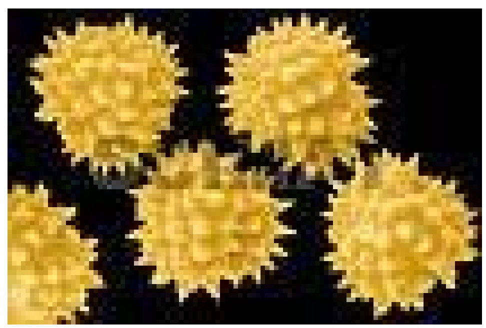






Streamlining reduces flow separation and minimizes pressure drag

But, an object with a large amount of surface area exposed to the flow experiences large friction drag



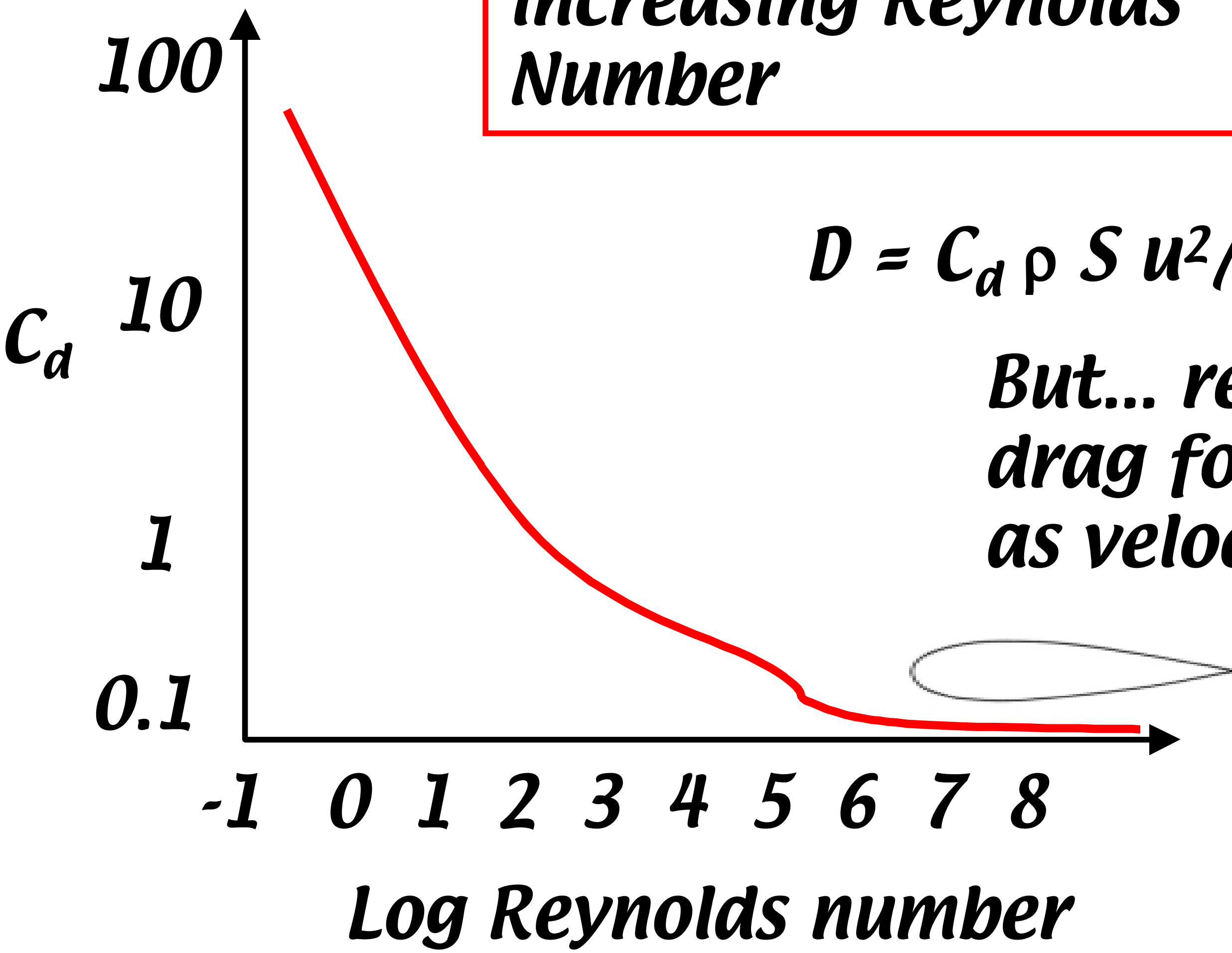
$$Re = \frac{\rho u L}{\mu}$$

Pressure stress: Shear stress

As shear stresses become more important, minimizing surface area to volume ratio may reduce drag more than streamlining

How does Reynolds number affect the drag coefficient?

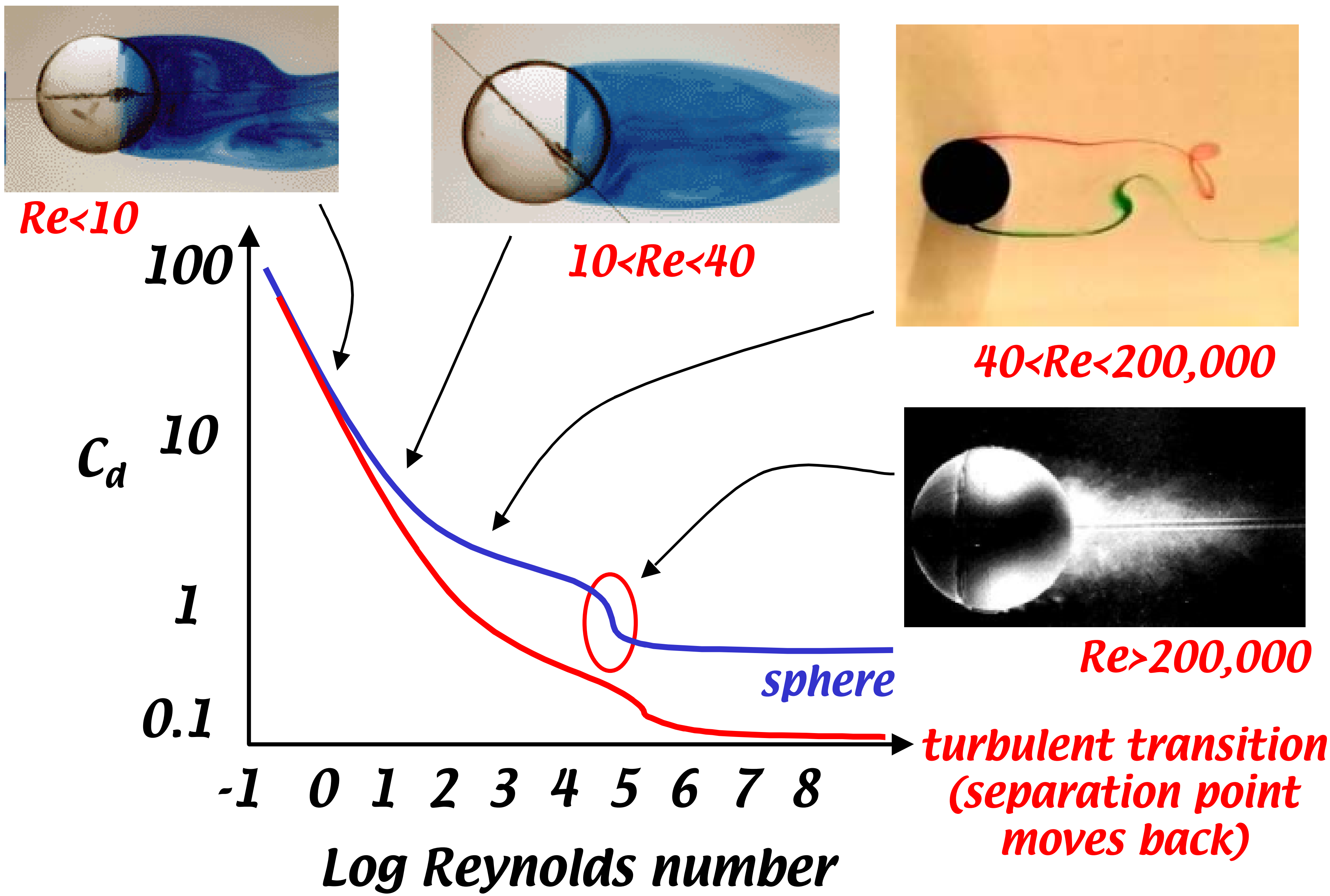
C_d for a streamlined body decreases with increasing Reynolds Number



$$D = C_d \rho S u^2/2$$

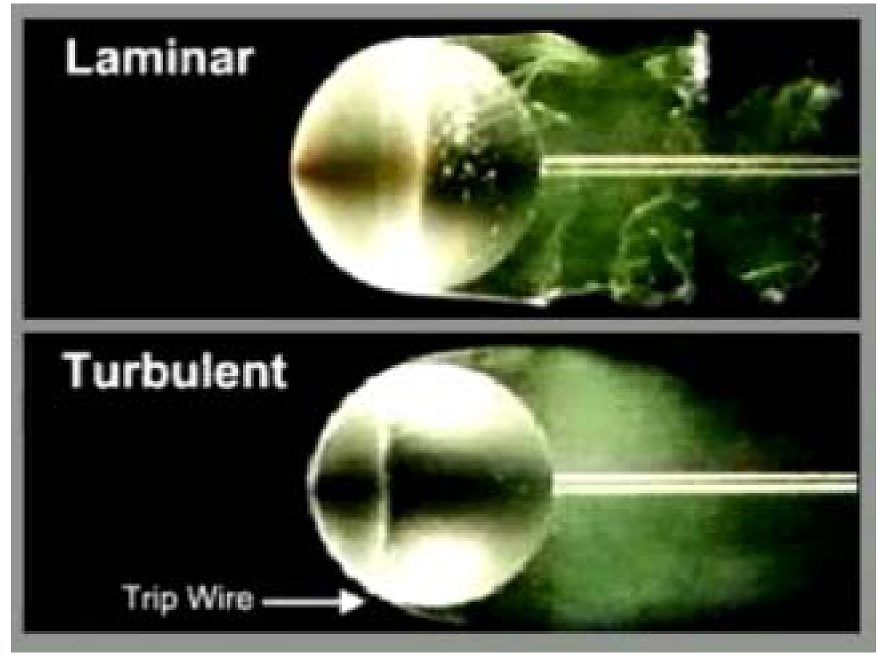
But... remember that drag force increases as velocity^2

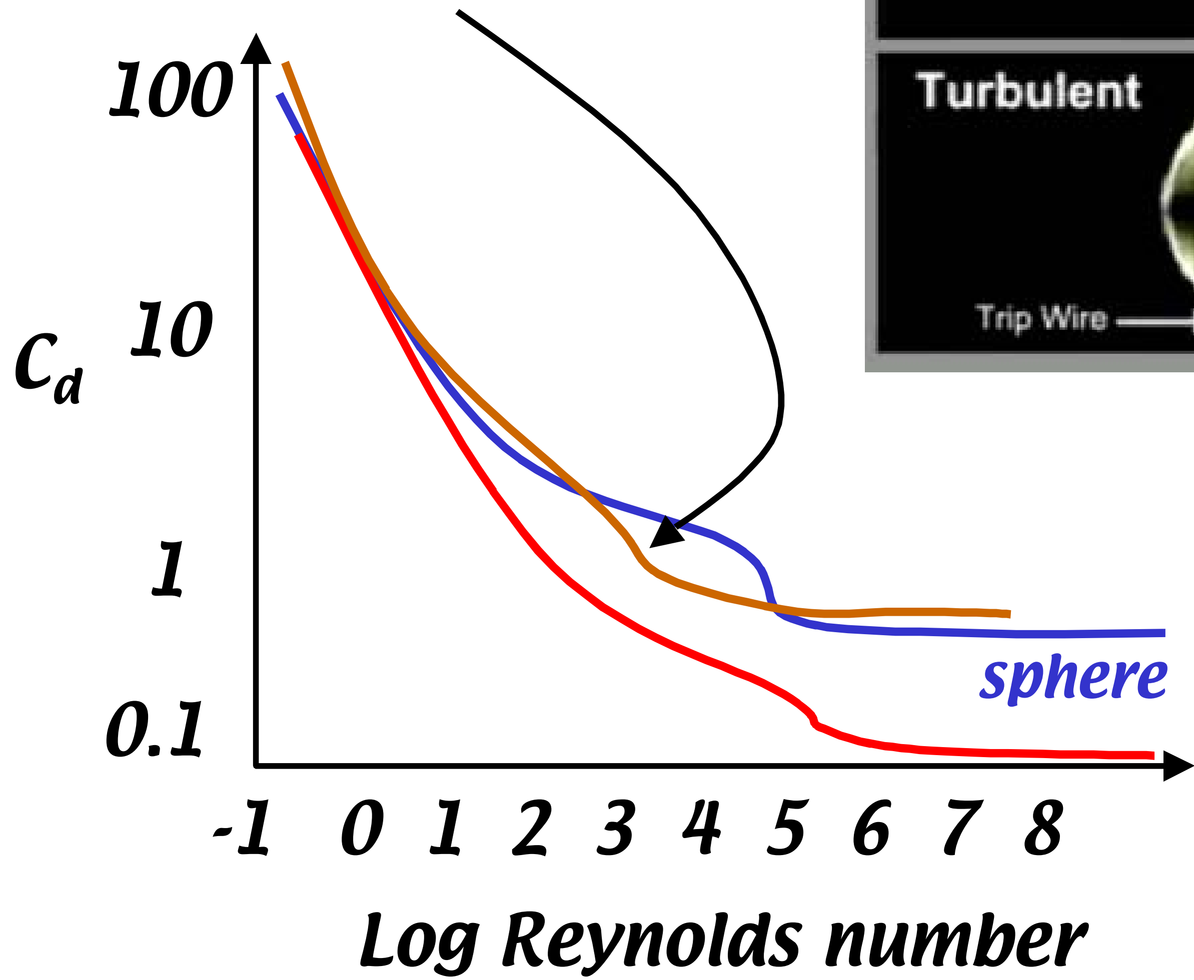
How does Reynolds number affect C_d of a bluff body?



How does Reynolds number affect C_d of a bluff body?

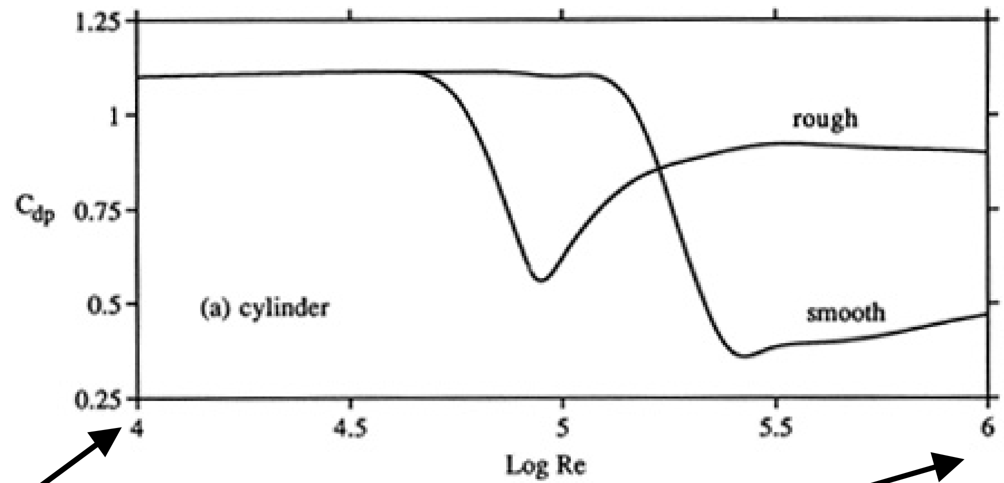
surface roughness and "turbulators" cause C_d to drop at lower Re

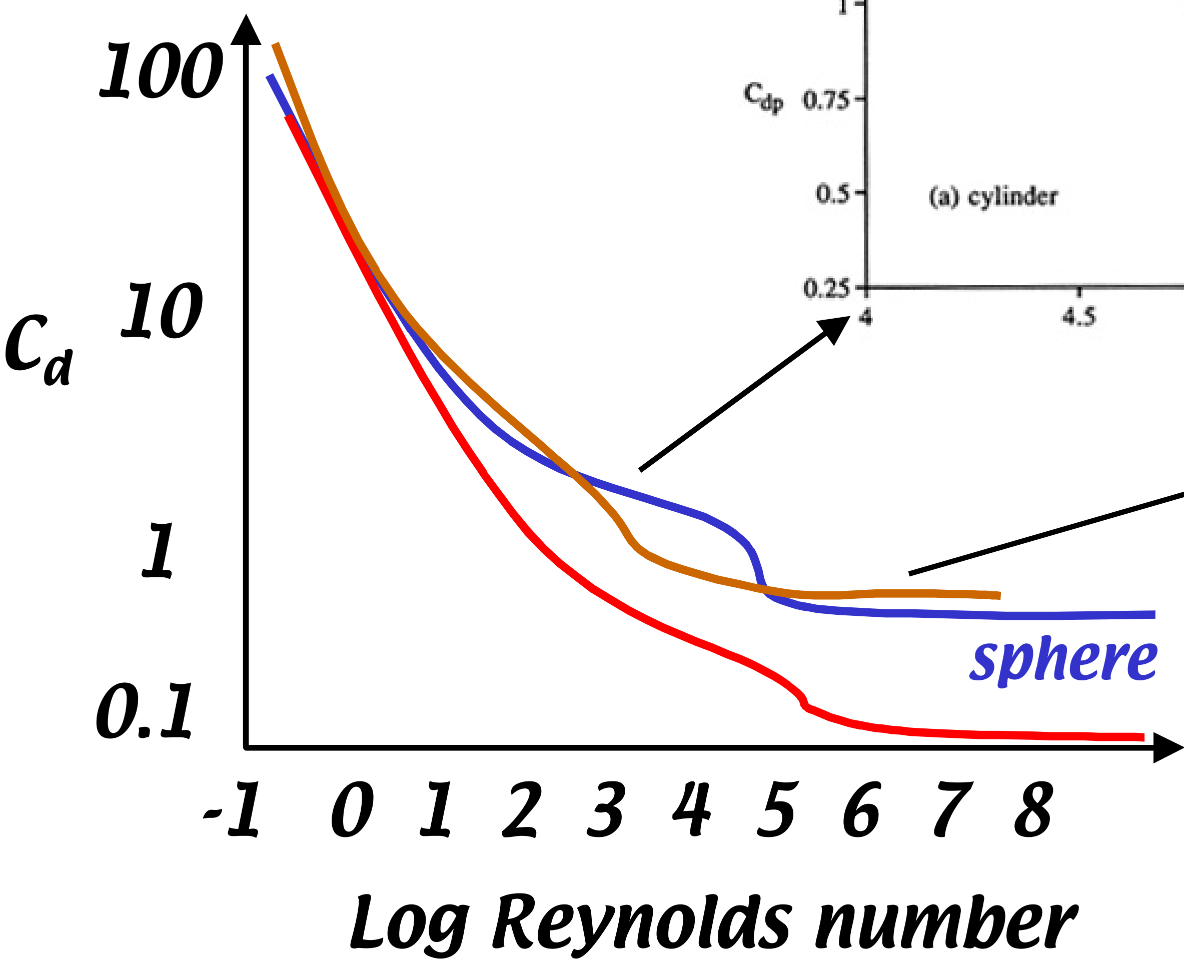




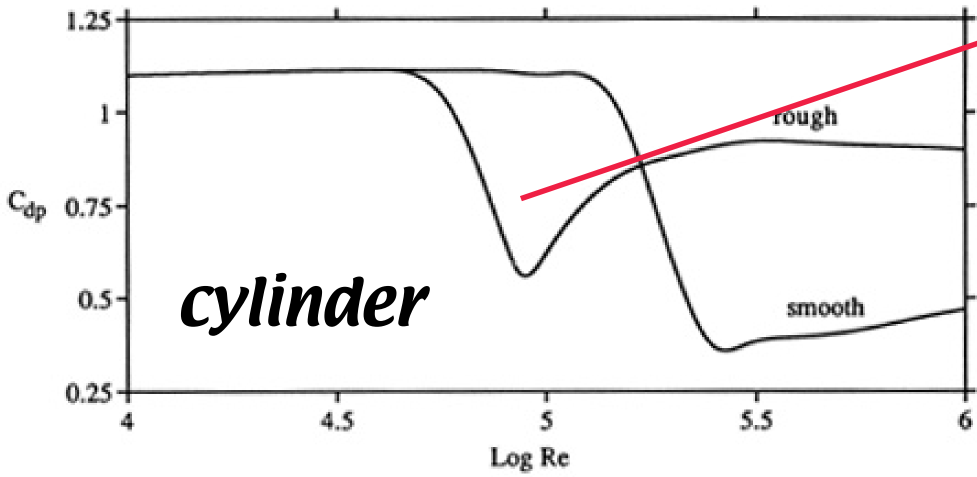
How does Reynolds number affect C_d of a bluff body?

surface roughness
and "turbulators" cause
C_d to drop at lower Re

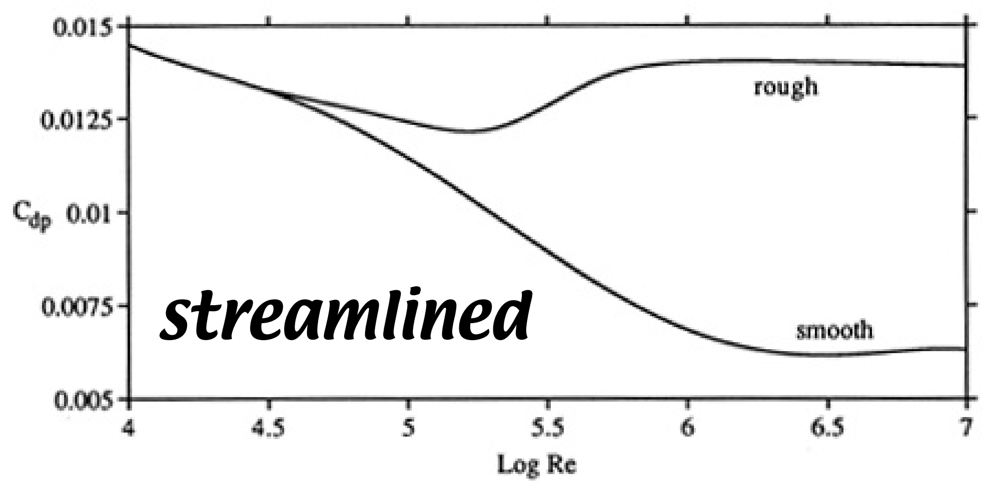




Surface roughness can reduce C_d in bluff bodies over a limited range of Re by increasing boundary layer turbulence and decreasing pressure drag



Re = 200,000



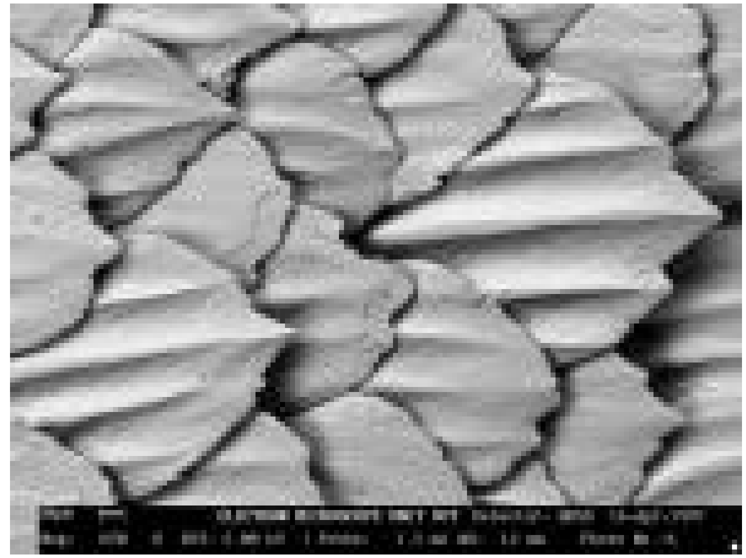
$$Re = \frac{\rho\, u\, L}{\mu}$$

$L = 0.01$ m

$1 \text{ m/s} < u < 10 \text{ m/s}$

$10^4 < Re < 10^5$

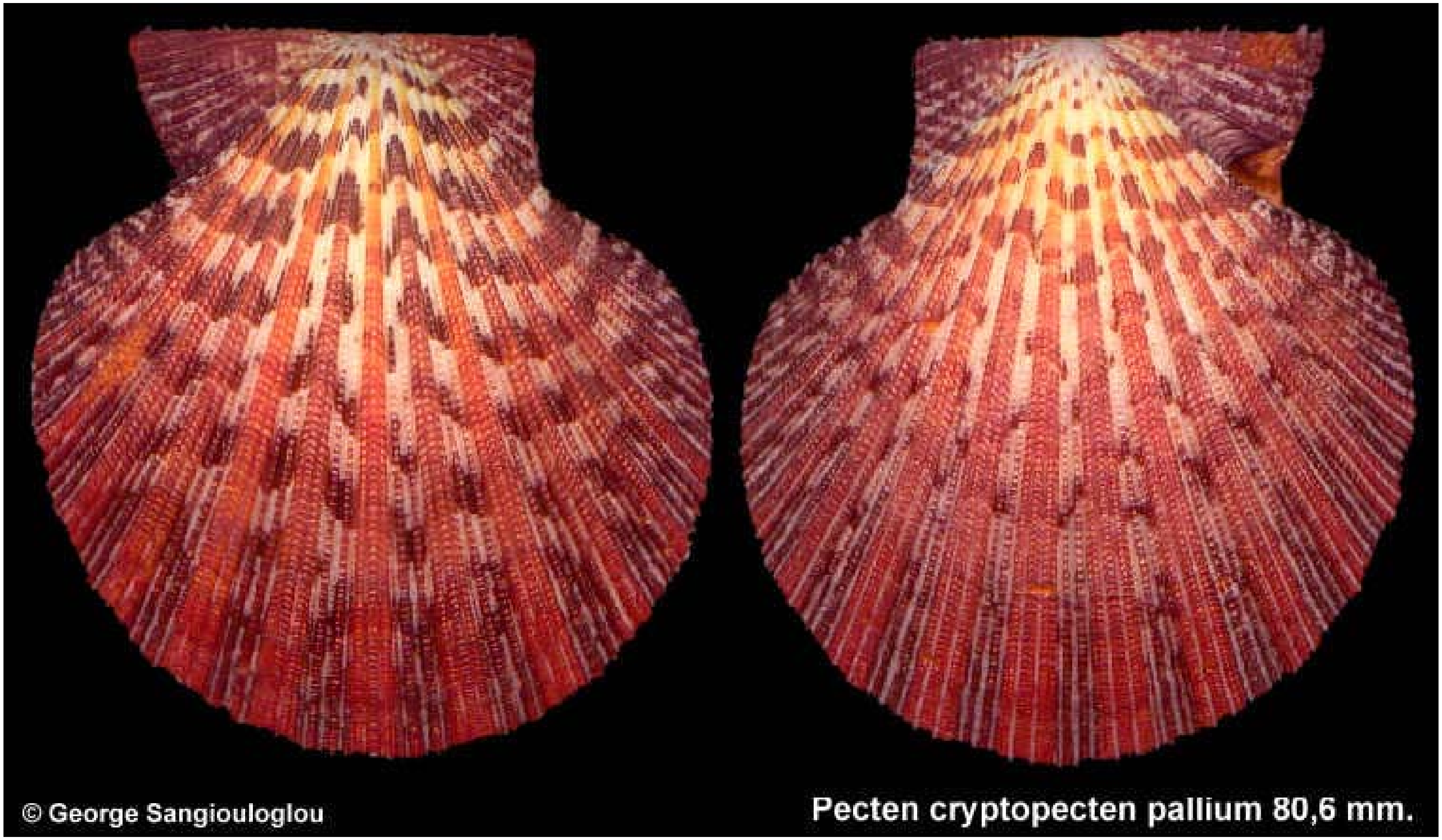
At other Reynolds numbers, microstructures on the surface may channel flow and reduce friction drag



Riblets - *artificial coatings with streamwise surface grooves based on shark skin can provide drag reductions up to 8%*

*Applied to racing boat hulls and wings of aircraft

Dimensions of riblets on some scallop shells appear to be optimized for drag reduction while swimming



E.J. Anderson, P.S. MacGillivray and M.E. DeMont (1997). Scallop shells exhibit optimization of riblet dimensions for drag reduction. Biological Bulletin 192, 341-344.

Does the "fast-skin" bodysuit by Speedo really help reduce drag on swimmers?

Speedo claims 7.5% drag reduction, due to reduced friction drag

The fabric is a biomimetic knitted construction that has ridges, where small vortices are formed. The ridges are scientifically calculated for height and width to the exact proportion of the Shark's dermal denticles, which is the most efficient configuration for SPEED!
(from Speedo: FAST-SKIN - THE FACTS, 2000)

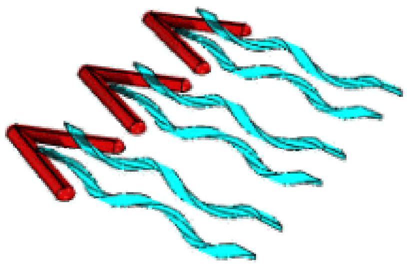
If true, this would lower race times by 1-1.5 s per 100 m!

But...at typical swimmers' Reynolds numbers, friction drag only accounts for about 3-5% of total drag

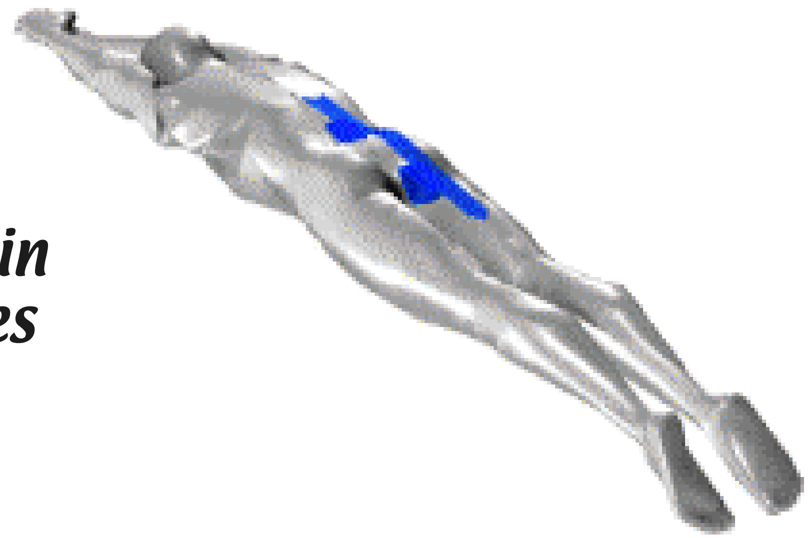
Source: Scientific Proceedings - Applied Program - XXth International Symposium on Biomechanics in Sports - Swimming

Does the “fast-skin” bodysuit by Speedo really help reduce drag on swimmers?

Maybe the suits actually reduce pressure drag, by increasing boundary layer turbulence and reducing flow separation



vortices could be generated in boundary layer by suit ridges

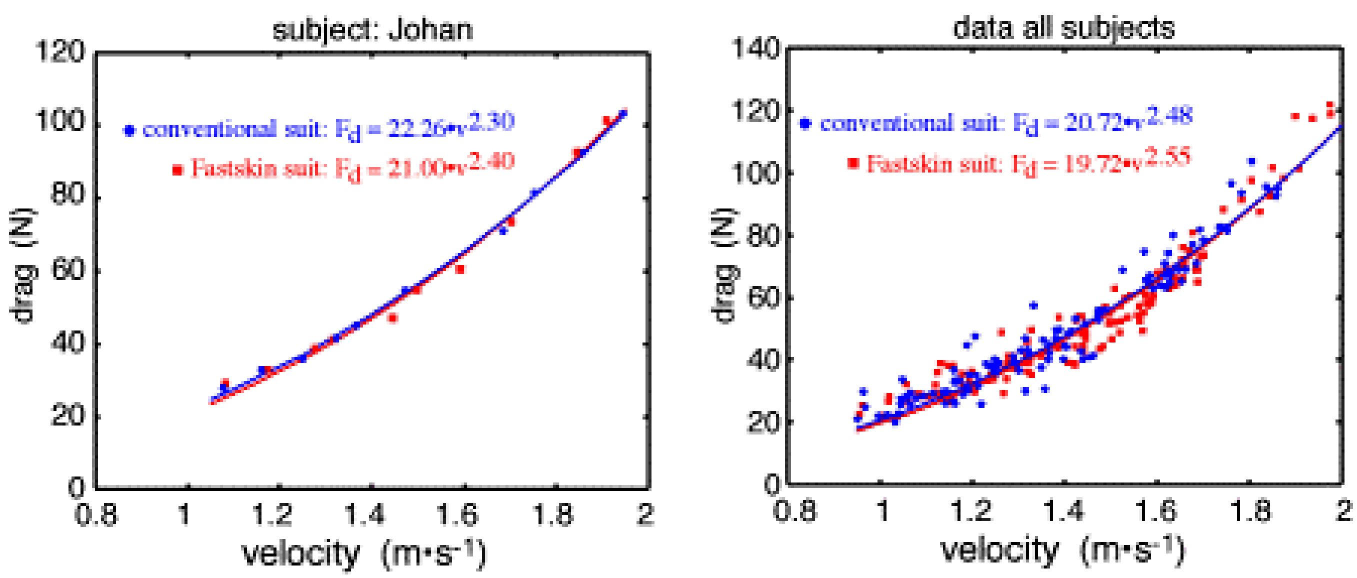


increased boundary layer turbulence could reduce flow separation in small of back and behind buttocks

Does the "fast-skin" bodysuit by Speedo really help reduce drag on swimmers?

Figure 7. Subject wearing Fast-skin" (left) and standard suit (right).

No significant reduction in drag when tested on 13 Dutch top-level swimmers

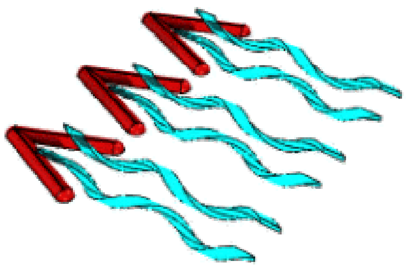


Why doesn't the "fast-skin" bodysuit by Speedo really help reduce drag on swimmers?

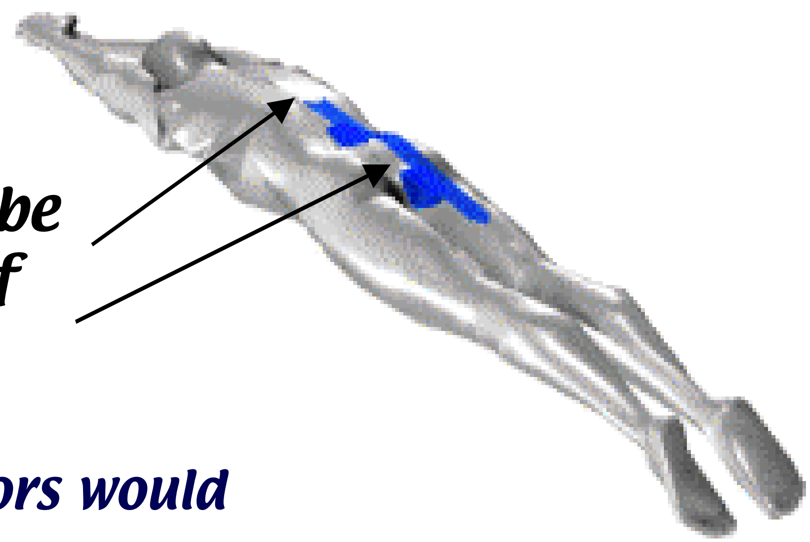
The boundary layer on the trunk of a swimmer has a thickness of about 4 mm when swimming at race pace.

Hence vortex generators must have a height of at least 4 mm to be effective.

The "denticles" on fast-skin only protrude about 0.5 mm)

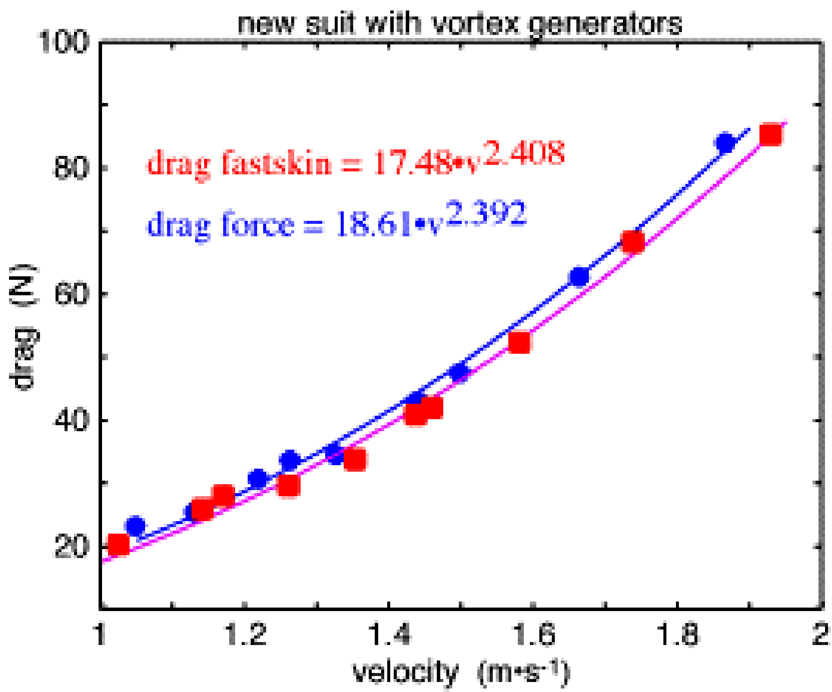


Larger vortex generators would be useful, but only just upstream of points where flow separation is likely to occur



(at other locations the generators would actually increase resistance)

New series of Speedo body suits was released in 2001, in which strips with vortex generators are positioned on chest and back.

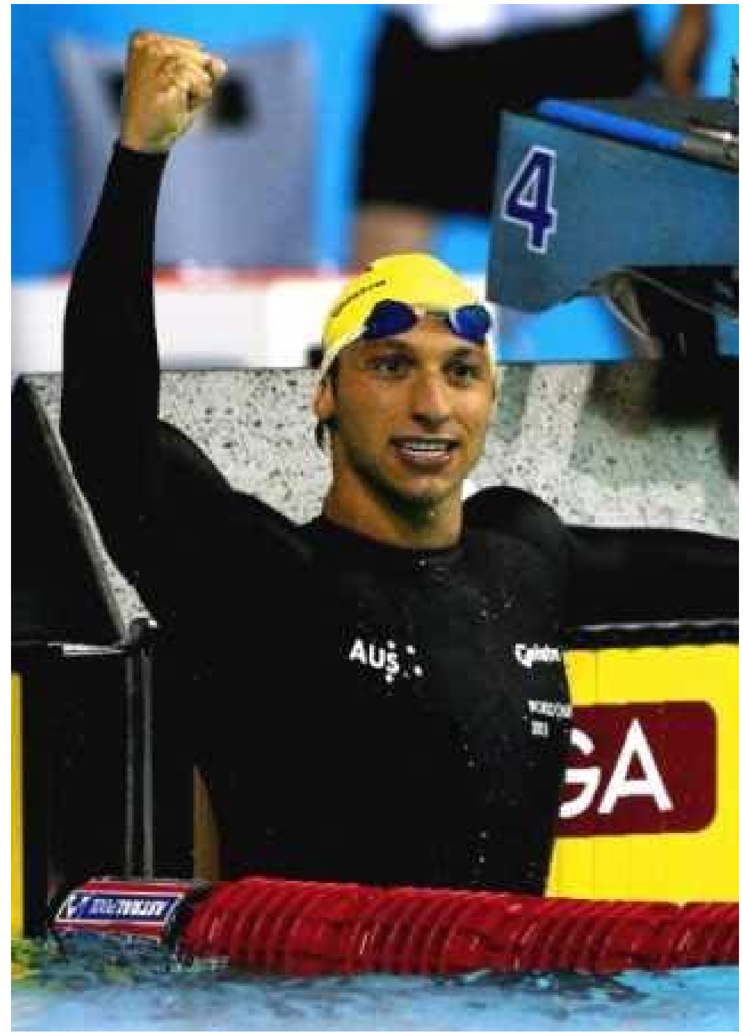


****tests on one subject suggested a modest drag reduction***

Source: Scientific Proceedings - Applied Program - XXth International Symposium on Biomechanics in Sports - Swimming

July 21, 2003

LONDON (Reuters) - Ian Thorpe's 400 meters freestyle victory on Sunday was the first achieved in the Adidas Jetconcept bodysuit



Adidas says new suit focuses on cutting form drag by adding 'riblets' of silicon that run from the underarm to the lower back and over the bottom.

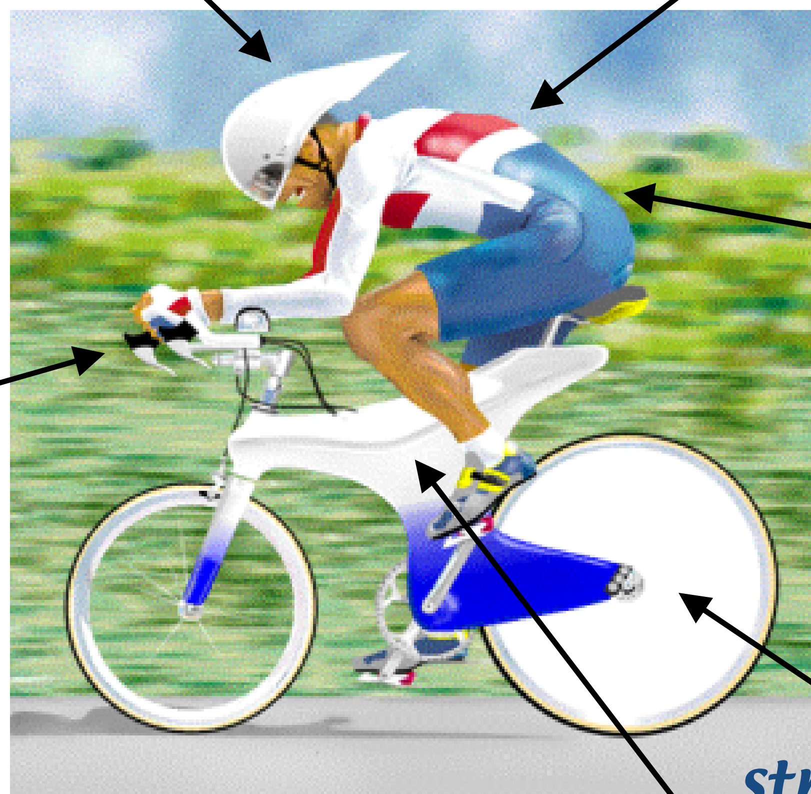
Tests in Finland and Australia showed the riblets could enhance performance by up to 3%

Does drag matter in air?
Drag reduction in bicycle riders

helmet can decrease aerodynamic drag by about 2%, even compared to a bald rider

proper body position can reduce drag by 31% over an upright riding position.

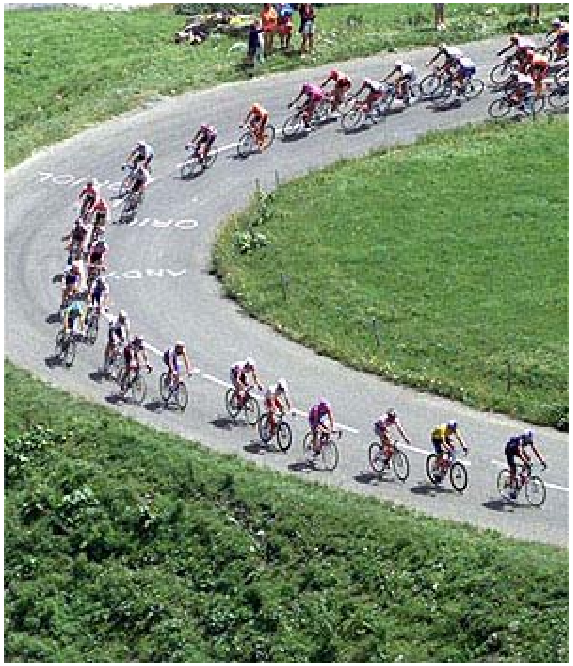
New handlebars allow riders to achieve an optimal aerodynamic position.



bodysuits reduce friction drag (small portion of total drag)

streamlining of bicycle and wheels reduces drag

"Drafting" to reduce drag in bicycle races



lead cyclist produces a turbulent wake behind - low pressure area with eddies

cyclist following very close (within a few inches) is pushed forward by low pressure and eddies

*lead cyclist also gains an advantage by having his eddy filled in

But...lead cyclist still expends 30-40% more energy than riders in the middle of a pack

Back to biology.....
Mechanisms of biological drag reduction

- Streamlining
- Adaptive shape change
- Surface microstructure
- Surface heating (effects on viscosity)

Friction drag depends on viscosity, and viscosity of water decreases with increasing temperature

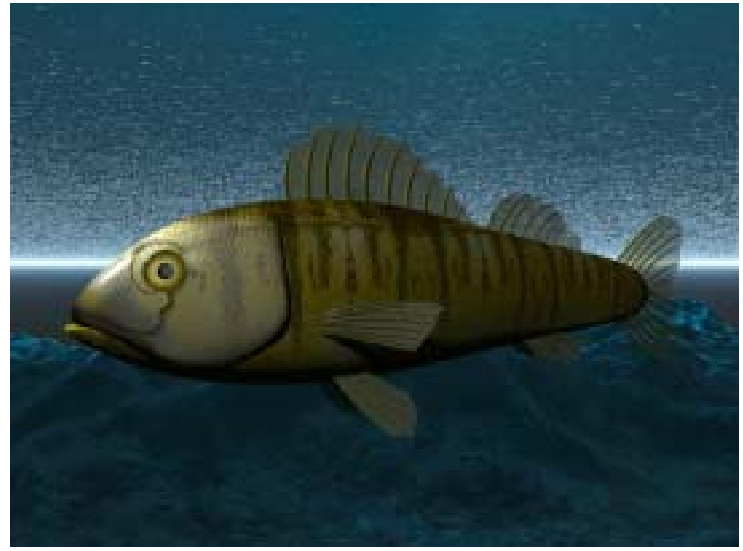
► Effect is very small

Back to biology.....
Mechanisms of biological drag reduction

- Streamlining
- Adaptive shape change
- Surface microstructure
- Surface heating (effects on viscosity)
- Mucous secretions (slimy fish and the mysterious slimy subs)

Adding long-chained polymers to the velocity gradient near a body can reduce friction drag

Fish slime can reduce drag
(Daniel, 1981)



But... slime also has many other functions:

- reduce parasites
- cover wounds
- maintain salt balance
- defensive

(and may be expensive to produce)

Back to biology.....

Mechanisms of biological drag reduction

- *Streamlining*
- *Adaptive shape change*
- *Surface microstructure*
- *Surface heating (effects on viscosity)*
- *Mucous secretions (slimy fish and the mysterious slimy subs)*
- *Compliant surfaces (dolphins and Sir James Gray's paradox)*

Drag reduction with compliant surfaces (dolphins and Sir James Gray's paradox)

Dolphins seemed to go faster than possible for estimated power output of muscles
-> Gray suggested compliant skin damped turbulence, producing laminar flow and reducing drag

Ends up that dolphins actually swim a little slower than thought and muscles produce more power than thought

After many years and many experiments (!), there is still no evidence for drag reduction via compliant surfaces

Back to biology.....

Mechanisms of biological drag reduction

- Streamlining
- Adaptive shape change
- Surface microstructure
- Surface heating (effects on viscosity)
- Mucous secretions (slimy fish and the mysterious slimy subs)
- Compliant surfaces (dolphins and Sir James Gray's paradox)
- Flow splitters (tail feathers)

“Splitter plate” behind an object in flow reduces turbulence and pressure drag

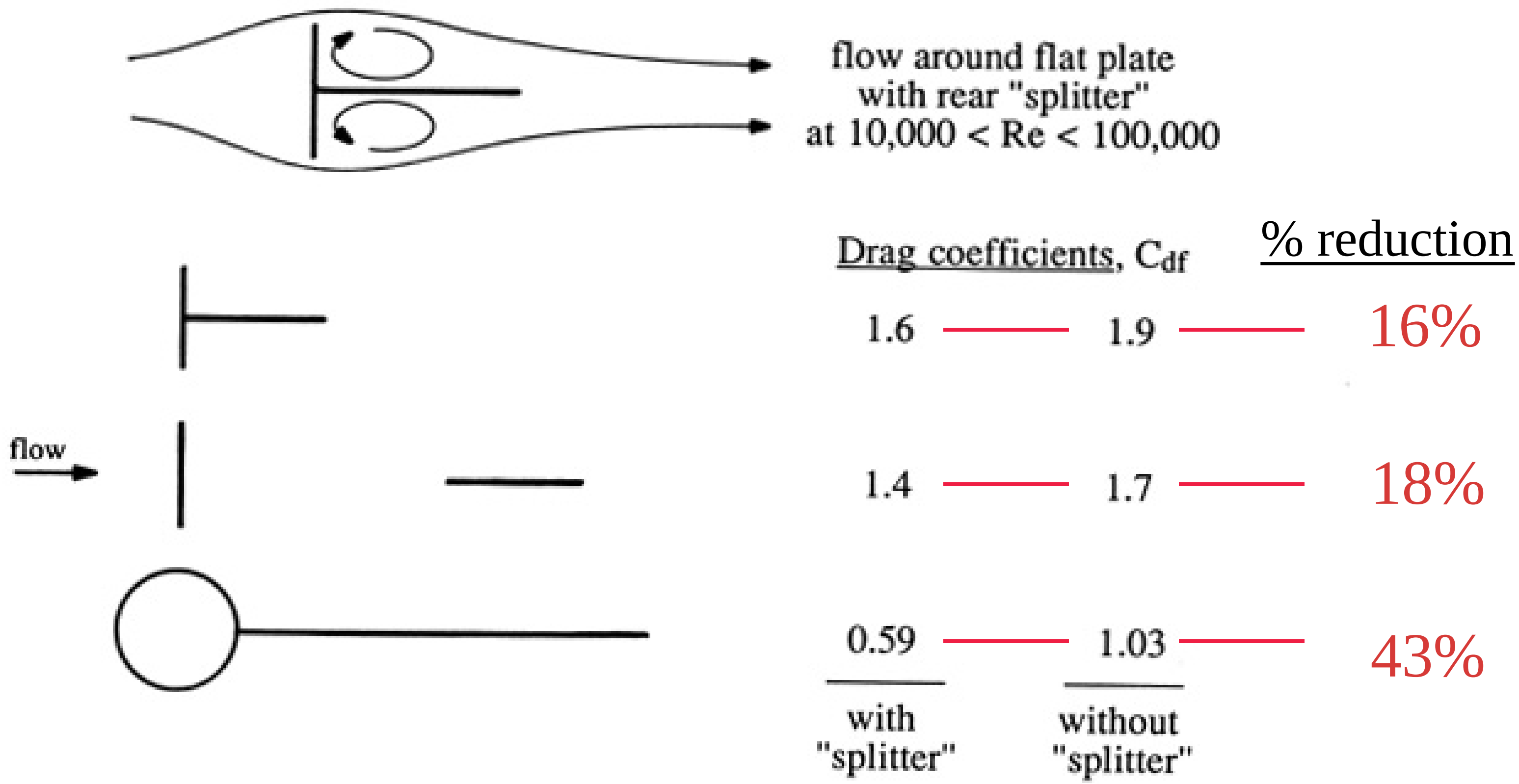
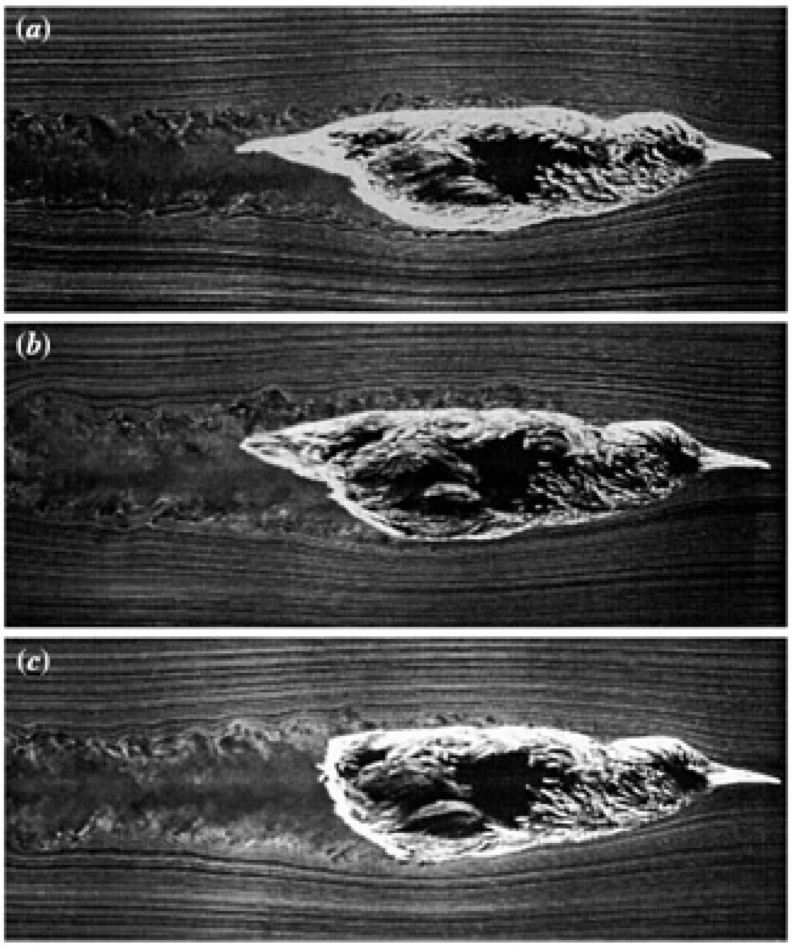


FIGURE 6.3. The influence of “splitter plates” on flow patterns and drag coefficients of long flat plates and cylinders. Reynolds numbers are based on maximum dimensions normal to flow and drag coefficients on frontal areas.

Tail feathers may split flow behind flying birds



"Dorsal boundary layer becomes increasingly turbulent...as the tail is progressively removed."

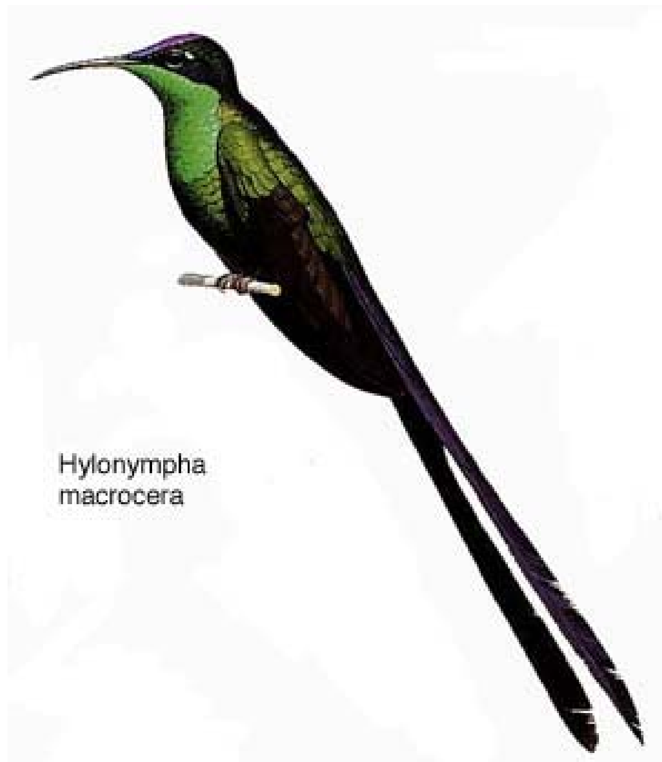
Tail removal increases body drag by ~35%!

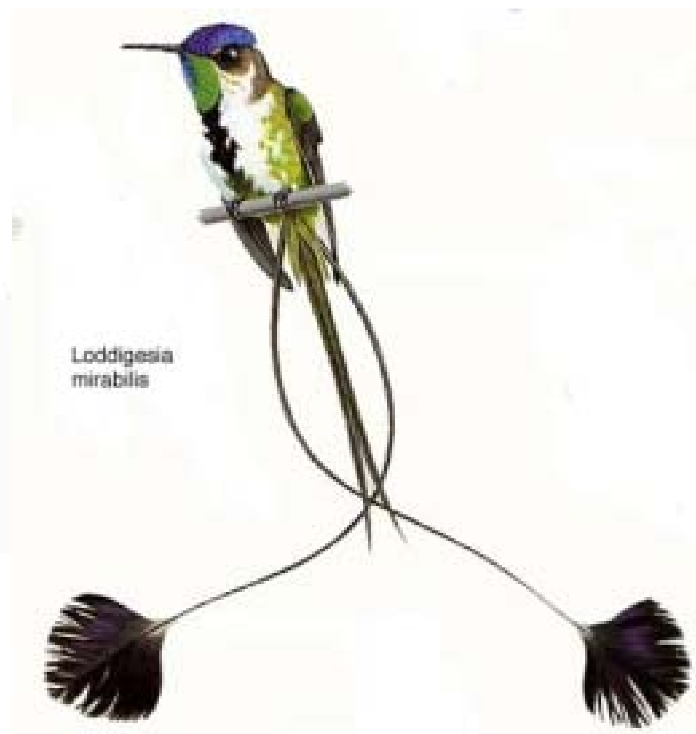
Caveat: flow field induced by wing flapping is ignored.

Maybury and Rayner, 2001

Hummingbirds: Family Trochilidae

About 320 species, mostly in South America





What if an organism wants to enhance drag?

- Pressure gradient associated with drag can aid in filter feeding

- Drag forces on appendages can be used to generate thrust (i.e. paddling, rowing)

- Drag forces can slow the descent of organisms that are air or water-dispersed (i.e. seeds, marine larvae)

Hollow structures with open side facing flow experience enhanced drag

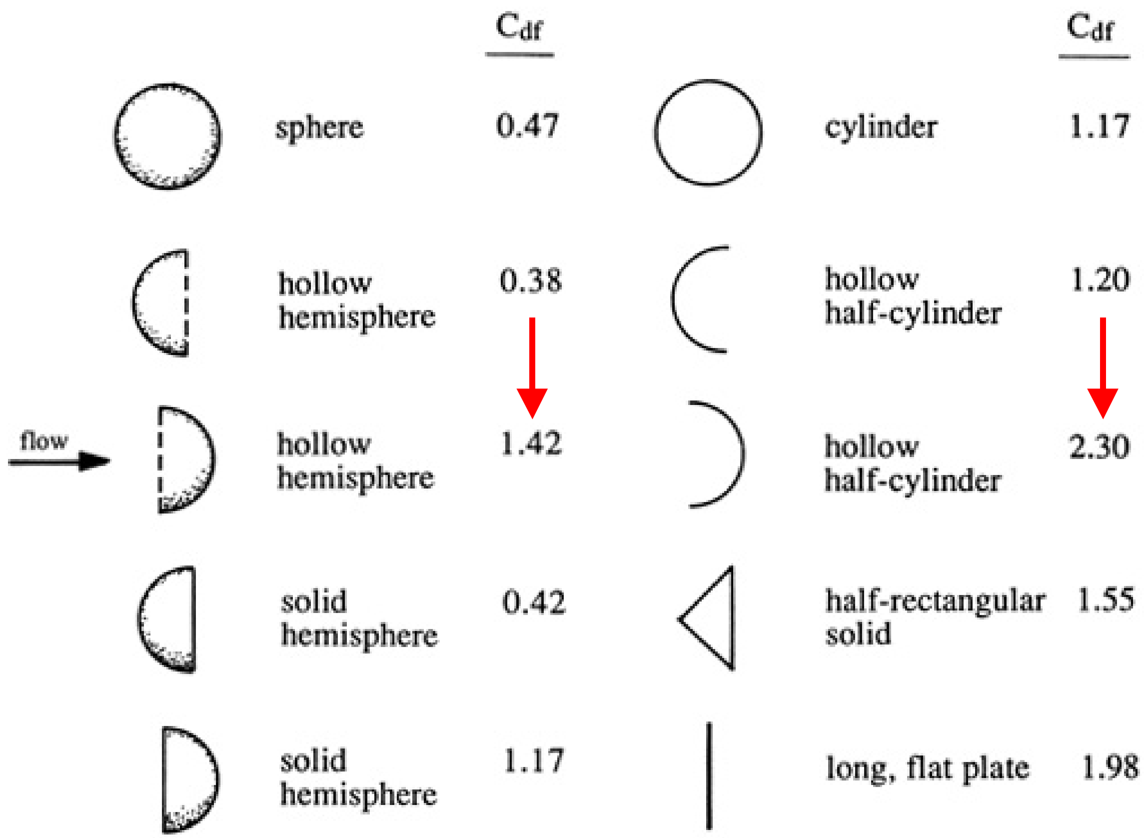


FIGURE 6.4. Drag coefficients, based on frontal area, for a variety of three-dimensional bodies and two-dimensional profiles at Reynolds numbers between 10^4 and 10^6. All the data may not be precisely comparable due to variations in the experimental conditions.

Filter feeders can increase cross-sectional area or change orientation of concavity to increase filtration pressure

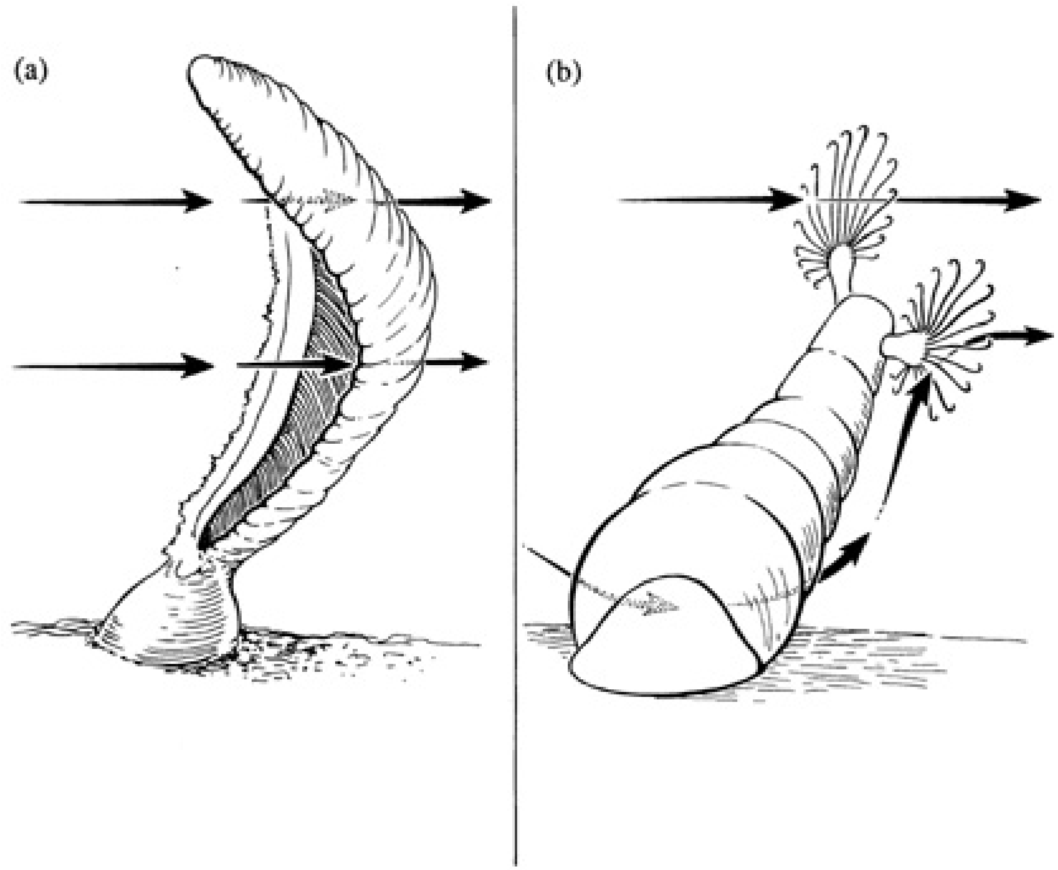
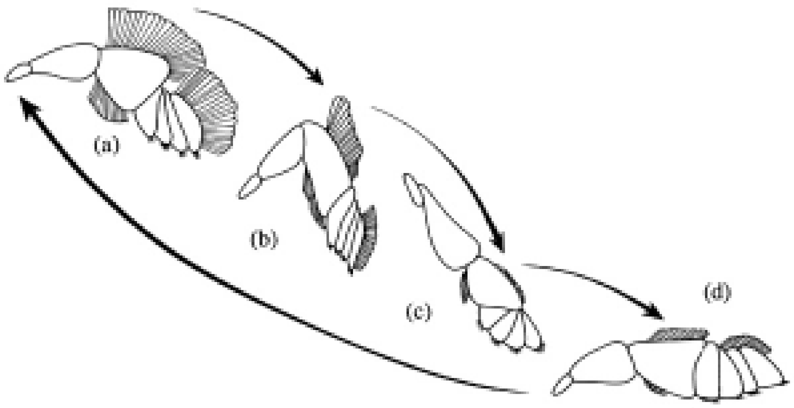


FIGURE 6.5. Living structures whose concave sides face upstream and which thus have high drag coefficients: (a) a sea pen, *Ptilosarcus*; (b) a larval black fly, *Simulium*.

Using drag for propulsion: paddling and rowing

$$D = C_d \rho S u^2/2$$

Drag is a mechanism by which swimming forces arise

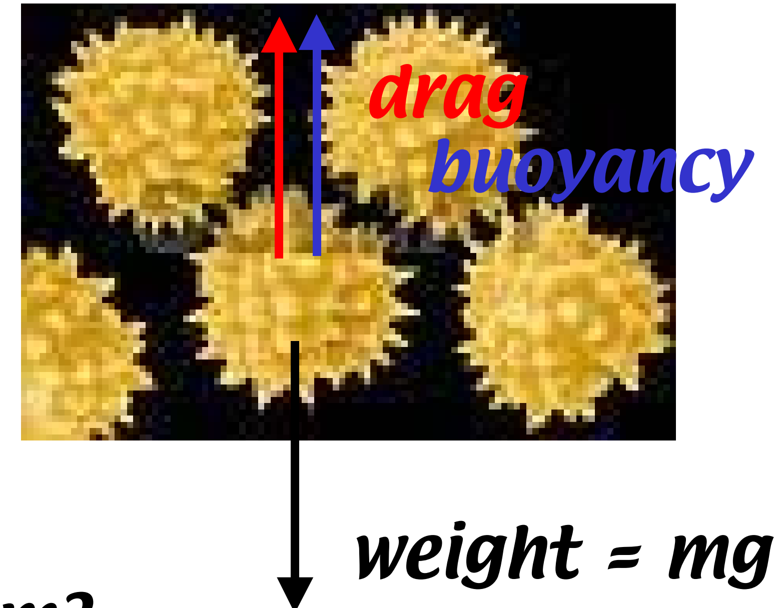


- ►Change area/shape between downstroke and upstroke
- ►Decrease velocity during recovery stroke
- ►Change fluid density during recovery stroke

Objects falling at terminal (steady) velocity experience drag and buoyant forces balancing their weight

$$D = 0.5\, C_d\, \rho_f\, S\, u^2$$

$$B = \rho_f\, V\, g$$



What is u at equilibrium?

$$mg = 0.5\, C_d\, \rho_f\, S\, u^2 + \rho_f\, V\, g$$

$$V \rho_o\, g = 0.5\, C_d\, \rho_f\, S\, u^2 + \rho_f\, V\, g$$

$$4\pi r^3 \rho_o\, g/3 = 0.5\, C_d\, \rho_f\, \pi r^2\, u^2 + 4\pi r^3 \rho_f\, g/3$$

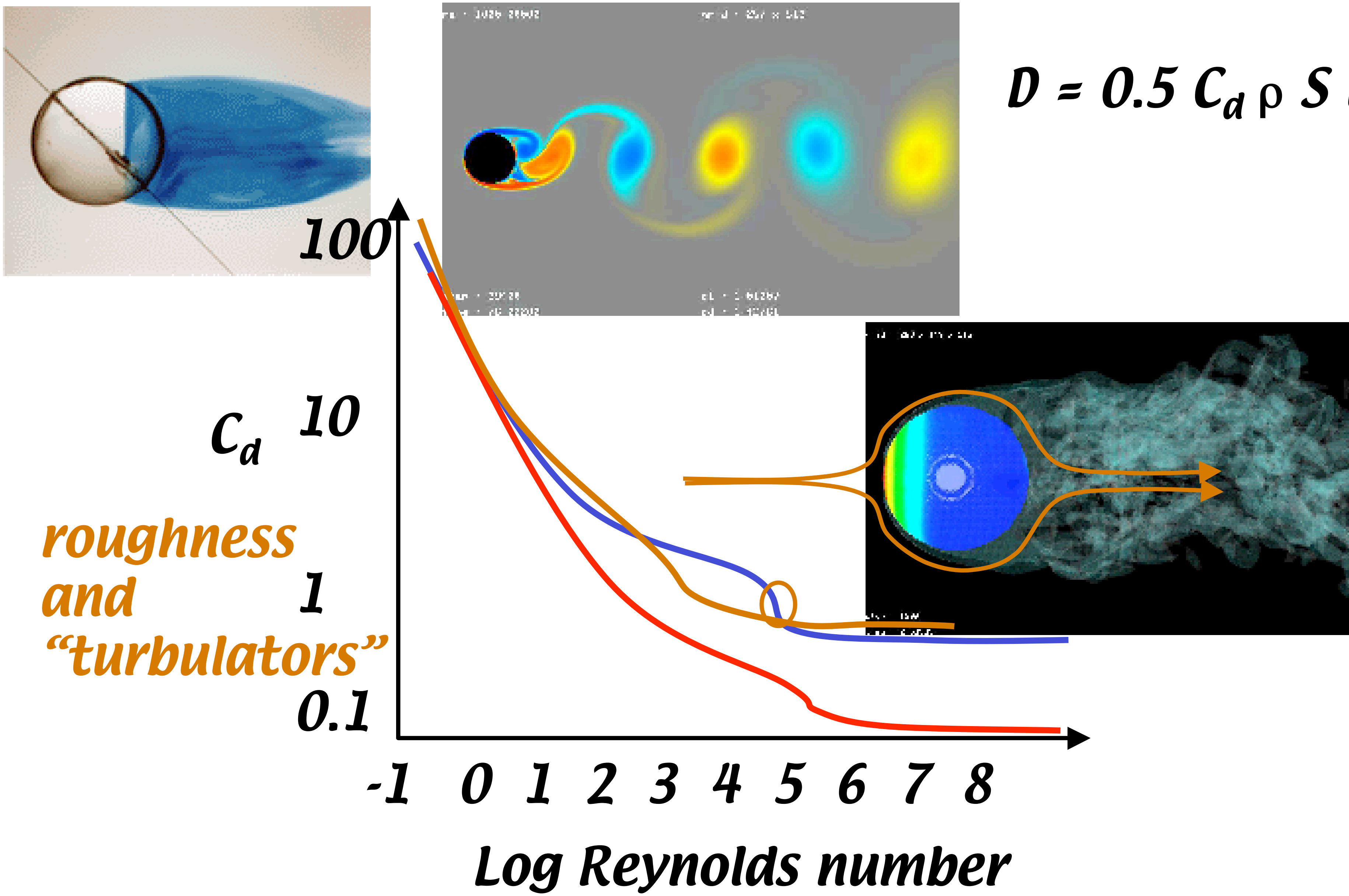
$$4r\,(\rho_o - \rho_f) g/3 = 0.5\, C_d\, \rho_f\, u^2$$

Biology 427 Bimechanics
Lift and circulation

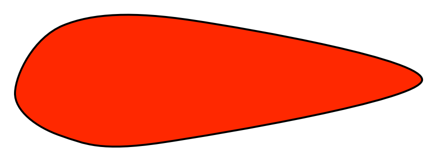
- Recap drag, shape, and the Reynolds number
- Return to lift and Bernoulli
- Basic definitions of wing shape
- The relationship between lift and circulation
- Mechanisms that promote or maintain circulation.
- The challenge of flapping flight

Check out p 484 on your CD text

$$D = 0.5\, C_d\, \rho\, S\, u^2$$

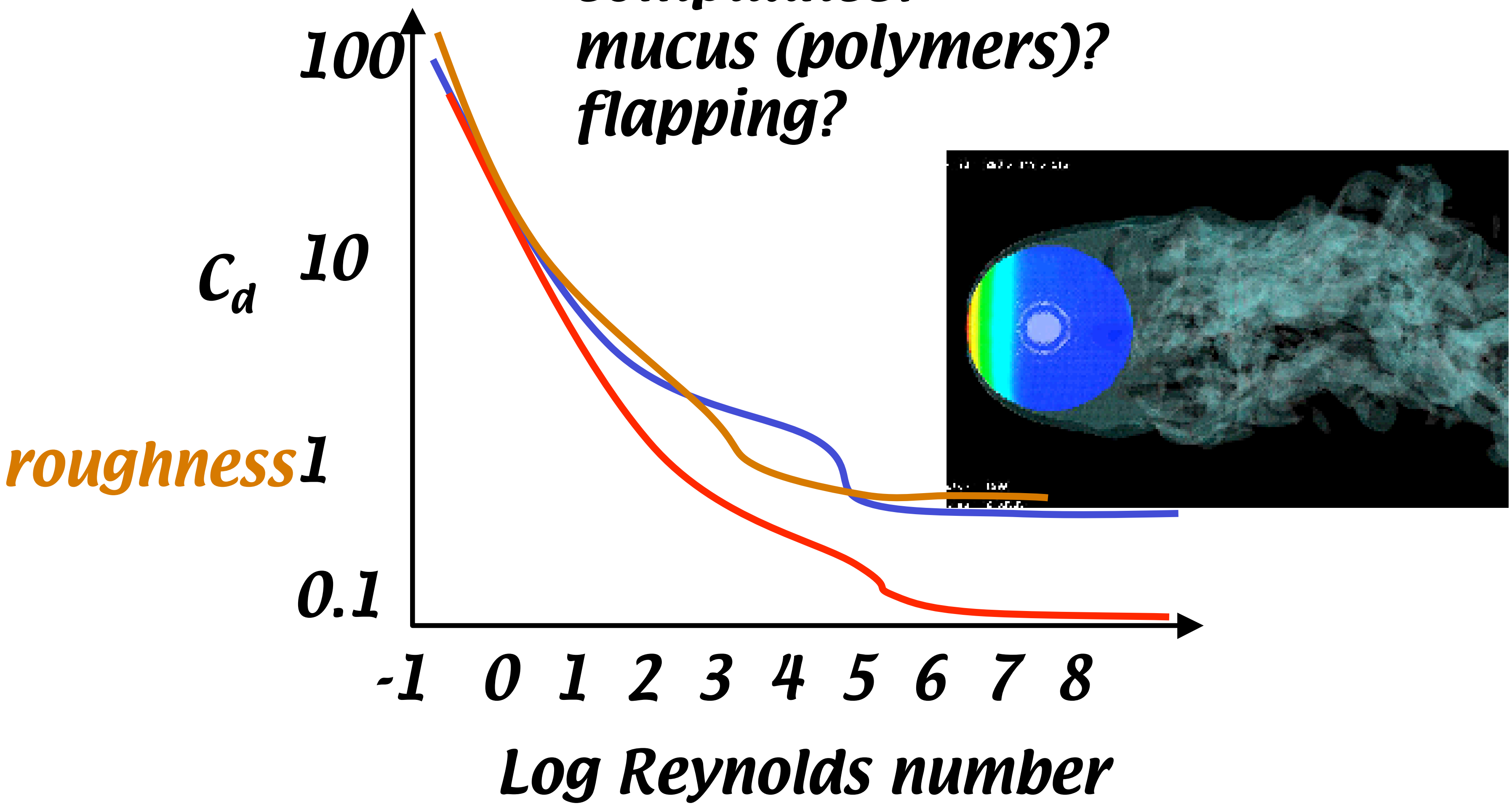


streamlined body: same surface area

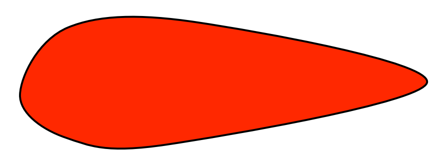


$D = 0.5\, C_d\, \rho\, S\, u^2$

Other factors:
temperature?
compliance?
mucus (polymers)?
flapping?

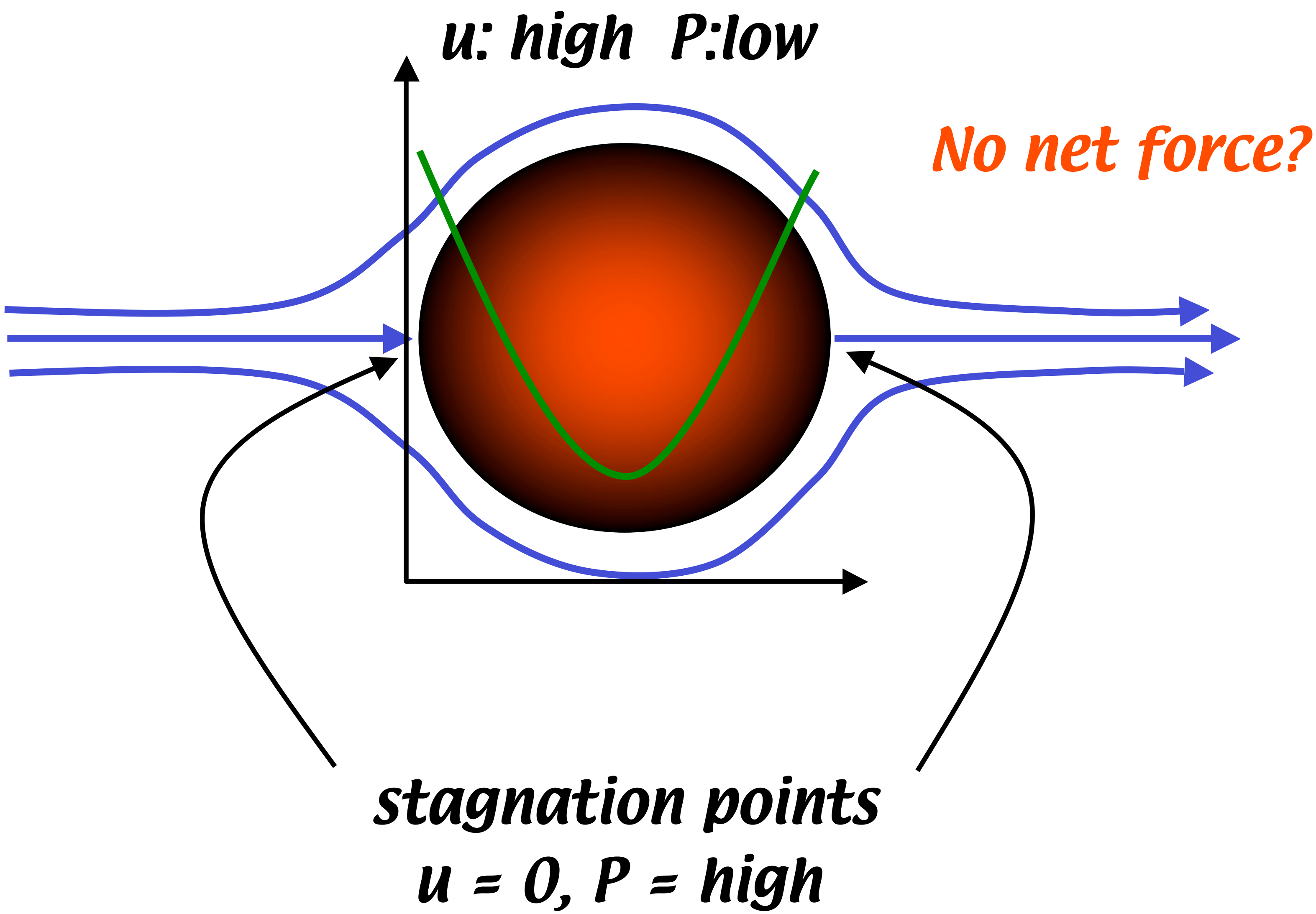


streamlined body: same surface area



D'Alembert's Paradox

$$(P_2 - P_1)/\rho = (u_1^2 - u_2^2)/2$$



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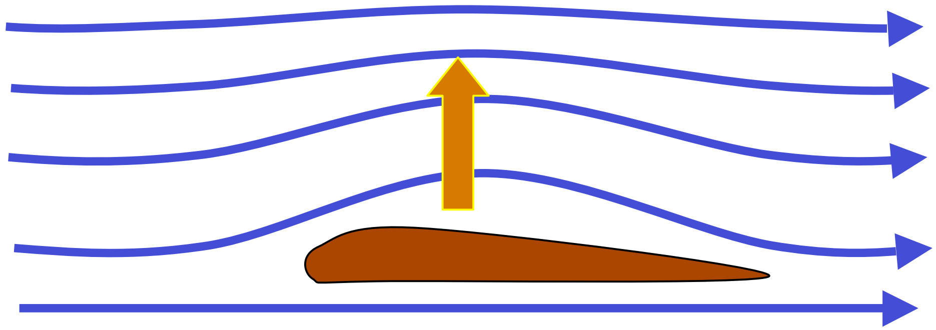
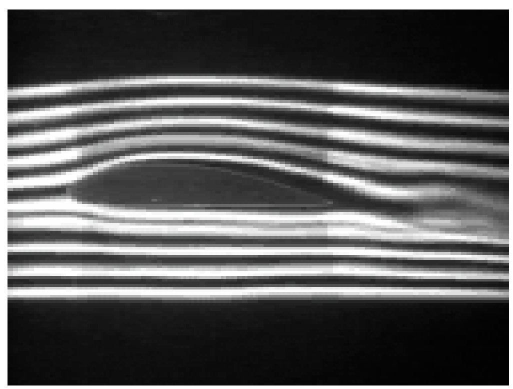
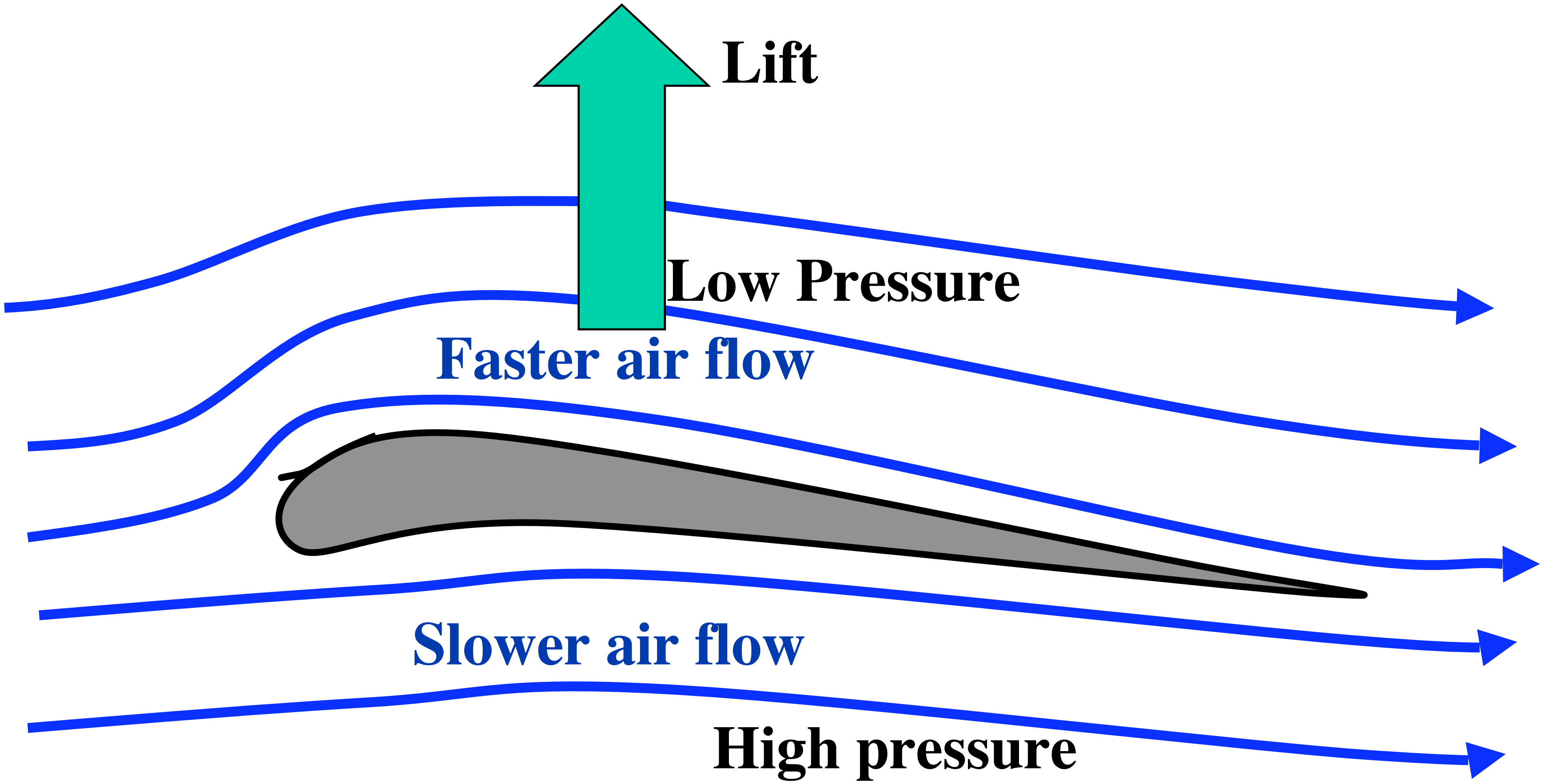




Lift and Circulation:



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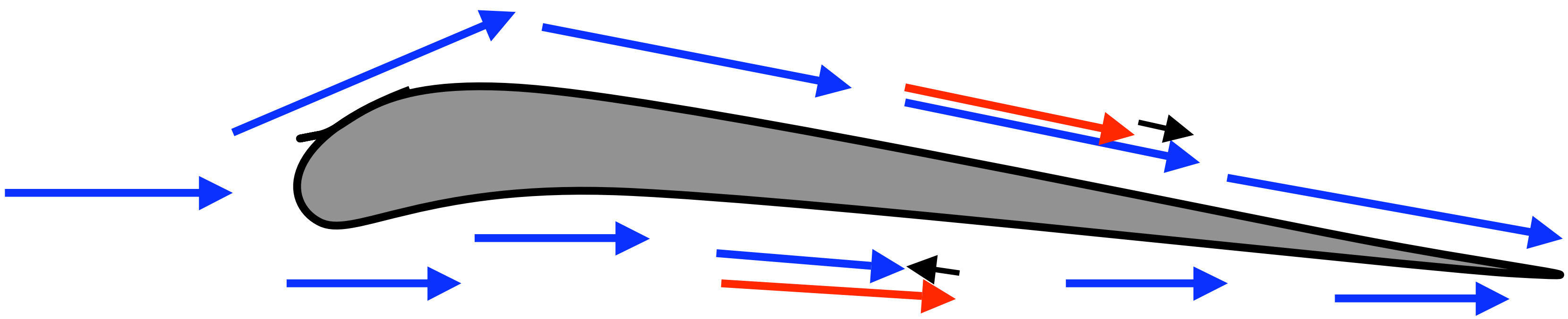
Lift and Circulation:

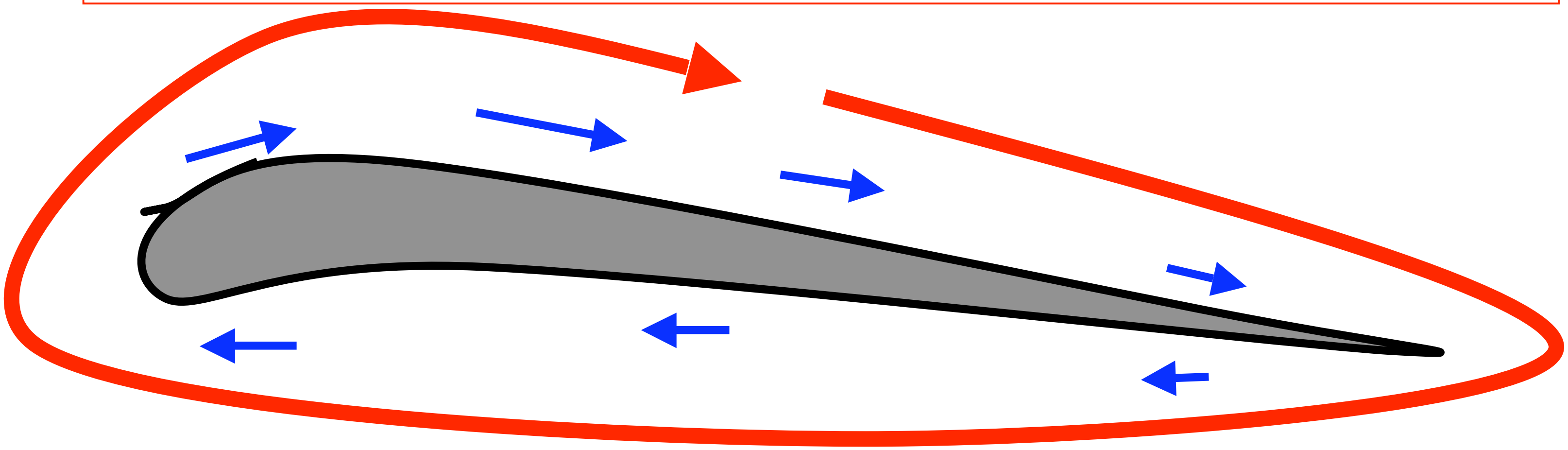


Subtract the mean velocity from all of these vectors

$$(P_2 - P_1)/\rho = (u_1^2 - u_2^2)/2$$

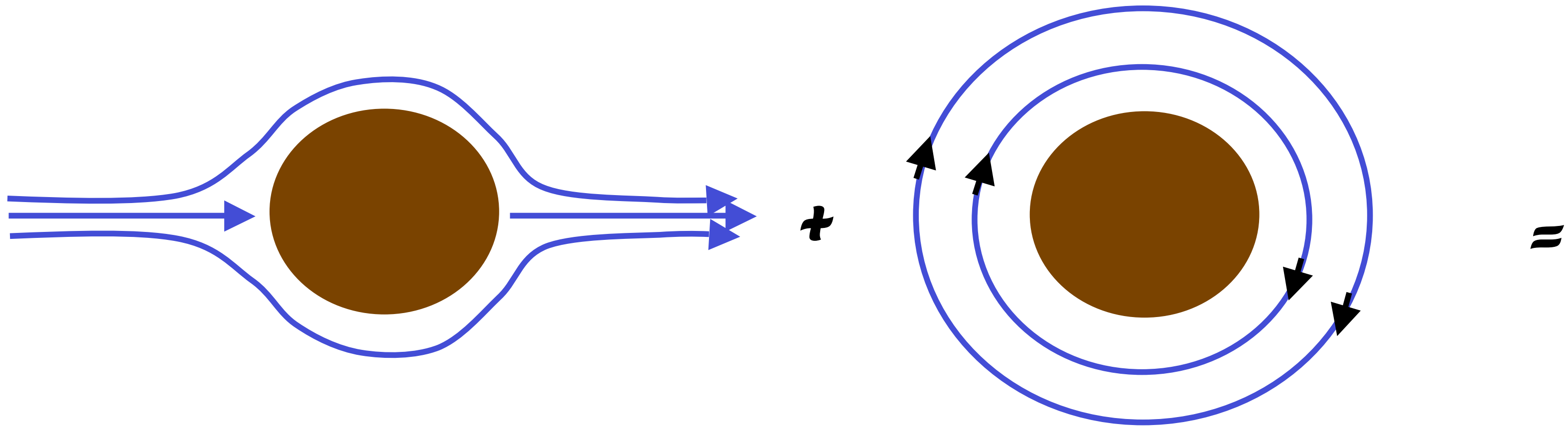
Lift and Circulation:

With the mean subtracted, there is and effective circulation (Γ)about the wing. Greater Γ implies a greater velocity difference

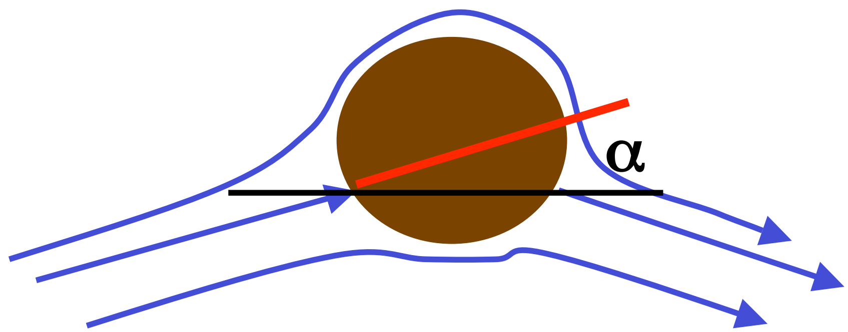


$$(P_2 - P_1)/\rho = (u_1^2 - u_2^2)/2$$

A different spin on circulation



$U_T = U\{\cos(\theta)/r^2,\sin(\theta)/r^2\}$ $U_R = \{0,\Gamma/(2\pi r)\}$



$U_T = U\{\cos(\theta)/r^2,\sin(\theta)/r^2 + \Gamma/(2\pi r)\}\ \}$

$(P_2 - P_1)/\rho = (u_1^2 - u_2^2)/2$

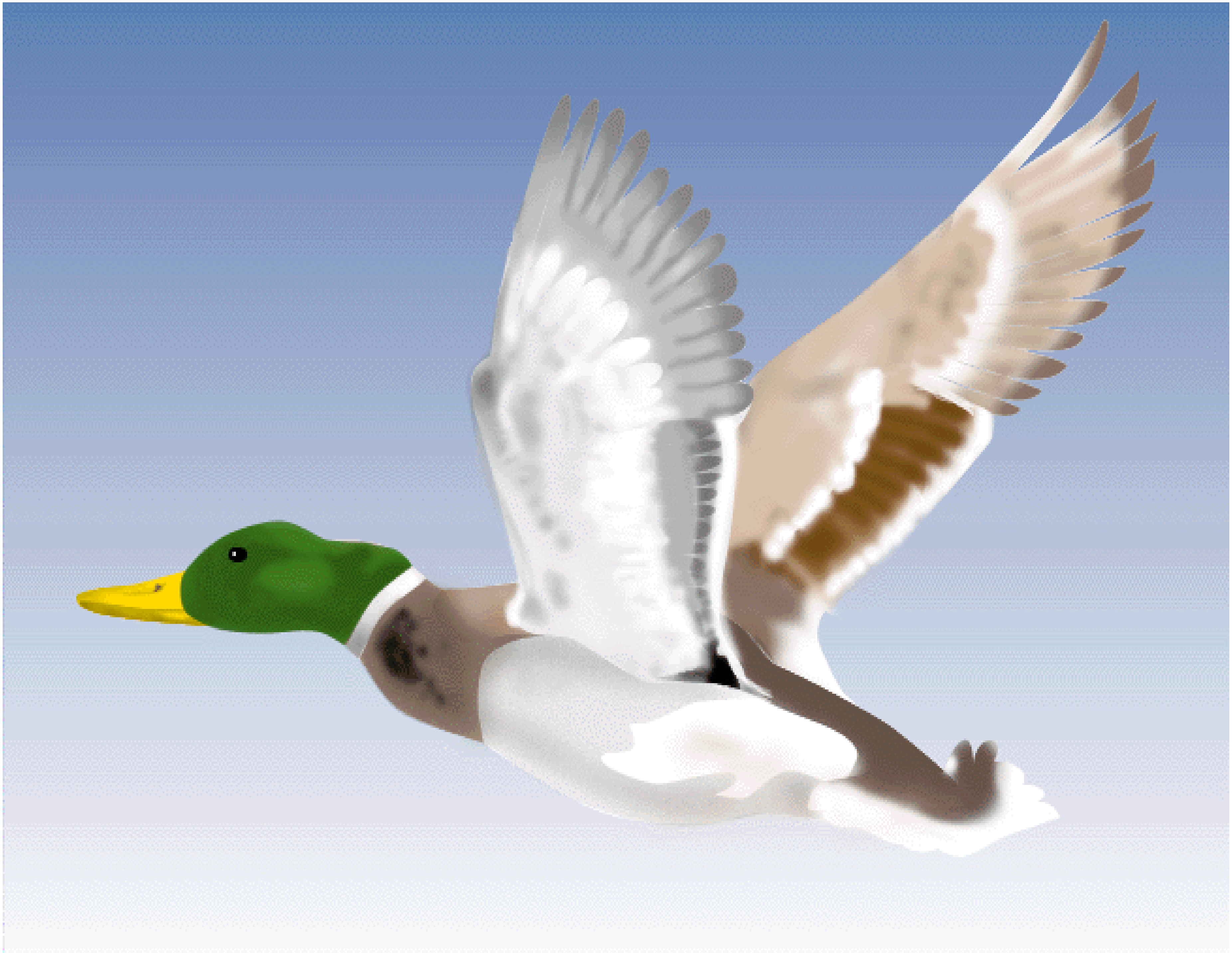
$L = 2\pi\rho U^2 \sin(\alpha)$
$\Gamma = \rho U \sin(\alpha)$
$L = 2\pi U \Gamma$

$L = 2 \pi \rho U^2 \sin(\alpha)$
$\Gamma = \rho U \sin(\alpha)$
$L = 2 \pi \; U \Gamma$

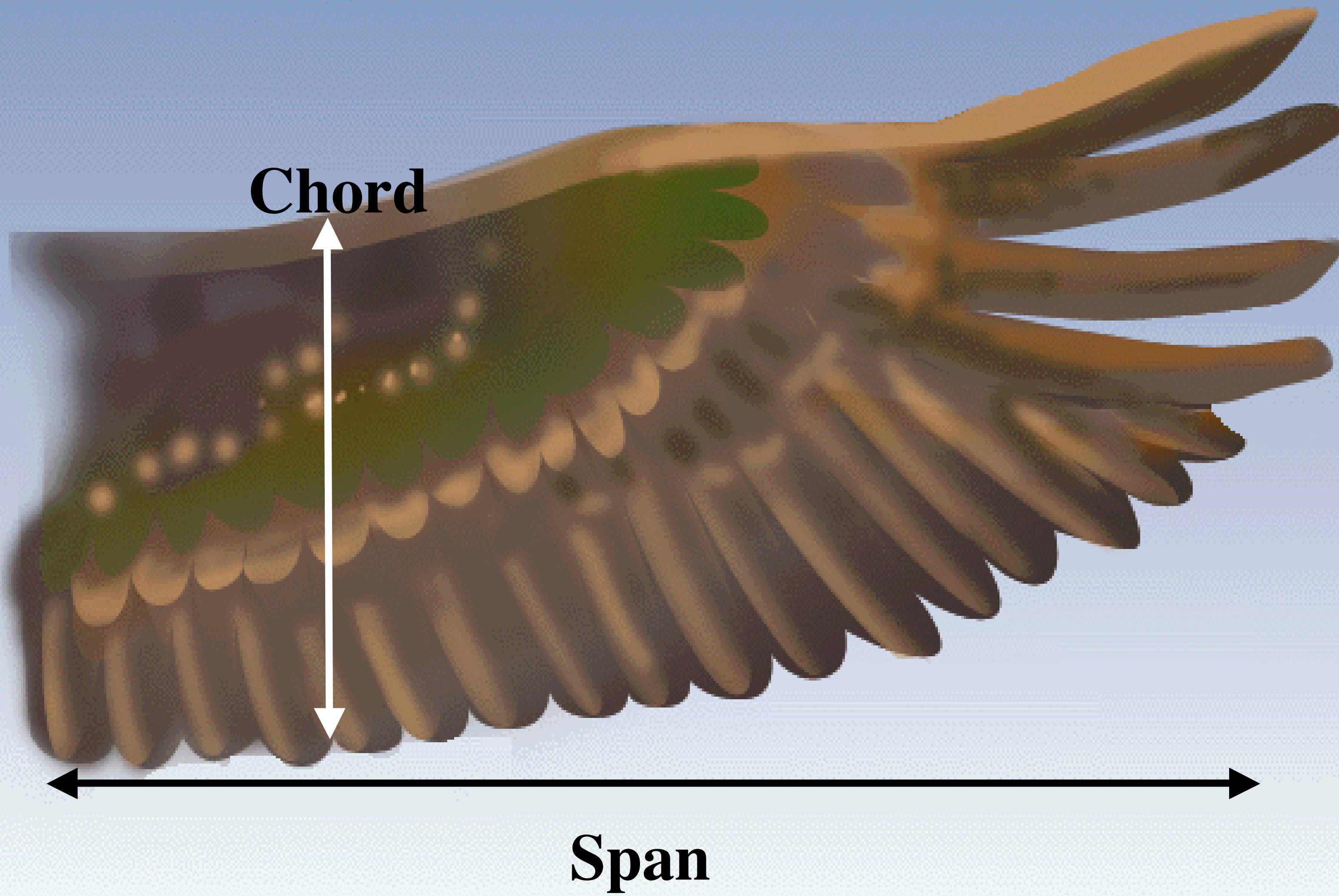
Message: lift can be measured by the amount of circulation held by a wing

Circulation is conserved (Kelvin's circulation theorem)
For every clockwise spin there is a counter clockwise one elsewhere in the fluid.

Dilemma: create circulation and maintain it.
Understand this in the context of flapping flight!



Aspect Ratio = $Span^2$/AREA



$L = 2\,\pi\,\rho\,U^2 \sin(\alpha)$

$\Gamma = \rho\,U \sin(\alpha)$

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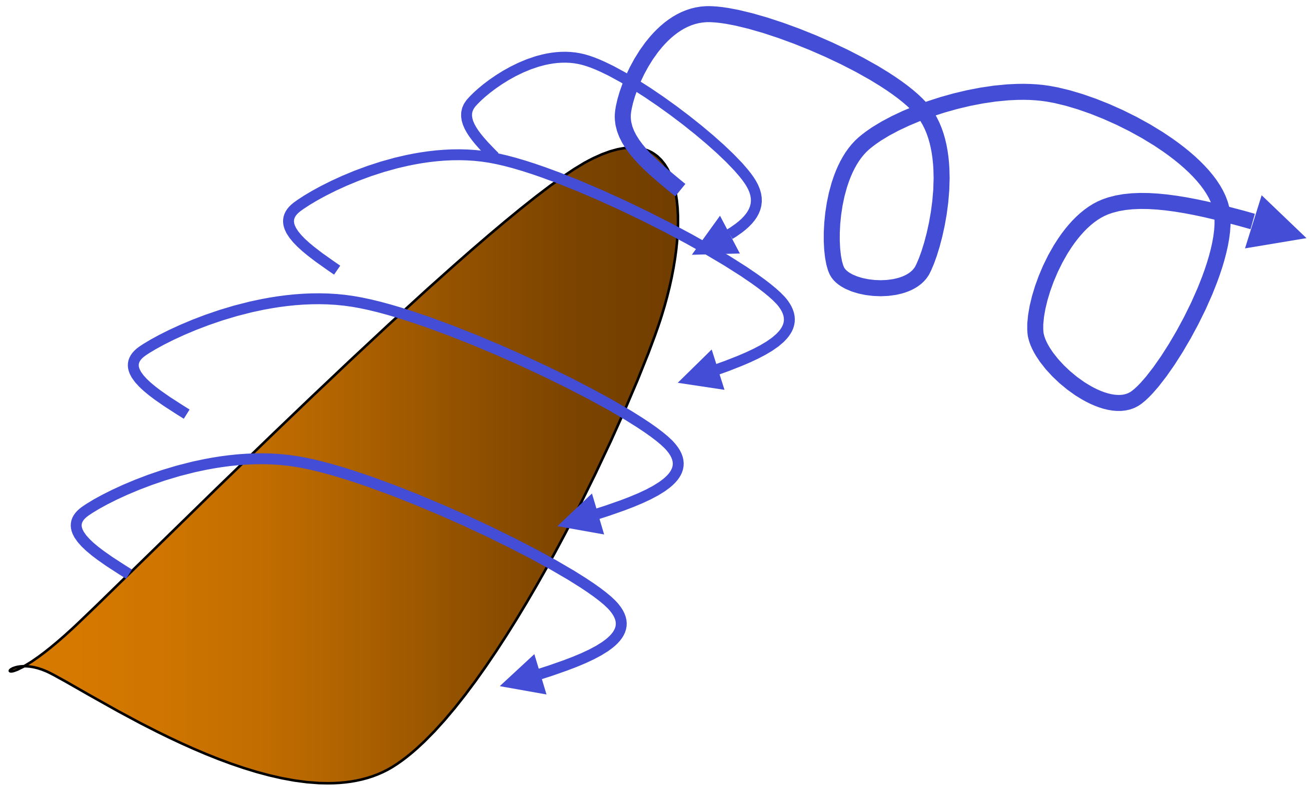
Message: lift can be measured by the amount of circulation held by a wing



Circulation can be lost from the wing as a tip vortex

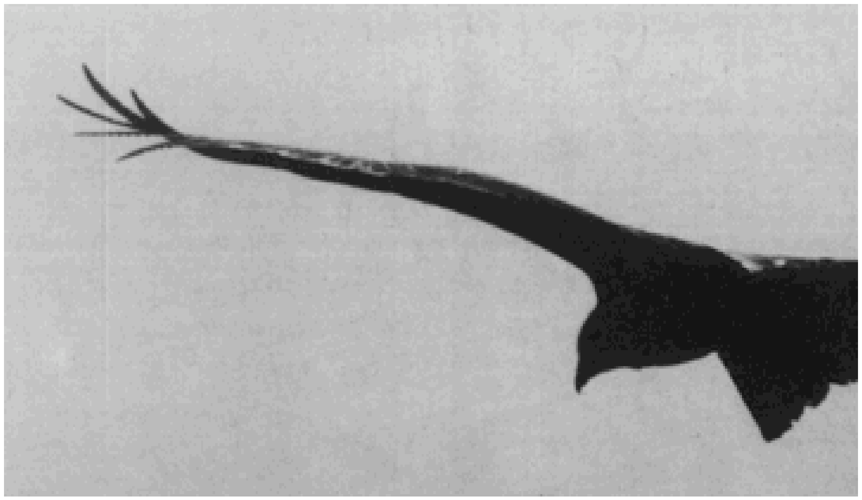
Higher aspect ratio wings loose proportionately less

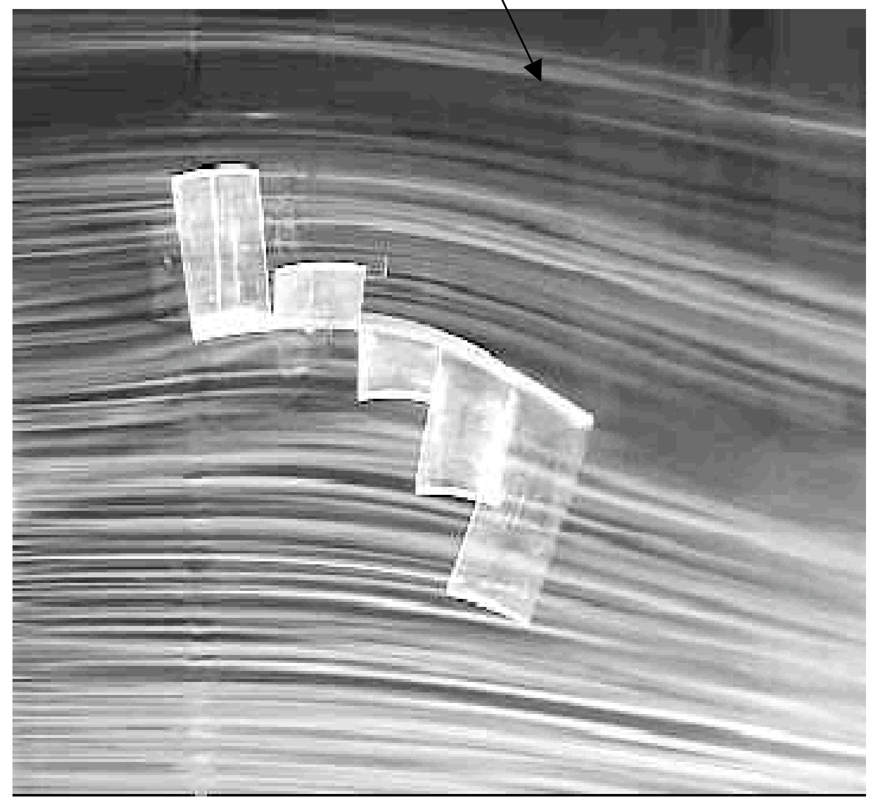
http://www.petersononline.com/birds/perspective/flight.html

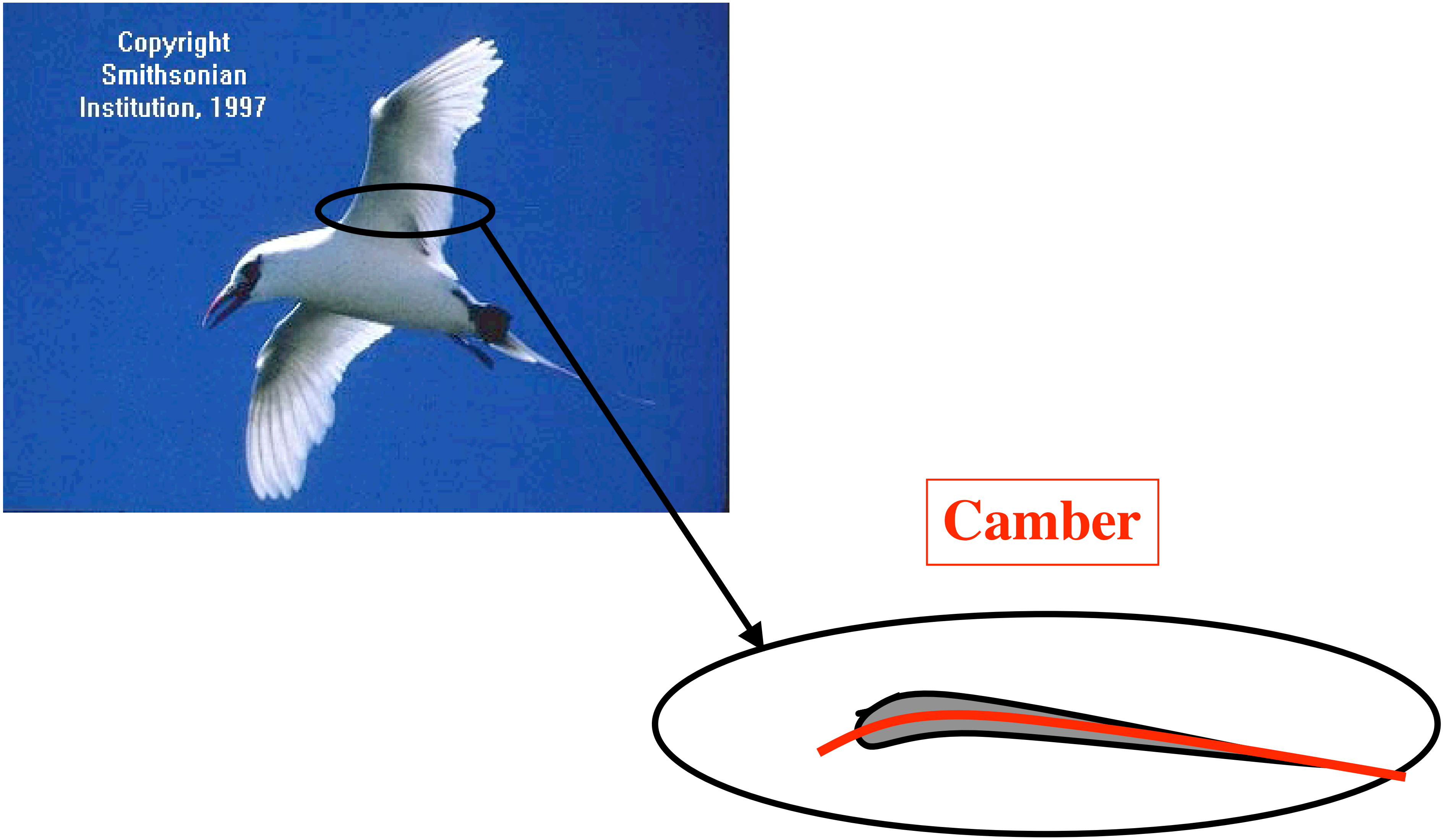
Increasing aspect ratio →

Limits to aspect ratio? Structural, flight mode …

http://lautaro.fb10.tu-berlin.de/user/michaels/michaels_eng.html





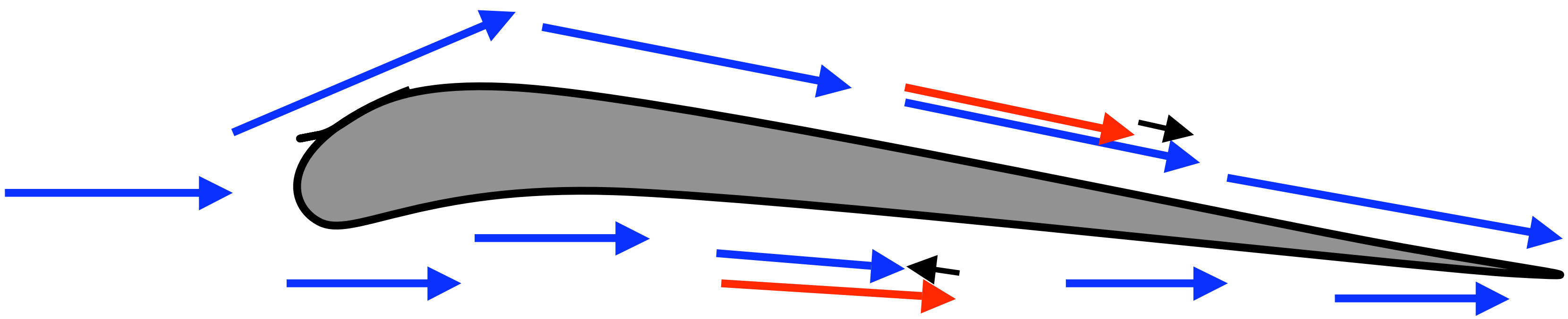


Let's look at the NASA's tool for understanding this.

Biology 427 Biomechanics
Lecture 20. Gliding flight: a soar topic

- Recap basics of lift and circulation
- The consequences of aspect ratio
- The lift coefficient (C_L)
- Drag coefficients for wings
- Drag and lift together (polar plots)
- Gliding flight

Lift and Circulation:



Subtract the mean velocity from all of these vectors

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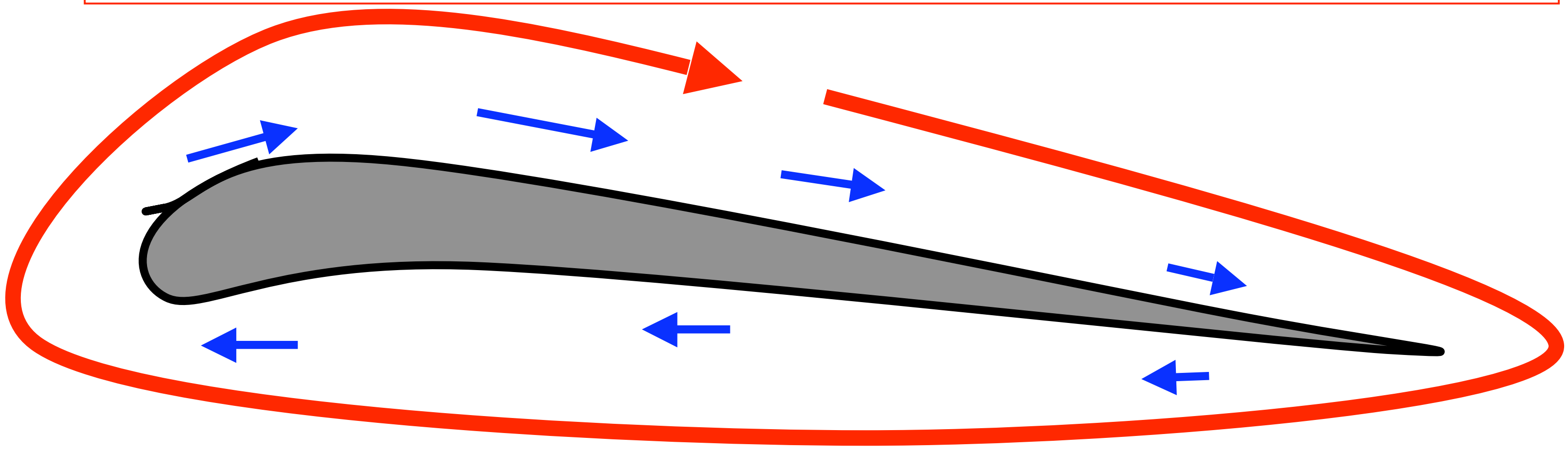


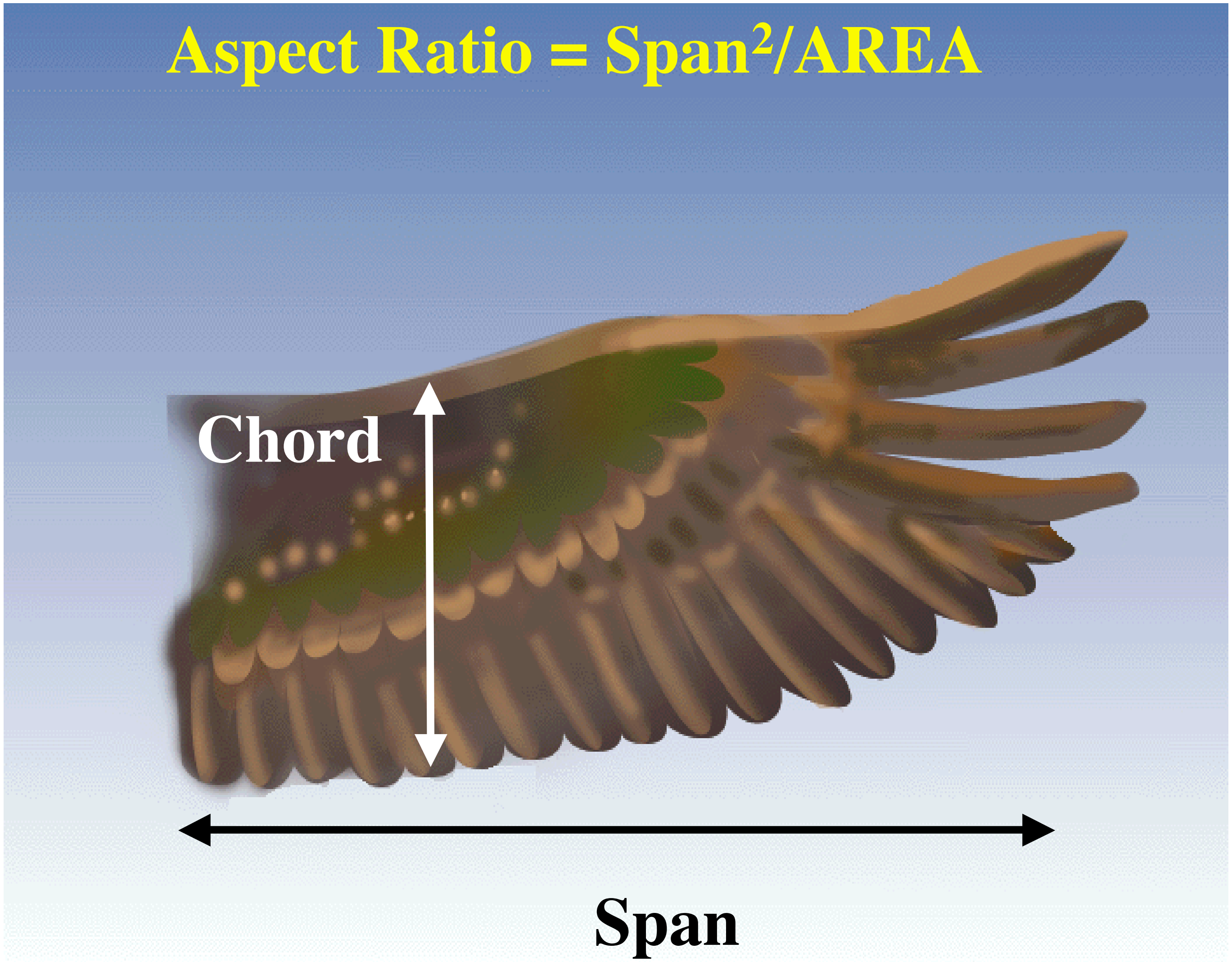
$$(P_2 - P_1)/\rho = (u_1^2 - u_2^2)/2$$

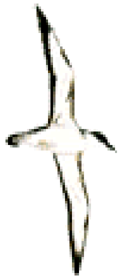
$L = 2\,\pi\,\rho\,U^2\,c\,\sin(\alpha)$
$\Gamma = 2\,\pi\,\rho\,U\,c\,\sin(\alpha)$
$L = \rho\,U\,\Gamma$

Message: lift can be measured by the amount of circulation held by a wing

Circulation is conserved (Kelvin's circulation theorem)
For every clockwise spin there is a counter clockwise one elsewhere in the fluid.

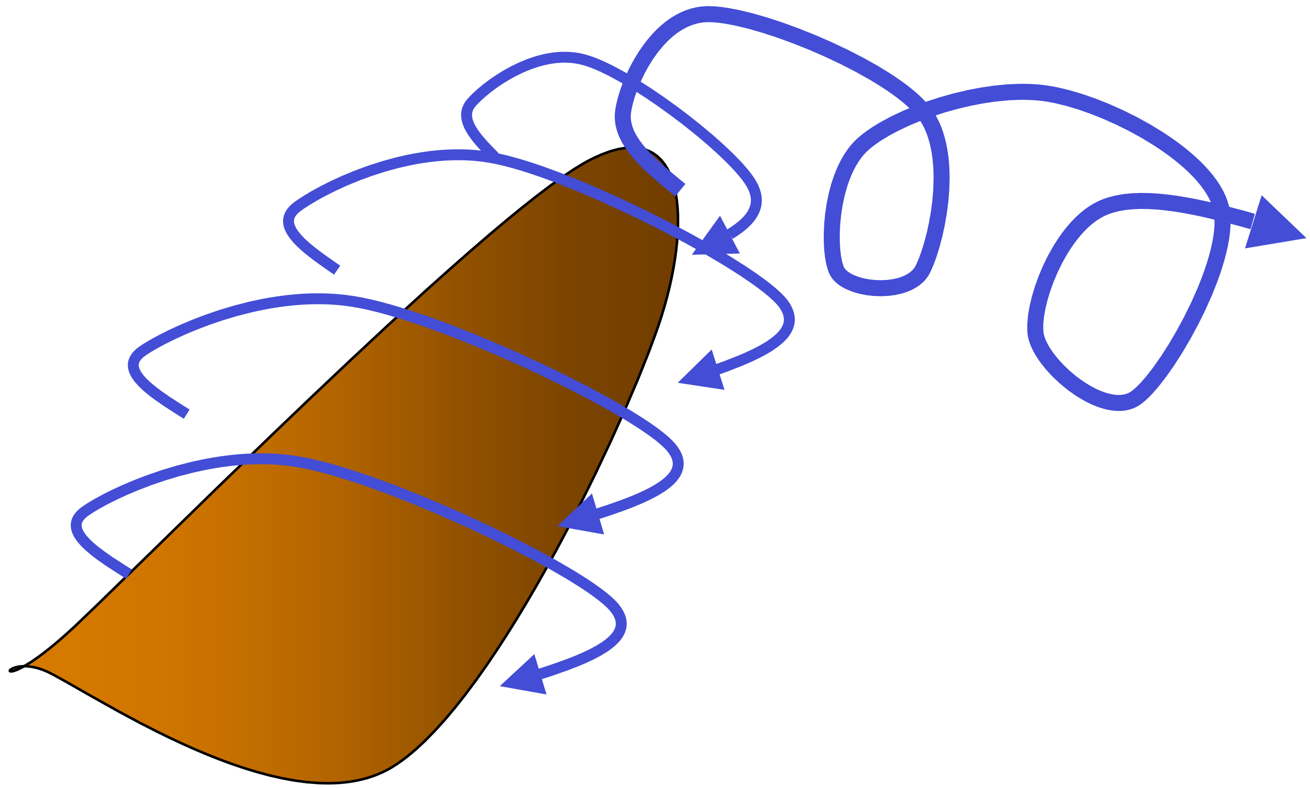
Dilemma: create circulation and maintain it.
Understand this in the context of flapping flight!


Aspect Ratio = Span²/AREA
Chord
Span



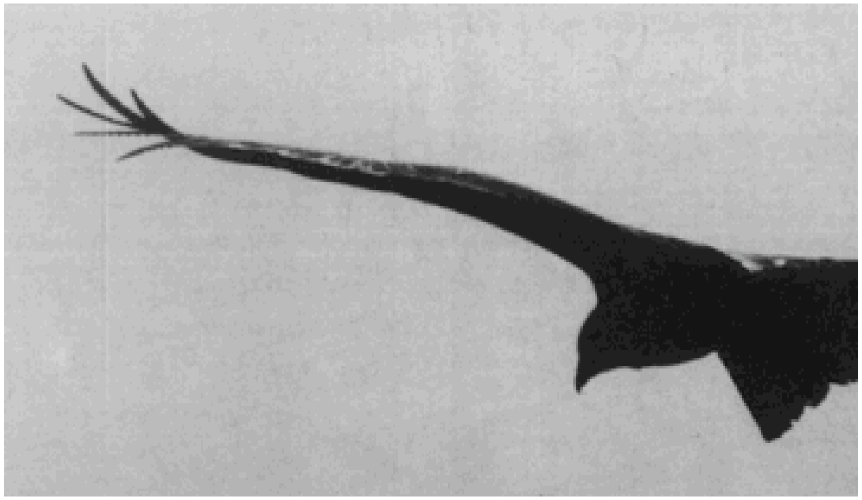
$$L = 2 \pi \rho U^2 c \sin(\alpha)$$
$$\Gamma = 2 \pi \rho U c \sin(\alpha)$$
$$L = \rho U \Gamma$$

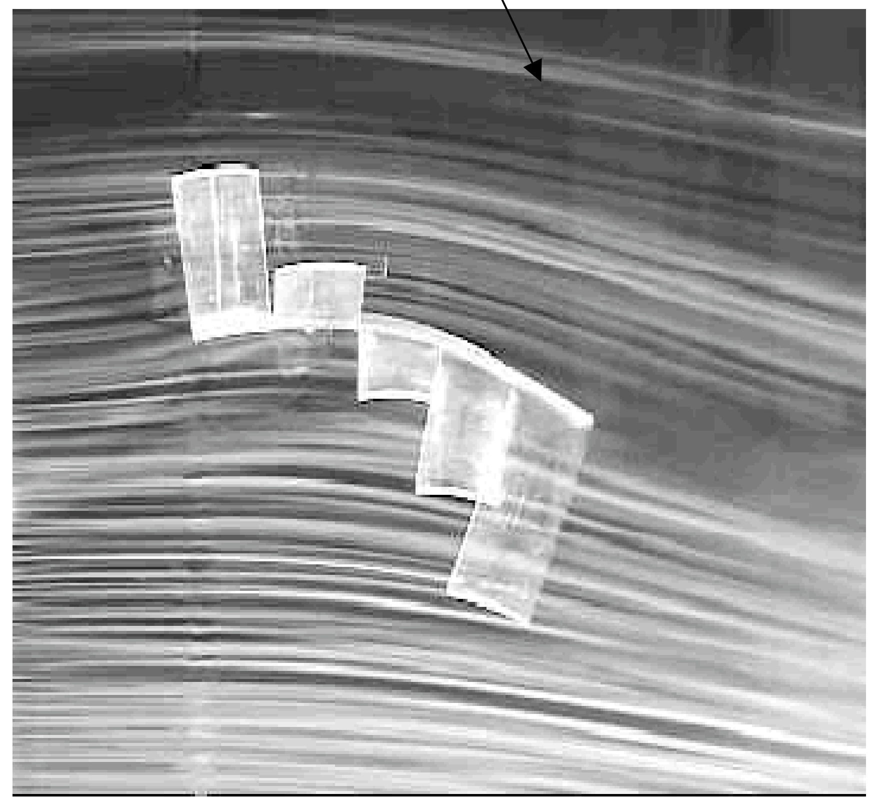
Message: lift can be measured by the amount of circulation held by a wing



Circulation can be lost from the wing as a tip vortex

Higher aspect ratio wings loose proportionately less http://lautaro.fb10.tu-berlin.de/user/michaels/michaels_eng.html





Formation flight -> recovers some lost circulation

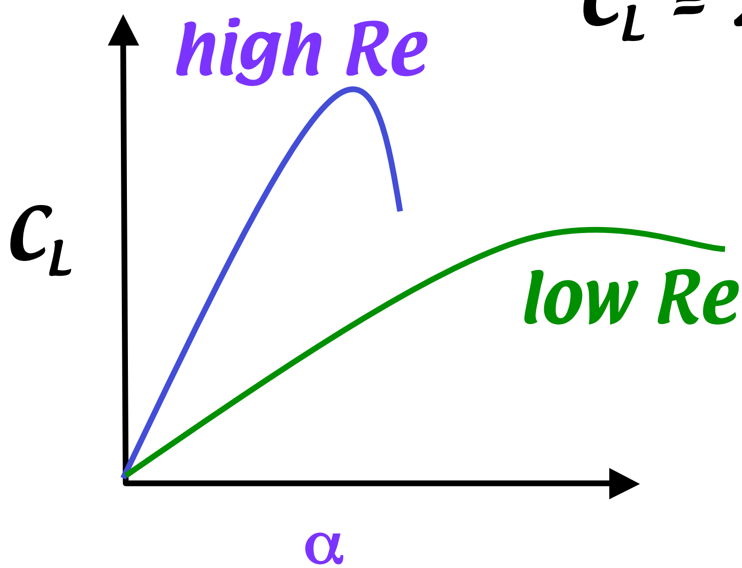
Ideal

$$L = 2 \pi \rho U^2 c \sin(\alpha)$$
$$\Gamma = 2 \pi \rho U c \sin(\alpha)$$
$$L = \rho U \Gamma$$

For real wings in real fluids, we cannot ignore viscosity and the finite span of the wings.

$$C_L = 2 L / \rho S U^2$$

planform area



shape, camber, texture, Re..

Real wings have drag as well (from two issues: viscosity of finite span). It's hard to predict it!

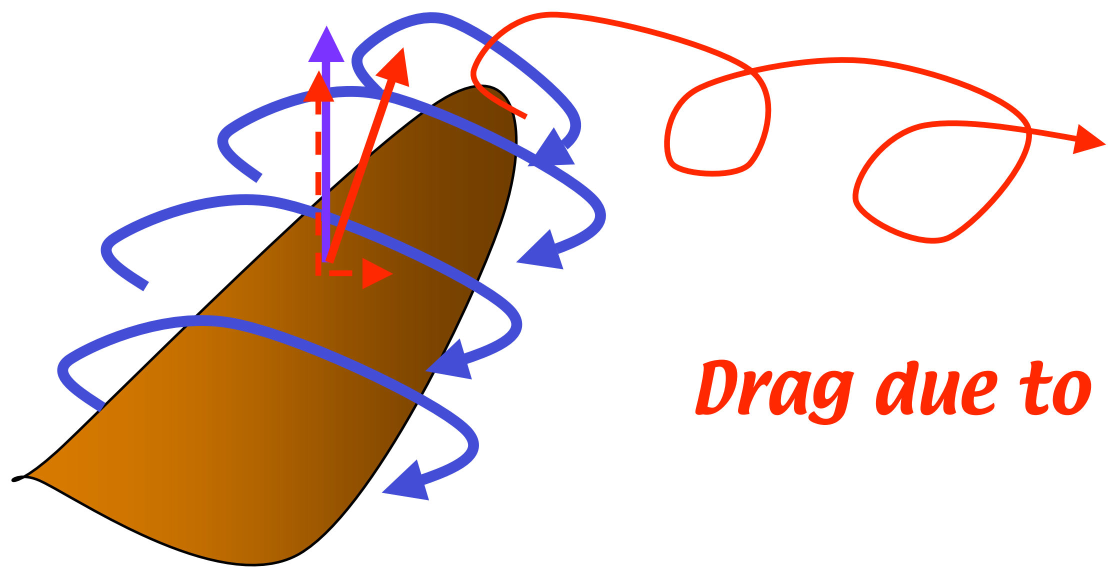
Two kinds of drag (profile drag and induced drag). Both depend on shape (A_R, camber), Re, angle..

$C_{DP} = 2\,D / \rho\,S\,U^2$

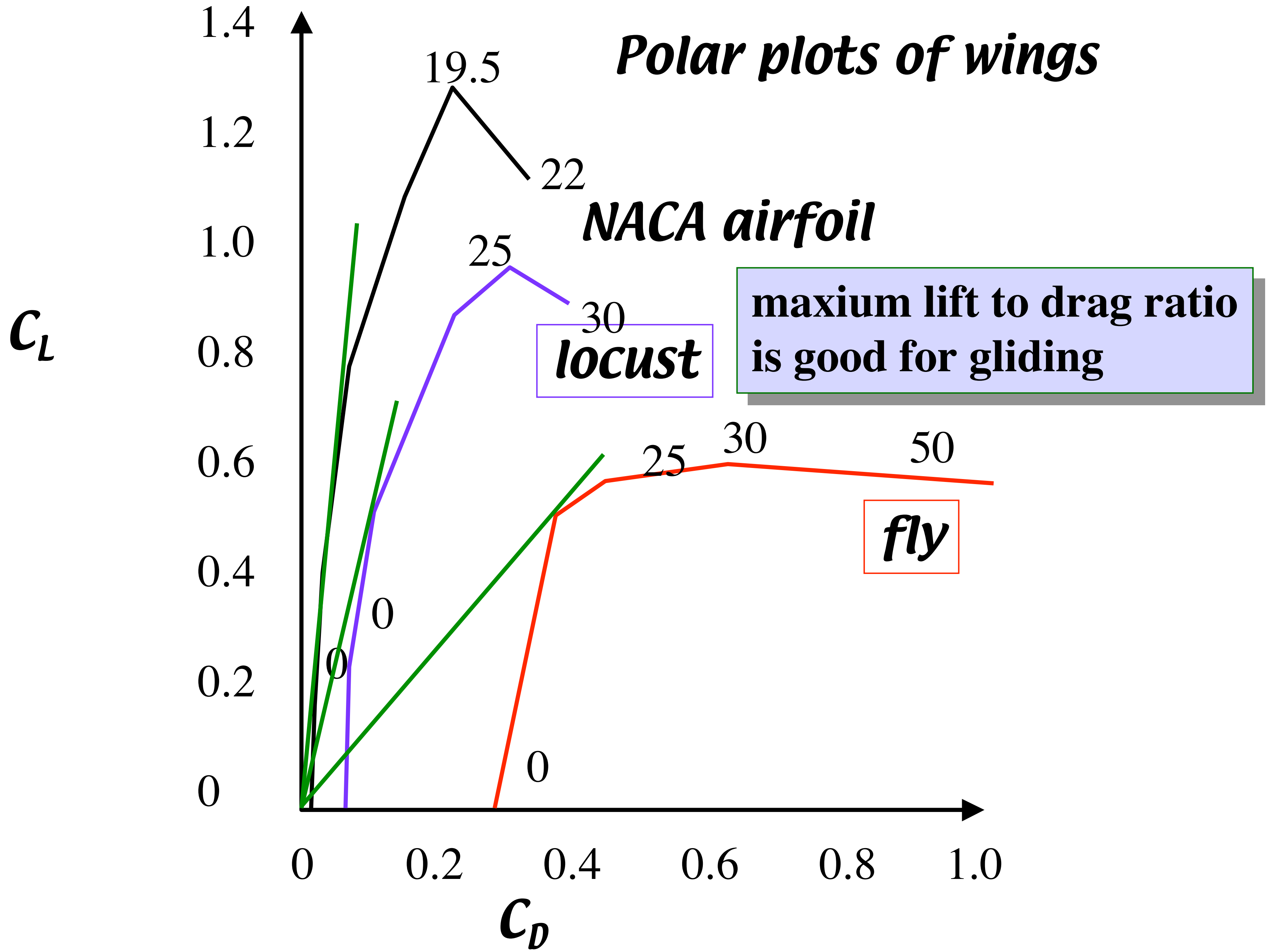
$C_{di} = C_L^2/(e\pi A_R)$

planform area

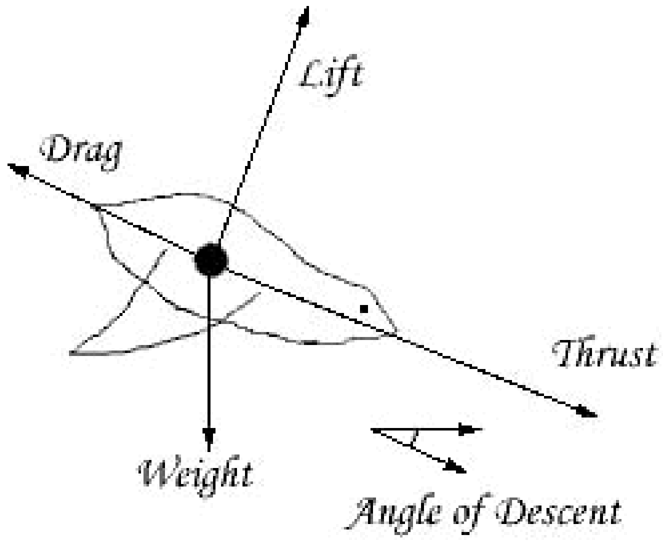
e ~ 0.8 - 0.9

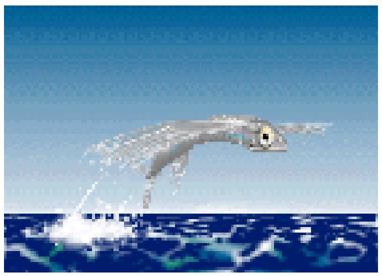


Drag due to lift



Polar plots of wings
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0
C_L
19.5
22
NACA airfoil
25
30
locust
maxium lift to drag ratio is good for gliding
25
30
50
fly
0
0
0
0
0.2
0.4
0.6
0.8
1.0
C_D





http://wings.ucdavis.edu/Book/Nature/beginner/index.html#gliding

Gliding

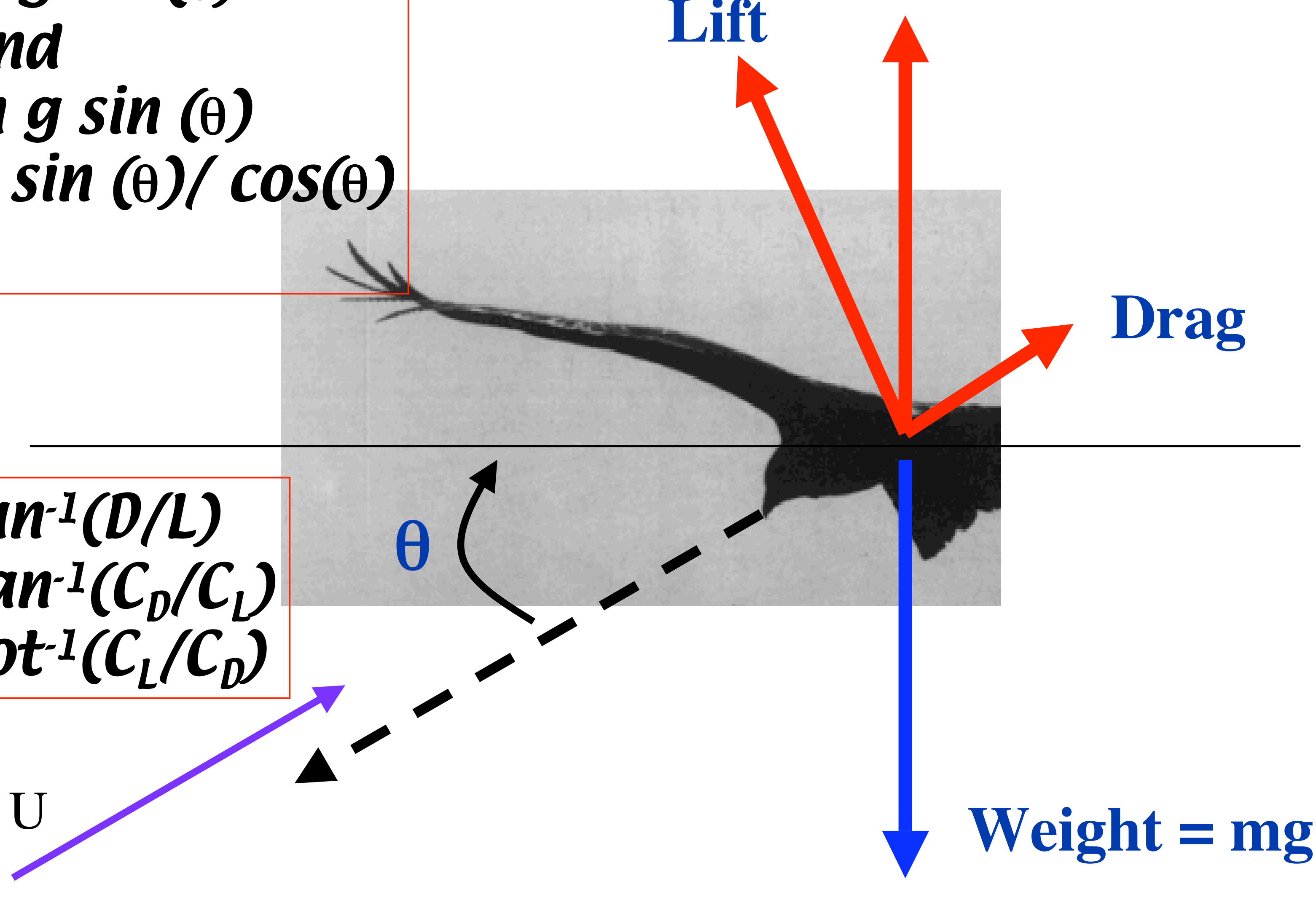
At equilibrium

$L = m\,g\,\cos(\theta)$

and

$D = m\,g\,\sin(\theta)$

$D/L = \sin(\theta)/\cos(\theta)$



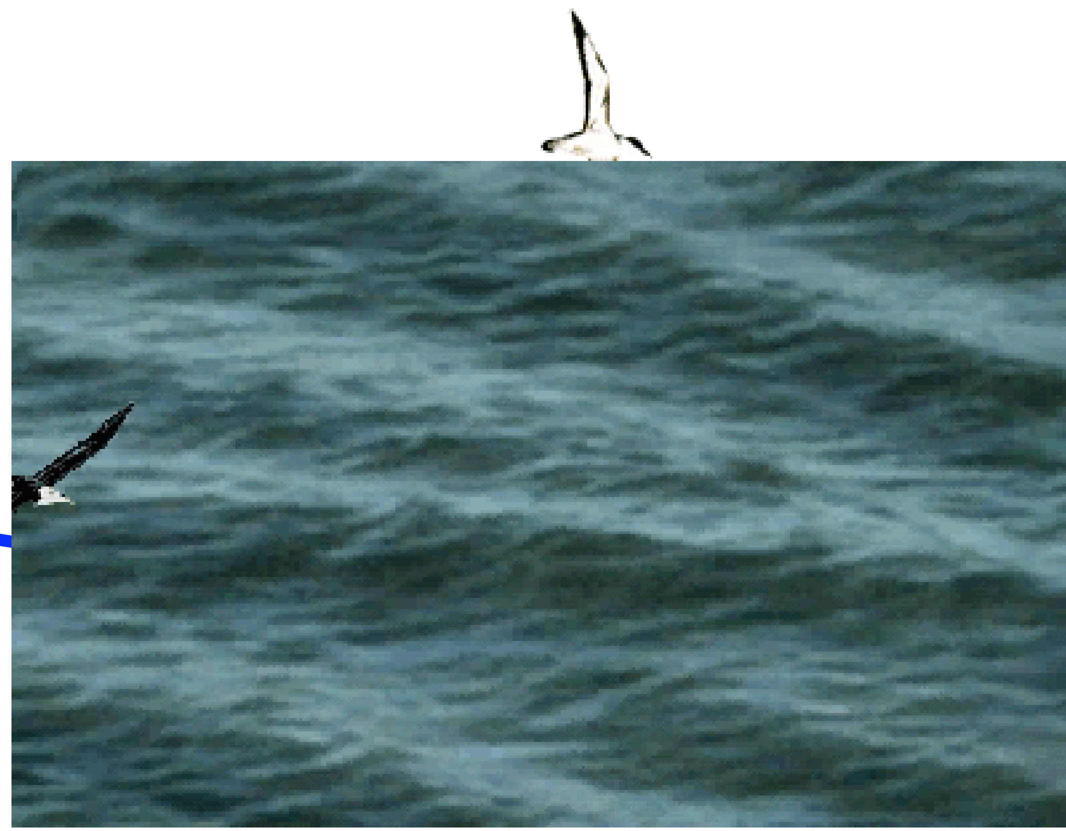
$\theta = \tan^{-1}(D/L)$

$= \tan^{-1}(C_D/C_L)$

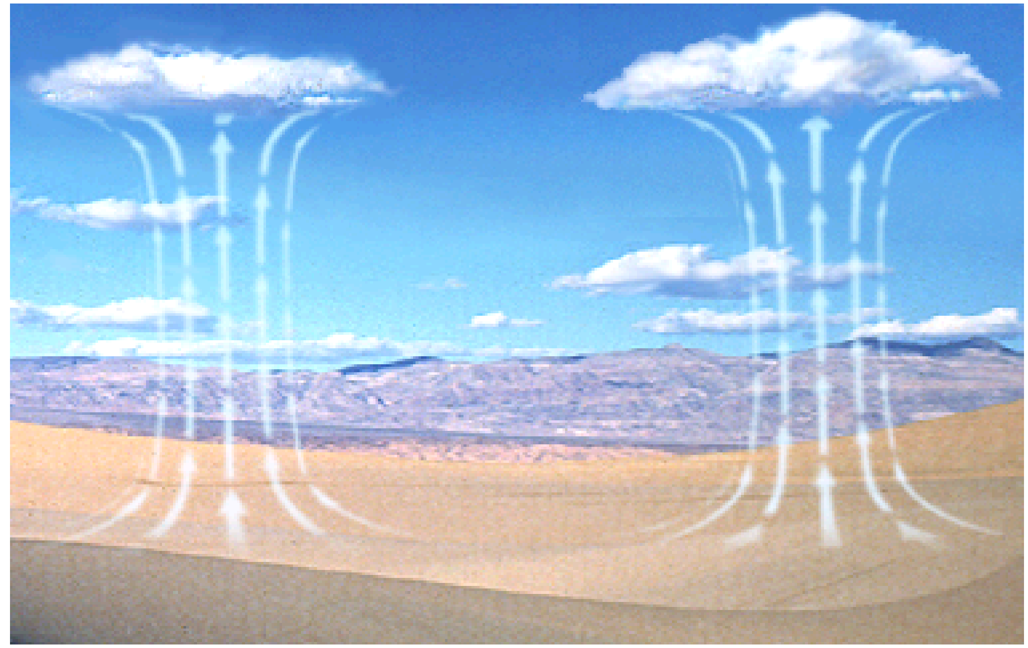
$= \cot^{-1}(C_L/C_D)$

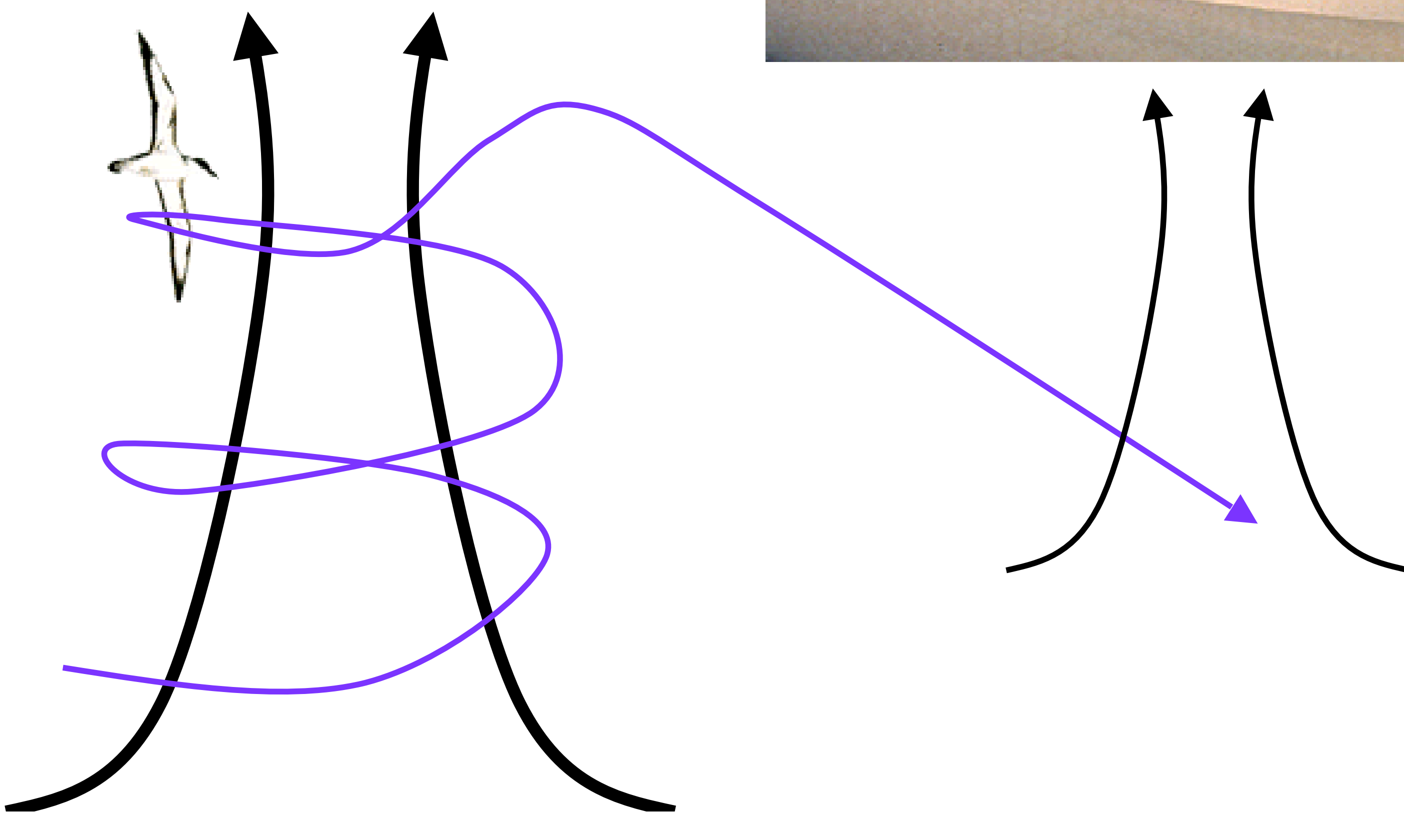
Soaring

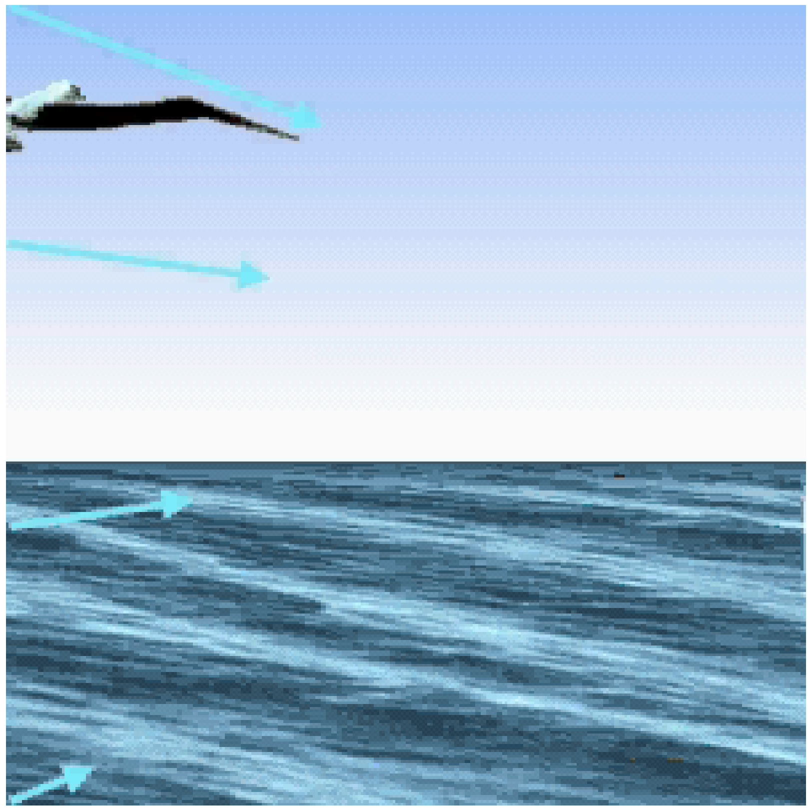
slope soaring

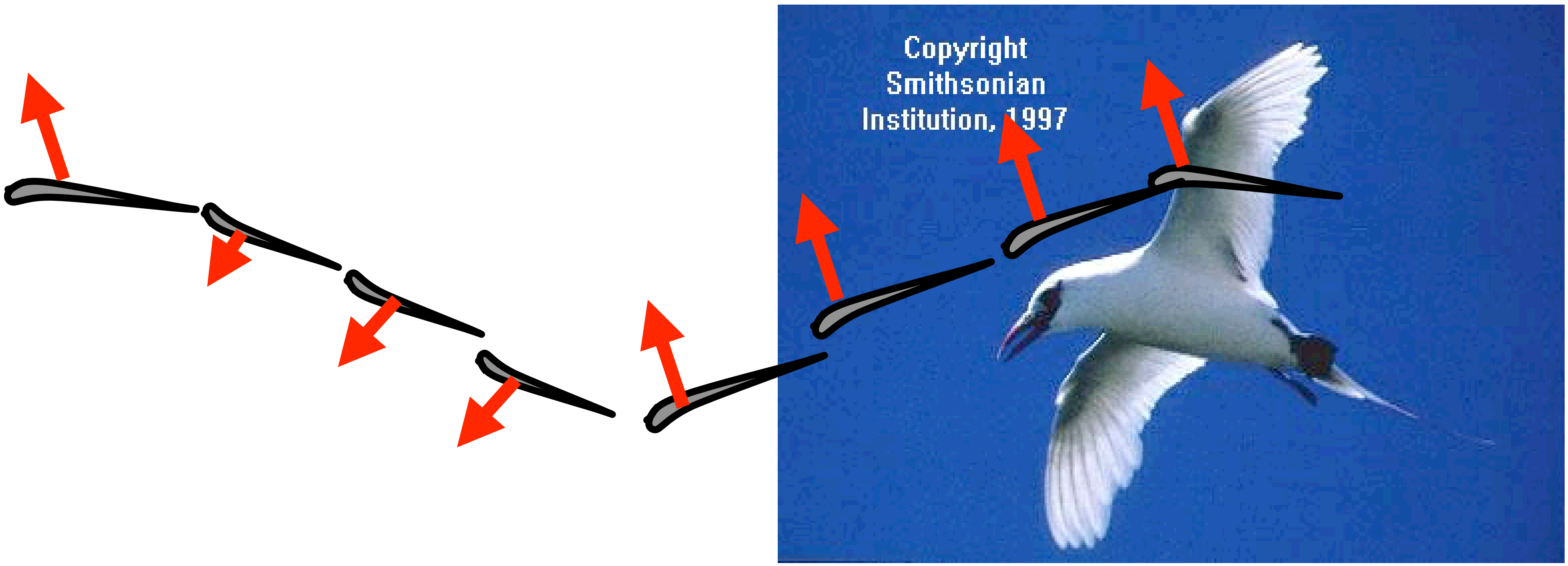


Thermal Soaring









Thrust from lift on a flapping wing

Biology 427 Biomechanics 2004
Lecture 21. Flapping flight fundamentals.

- Recap lift coefficients, gliding and soaring.
- Lift and thrust from flapping wings
- Quasi-steady vs. unsteady flows
- Methods of unsteady force production in flapping wings
- Modeling unsteady force production

*Special seminar by Bob Full on Friday at 11:30 in this room:
"Bipedal Bugs, Galloping Ghosts and Gripping Geckos: BioInspired Computer Animation, Robotics, Artificial Muscles and Adhesives."

Real wings have drag as well (from two issues: viscosity and finite span). It's hard to predict it!

Two kinds of drag (profile drag and induced drag). Both depend on shape (A_R, camber), Re, angle..

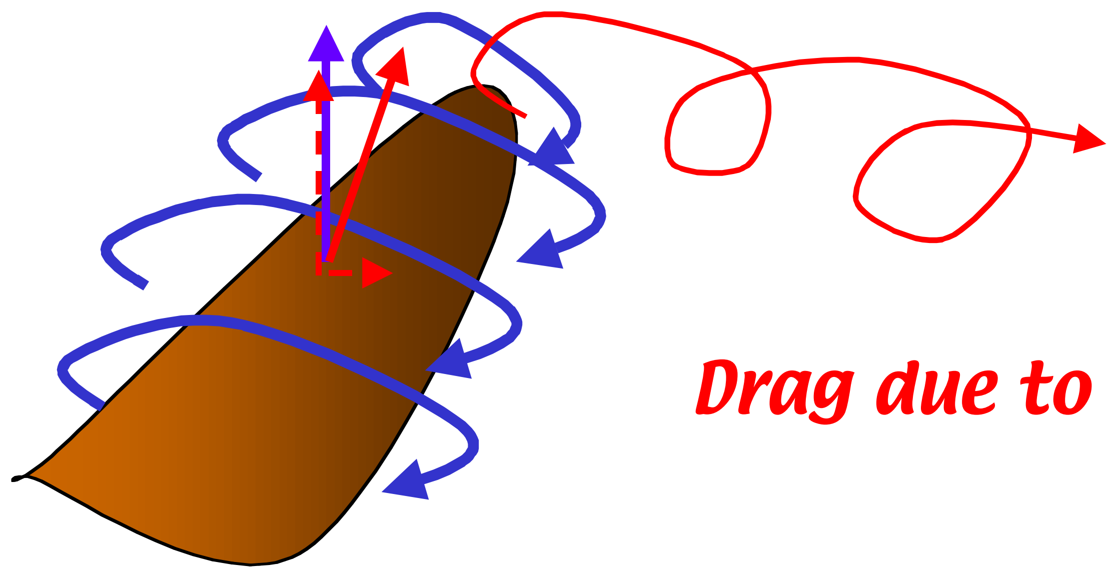
$C_{DP} = 2D / \rho S U^2$

$C_{Di} = C_L^2/(e\pi A_R)$

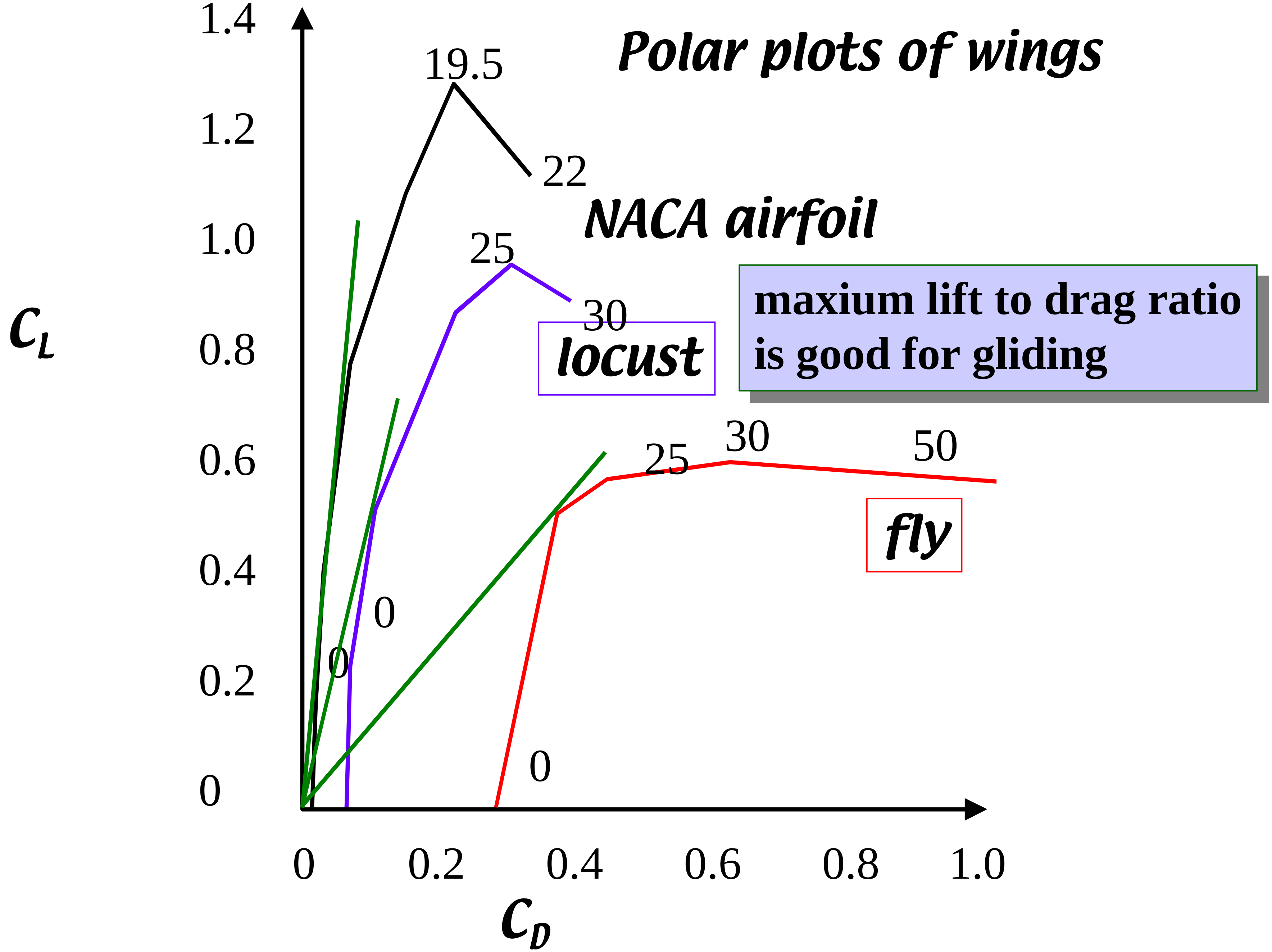
planform area

(pressure and viscous drag)

$e \sim 0.8 - 0.9$



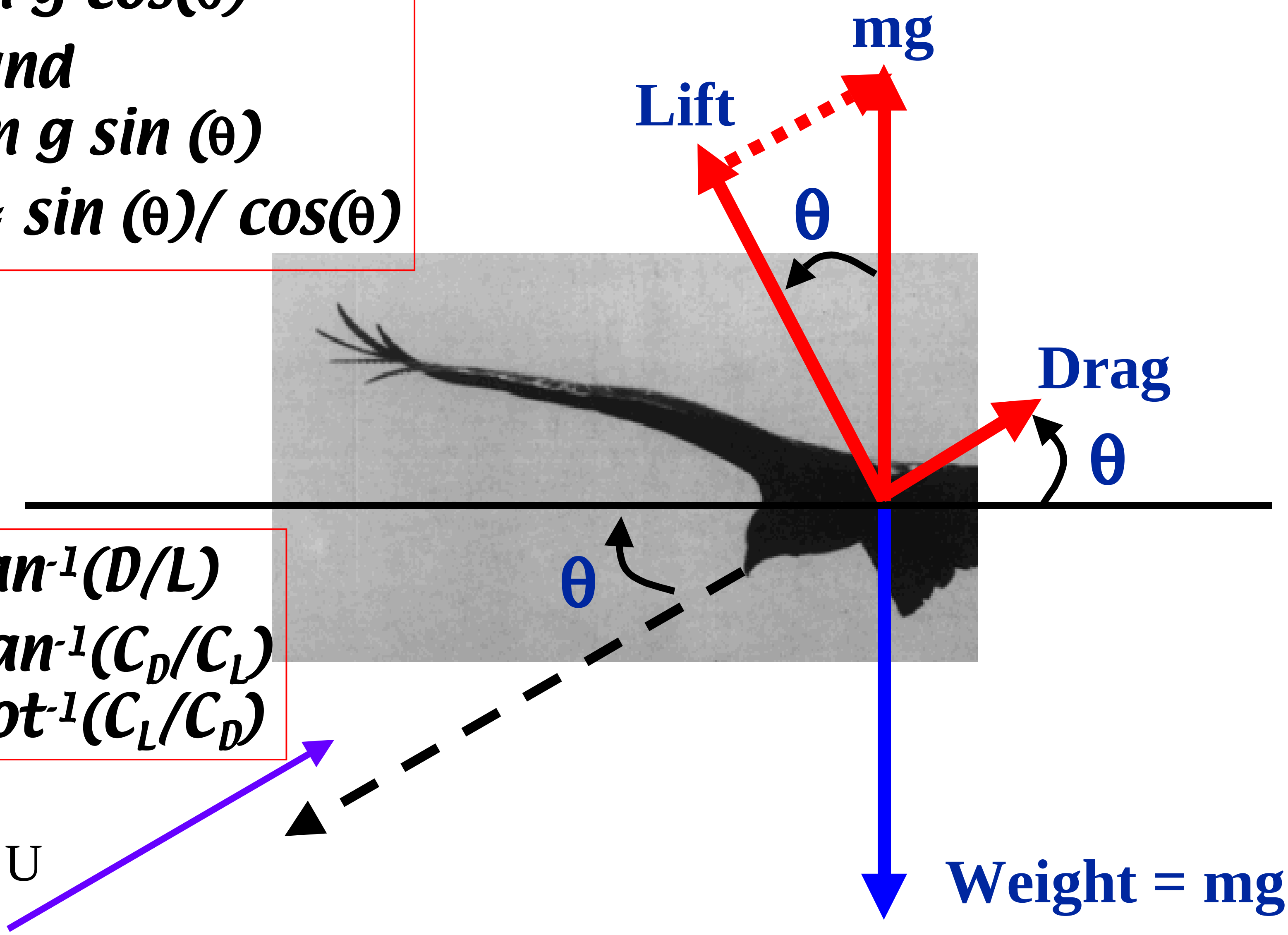
Drag due to lift



Polar plots of wings
C_L
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0
19.5
22
NACA airfoil
25
30
locust
maxium lift to drag ratio is good for gliding
30
25
50
fly
0
0
0
0
0.2
0.4
0.6
0.8
1.0
C_D

At equilibrium
$L = m\, g \cos(\theta)$
and
$D = m\, g \sin(\theta)$
$D/L = \sin(\theta)/\cos(\theta)$

Gliding

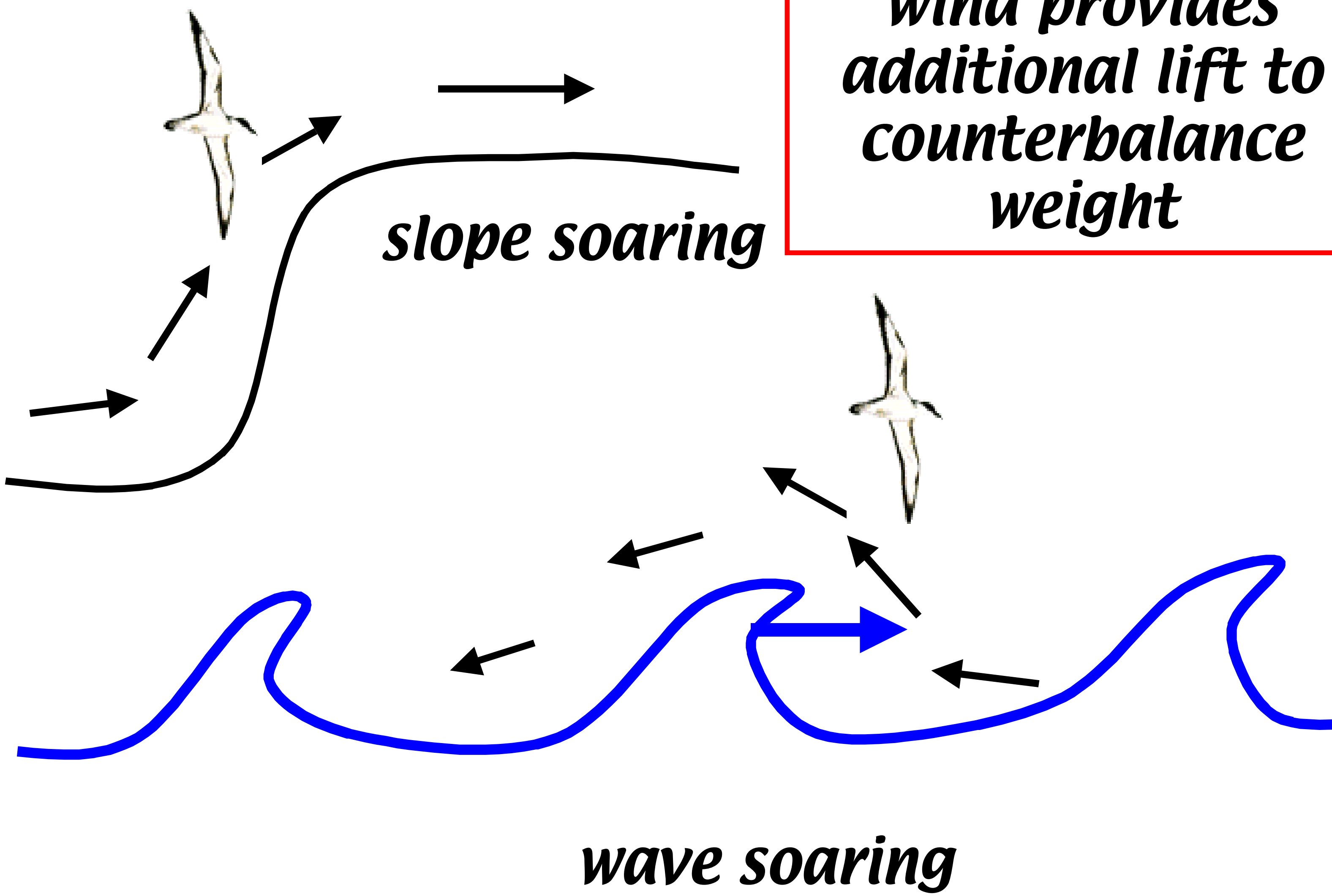


$\theta = \tan^{-1}(D/L)$
$= \tan^{-1}(C_D/C_L)$
$= \cot^{-1}(C_L/C_D)$

Glide angle is independent of weight!

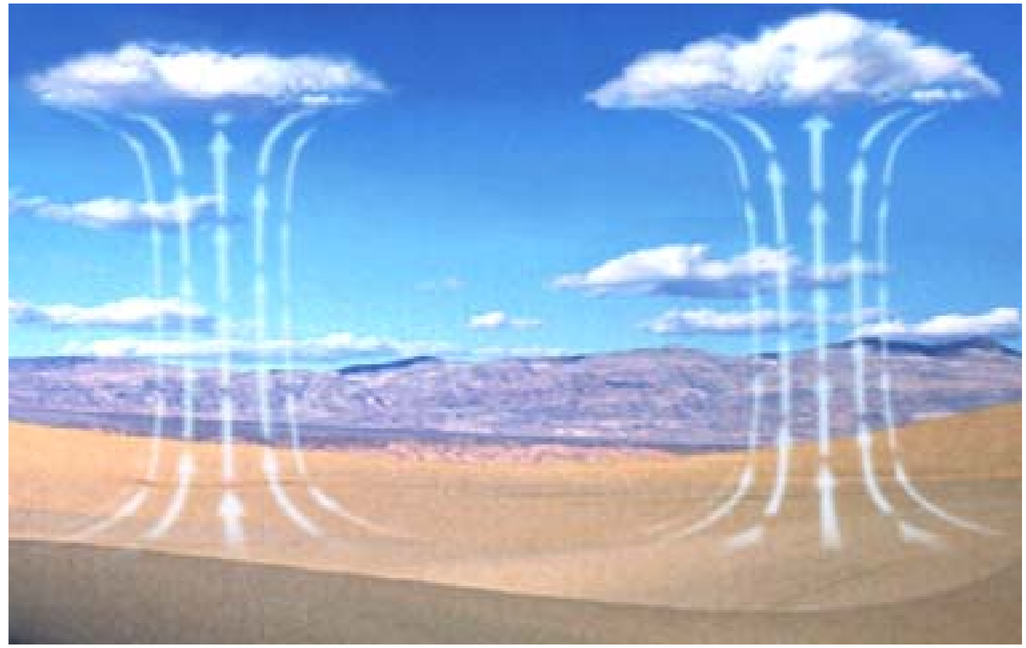
Soaring

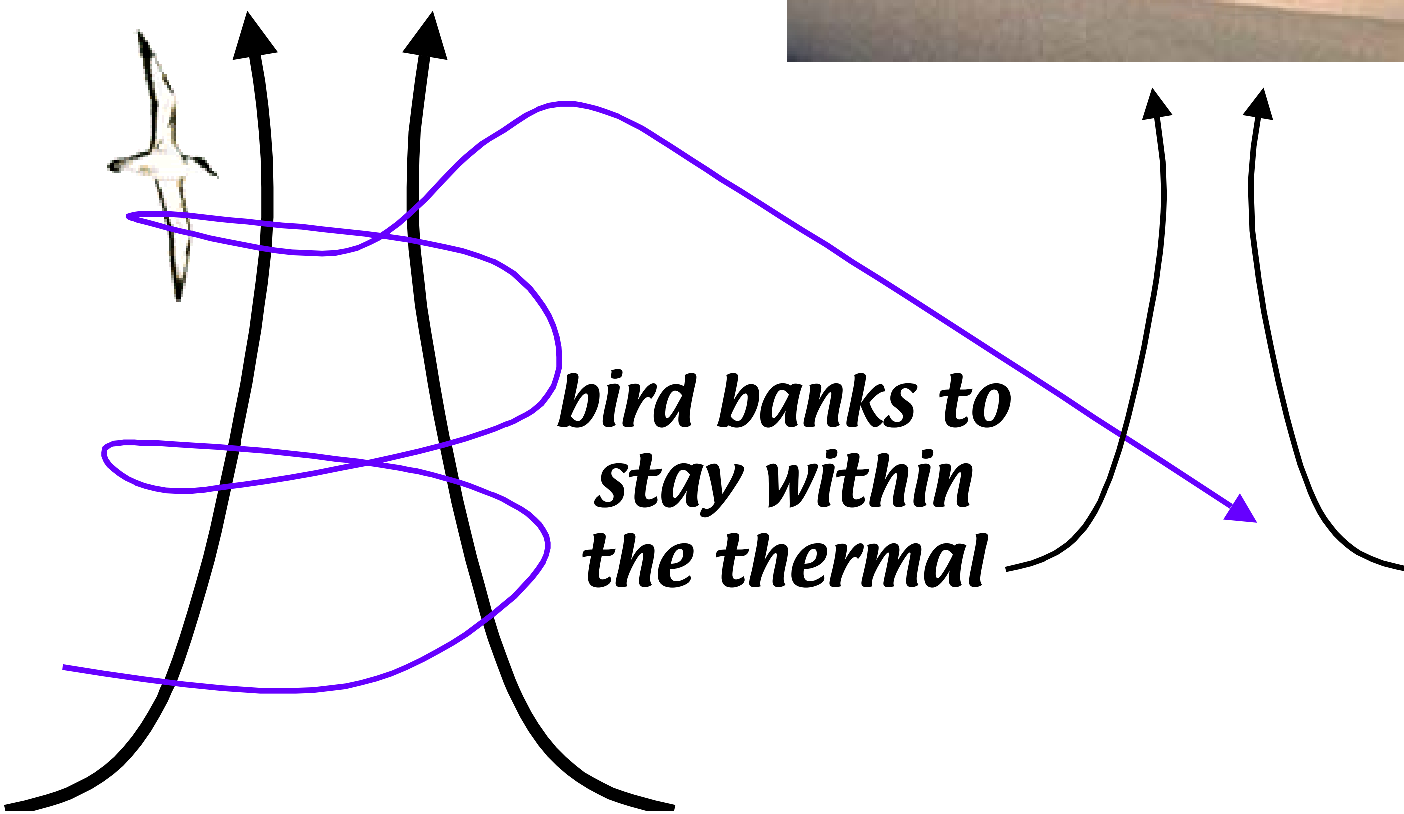
Upward velocity of wind provides additional lift to counterbalance weight



Thermal Soaring

Upward velocity of warm air provides enough extra lift to raise the bird

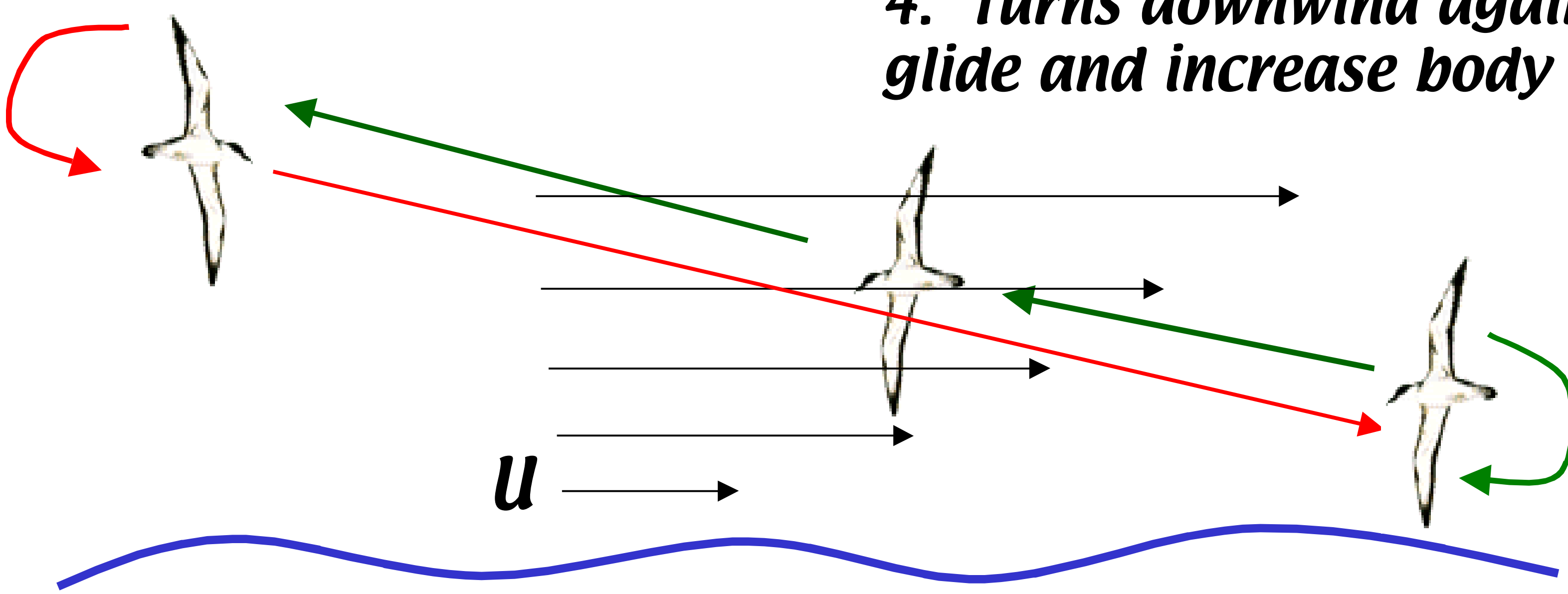




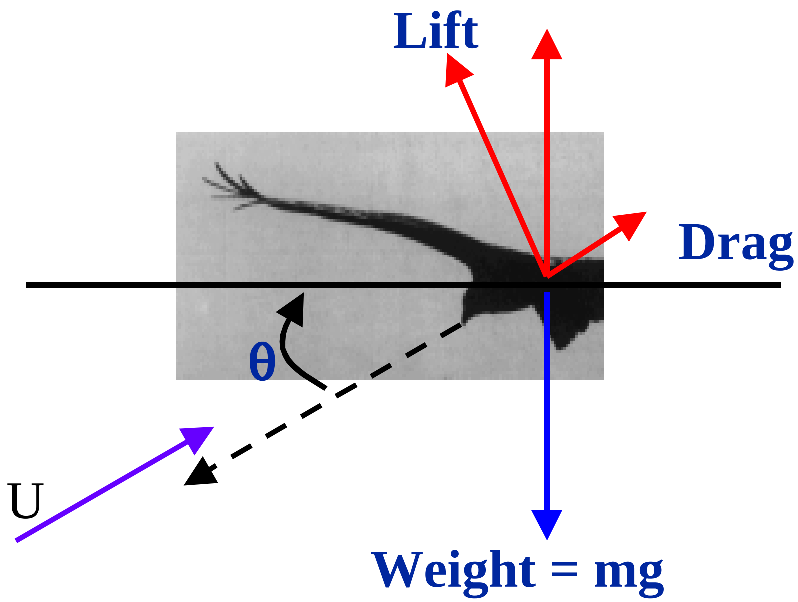
Dynamic Soaring

**takes advantage of a vertical velocity gradient in air rather than actual vertical movement of air*

1. *Bird glides down towards surface, increasing body velocity*
2. *Turns upwind and generates lift based on velocity gained during descent*
3. *Rises into higher velocities as moves up in gradient, allowing continued lift generation*
4. *Turns downwind again to glide and increase body velocity*



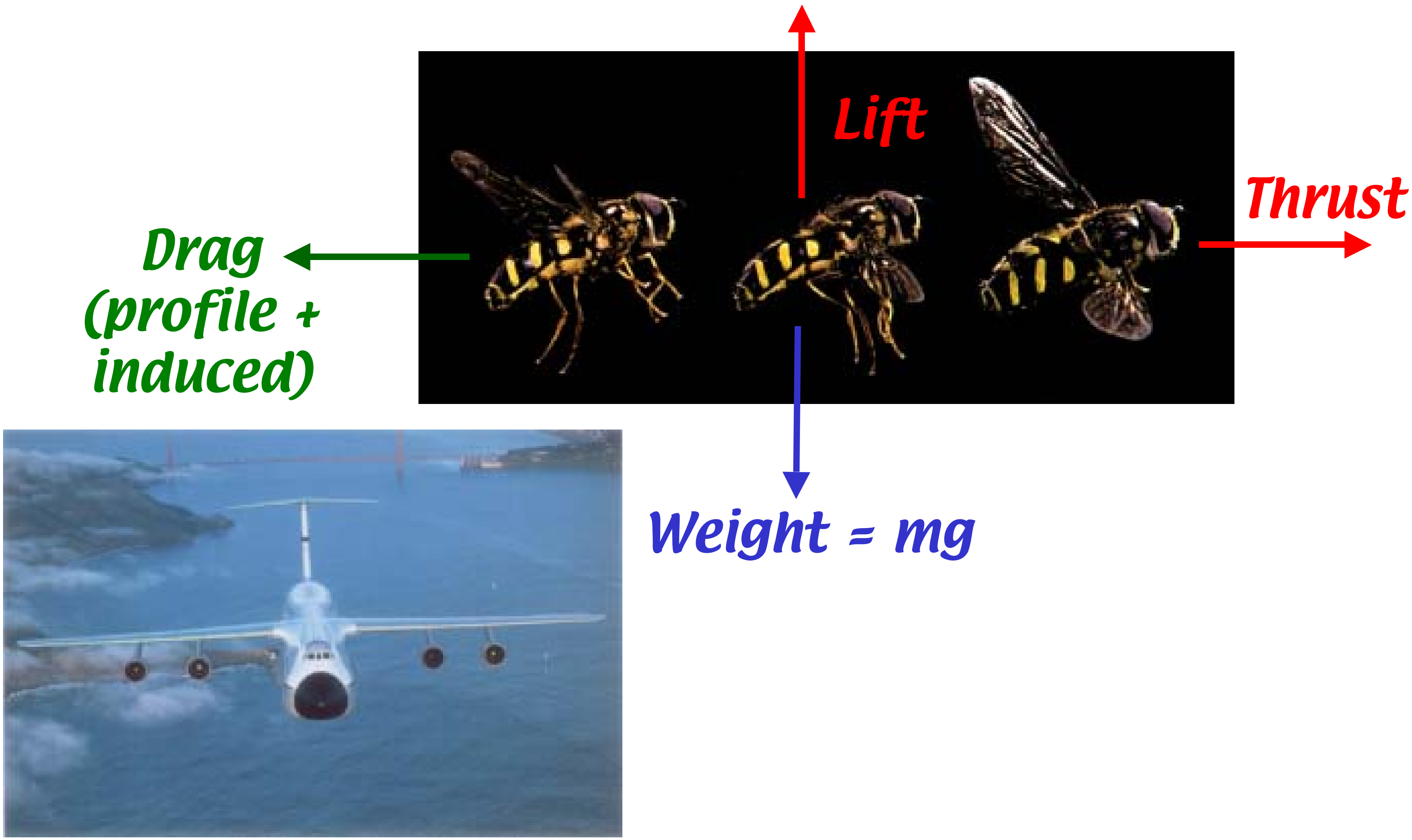
Armed with lift coefficients, we can analyze gliding and soaring performance of "fixed wing" animals.



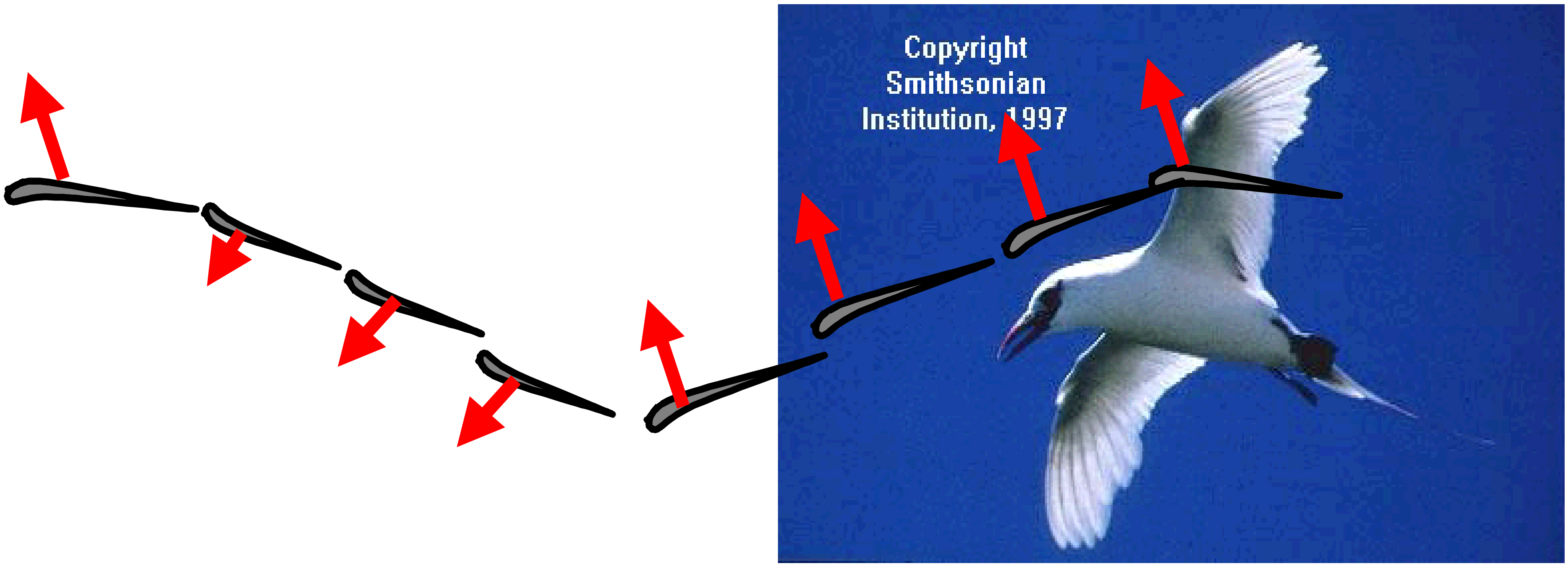
But… in most cases animals can't generate enough lift without flapping their wings to increase local air velocity

In flapping flight the velocity of wing with respect to the air varies both temporally (wing moves up and down) and spatially (along span of wing)

To further complicate matters, flying animals must generate both lift and thrust (forward force to counteract drag) with their wings



Thrust from lift on a flapping wing



for level flight at a steady speed (no accelerations):

mean lift = weight

the mean upward force = mg

mean thrust = drag

the mean forward force = $\frac{1}{2} \rho u^2 S_{body} C_{D, body} + \frac{1}{2} \rho u^2 S_{wing} C_{D, wing} + \frac{1}{2} \rho u^2 S_{wing} C_{Di}$

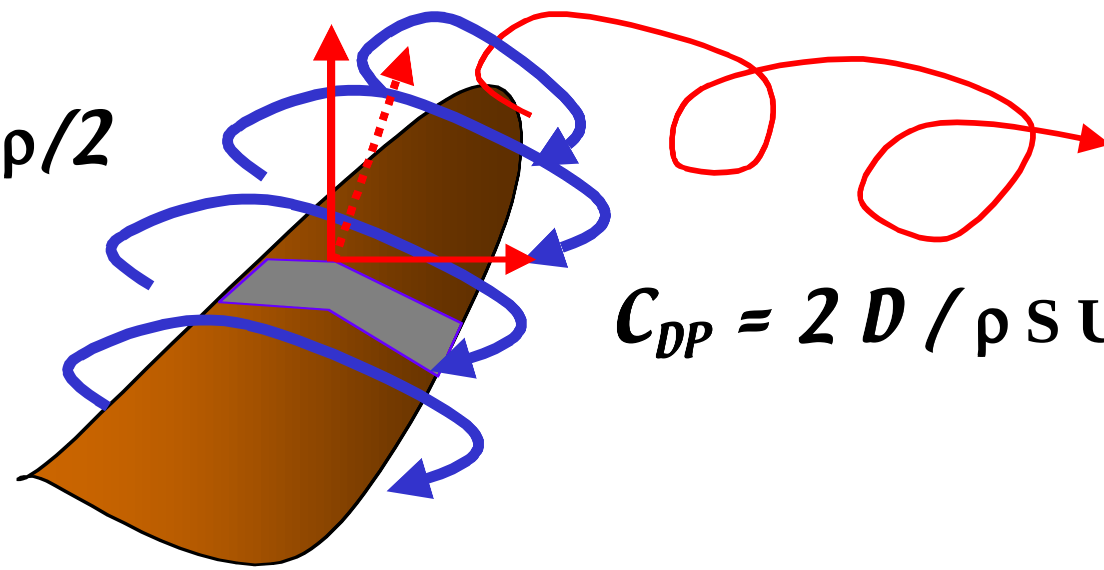



We understand how to calculate forces for steady flow. Can we use this approach to analyze flapping flight?

Quasi-steady blade-element approach:
calculate the steady lift and drag forces on each segment of a wing and sum these over the entire wing at each instant in time.

$$C_{Di} = C_L^2/(e\pi A_R)$$

$$L = C_L u^2 S \rho/2$$



$$C_{DP} = 2\,D\,/\,\rho\,S\,U^2$$

We understand how to calculate forces for steady flow. Can we use this approach to analyze flapping flight?

Works well in some cases, i.e. fast forward flight with relatively low flapping frequencies (large birds, whales, etc.)

But, Ellington (1986) showed that average lift coefficient of many flying insects is greater than maximum measured steady lift coefficient!

Three possible fluid flow situations.......

- ***Steady flow*: velocity is constant at any point ($u=0$, $du/dt = 0$)**

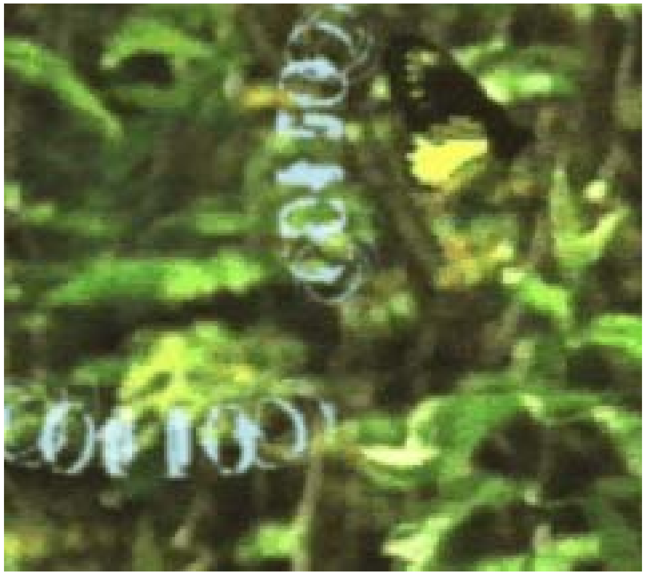
- ***Quasi-steady flow*: velocity varies, but forces equilibrate instantly ($F \sim u^2$)**

- ***Unsteady flow*: velocity varies and forces depend upon acceleration, time and other factors**

How can we quantify the unsteady fluid forces produced by flapping wings?

***WAKE ANALYSIS* relies on the fact that the wake behind (or under) a flying animal contains all of the information about momentum changes in the fluid (and thus forces produced by the wings)**

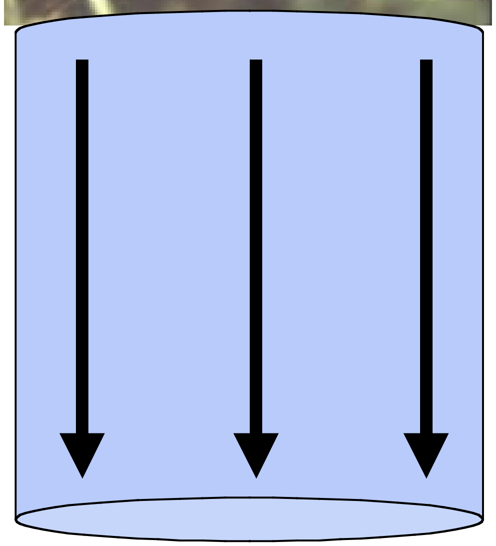
force generation during downstroke only



lift during one stroke and thrust during the other

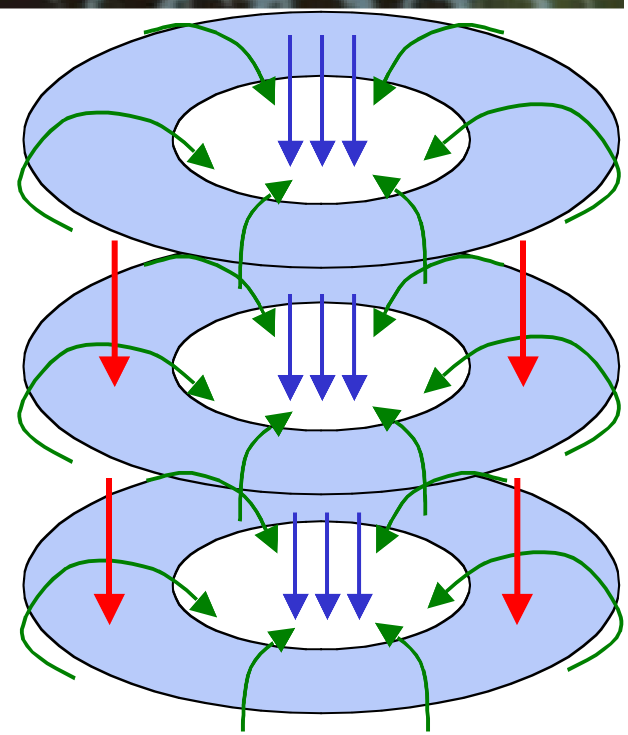
twist wings to produce lift during both strokes

Vortex models equate momentum flux with a hovering animal's weight to estimate circulation



momentum jet = weight of animal

momentum in wake has translational, circulational, and induced components



The reduced frequency parameter is a measure of the unsteady component of motion

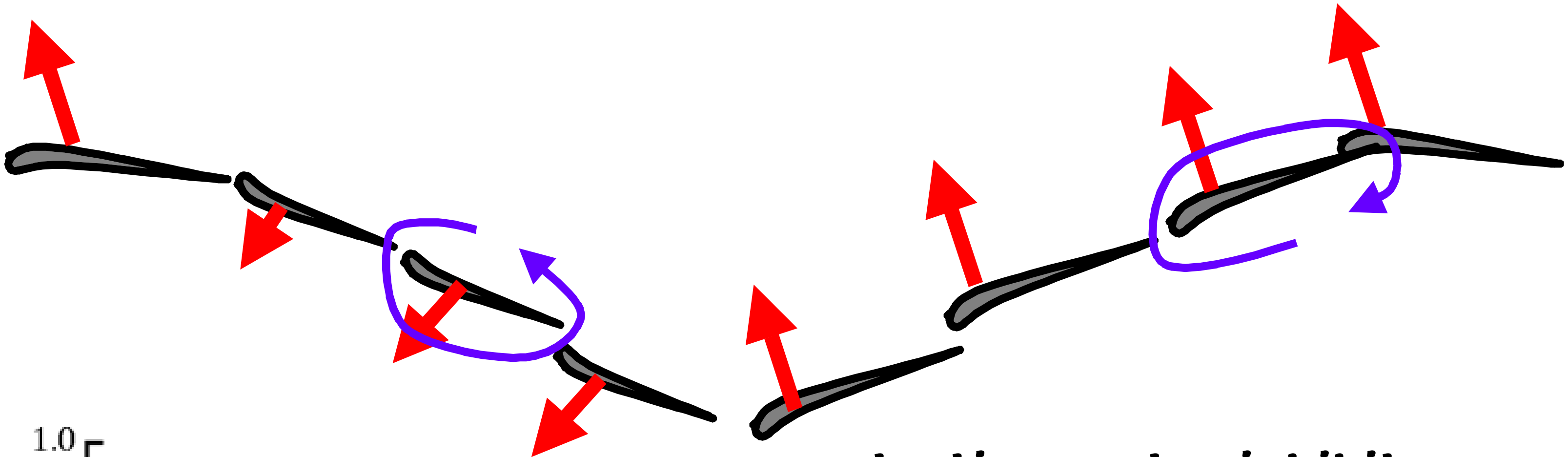
$$\sigma = \omega L/u$$

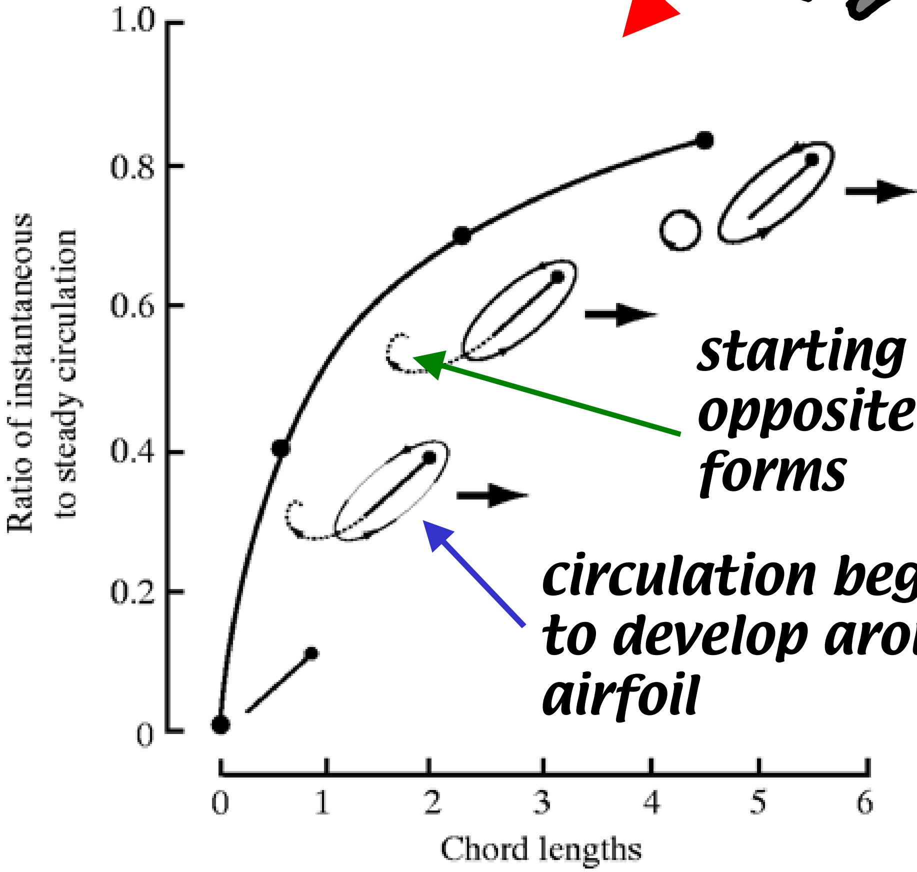
($\omega = 2\pi$*flapping frequency)

oscillatory motion/forward motion

A trade-off:
High frequency motions lead to high relative velocities (and lift).
But, these only happen with flapping, a motion that necessarily requires changes in the direction of circulation - and circulation takes time to develop.

Problem: circulation takes time to develop





starting vortex inhibits circulation around wing until vortex is shed as wing moves forward

starting vortex with opposite circulation forms

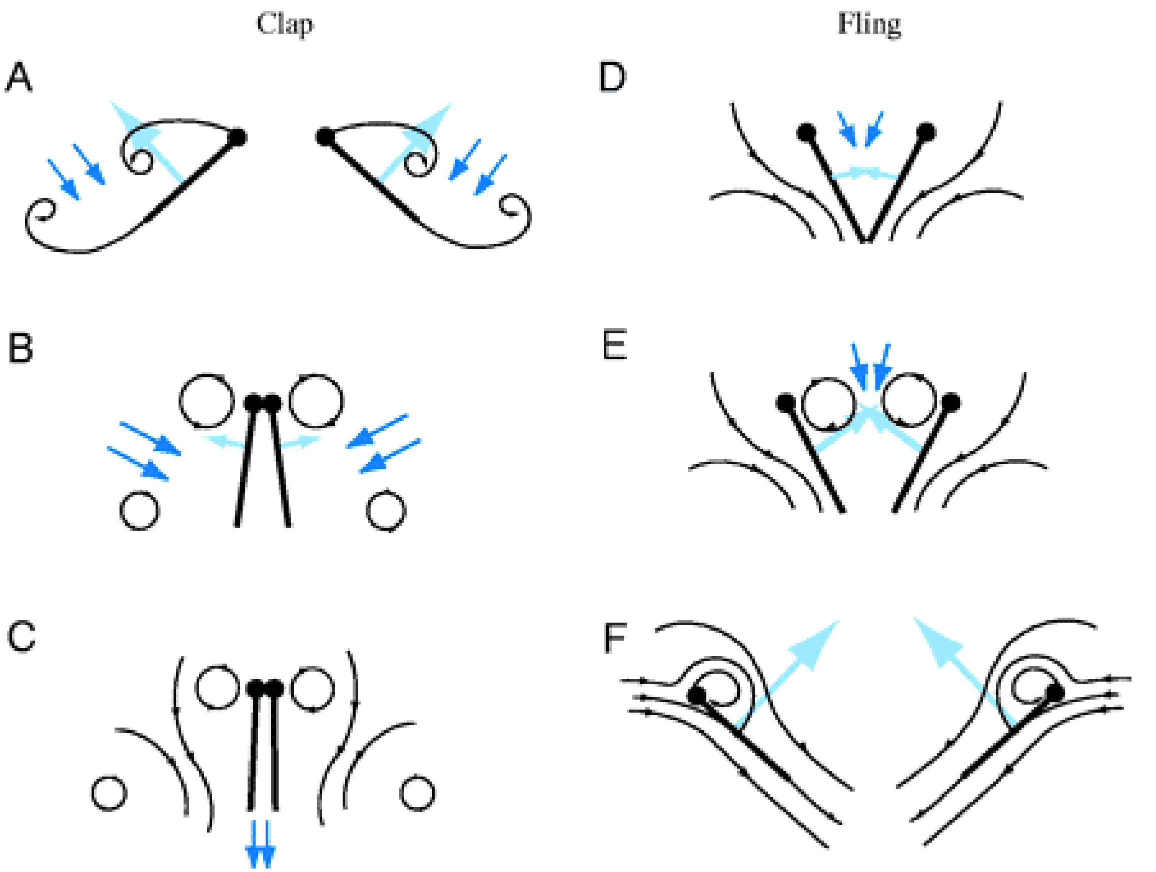
circulation begins to develop around airfoil

Wagner effect

$$\Gamma \sim (\nu t)^{1/2}$$

$$(\nu = \mu/\rho)$$

"Clap and fling" could help promote circulation



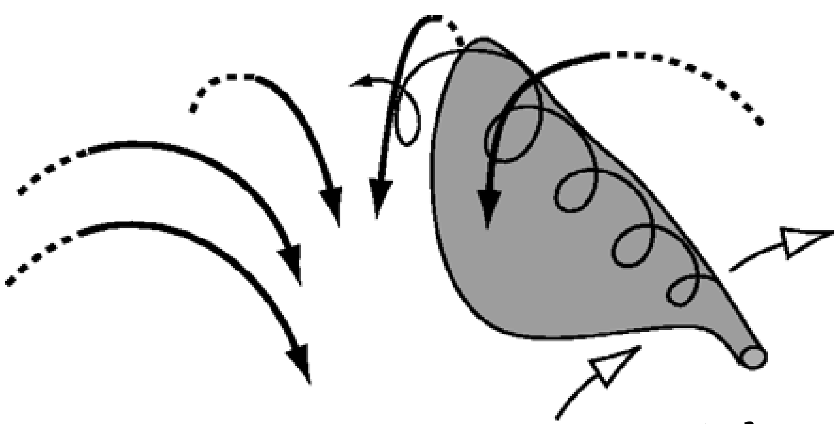
As wings reach top of stroke, bring together leading edges first and shoot jet of air out between wings

Fling or peel apart wings from leading edges first - fluid rushes into gap and may help promote growth of circulation in next stroke

But...
-only seen in a limited number of insects
- Wagner effect may not be significant at relevant Reynolds numbers anyway

How do flying insects generate so much lift?

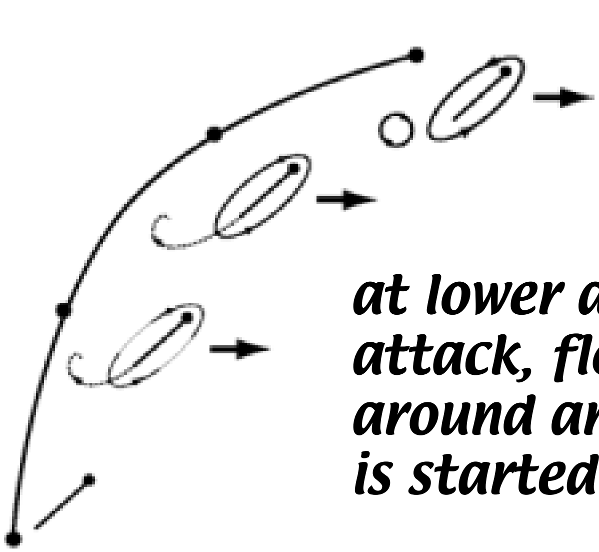
First clue came from "the flapper" - a Reynolds-scaled (large) robotic hawkmoth (Ellington et al., 1996)



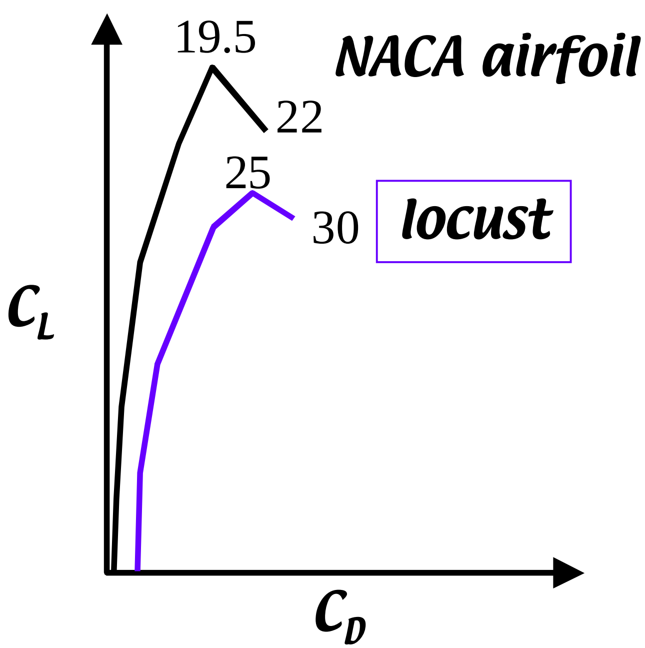
Smoke released from the leading edge of the flapper revealed an attached vortex along the leading edge of the wing

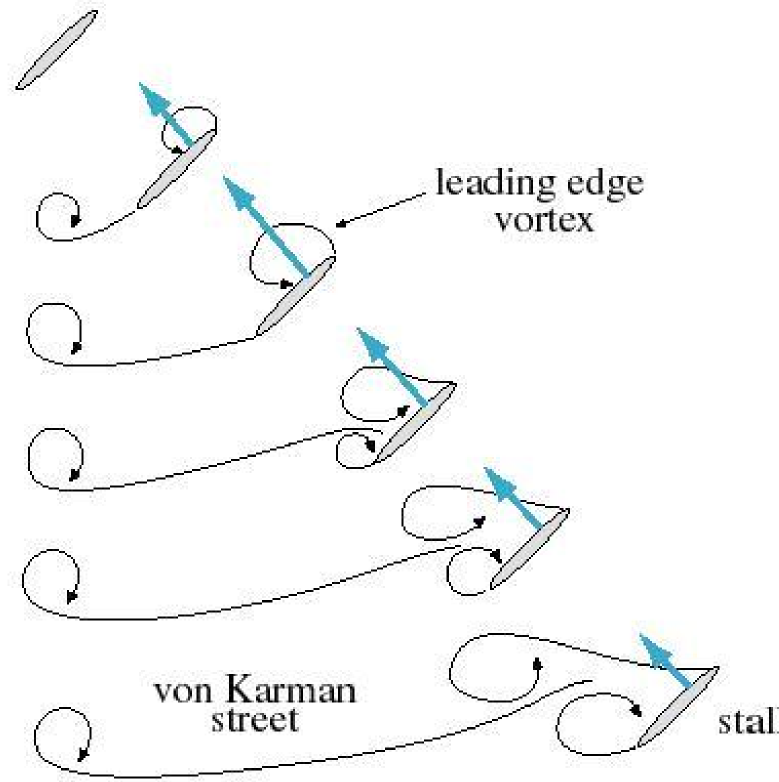
▶ **This attached vortex leads to higher lift**

Leading edge vortices and delayed stall



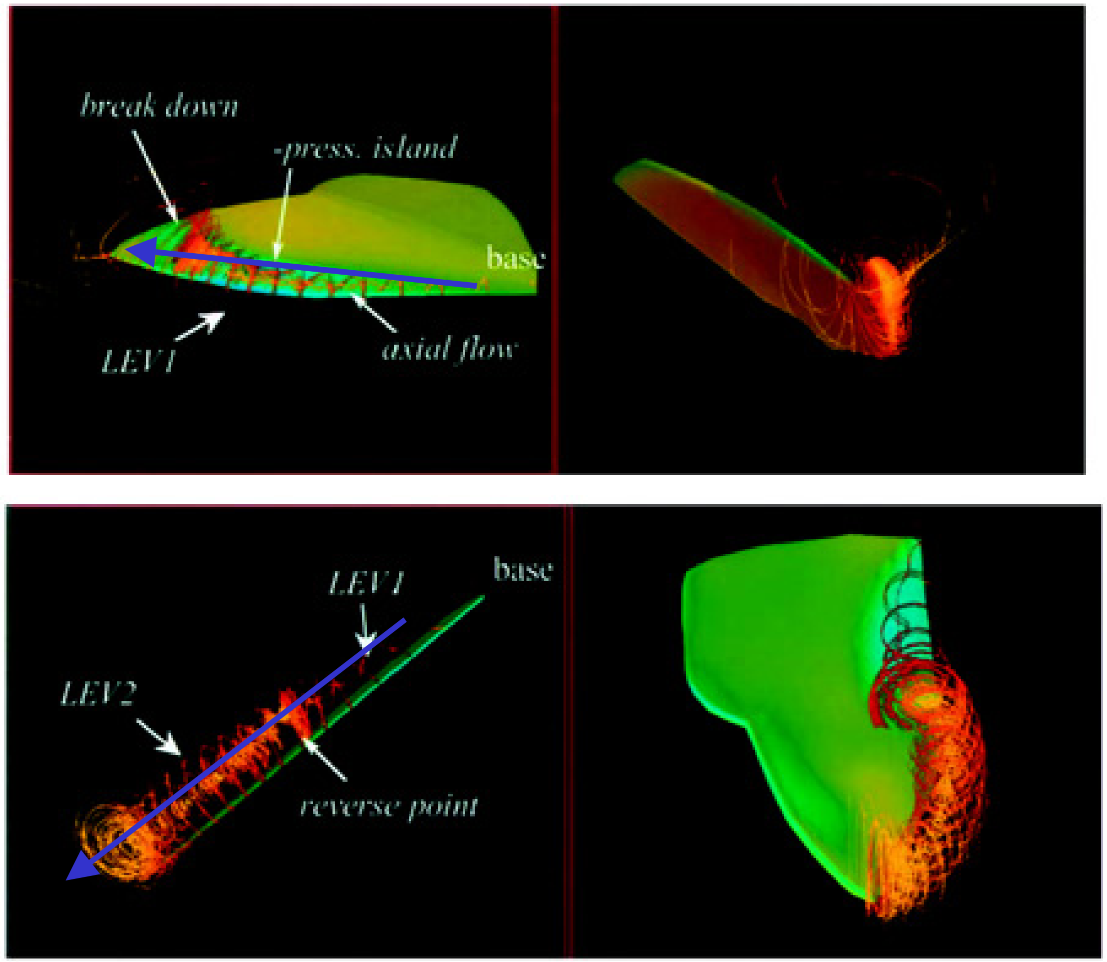
at lower angles of attack, flow circulates around an airfoil that is started from rest





- at higher angles of attack, flow separates at the leading edge and forms a leading edge vortex
- the leading edge vortex grows and is shed from the wing, leading to stall

Leading edge vortices and delayed stall



CFD (computational) model of flow around a flapping hawkmoth wing
(Liu et al., 1998)

But, the leading edge vortex on hawkmoth (and Drosophila) wings remains attached, allowing higher lift generation at high angles of attack!

How is the leading edge vortex stabilized?

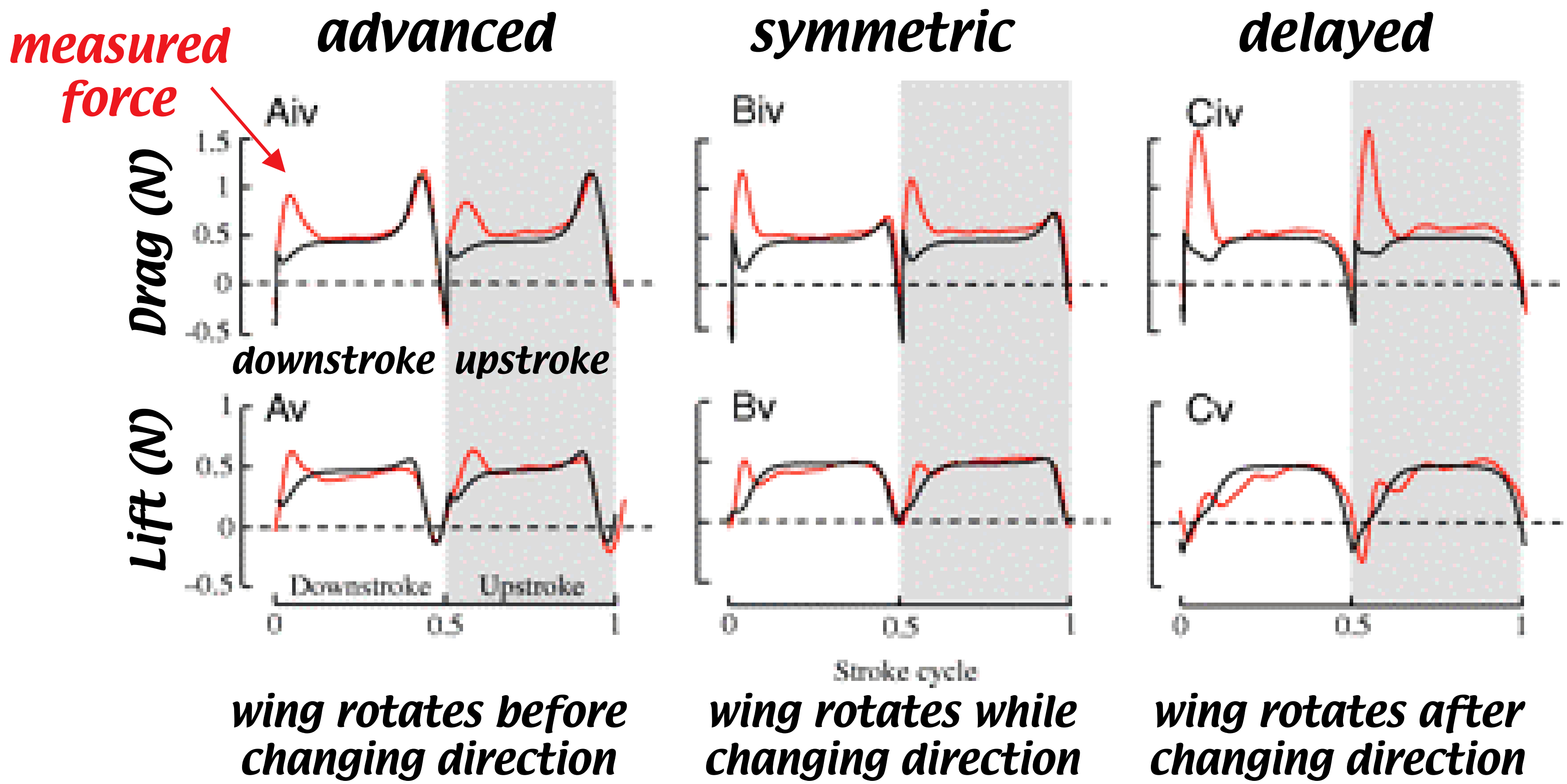
▸spanwise flow due to flapping appears to stabilize leading edge vortex in hawkmoths

▸But this does not seem to be the case in Drosophila - different mechanism at lower Re?

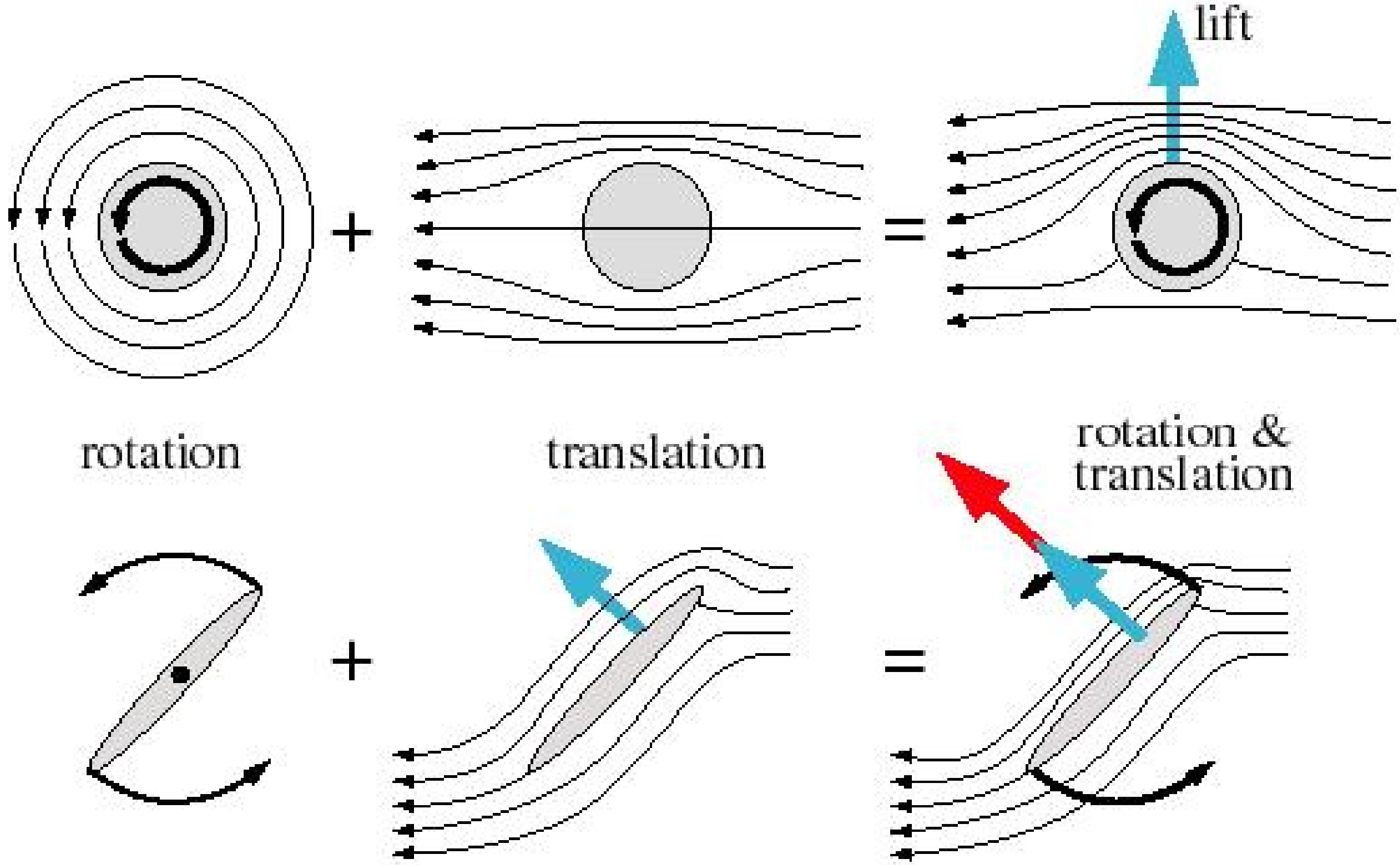
How do flying insects generate so much lift?

Force measurements and flow visualization of "robo-fly" (dynamically scaled Drosophila wing) have revealed additional mechanisms of unsteady lift generation

Timing of wing rotation affects force production



Rotational forces can augment lift production



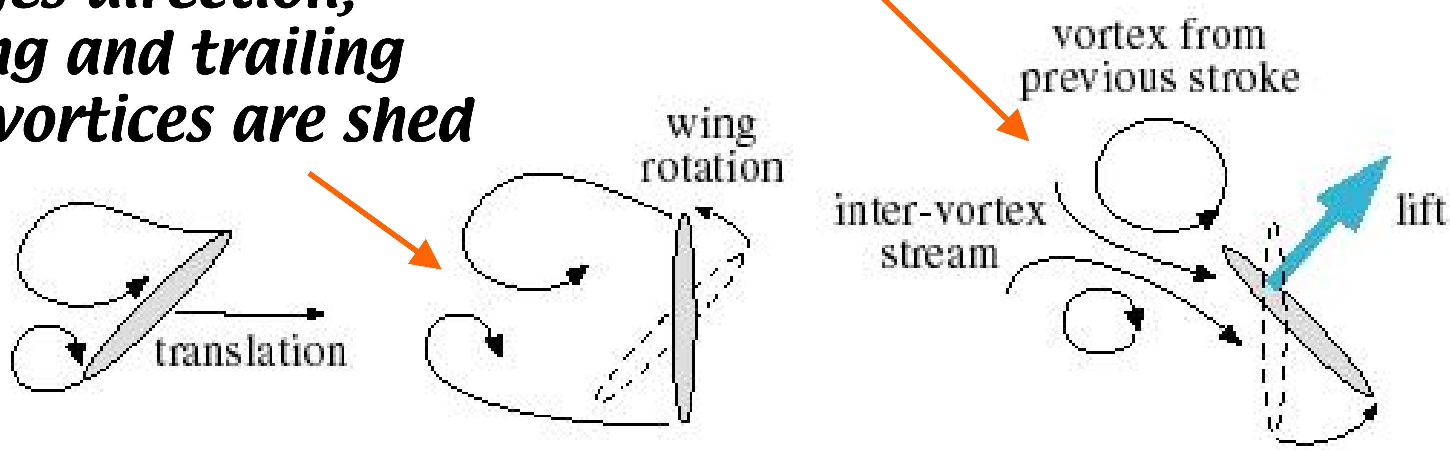
***subtle changes in the timing of rotation can produce large differences in force production that may aid in maneuvering**

Wake recapture: building better vortices by recycling fluid momentum

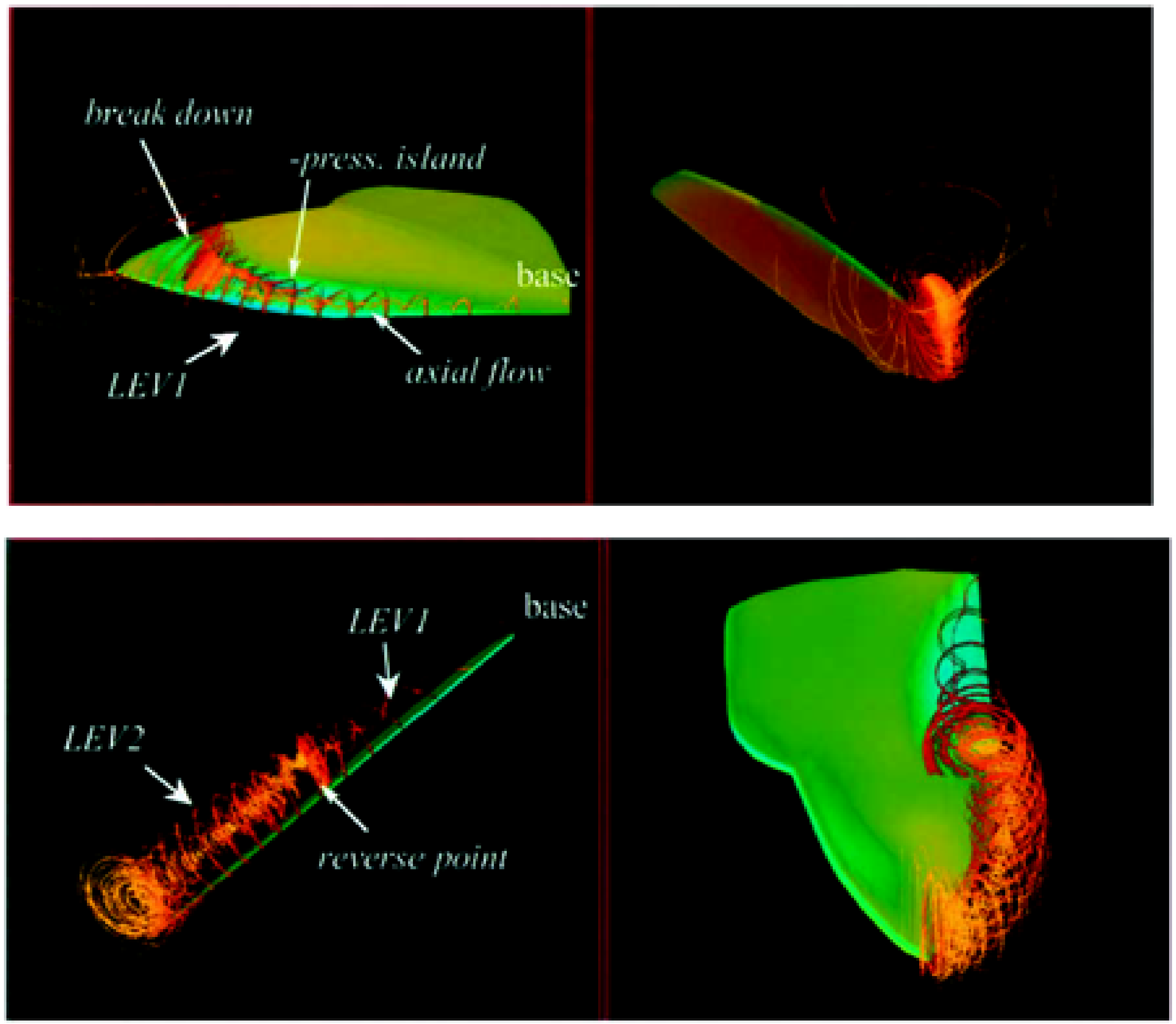
If wing reverses direction quickly, it will interact with the induced flow between these shed vortices

This inter-vortex flow increases the relative velocity of air hitting the wing, leading to higher lift production

As wing stops and changes direction, leading and trailing edge vortices are shed



Can we model unsteady force production by flapping wings without performing a full computational fluid analysis?

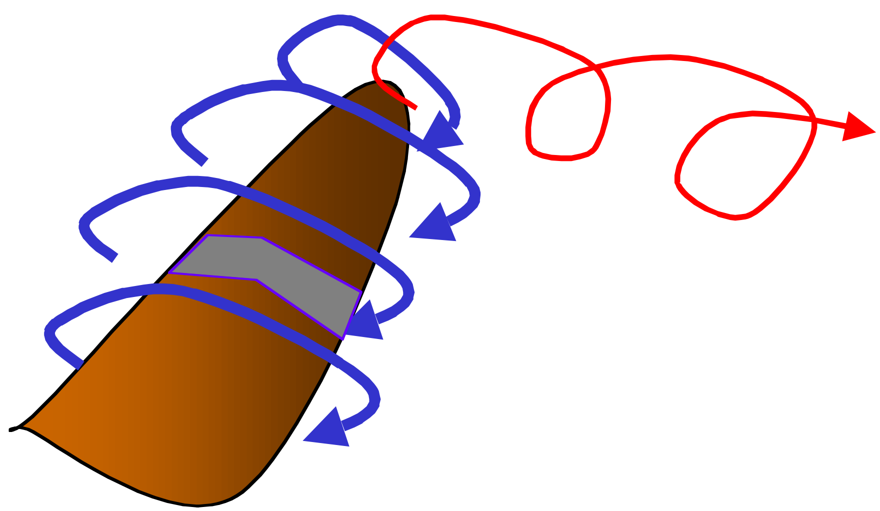


Mechanisms of unsteady force production:

1. ***translation***
2. ***rotation***
3. ***wake capture***

Can we model unsteady force production by flapping wings without performing a full computational fluid analysis?

Back to blade element analysis: calculate the lift and drag forces on each segment of a wing and sum these over the entire wing at each instant in time.



But this time:

- ▸ use unsteady force coefficients for translational motion (high angle of attack and delayed stall)
- ▸ calculate rotational forces generated at stroke reversals

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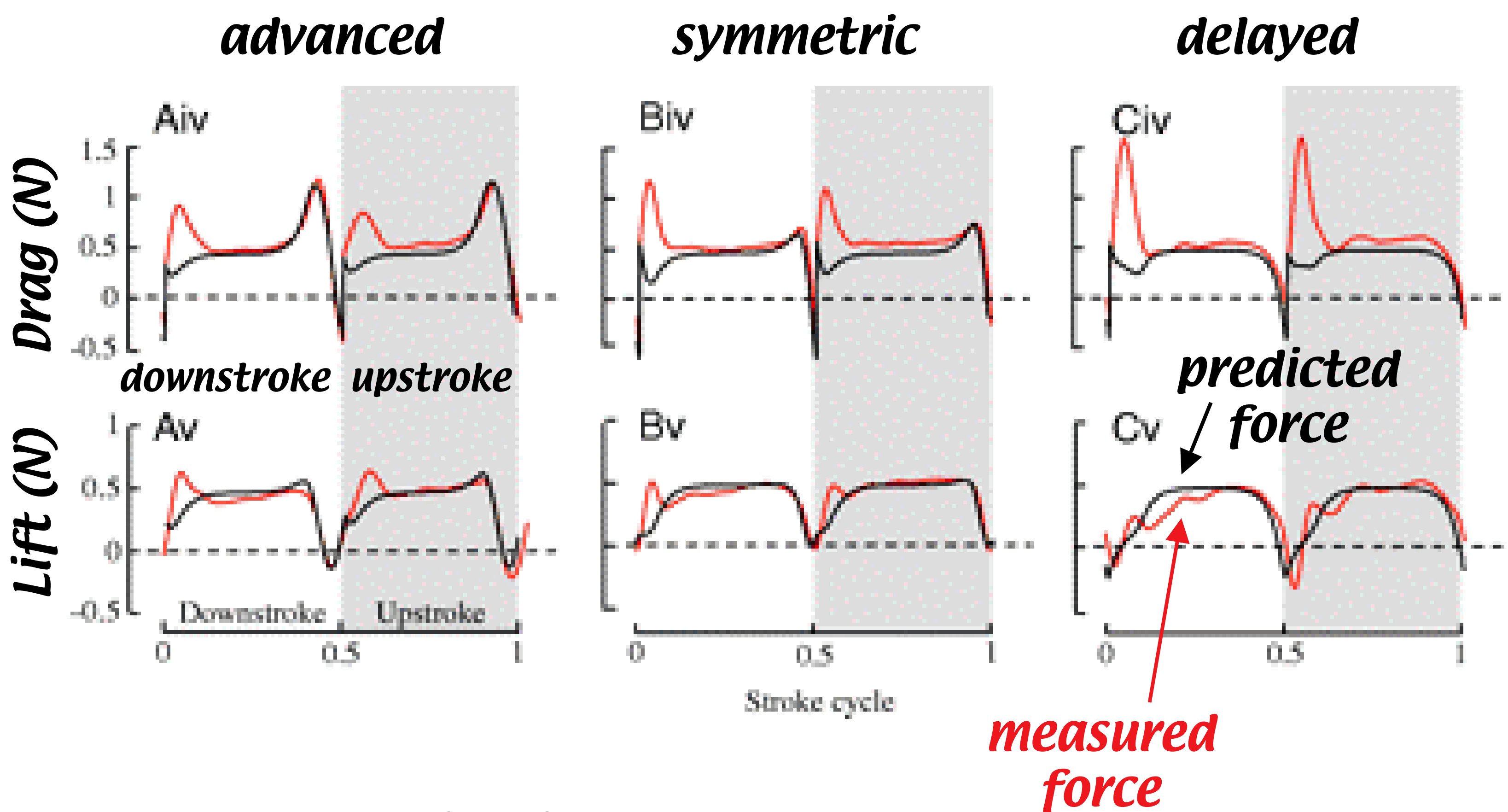
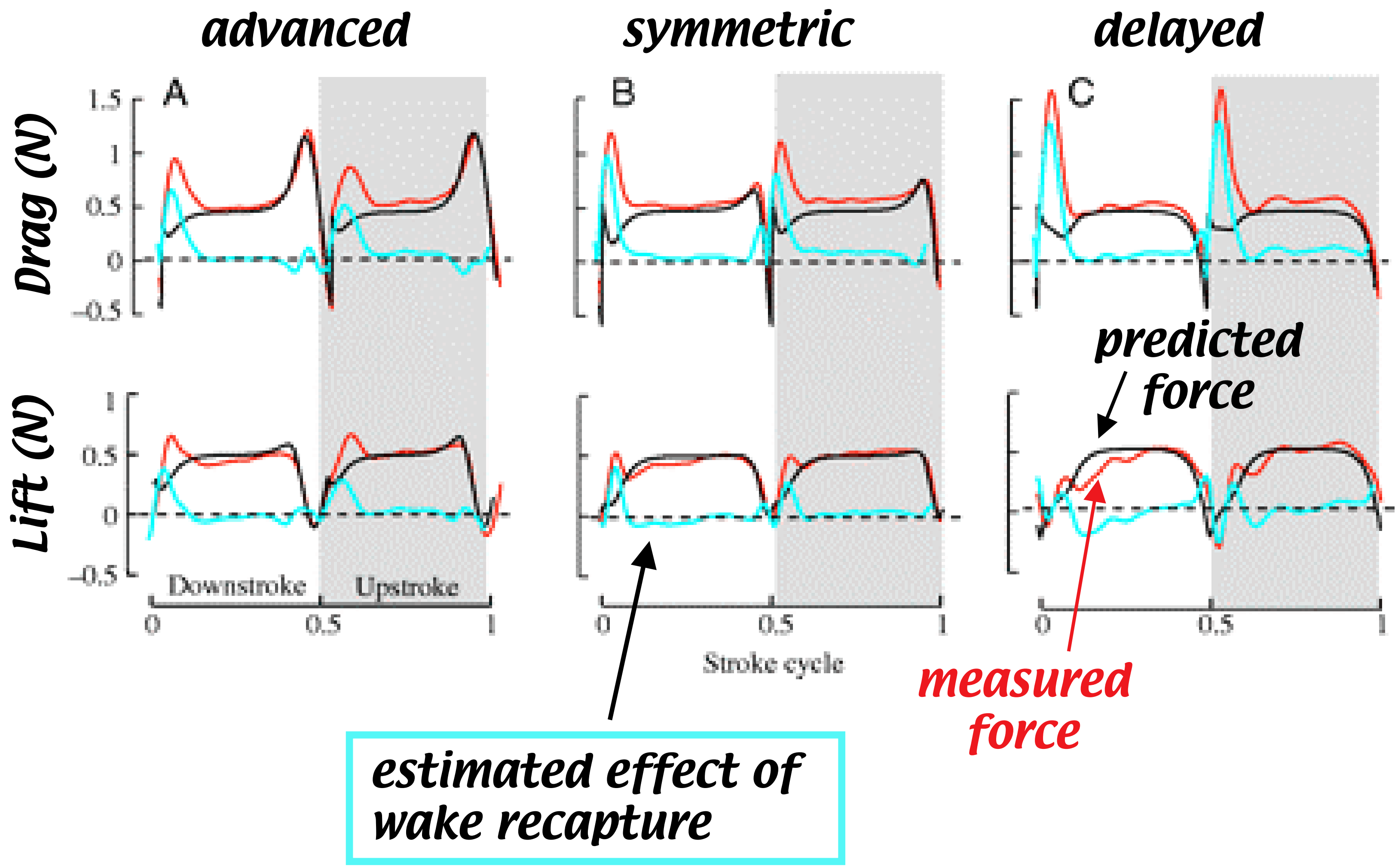


Blade element analysis with unsteady force coefficients and rotation predicts forces well in some cases

Sane and Dickinson (2002)

Wake capture accounts for the difference between measured and predicted forces

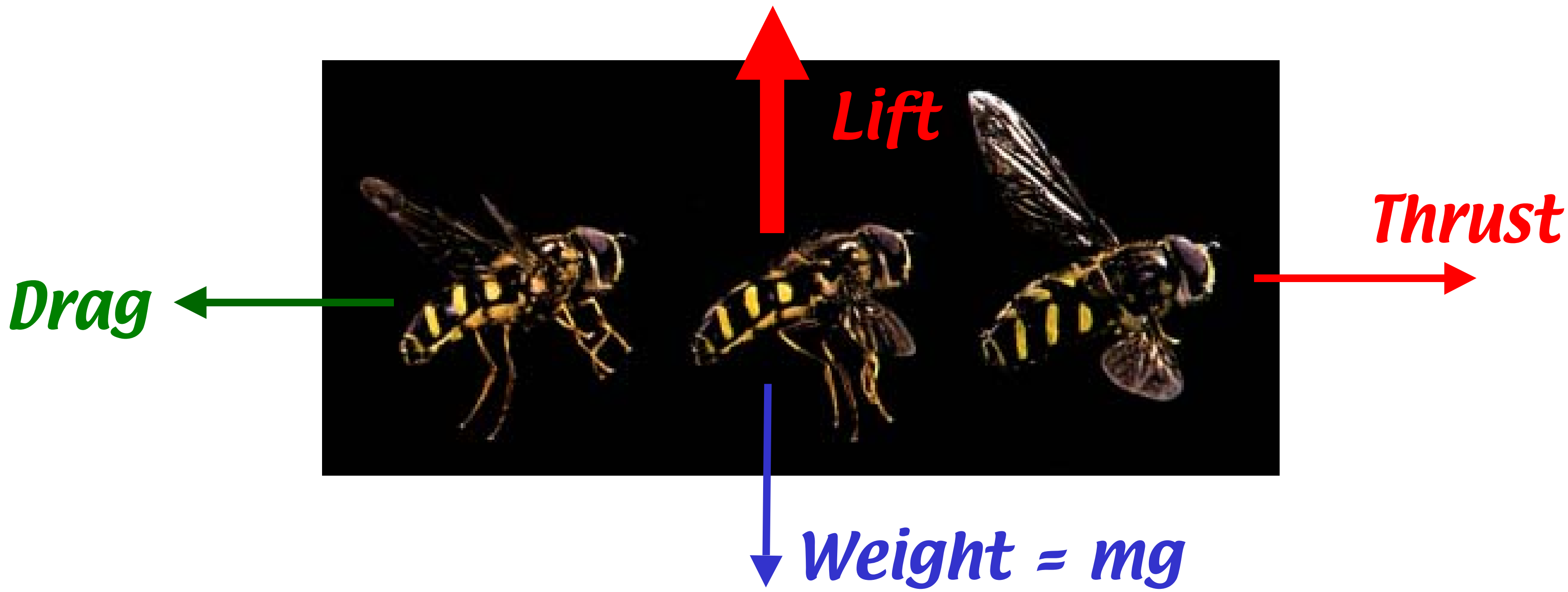


Sane and Dickinson (2002)

Biology 427 Biomechanics 2004
Lecture 22. Swimming dynamics and unsteady flows

- Modeling unsteady flapping flight
- Differences between flight and swimming
- Mechanisms of producing thrust in water:
    - ▸Jet reaction mechanisms
    - ▸ Drag-based swimming and added mass forces
    - ▸ Lift-based (oscillatory) and undulatory swimming

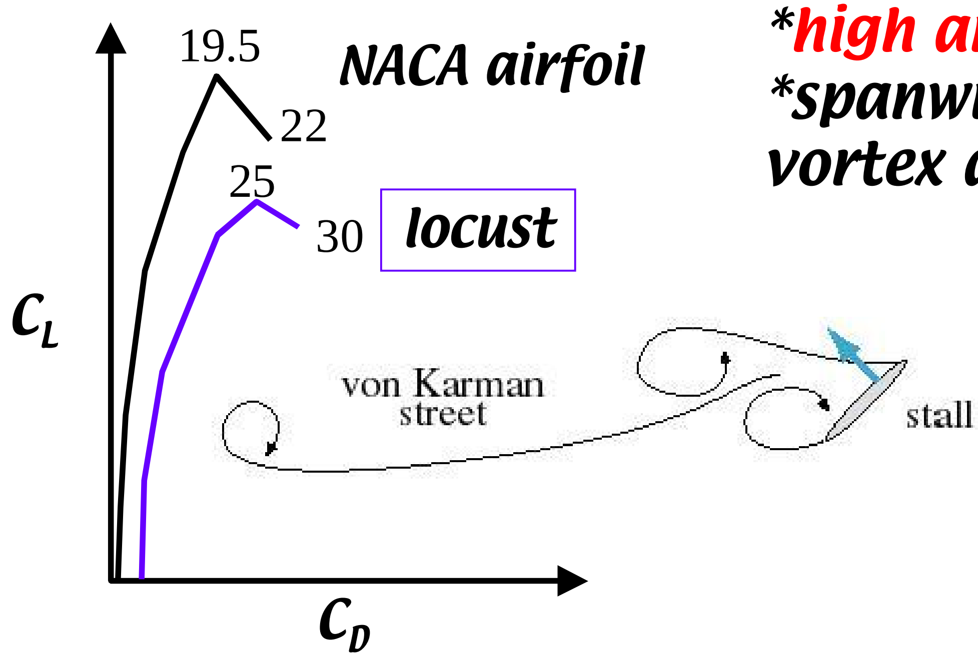
Flying animals must generate both lift and thrust (forward force to counteract drag) with their wings



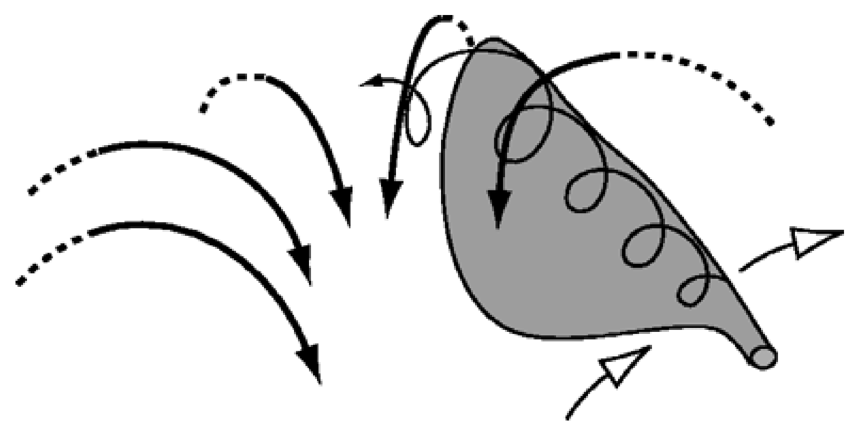
Average lift coefficients of many flying insects are greater than maximum steady lifts coefficients - insects do not generate lift by conventional, steady mechanisms!

How do flying insects generate so much lift?

1. Leading edge vortex and delayed stall

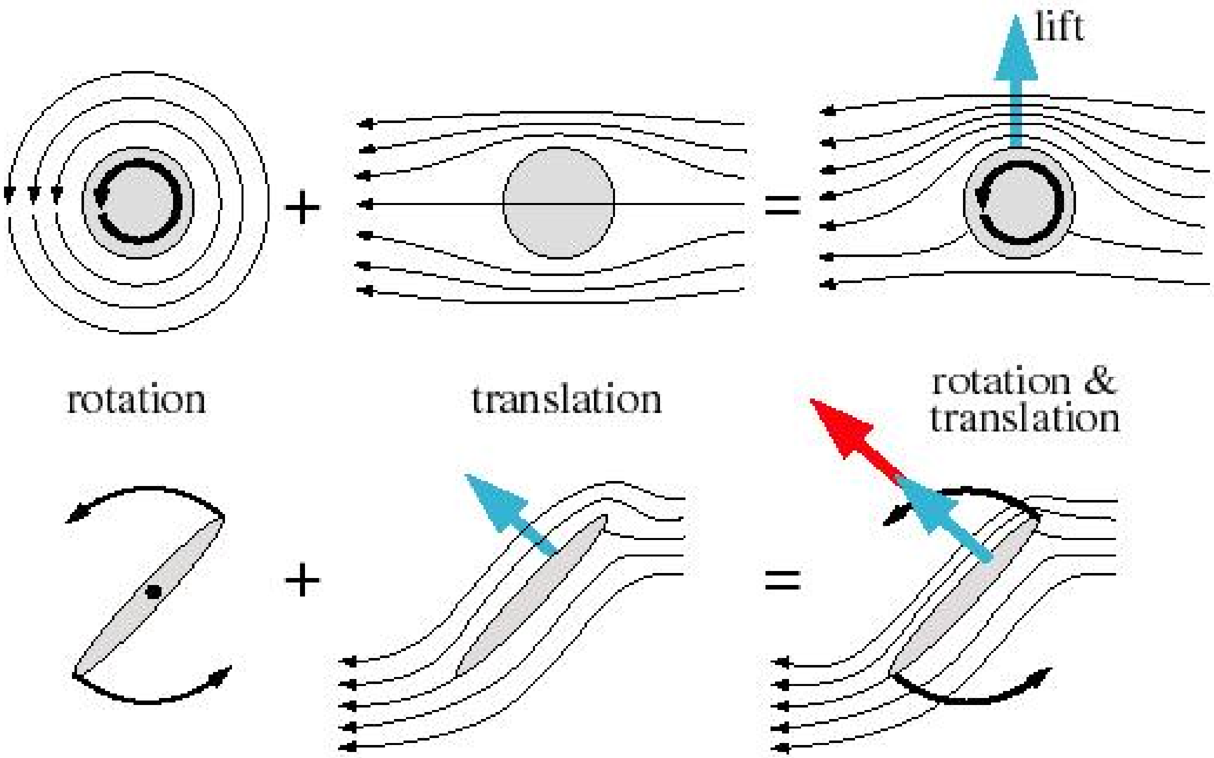


*high angle of attack provides more lift
*spanwise flow stabilizes leading edge vortex and delays stall



How do flying insects generate so much lift?

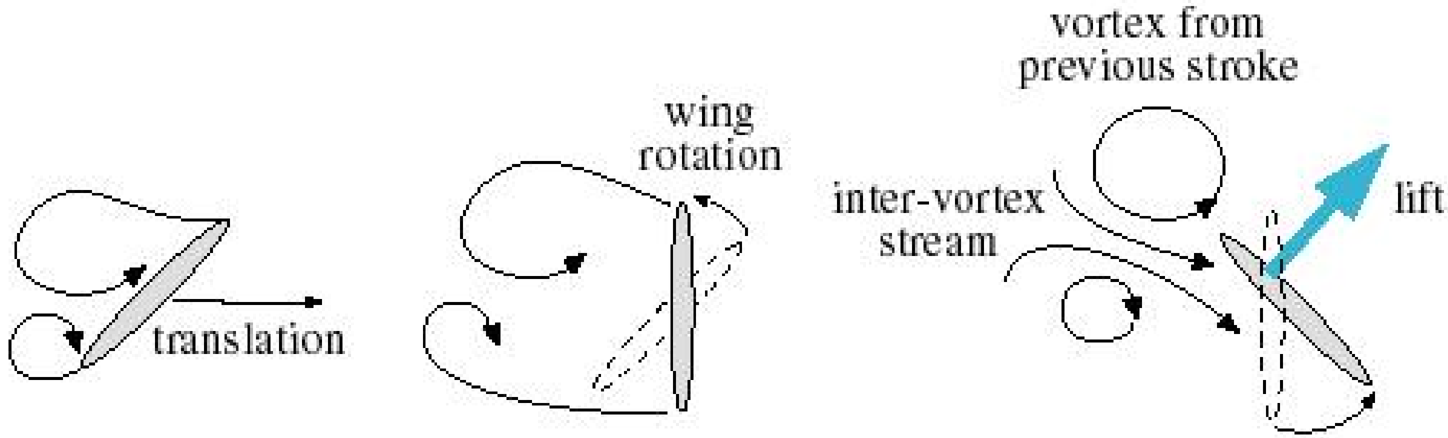
1. Wing rotation



*Rotational forces can augment lift production
* Timing of wing rotation affects force production

How do flying insects generate so much lift?

1. Wake capture



***As wing changes direction, it sheds vortices into the wake and then moves through this higher velocity fluid, increasing lift production**

We can calculate all of the forces produced by a moving fluid by solving the full 3-D Navier-Stokes equation numerically (Computational Fluid Dynamics)

$$\rho \frac{D\vec{u}}{Dt} = -\vec{\nabla} P + \mu \vec{\nabla}^2 \vec{u} + \rho \vec{g}$$

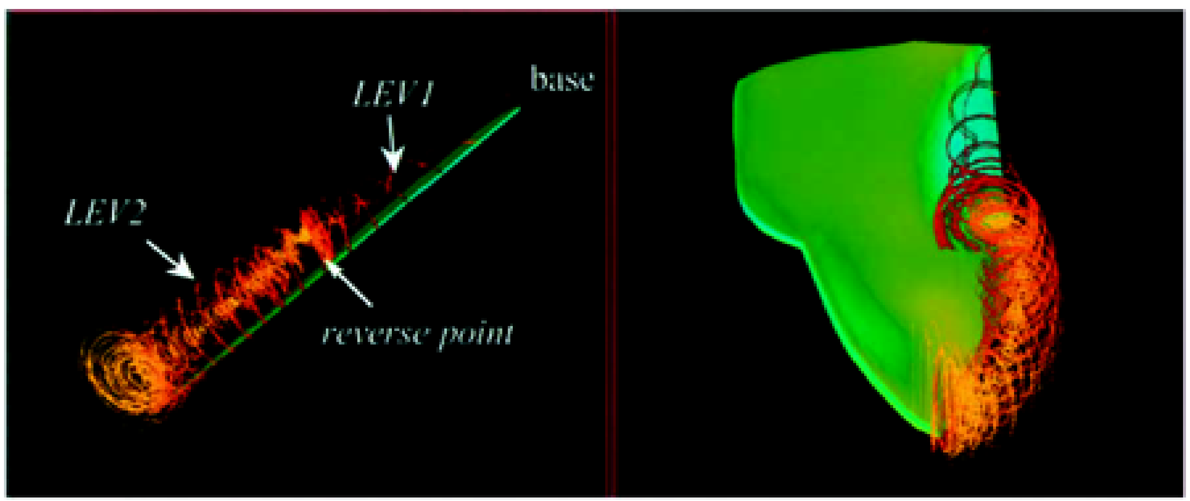
**solve for each speck of fluid in each time step!*

*mass/vol * acceleration (force)*

gradient in pressure/vol

*viscosity*gradient in shear/vol*

*mass*gravity /vol*

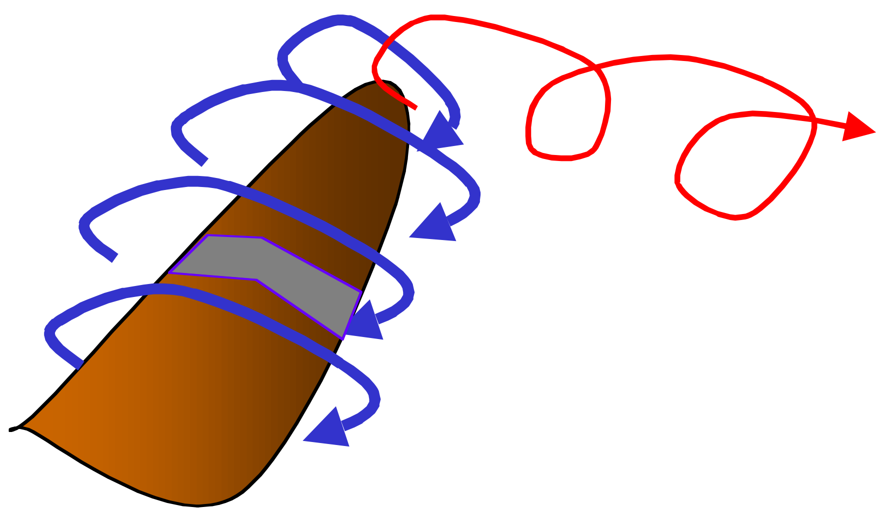


But...

this is extremely time and computer-intensive, and only applies to the exact situation you choose to solve

Can we create a simpler, analytical model of unsteady flapping flight that could predict force production in many different cases?

Back to blade element analysis:
calculate the lift and drag forces on each segment of a wing and sum these over the entire wing at each instant in time.



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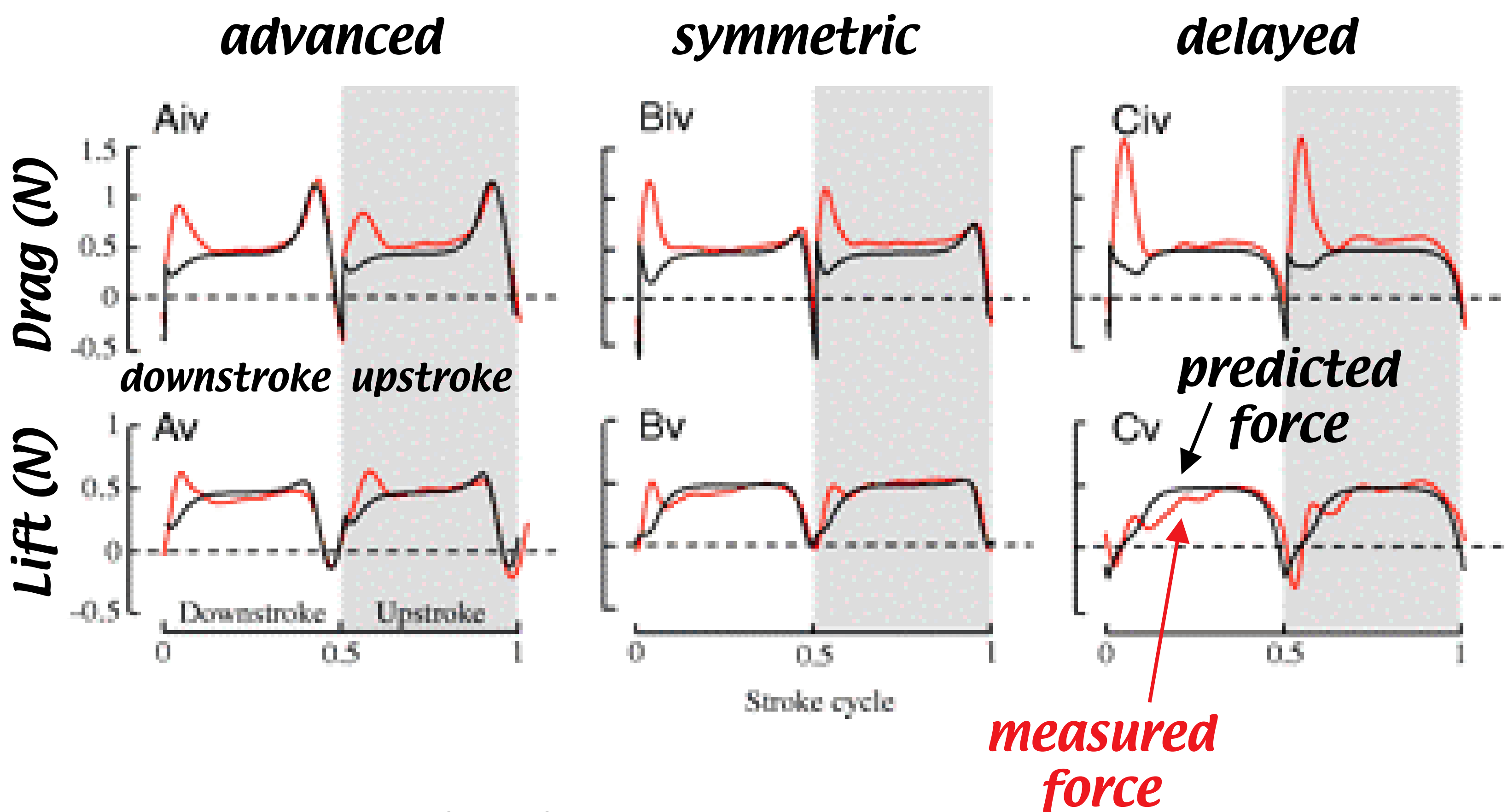
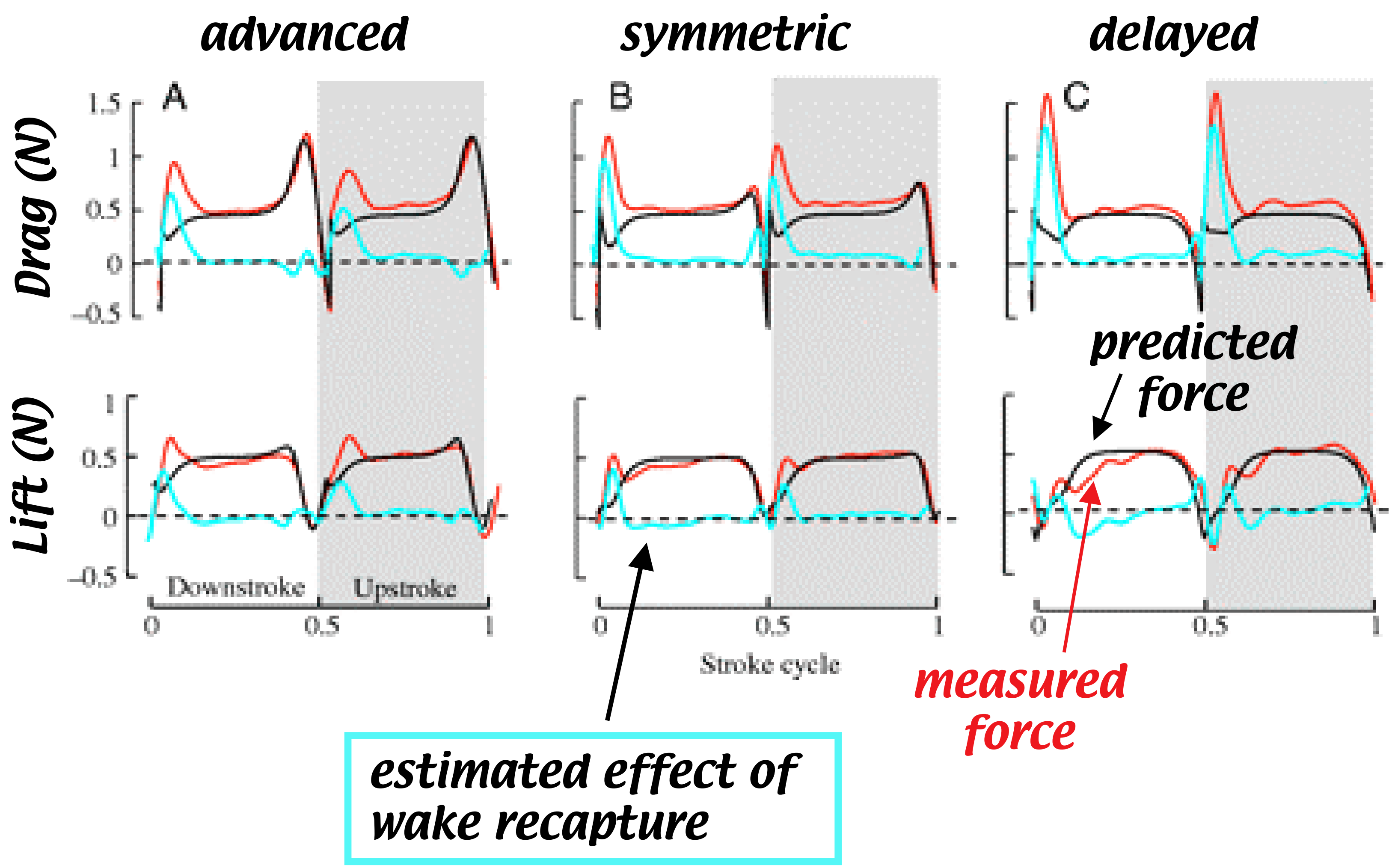


Blade element analysis with unsteady force coefficients and rotation predicts forces well in some cases

Sane and Dickinson (2002)

Wake capture accounts for the difference between measured and predicted forces - It may be possible to predict unsteady forces produced by flapping flight!

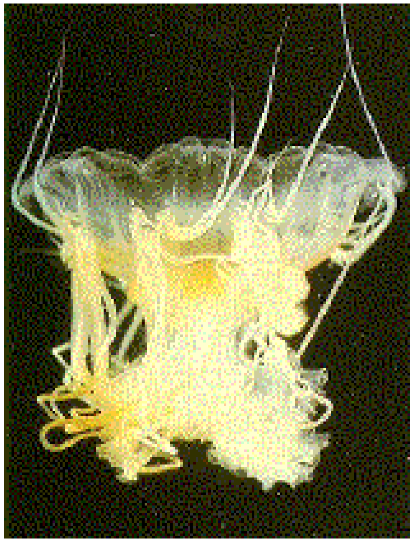


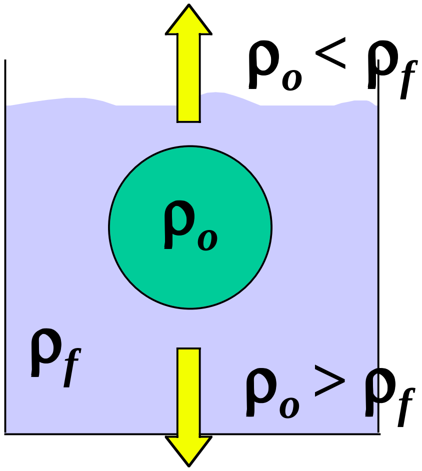
Sane and Dickinson (2002)

How does swimming differ from flight?

All fluids (air or water) follow the same physical rules, but the density of most biological tissues is much closer to that of water

ρair = 1.2 kg/m^3
ρwater = 1000 kg/m^3
ρseawater = 1000 kg/m^3
ρfat = 940 kg/m^3, but
ρbone = 1700 kg/m^3 -> 2500 kg/m^3





F_{total} = mg = $(\rho_f - \rho_o)Vg$
where ρ_f = density of fluid
and ρ_o = density of object

How does swimming differ from flight?

All fluids (air or water) follow the same physical rules, but the density of most biological tissues is much closer to that of water

ρ*air = 1.2 kg/m*^{3}
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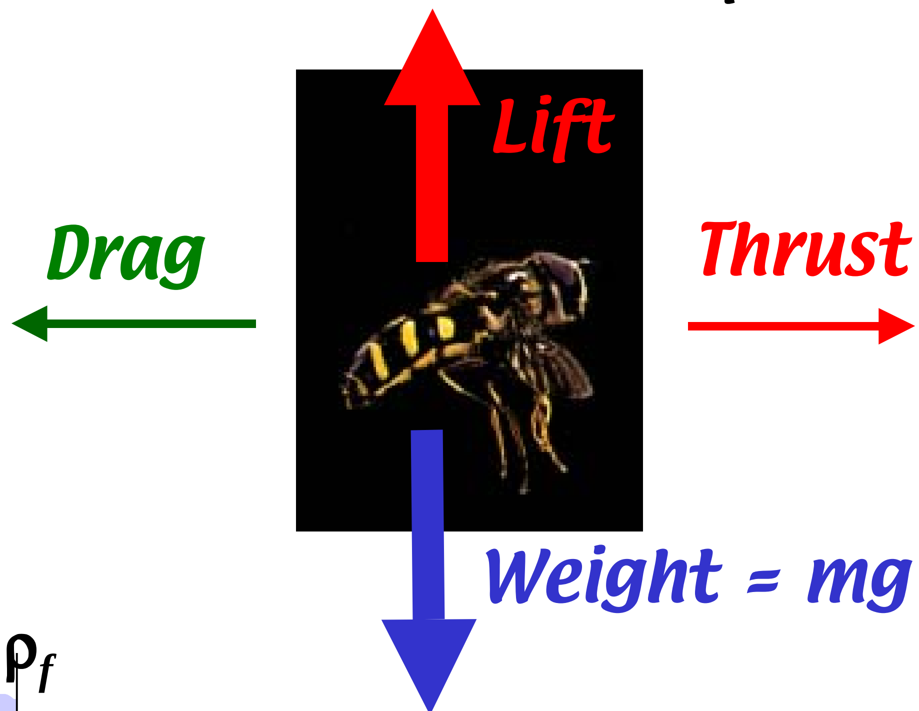

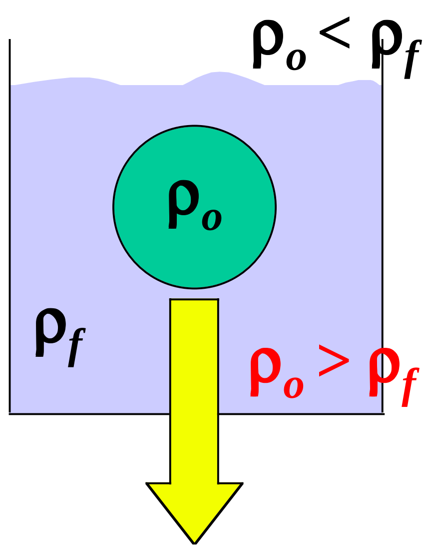

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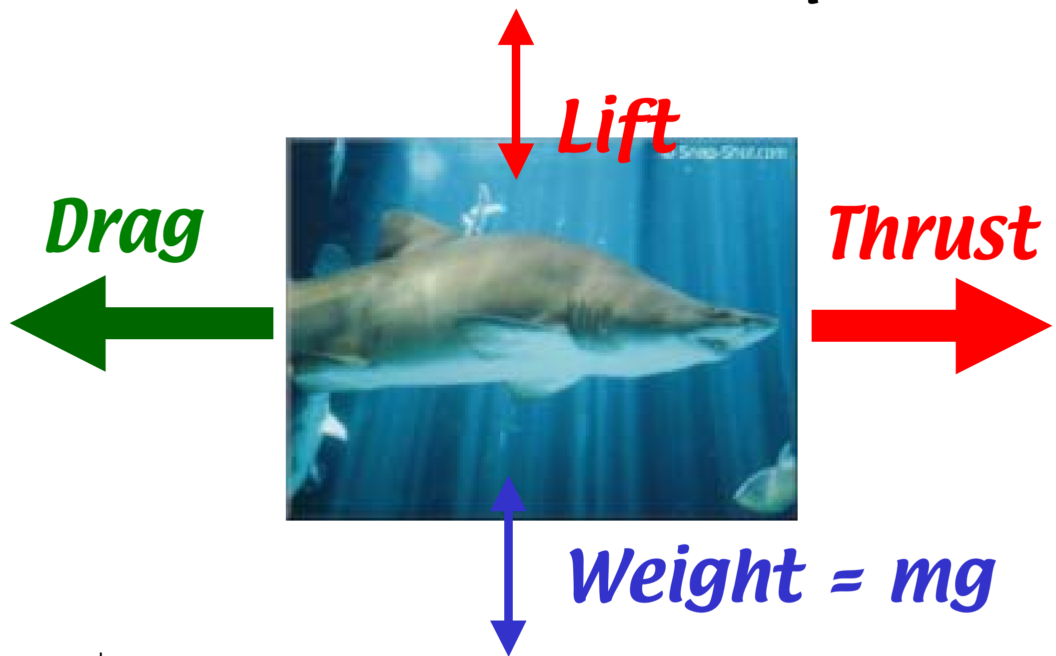
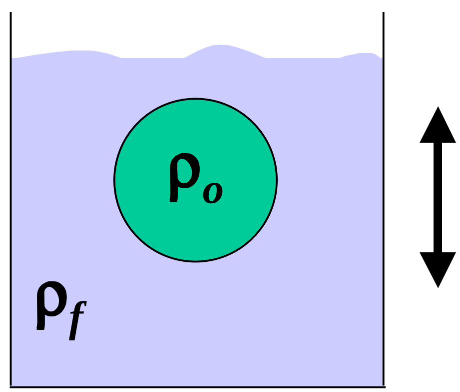
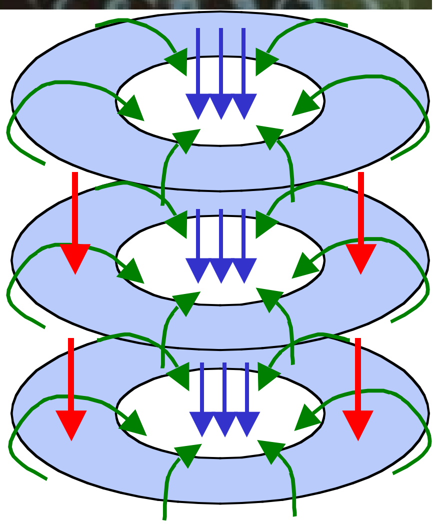




slightly positively buoyant,
slightly negatively buoyant,
or neutrally buoyant
(depends on tissues
and air spaces)

Weight support is less of an issue in swimming



Need to impart rearward momentum to water so the animal will move forward

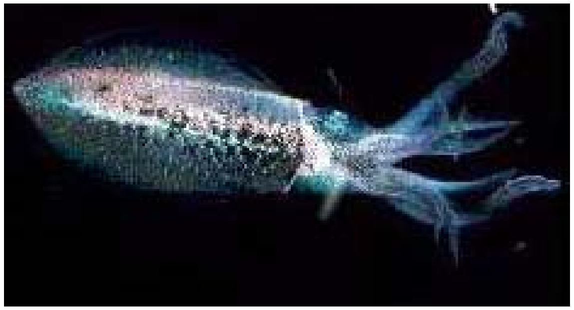
F = change in momentum = $d(mu)/dt$

How do animals generate forward thrust in water?

How do animals generate forward thrust in water?

Impart rearward momentum to water by:

1. **jet propulsion** - shoot a jet of water backwards out of your body



2. **drag-based swimming ("rowing")** - push water backwards with an appendage

3. **lift-based swimming** accelerate water backwards over a hydrofoil held at an appropriate angle

4. **undulating** - rolling water backwards along a waving fin or body

Jet reaction mechanisms

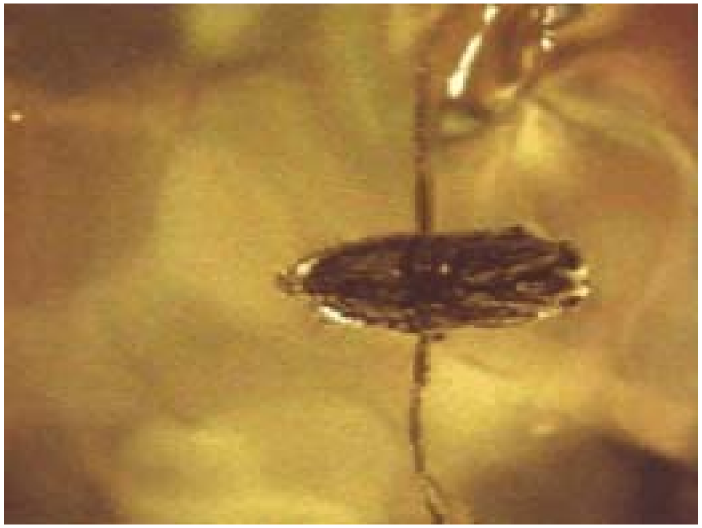
F = change in momentum = d(mu)/dt

Thrust = d(mu)/dt
= m du/dt + u dm/dt

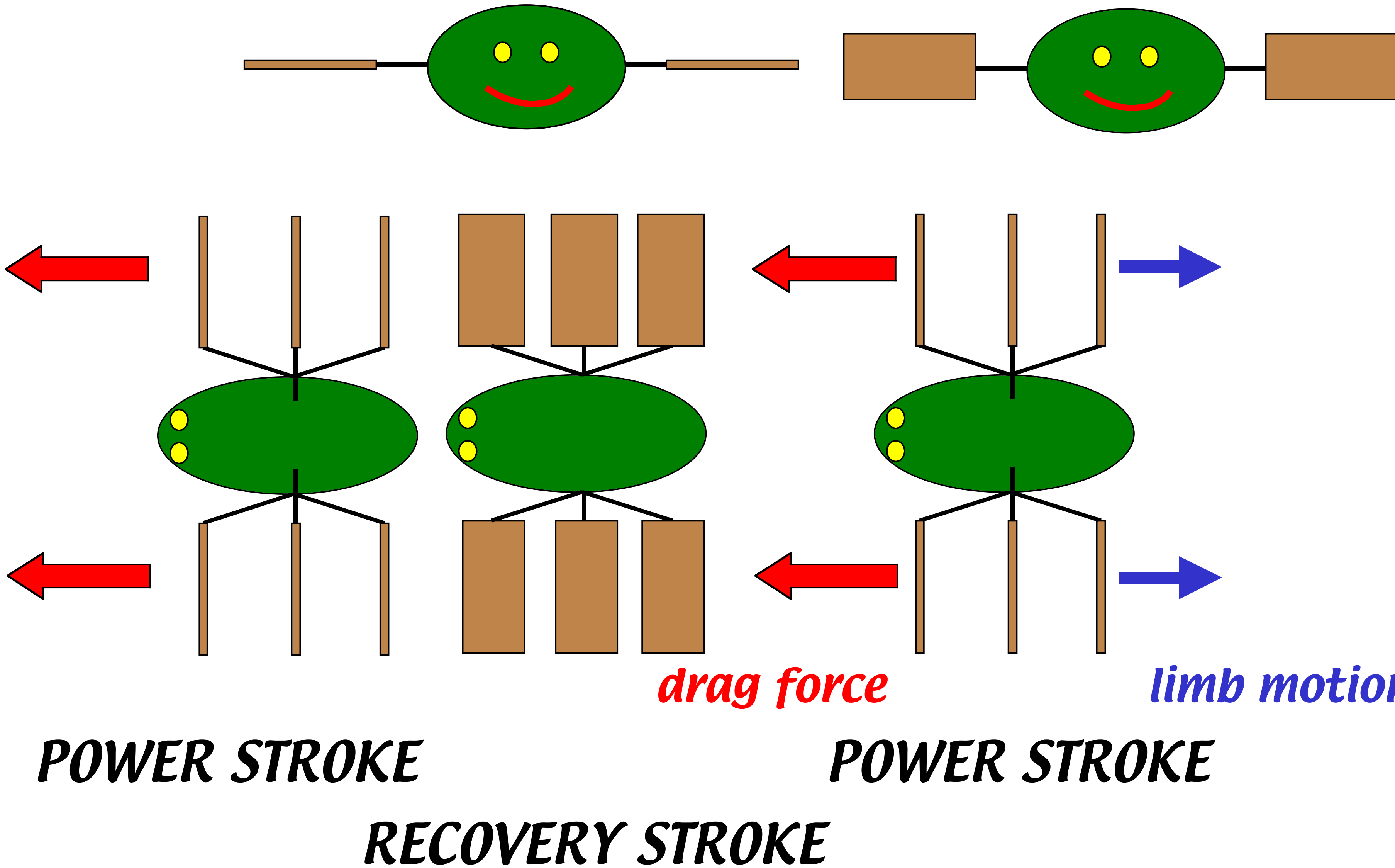
** in jet reactions, the total mass of the animal changes, as well as the velocity*

Drag-based swimming - *Water is pushed back by an appendage oriented perpendicular to flow*

** Drag on rearward-moving appendage produces forward motion of animal*



Drag-based swimming

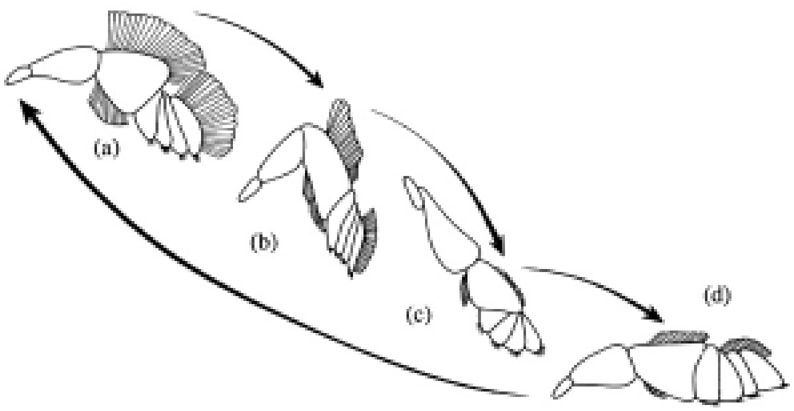


*rotate appendage so it experiences less drag when moving forward

Using drag for propulsion: paddling and rowing

$$D = C_d \rho S u^2/2$$

Mechanisms for reducing drag on the recovery stroke:



- ►*Change area/shape between downstroke and upstroke*
- ►*Decrease velocity during recovery stroke*
- ►*Decrease fluid density during recovery stroke*

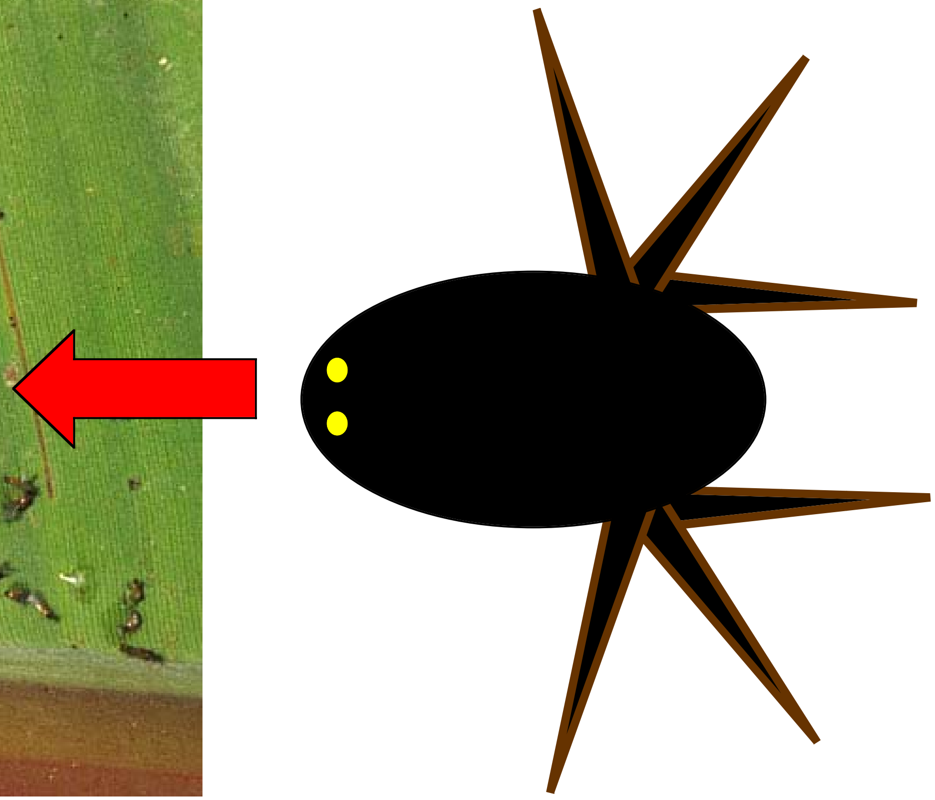
Drag-based swimming

copepod

horse

water beetle

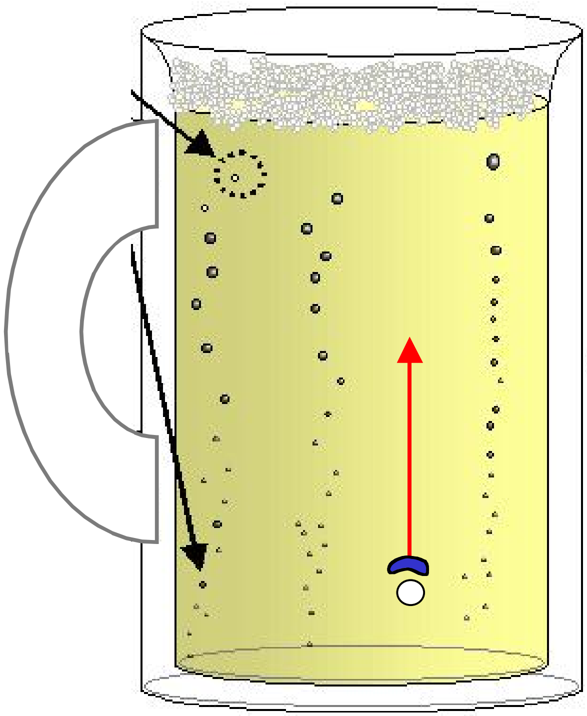
But… some dytiscid beetles swim without changing the area or orientation of their legs on the recovery stroke



$$\text{Thrust} = C_D\, \rho\, S\, u^2/2 + \text{“something else”}$$

What is the "something else" that contributes to drag-based swimming?

Consider a bubble rising in a glass of beer.....



Buoyant force:

$F_{total} = (\rho_f - \rho_o)Vg$

where ρ_f = density of fluid displaced

and ρ_o = density of object

bubble Volume = 1 mm^3 = 1 x 10^{-9} m^3

ρ_{bubble} = 1.2 kg/m^3; m_{bubble} = 1.2 x 10^{-9} kg

ρ_{beer} = 1000 kg/m^3

$F_{total} = (\rho_{beer} - \rho_{bubble})\, V g$ = 9.8 x 10^{-6} N

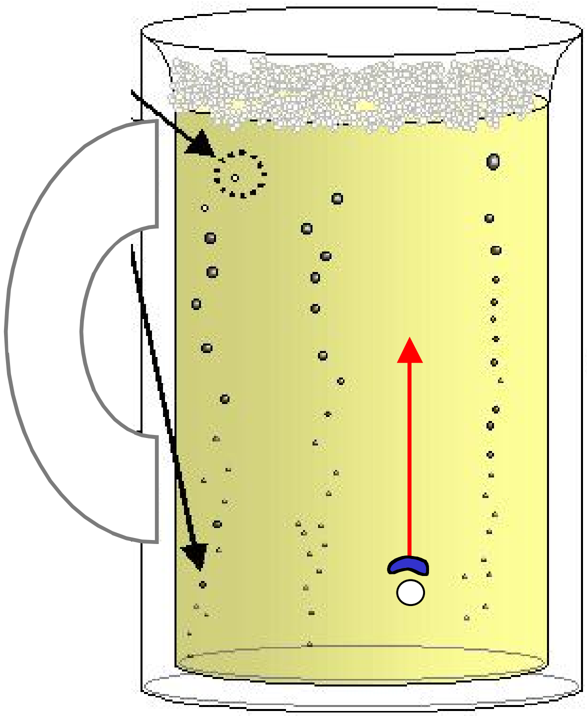
$F_{total} = m_{bubble}\, a$

a = 8200 m/s^2 = **830 x gravity!**

**bubble also has to accelerate the mass of fluid in front of it, and this fluid has inertia (resists acceleration or deceleration)*

What is the "something else" that contributes to drag-based swimming?

Consider a bubble rising in a glass of beer…..



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ρ_{beer} = 1000 kg/m^3

$F_{total} = (\rho_{beer} - \rho_{bubble})\, V g = 9.8 \times 10^{-6}$ N

$F_{total} = m_{virtual}\, a$

$m_{virtual} = \rho_{bubble} V + \alpha \rho_{beer} V$

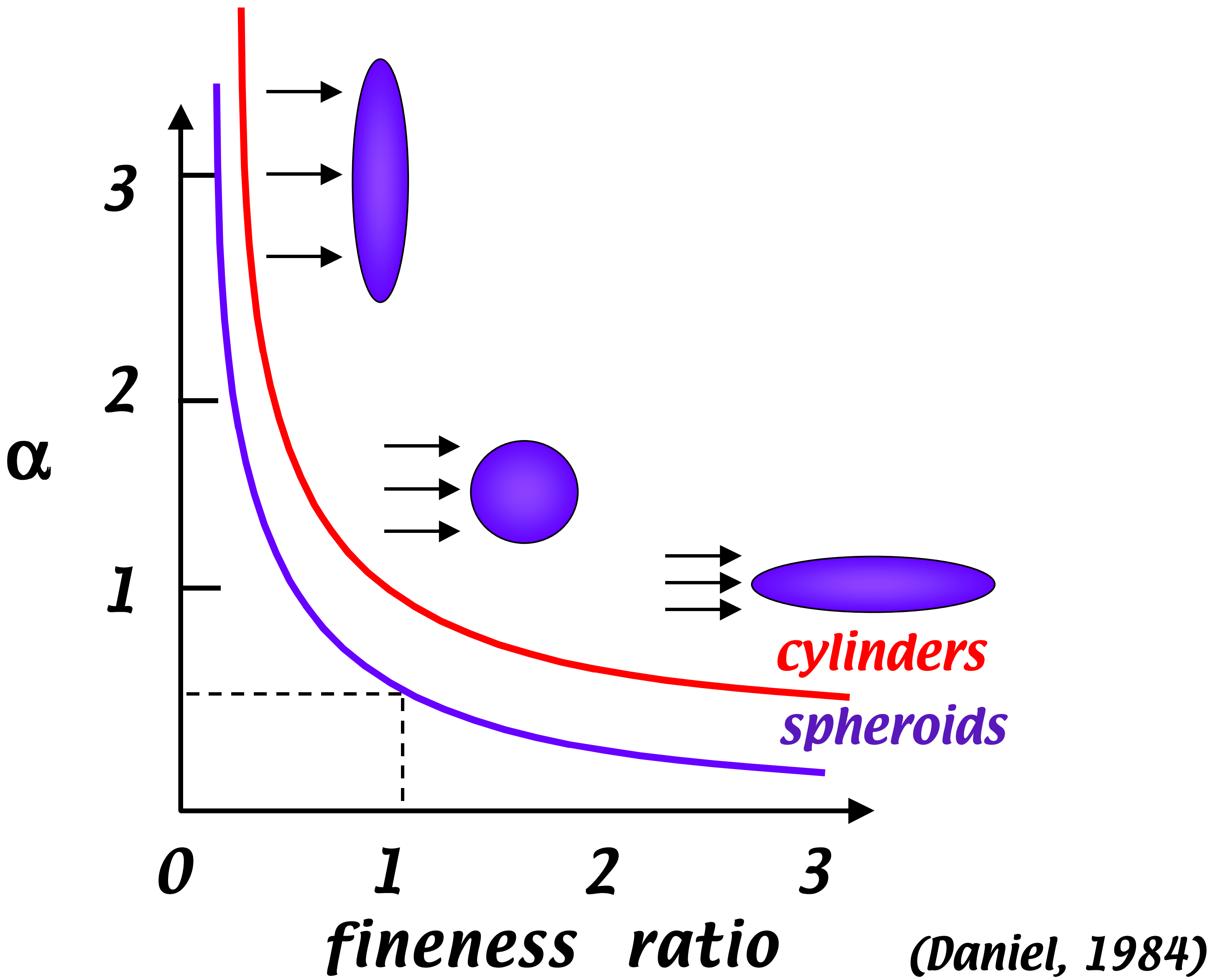
$= 0.5 \times 10^{-7}$ kg

a = 20 m/s^2 = **2 x gravity**

"added mass" for a sphere = 1/2 volume displaced by object (α = 0.5)

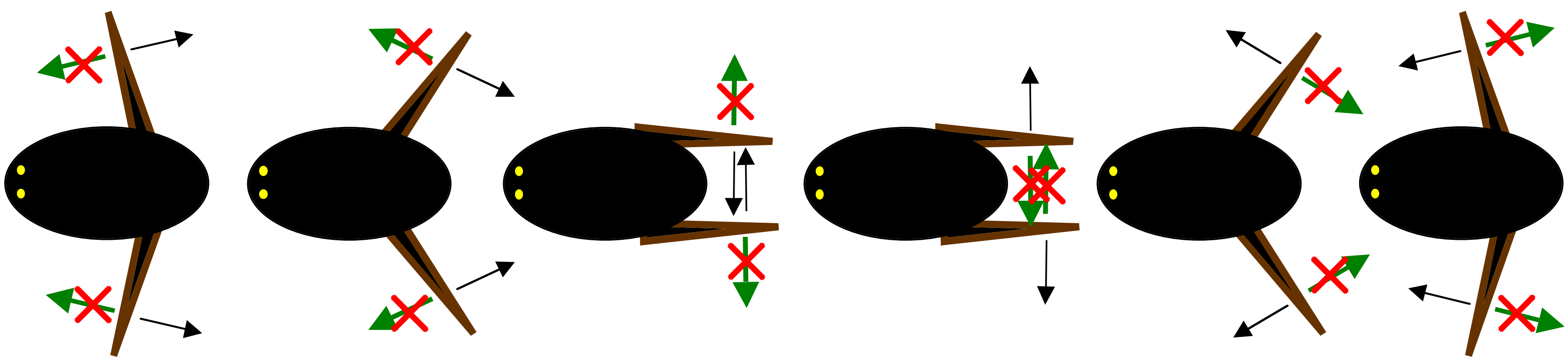
"virtual mass" = mass of object + added mass of fluid

The *added-mass coefficient* (α) depends on the shape of the object



Back to the dytiscid beetle.....

Drag opposes velocity of limb
(always opposite to direction of motion)



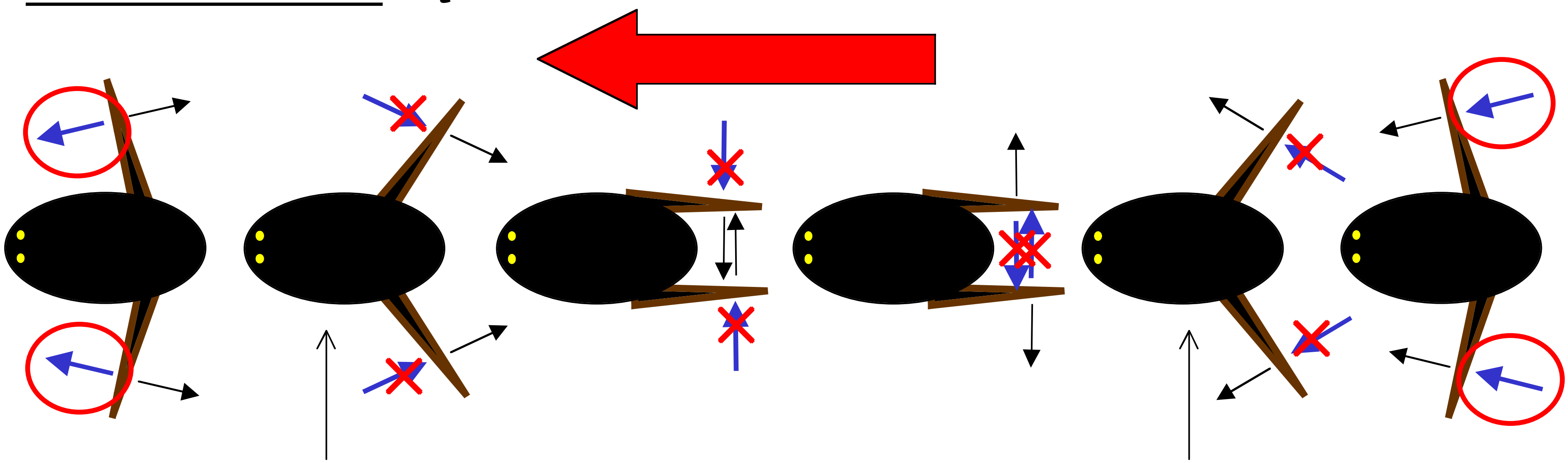
Thrust = $C_D \rho S u^2/2$ + "something else"

Thrust = Drag + Added mass force

Back to the dytiscid beetle.....

Drag opposes velocity of limb
(always opposite to direction of motion)

Added mass force opposes acceleration or deceleration of limb



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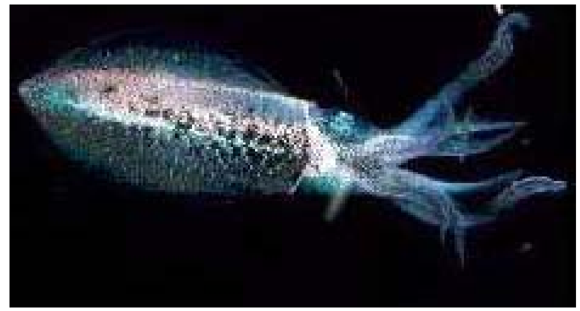

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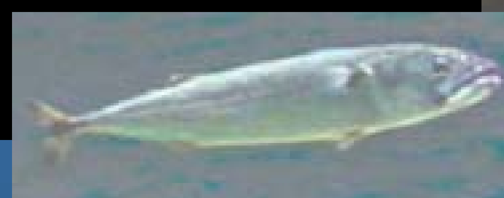
Swimming in fish and mammals

Lift-based swimming with hydrofoils (flippers, tail, fins....)

Fish swimming - body/caudal fin (tail) propulsion



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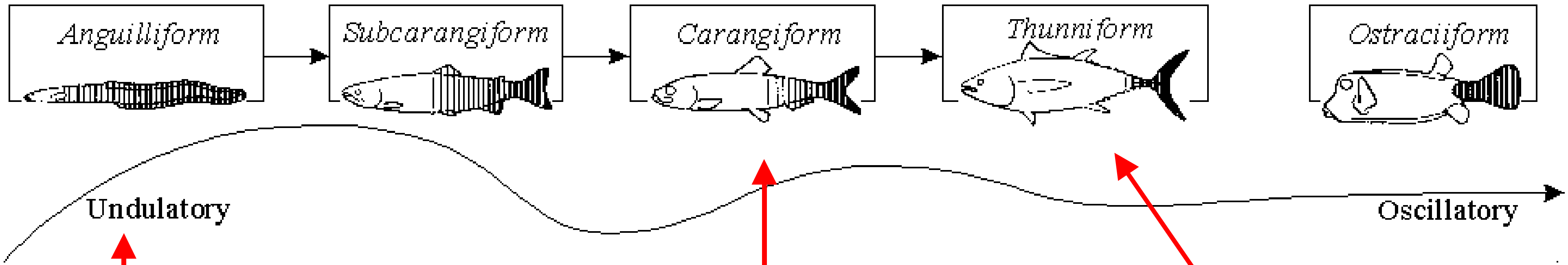
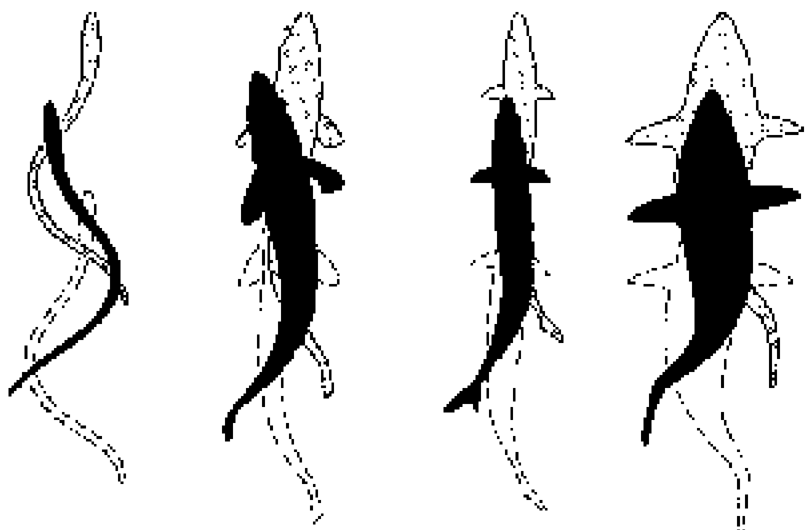


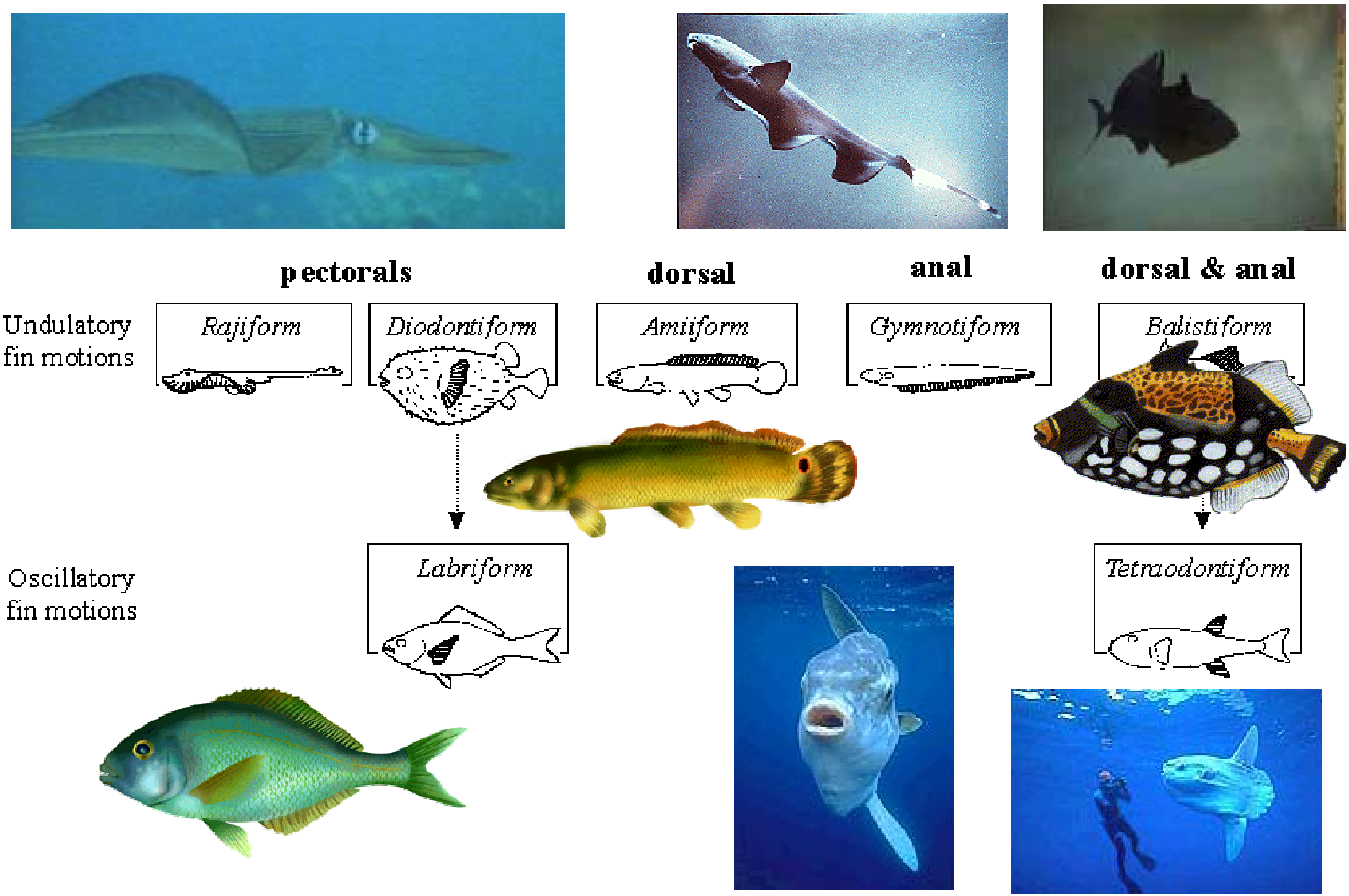
pass waves down large part of body length
****high cost of transport, but fast accelerations and maneuverable***
(eels, limbless amphibians, aquatic snakes, smooth polychaetes)

good generalist design
****fairly fast and efficient, but also maneuverable***
(jacks, perches, trout, cichlids)

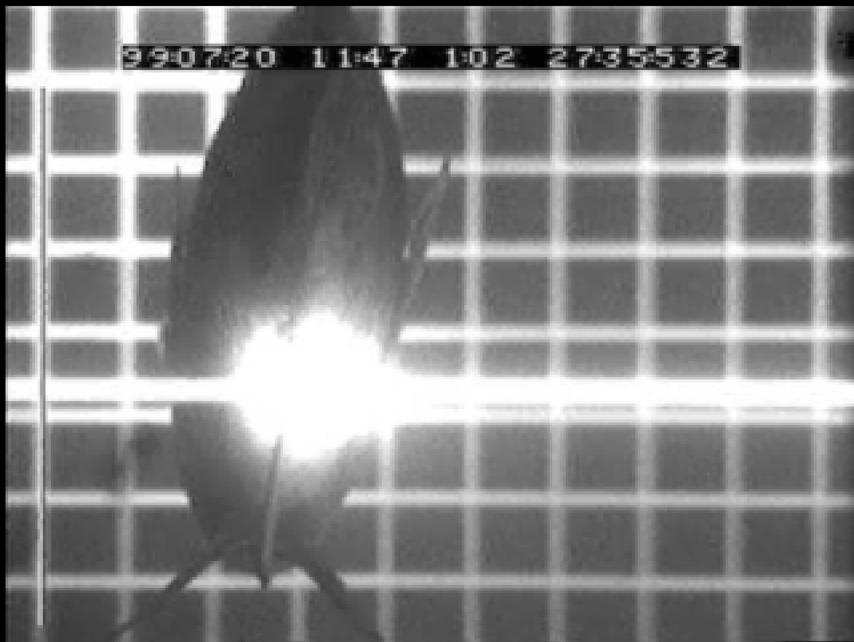
large pelagic fish
****very fast and very efficient***
(tunas, mackerels, marlins, dolphins, whales, sharks)



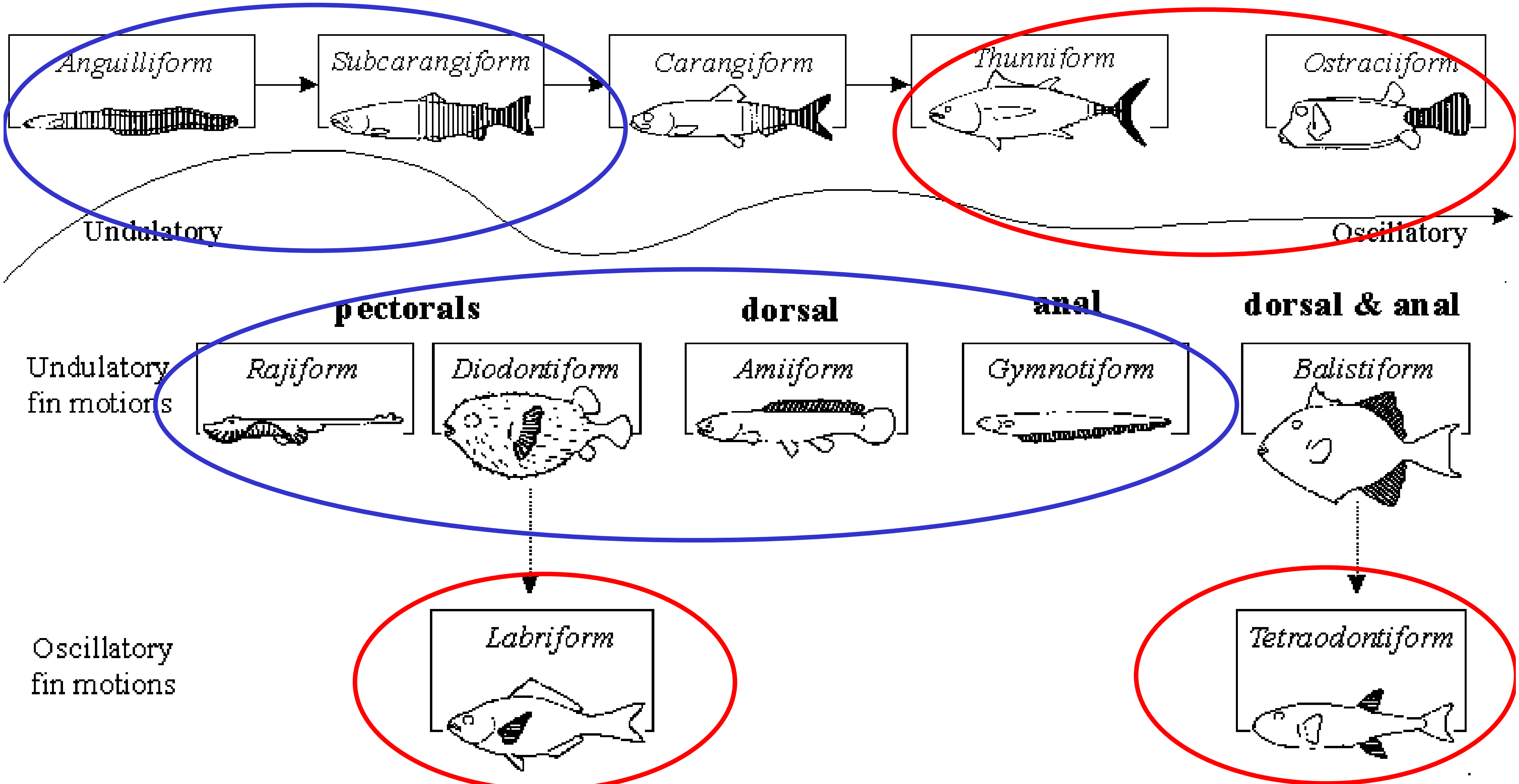
Fish swimming - median/paired fin propulsion



Fin movements are often complex



Lift often dominates forces produced by oscillatory motions - fluid is accelerated backwards over hydrofoil



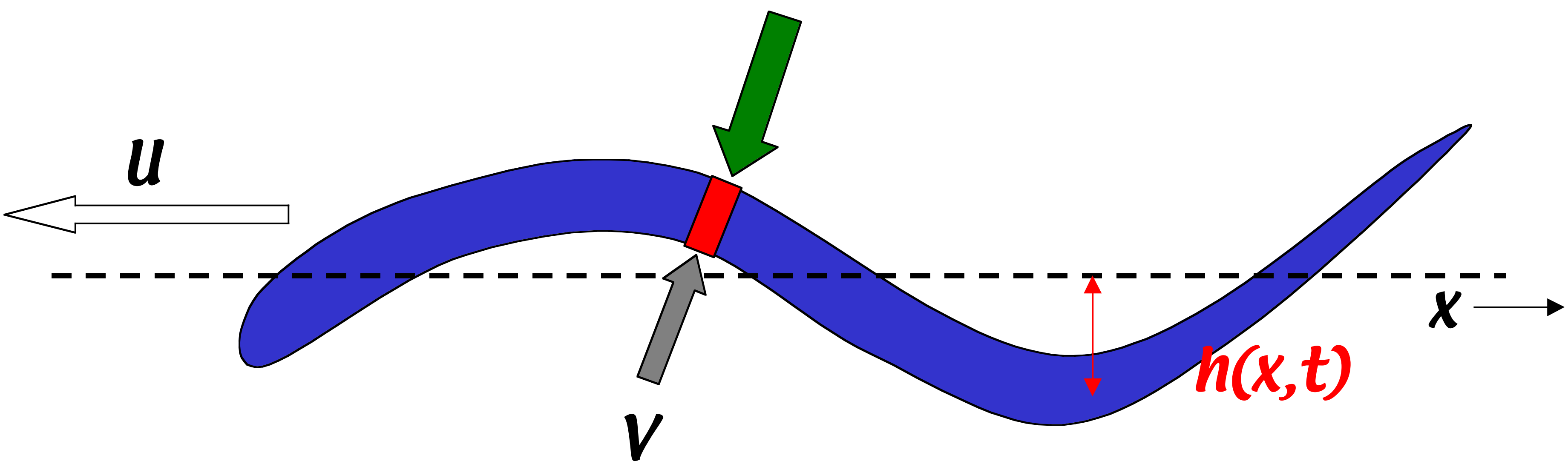
Undulatory motions pass momentum backwards with each wave - one vortex on each side per full wave is shed into the wake

Forces produced by undulatory motions can be calculated by adding the lateral forces produced by each individual segment

Lateral force per unit length

$V = dh/dt + u\, dh/dx$

$T = d(m'V)/dt + U\, d(m'V)/dx$



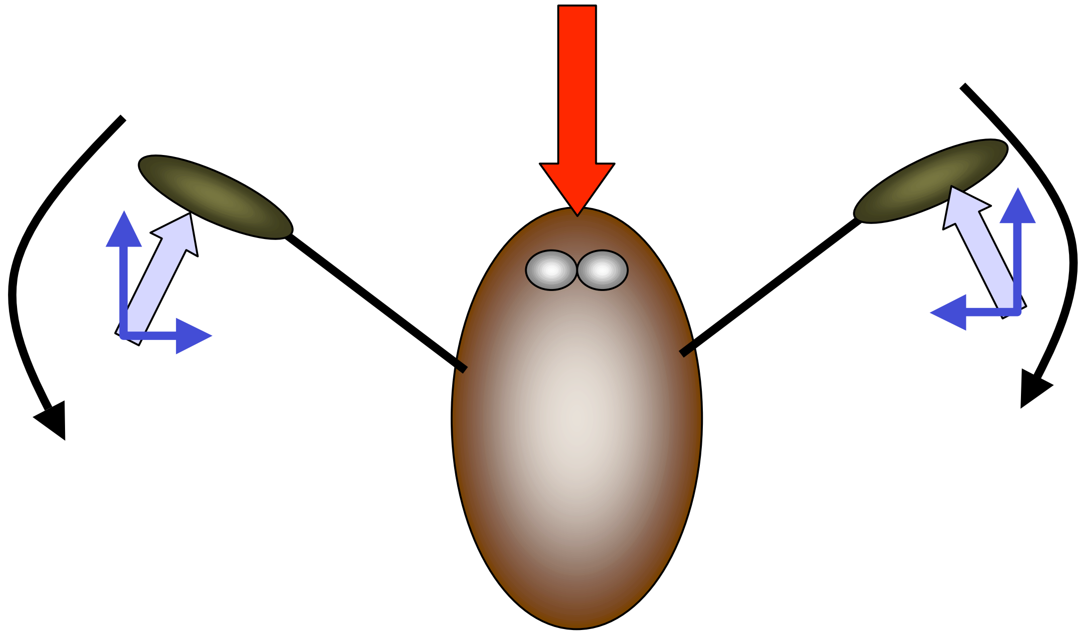
Lighthill's slender body theory:

Thrust = $m'(V^2/2 - V\, dh/dt)$ at the tail

Biology 427
Lecture 23. Life at Low Reynolds Numbers

- Recap High Re Number Swimming
- Low Reynolds Number Phenomena
- Ciliary locomotion
- Dilemmas about force generation
- Regulation of cilia and flagella

Balance of forces (thrust and "drag")for a swimmer!



$$Thrust = C_D \rho\ S\ u^2/2 + \text{“something else”}$$
$$= C_D \rho\ S\ u^2/2 + \alpha \rho\ V\ du/dt$$
$$\text{“Drag”} = C_{Dbody} \rho\ S_{body}\ u_{body}{}^2/2 + \alpha_{body} \rho\ V_{body}\ du_{body}/dt$$

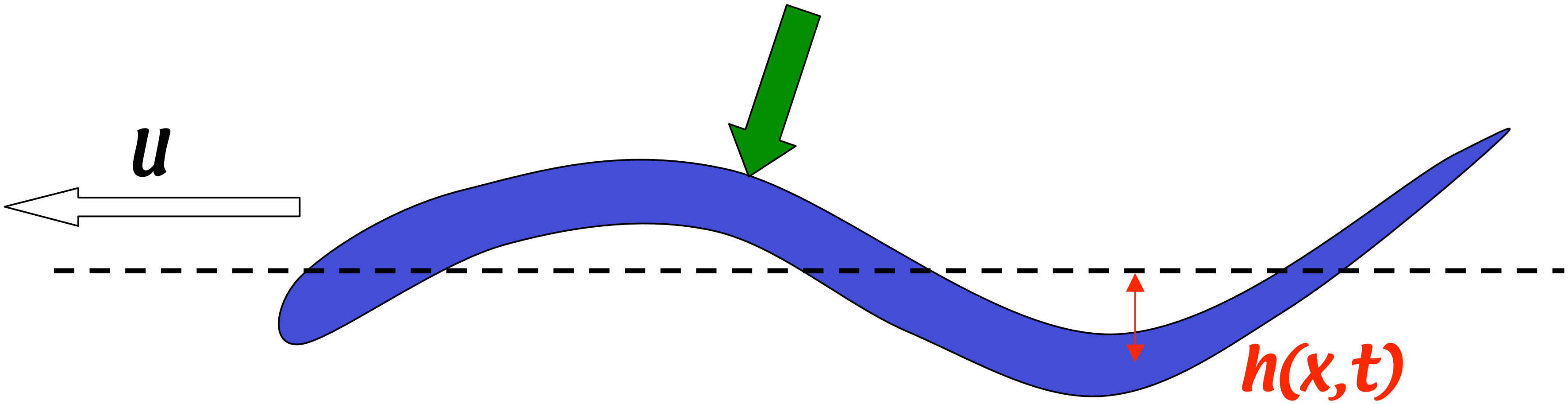
$$Thrust = Drag$$

More complicated for anquilliform swimming

Lateral force per unit length

$V = dh/dt + u\, dh/dx$

$T = d(m'V)/dt + U\, d(m'V)/dx$



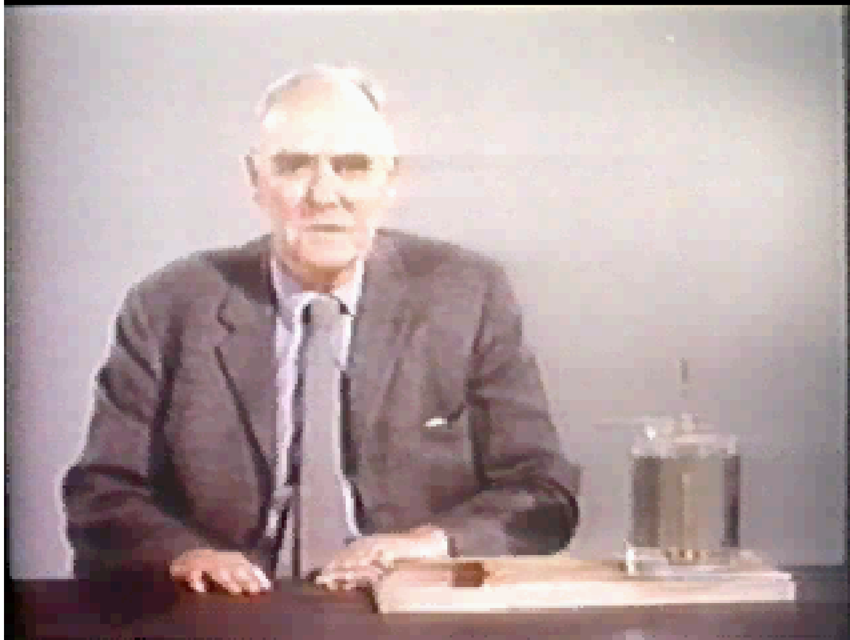
Lighthill's slender body theory:

Thrust = $m'(V^2/2 - V\, dh/dt)$ at the tail!

a demonstration

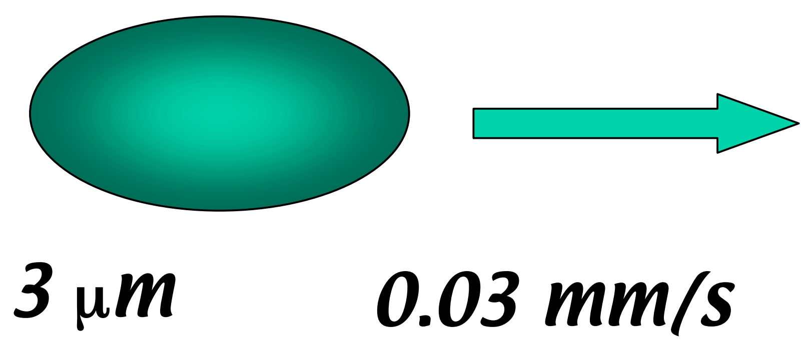
a small reading from Vogel

A reading and some movies



E. coli: how far does this glide?

$$m\, du/dt = -6 \pi R \mu u$$



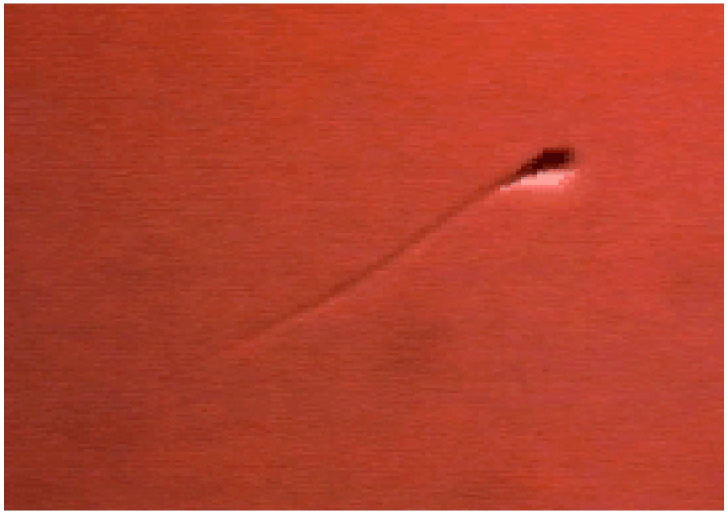
Swimming at Low Reynolds numbers (<1)

Phenomenological issues:

- flow is reversible
- flow equations are linear
- inertia is negligible
- disturbances are manefest over huge relative distances.
- boundaries are all important
- shape matters considerably less

A sphere:

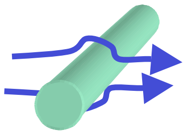
	Low Re	High Re
$C_D =$	$24/Re$	0.1
$D =$	$6 \pi r \mu U$	$0.1 \quad 0.5 \rho \pi r^2 U^2$



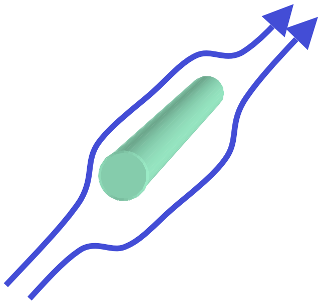
Two important questions:

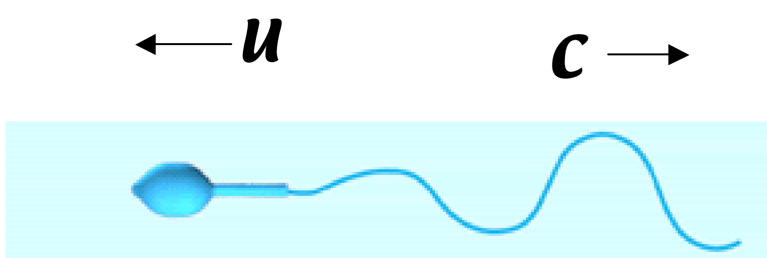
- What are the cellular mechanisms that generate force?
- What are the fluid dynamic mechanisms that propel the animal?

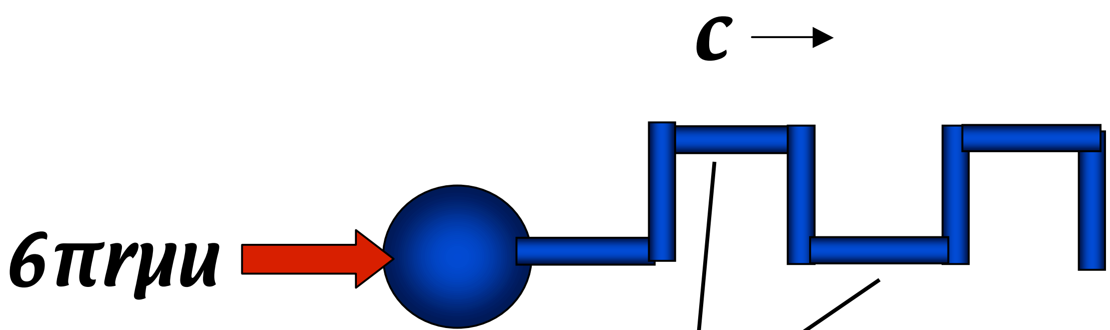
$$D = \frac{4 \pi \mu U l}{\ln(l/a) + 0.193}$$



$$D = \frac{2 \pi \mu U l}{\ln(l/a) - 0.897}$$



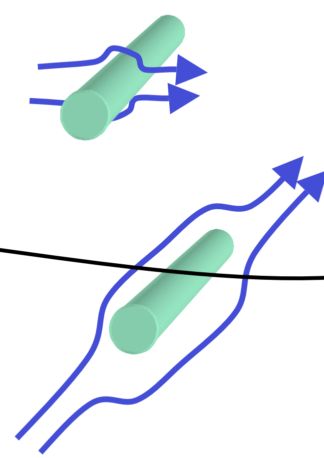




$$U = u - c$$

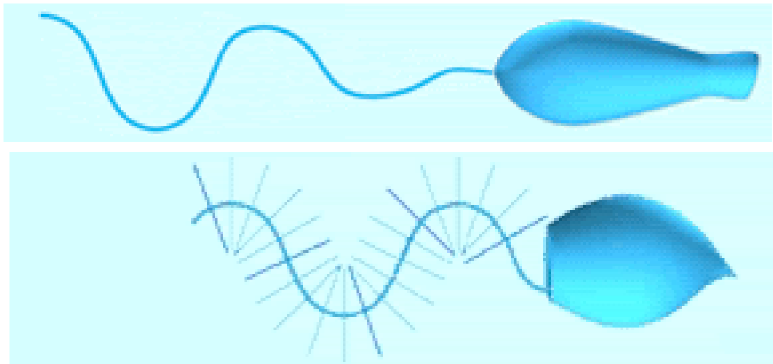
$$D = \frac{4\,\pi\,\mu\,U\,l}{\ln(l/a) + 0.193}$$

$$D = \frac{2\,\pi\,\mu\,U\,l}{\ln(l/a) - 0.897}$$



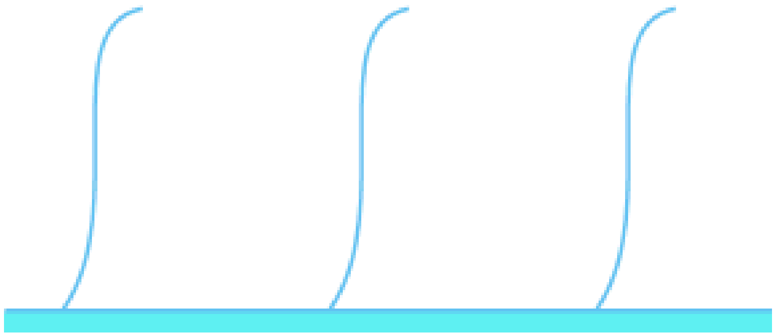
Total Rate of Work?

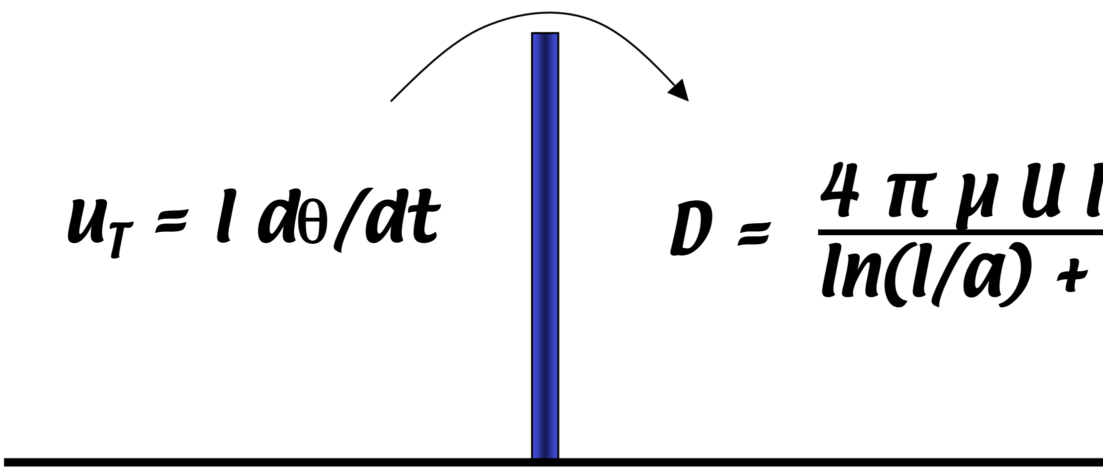
$$W = 6\pi r \mu u^2$$



mastigonemes

parapodia



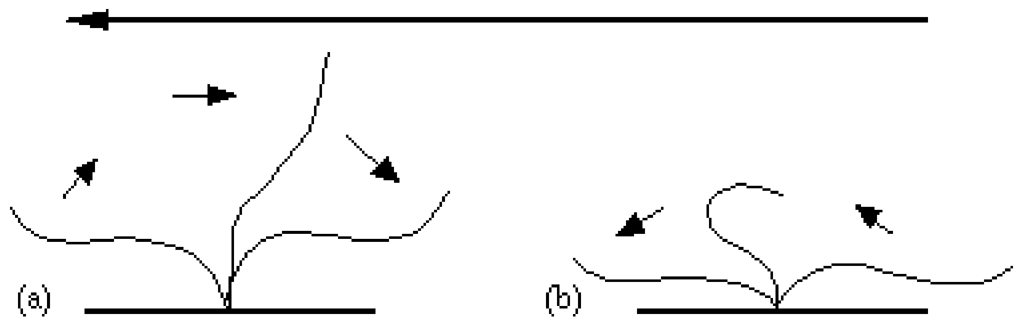


$$u_T = l \, d\theta/dt$$

$$D = \frac{4 \pi \mu U l}{\ln(l/a) + 0.193}$$

Problems:

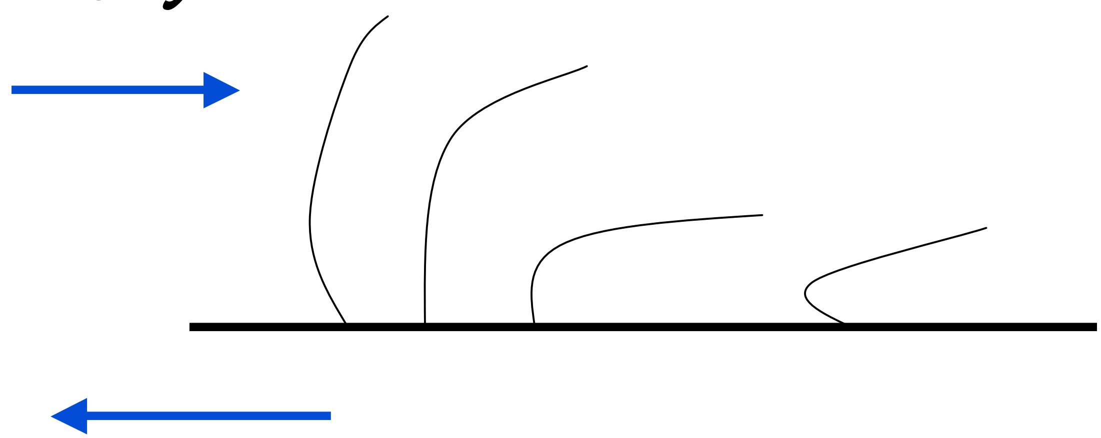
- boundaries
- density of cilia
- mucus
- and several important regulatory issues



The "oar-like" motion of cilia involves *a power stroke* (a) followed by a *recovery stroke* (b). The large arrow indicates the direction of motion of the cell.

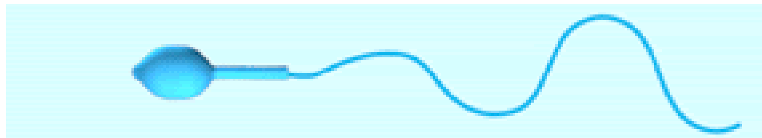
ciliary metachrony

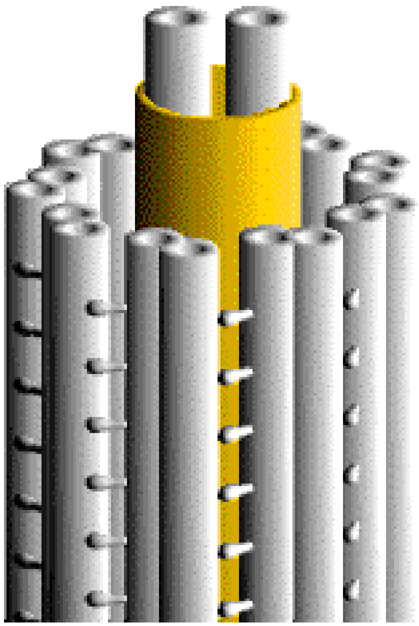
symplectic

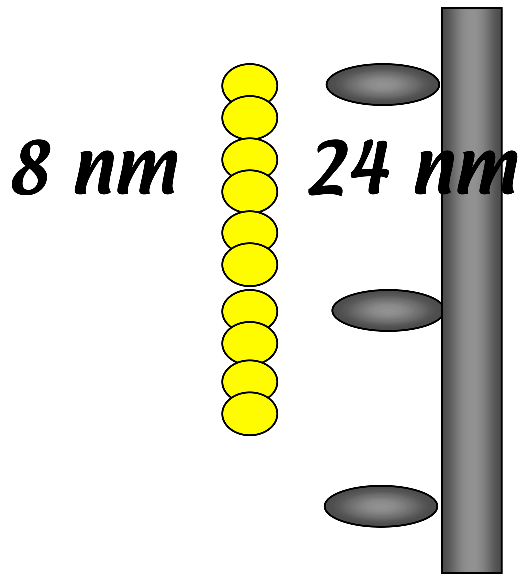


antiplectic

how are waves controlled?







tubulin dimer subunits and dynein motors

Biology 427

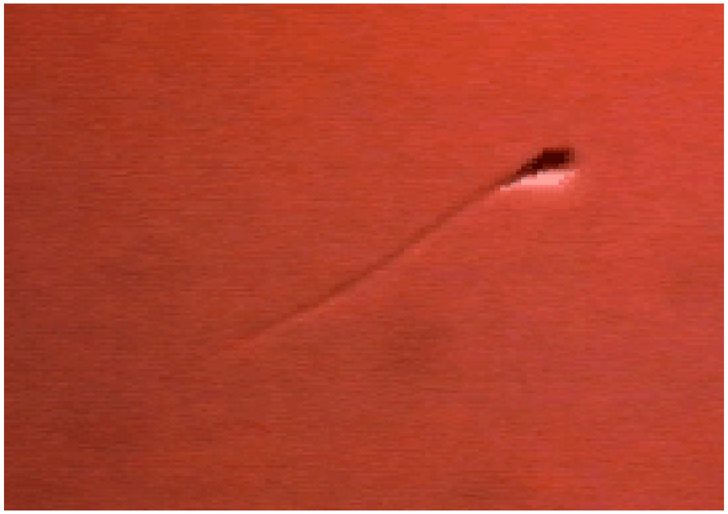
Lecture 24. More Low Reynolds Numbers

- Recap low Reynolds numbers
- Ciliary and flagellar mechanisms
- Fluid flow governs heat and mass transport
- An example of a low Reynolds number creature

Swimming at Low Reynolds numbers (<1)

Phenomenological issues:

- *flow is reversible*
- *flow equations are linear*
- *inertia is negligible*
- *disturbances are manifest over huge relative distances.*
- *boundaries are all important*
- *shape matters considerably less*



Two important questions:

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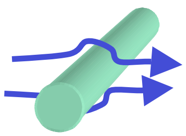
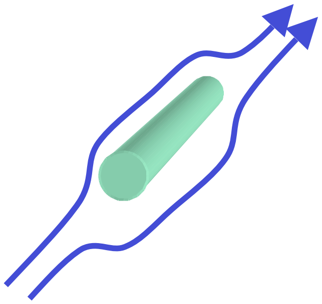
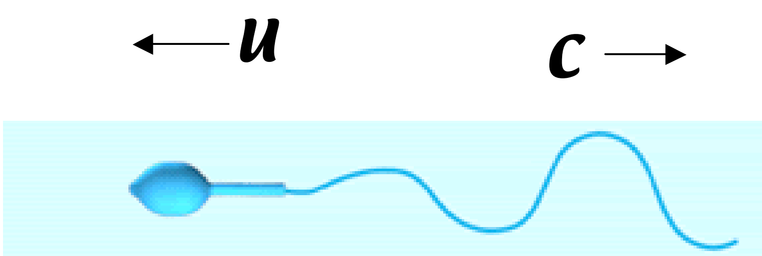
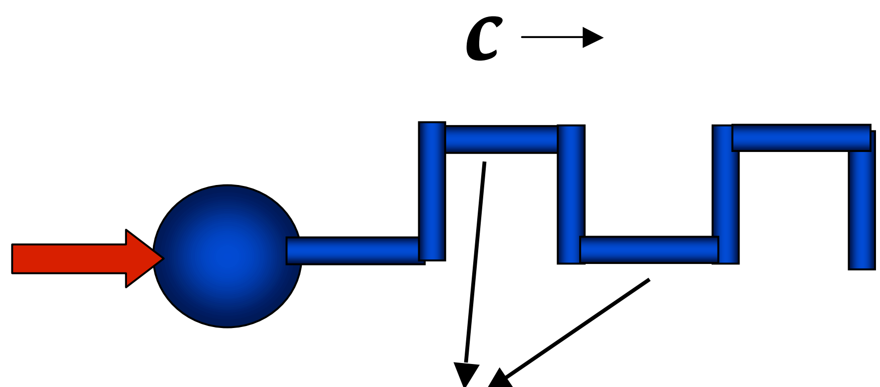
$$D = \frac{4 \pi \mu U l}{\ln(l/a) + 0.193}$$



$$D = \frac{2 \pi \mu U l}{\ln(l/a) - 0.897}$$





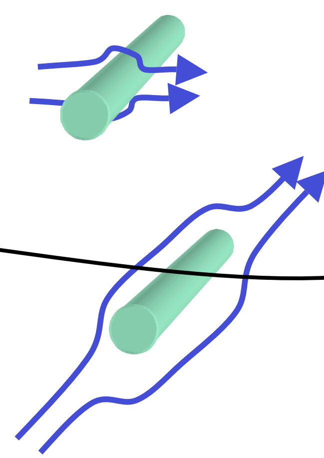


$6\pi r\mu u$

$U = u - c$

$$D = \frac{4\,\pi\,\mu\,U\,l}{\ln(l/a) + 0.193}$$

$$D = \frac{2\,\pi\,\mu\,U\,l}{\ln(l/a) - 0.897}$$



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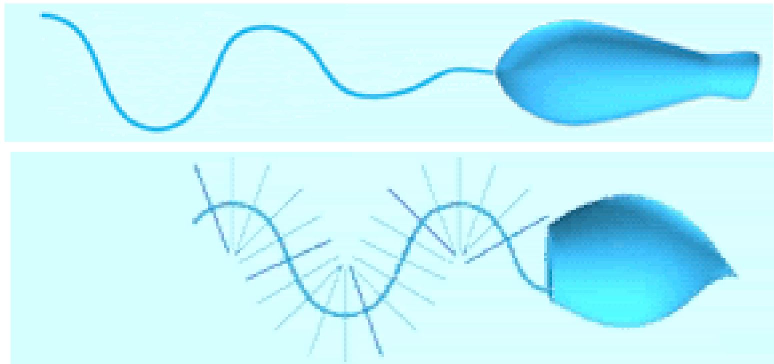
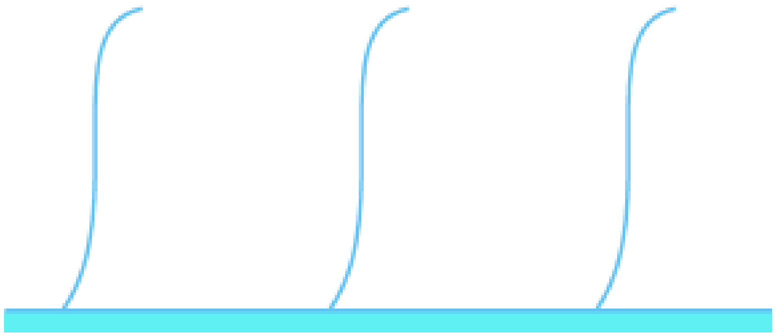
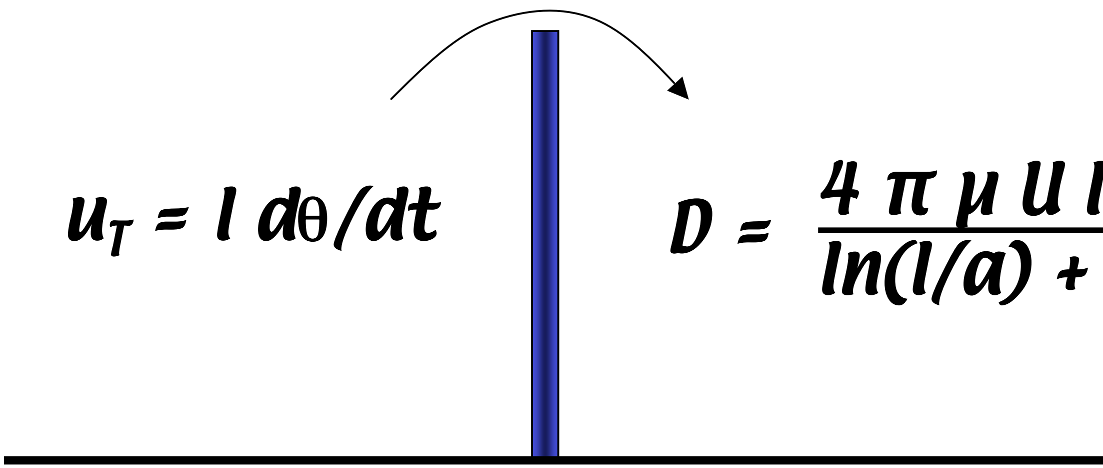


mastigonemes

parapodia





$$u_T = l\, d\theta/dt$$

$$D = \frac{4 \pi \mu U l}{\ln(l/a) + 0.193}$$

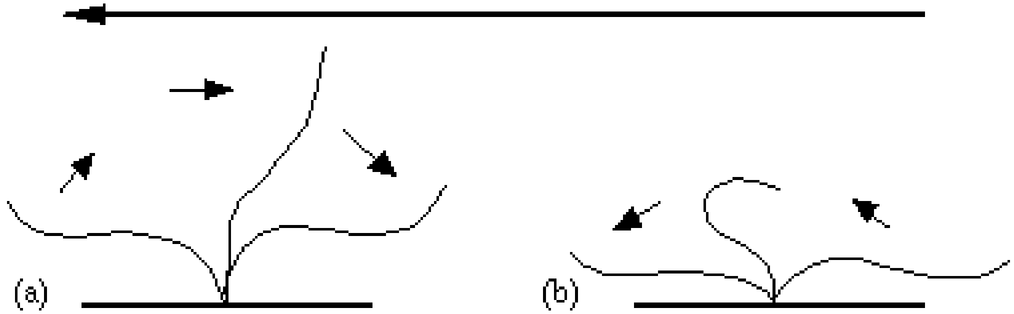
Problems:

boundaries

density of cilia

mucus

and several important regulatory issues



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ciliary metachrony

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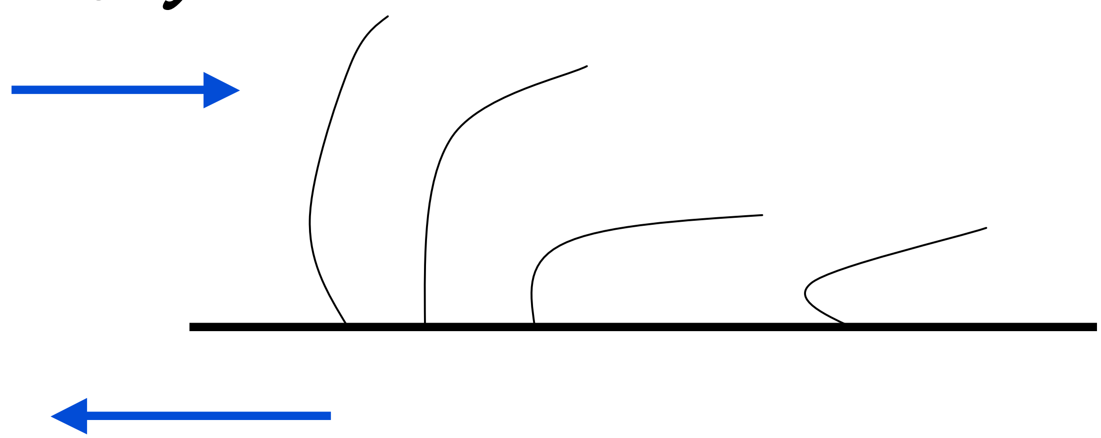
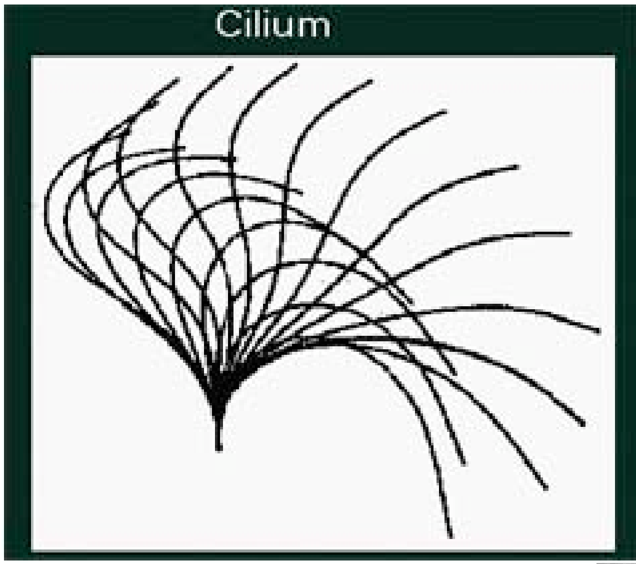
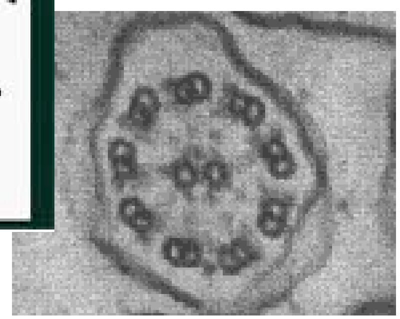


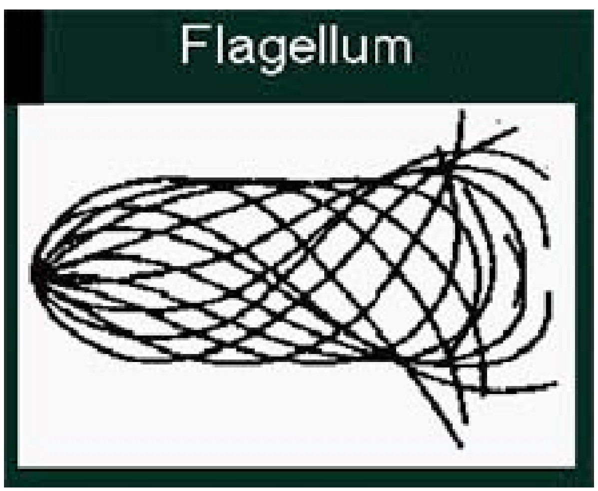
antiplectic

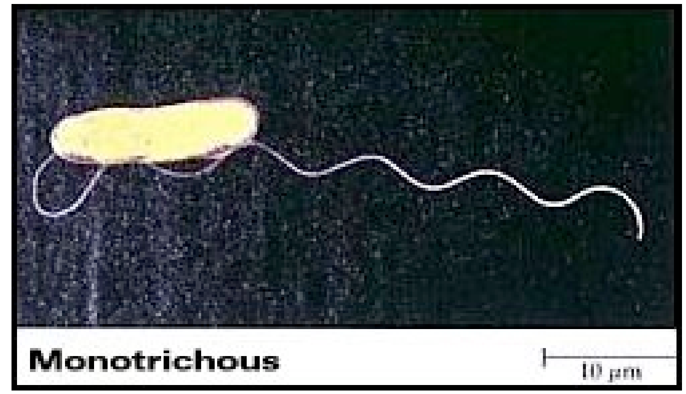
Laeoplectic and dexioplectic

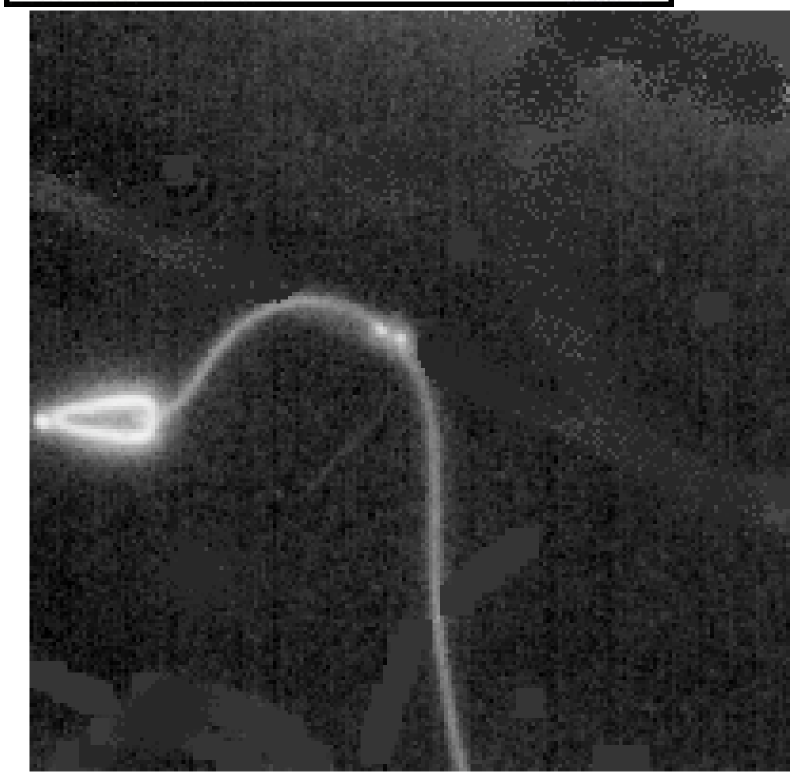
http://www.cco.caltech.edu/~brokawc/Demo1/BeadExpt.html

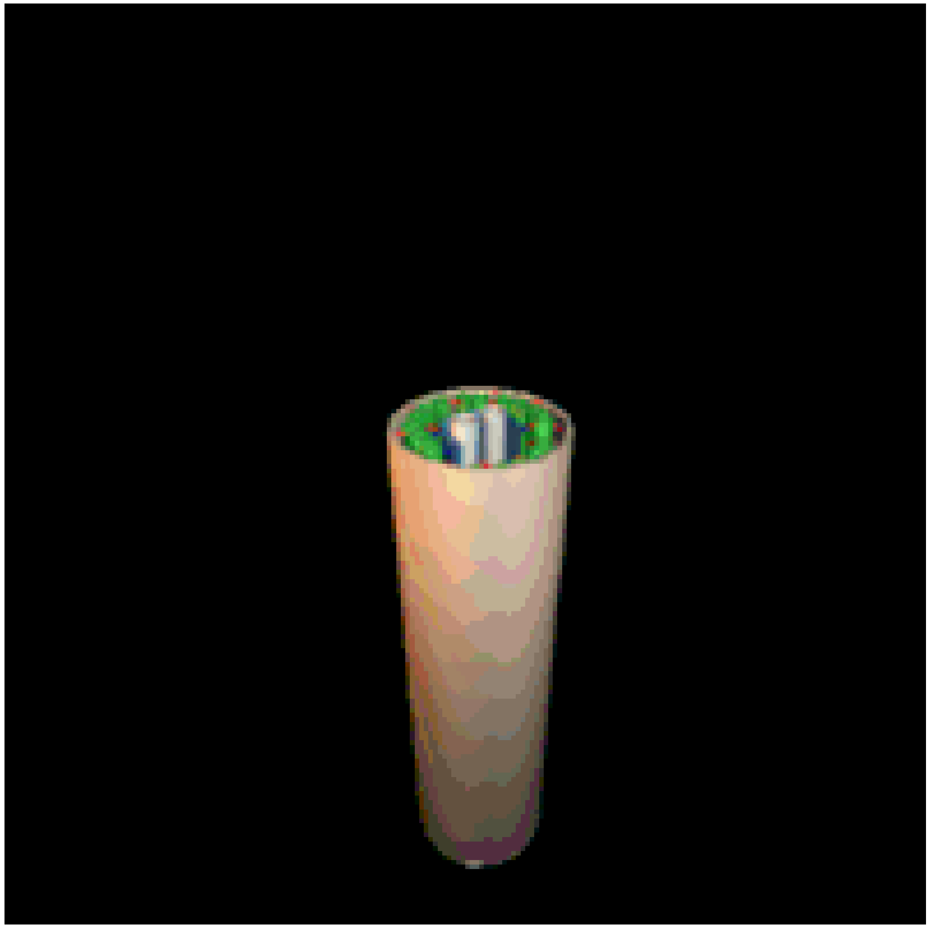




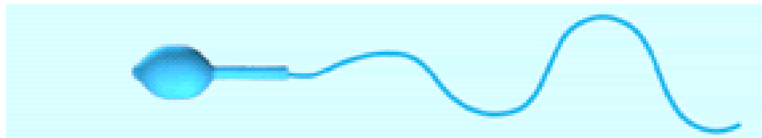


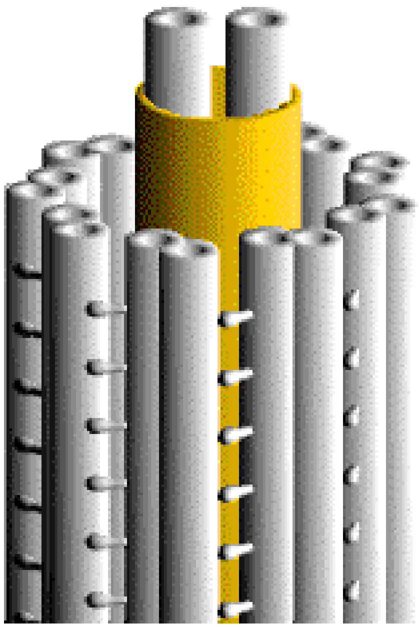


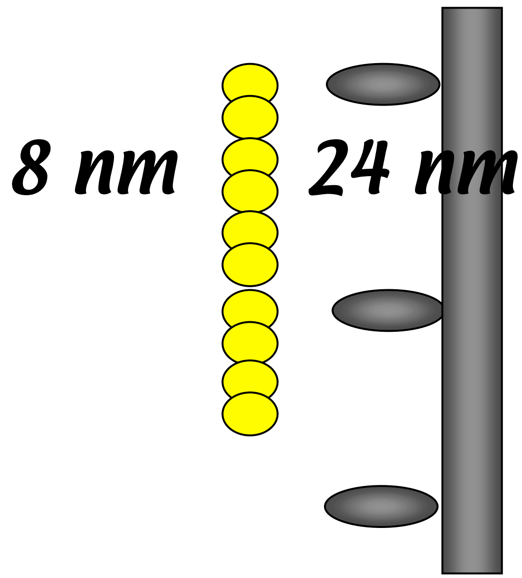


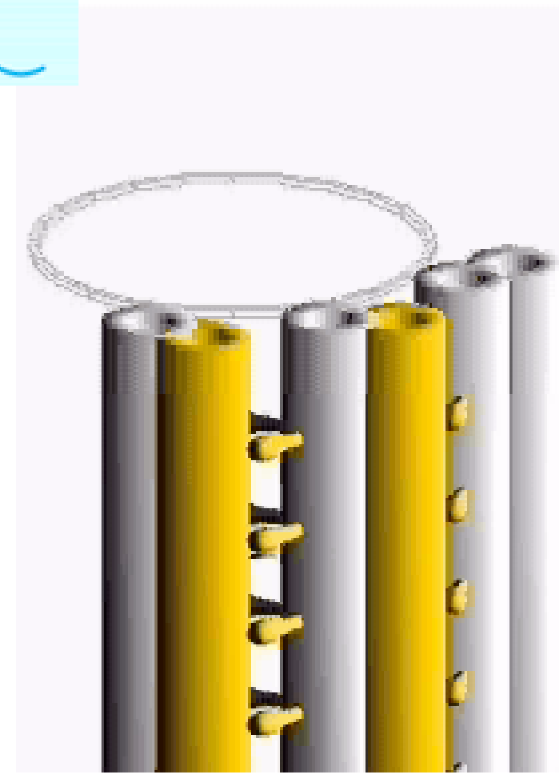


how are waves controlled?









tubulin dimer subunits and dynein motors

If you were unicellular, why would you swim?

Good

- Gets to new places for food
- Gets out of oxygen poor regions
- Avoids chemosensing predators
- Finds mates (sperm and egg)

Bad

- Movement requires energy $(6\pi r \mu U)U$
- signals mechanosensing predators
- May leave nice regions.

Flux of nutrients or gases

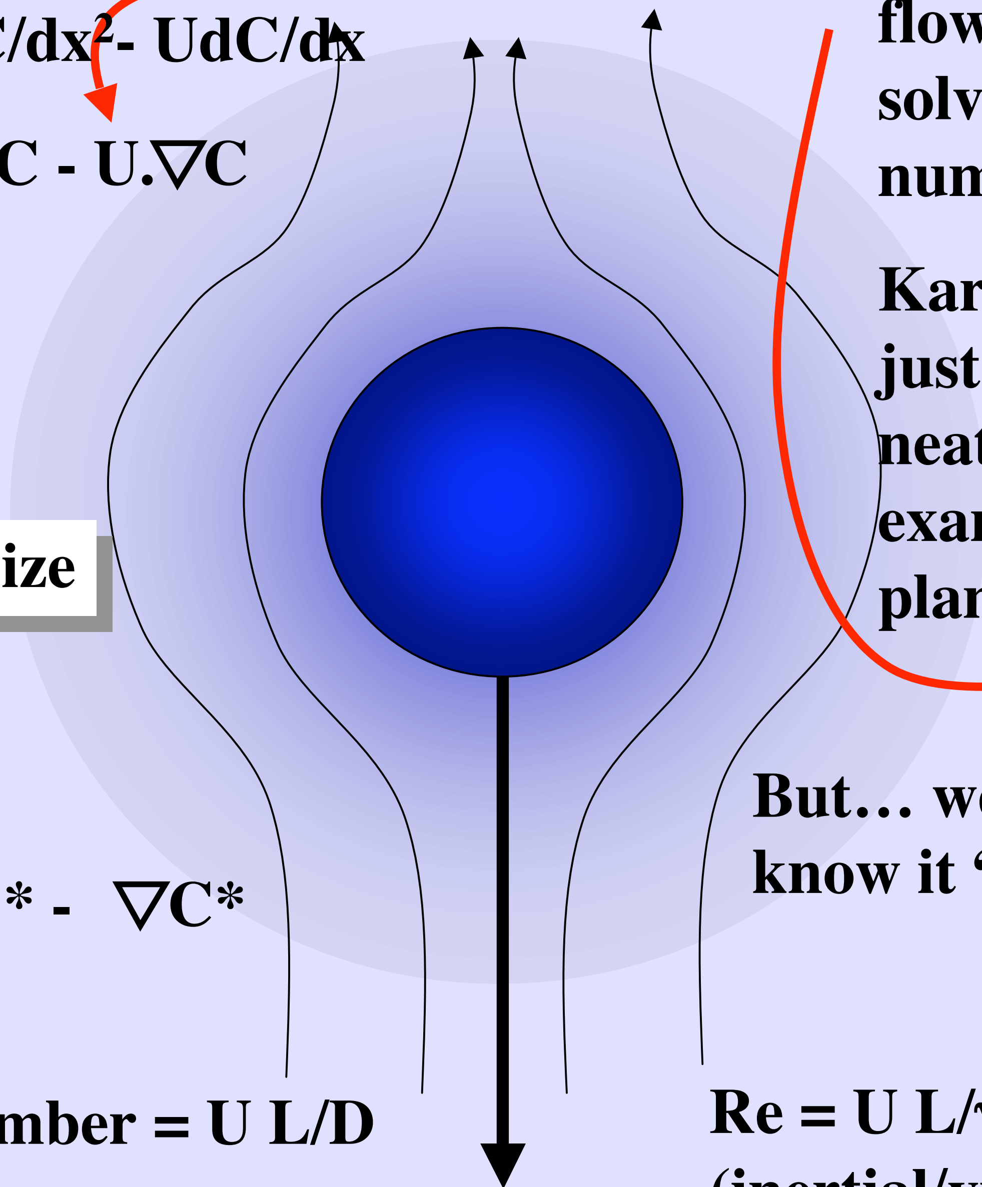
$\partial C/\partial t = D\, d^2C/dx^2 - U dC/dx$

$\partial C/\partial t = D\nabla^2 C - U.\nabla C$

nondimensionalize

$0 = \quad Pe\nabla^2 C^* - \nabla C^*$

Pe = Peclet number = U L/D



If you know the flow field, you could solve this numerically….

Karp et al (1996 did just that for some neat spherical examples. (passive plankton)

But… we don't always know it "easily"

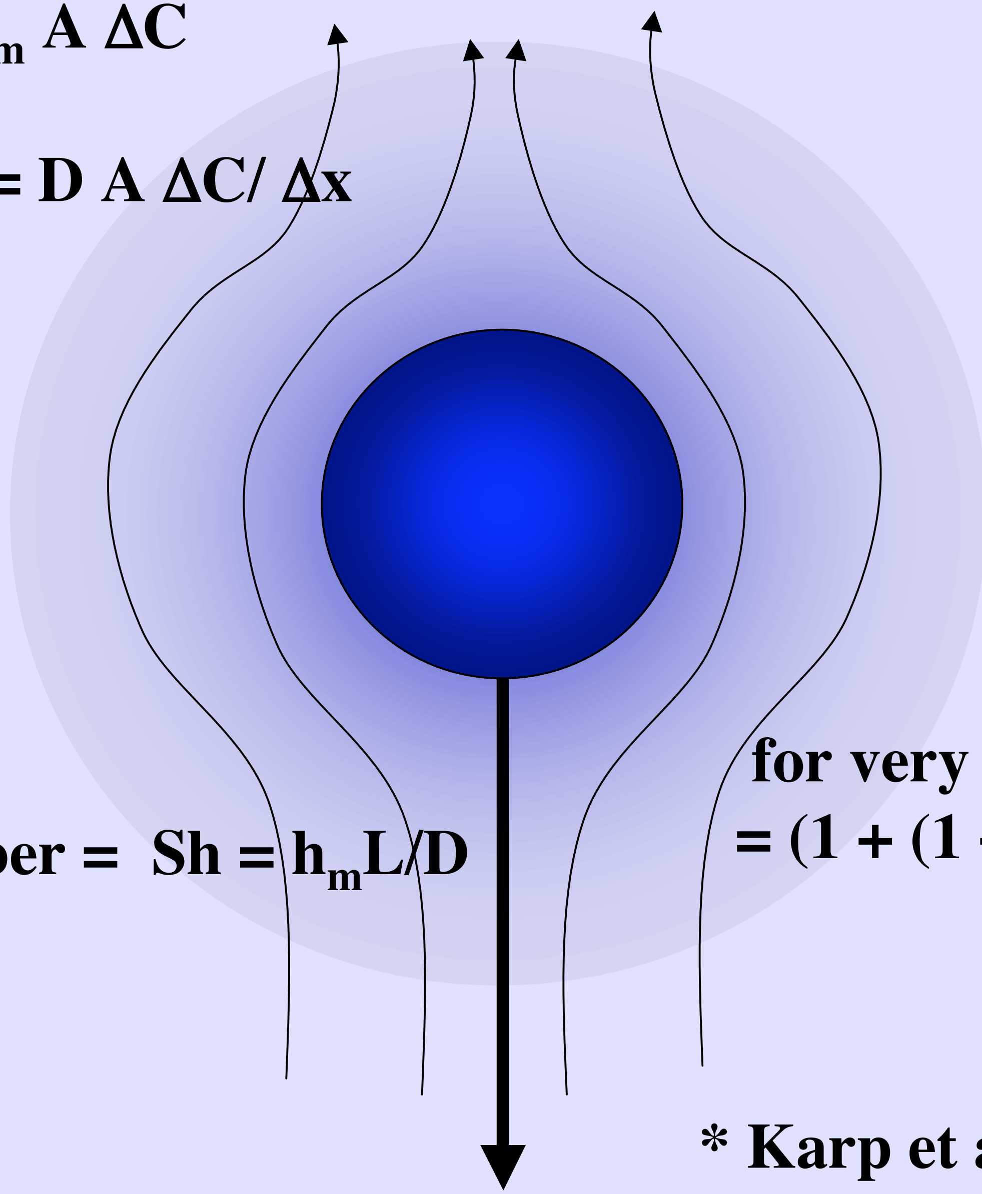
$Re = U L/\nu$

(inertial/viscous stresses)

The total flux is some amalgam of advective and diffusive fluxes

Total Flux $= h_m \, A \, \Delta C$

Diffusive Flux $= D \, A \, \Delta C / \Delta x$



Sherwood Number $= Sh = h_m L/D$

for very low Re*
$= (1 + (1 + 2\,Pe)^{1/3})/2$

*** Karp et al. 1996;**
Clift et al. 1978

Why swim?
Balance of oxygen gains and losses

Total flux of O_2

$$O_{2in} = h_m \, A \, \Delta C$$
$$= Sh \, D \, A \, \Delta C/R$$
$$= (1 + (1 + 2\,Pe)^{1/3}) \, D \, A \, \Delta C/2L$$

$$Pe = UL/D$$

great for eggs, plankton sinking ….

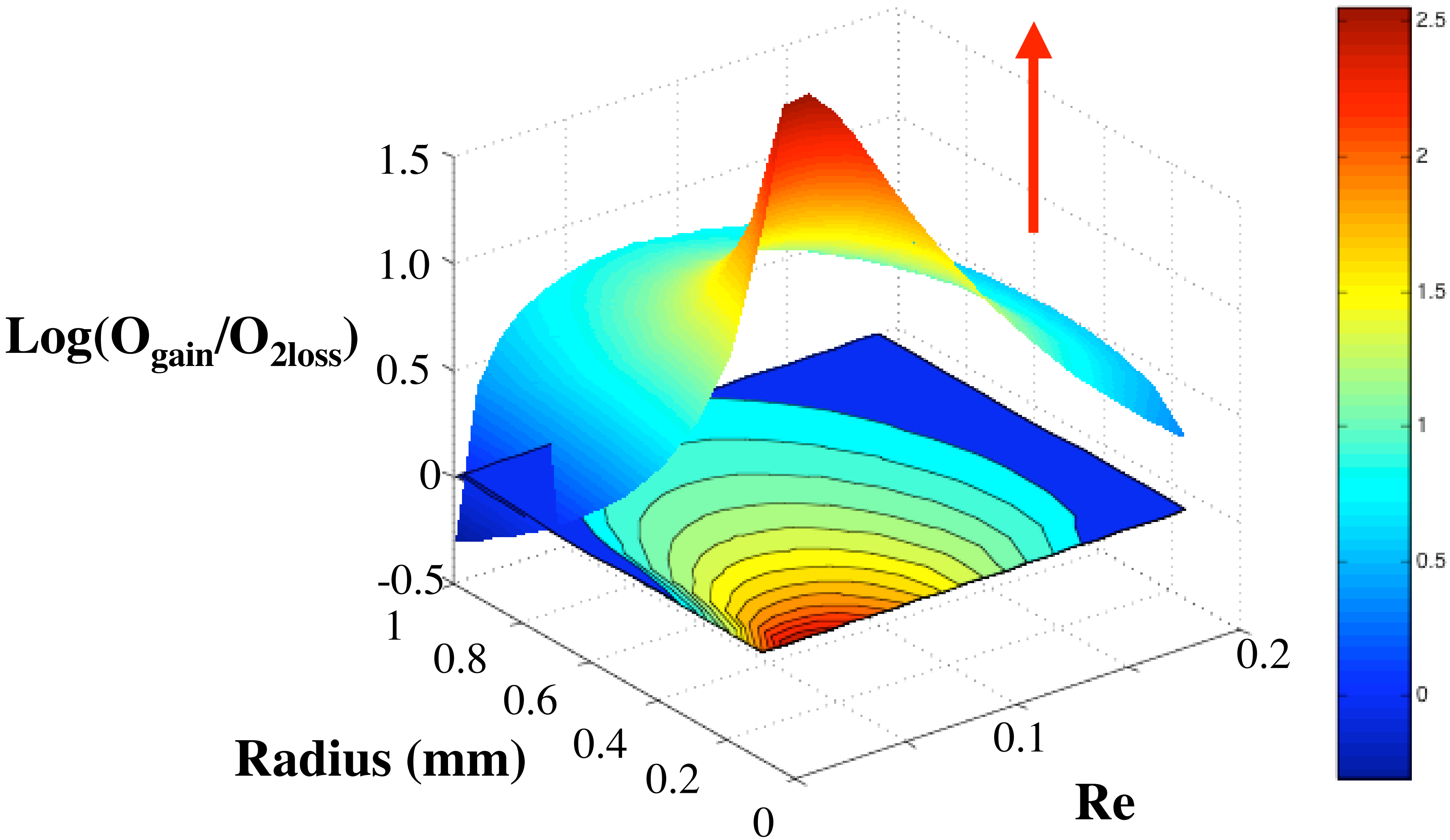
But

$$O_{2out} = \text{Drag } U + \text{metabolism} \quad = 6\,\pi\,\mu\,R\,U^2/\eta + k\,r^{3b}$$

$$O_2\text{ratio} = \frac{(1 + (1 + 2\,Pe)^{1/3}) \, D \, A \, \Delta C/2L}{6\,\pi\,\mu\,R\,U^2 + k\,r^{3b}}$$

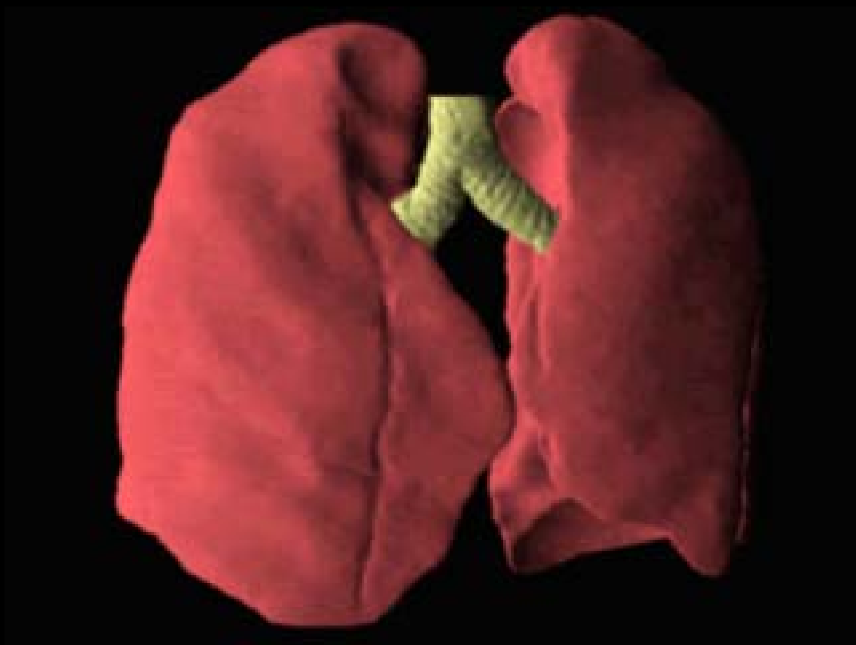
if > 1 ….

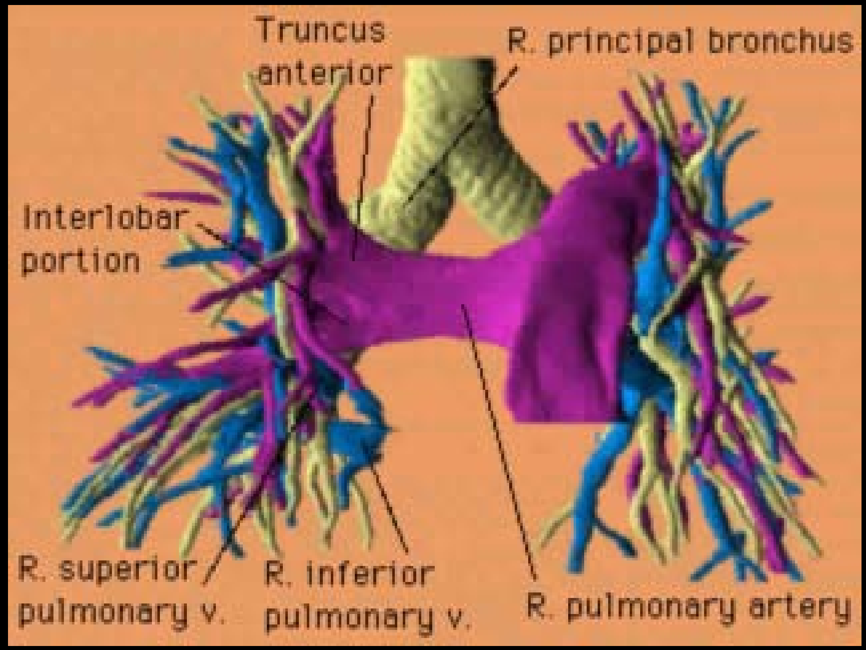
Not a bad idea to swim when small and slow



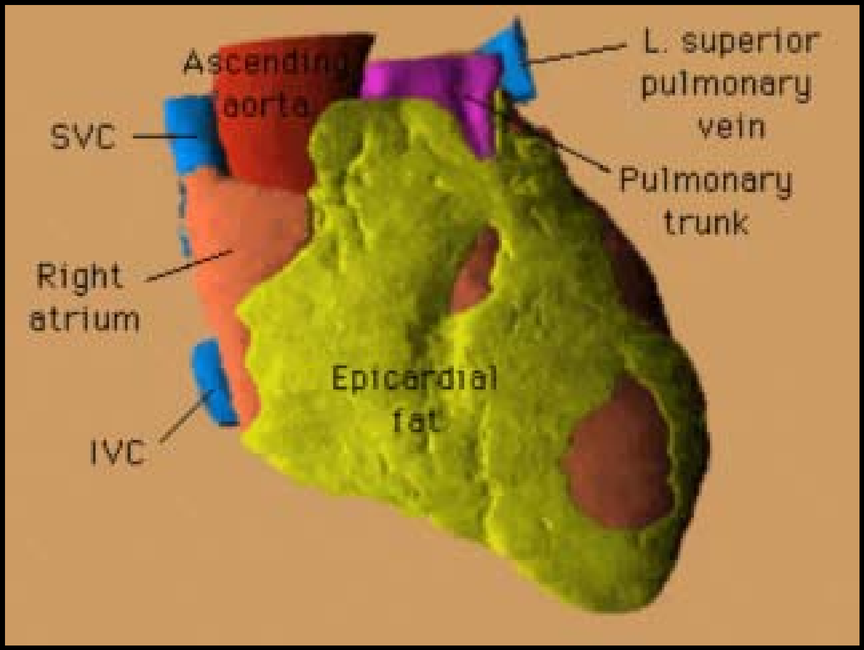
Biology 427 Biomechanics 2004
Lecture 25. Internal biofluiddynamics: vessel flows.

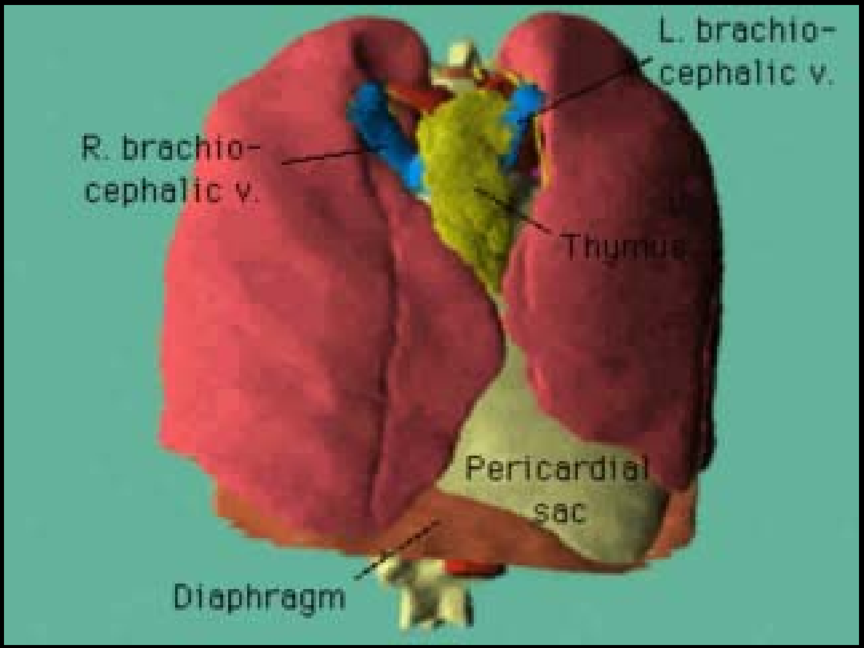
- Basic rules for biological plumbing: velocity profiles in tubes
- Volumetric flow rate and the Hagen-Poiseuille law
- Increasing surface area for diffusive processes
- Shear stress and aortic dissection
- Turbulent flow in biological vessels
- Collapsible tubes and the jugular vein of the giraffe





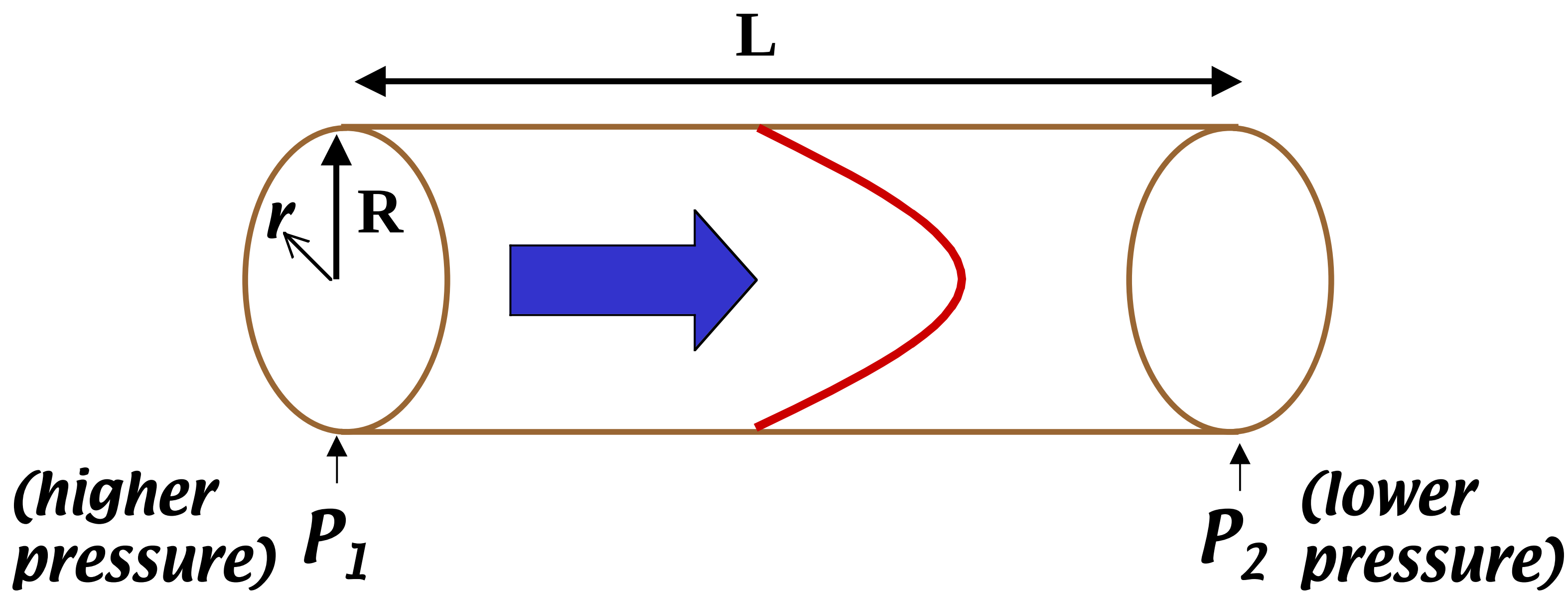
Digital Anatomist Interactive Atlas
http://www9.biostr.washington.edu/da.html





Digital Anatomist Interactive Atlas
http://www9.biostr.washington.edu/da.html

Rigid circular vessel of constant radius a



Steady flow: $u(r)$ = const, $du/dt = 0$

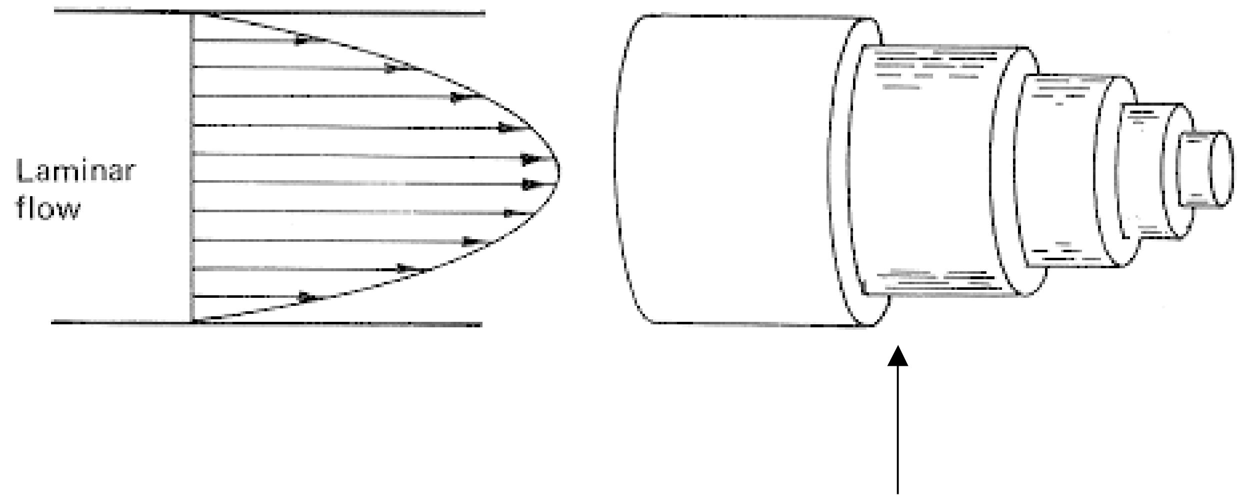
Pressure gradient along length: $\Delta P/L$ (dP/dx) $\Delta P = P_1 - P_2$

Newtonian flow : $\tau = \mu \, du/dr$ $(0 \leq r \leq R)$

No slip condition: $u(r) = 0$ at $r = R$

Where is the flow maximum?
Centerline of tube
What is the velocity profile?
Parabolic

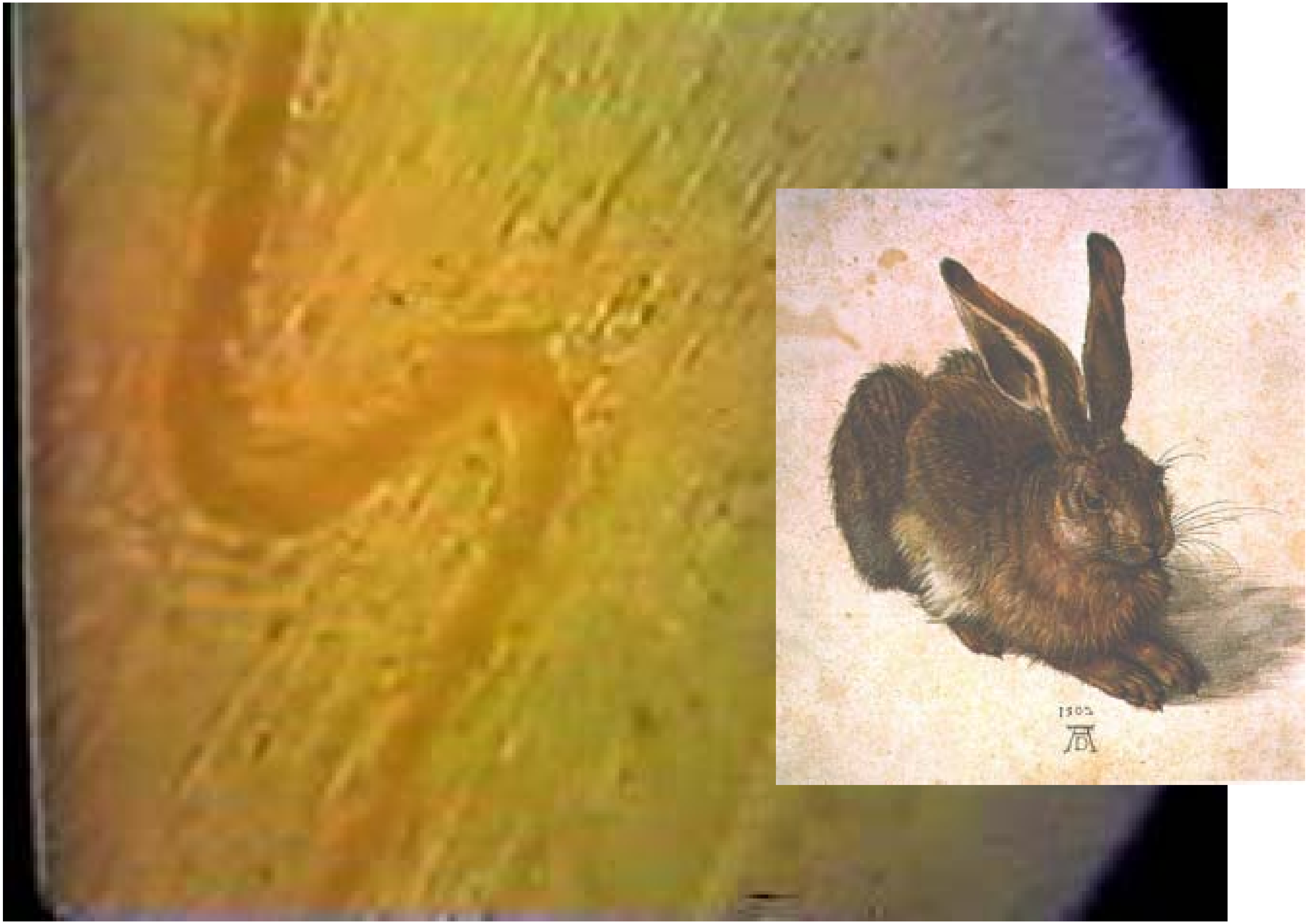
Parabolic profile of laminar flow in a rigid tube



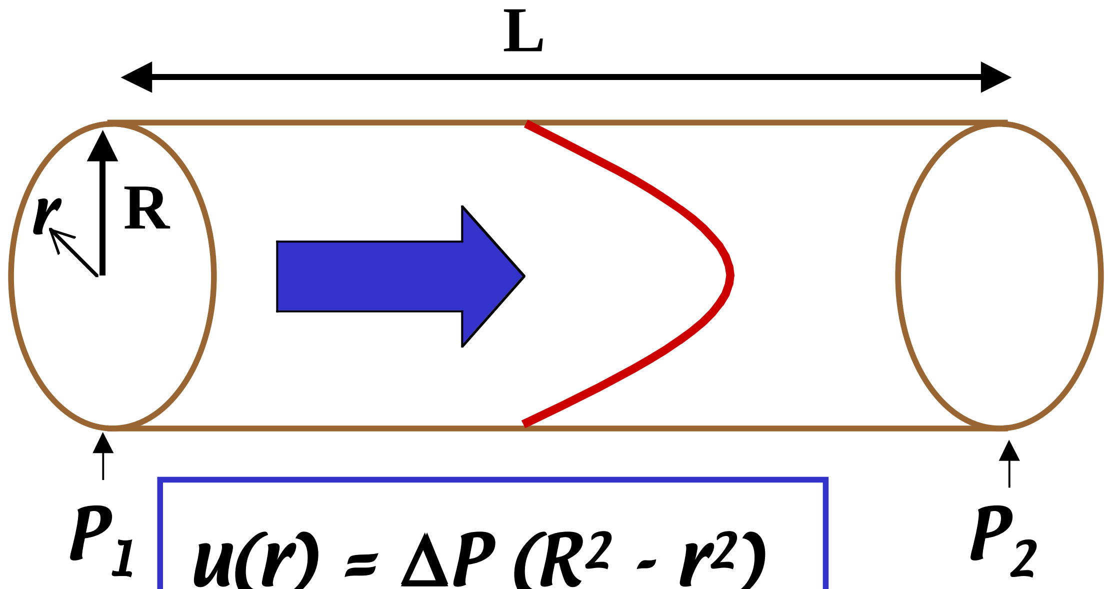
concentric layers (laminae) of fluid slip past one another, with the more central layers moving faster that the layers near the walls

Laminar flow in blood vessels of a rabbit's ear....

Laminar flow in blood vessels of a rabbit's ear....



What is the velocity of fluid flow through the tube?



What is the overall flow per time through the tube?

$$u(r) = \frac{\Delta P}{L} \frac{(R^2 - r^2)}{4\mu}$$

Volume flow rate (volume/time) = u*area

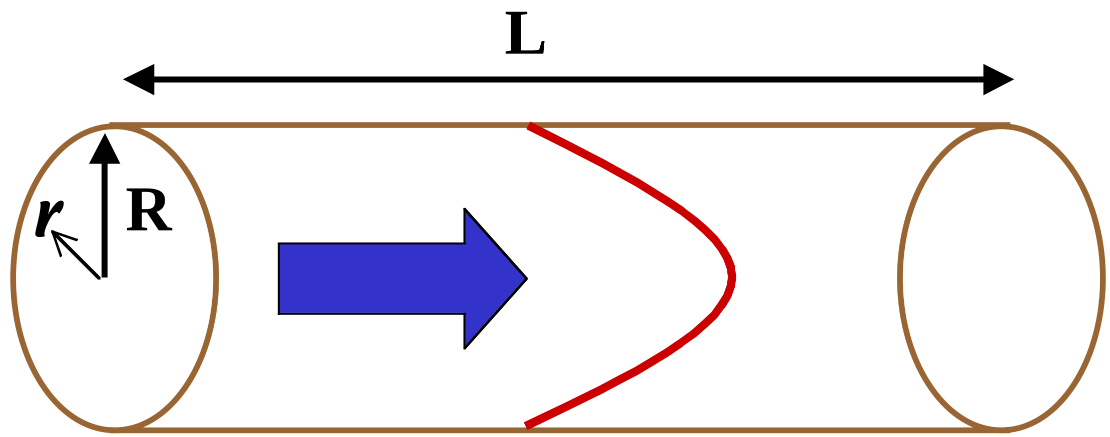
$Q = 2\pi \int u(r)\, r\, dr$ velocity of each layer ($u(r)\, 2\pi r$), integrate over all layers

$$Q = \frac{\Delta P}{L} \frac{\pi R^4}{8\mu} \; !$$

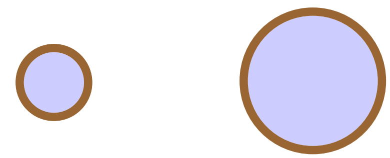
Hagen-Poiseuille law

Why does flow rate increase with radius⁴?

$$Q = \frac{\Delta P}{L} \frac{\pi R^4}{8\mu}$$



L = 1

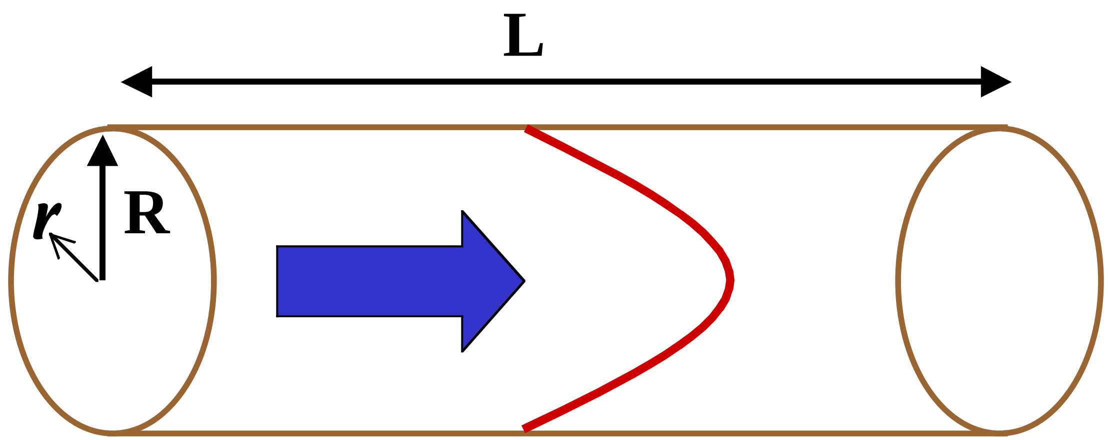


As radius is doubled, cross-sectional area is quadrupled:

Bigger tube also has less wall relative to its volume

radius	3	6
x-s area (πr^2)	28.26	113.04
wall area ($2\pi rL$)	18.84	37.68
volume ($\pi r^2 L$)	28.26	113.04
wall:volume	0.6667	0.333

What is the velocity of fluid flow through the tube?



$$u(r) = \frac{\Delta P}{L}\frac{(R^2 - r^2)}{4\,\mu}$$

$$Q = \frac{\Delta P}{L}\frac{\pi R^4}{8\mu}$$

What is the maximum velocity?

(u(r) with r = 0)

$$u_{max} = \frac{\Delta P}{L}\frac{R^2}{4\,\mu}$$

u_{max} = 2x u_{avg} !

What is the average velocity?

total flow rate/
cross-sectional area:
Q = u*area

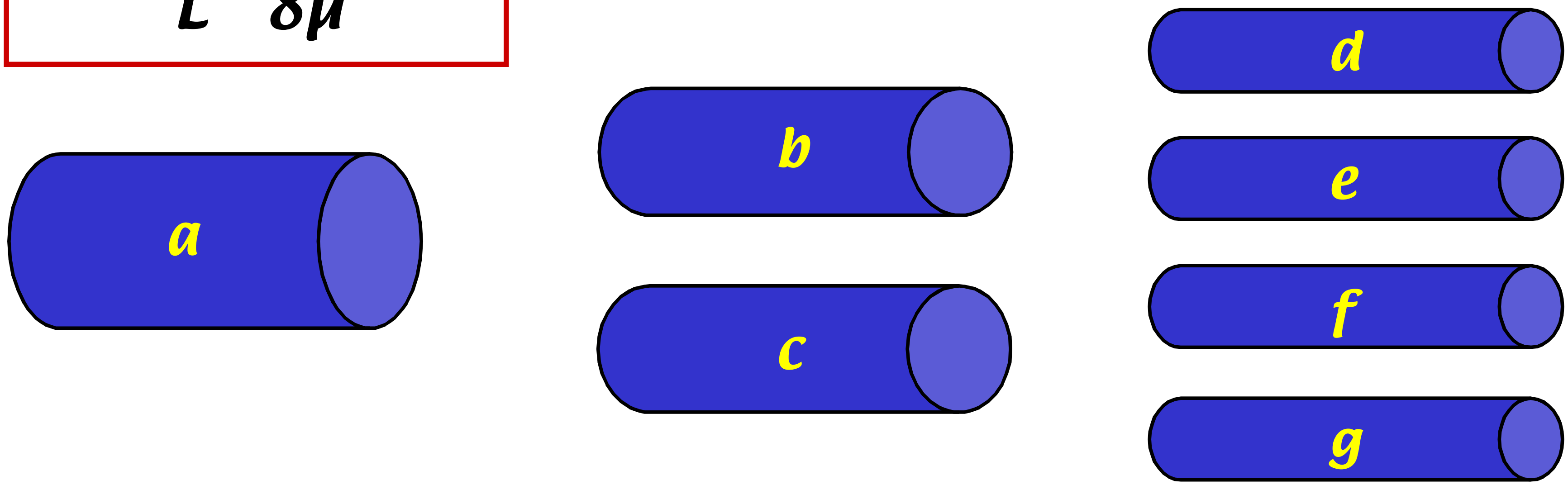
$$u_{avg} = \frac{Q}{\pi R^2} = \frac{\Delta P}{L}\frac{\pi R^4}{8\,\mu} * \frac{1}{\pi R^2} = \frac{\Delta P}{L}\frac{R^2}{8\,\mu}$$

What happens if one large tube is split into several smaller tubes with the same total area?

$$Q = \frac{\Delta P}{L} \frac{\pi R^4}{8\mu}$$

Flow rate is one half!

Flow rate is one quarter!



$R_a = 1$
$area_a = 3.14$

$area_{b+c} = 3.14$
$R_{b,c} = 0.71$

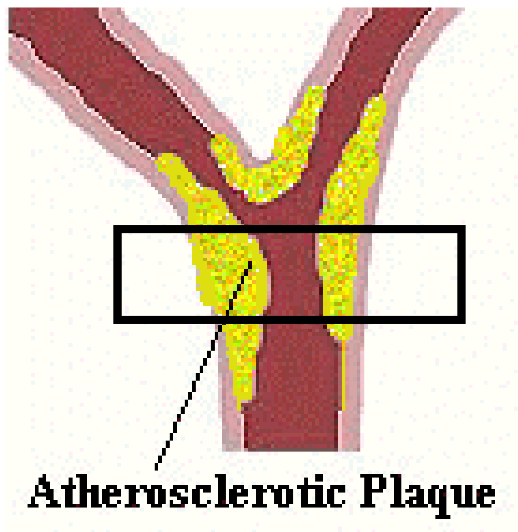
$area_{d+e+f+g} = 3.14$
$R_{d,e,f,g} = 0.50$

$Q_a \propto R^4 \propto 1$

$Q_{b+c} \propto R_b^4 + R_c^4 \propto 0.5$

$Q_{d+e+f+g} \propto R_d^4 + R_e^4 + R_f^4 + R_g^4 \propto 0.25$

What happens if there is a 5% decrease in the radius of a blood vessel?



$$Q = \frac{\Delta P}{L} \frac{\pi R^4}{8\mu}$$

A 22% increase in the pressure for a given flow

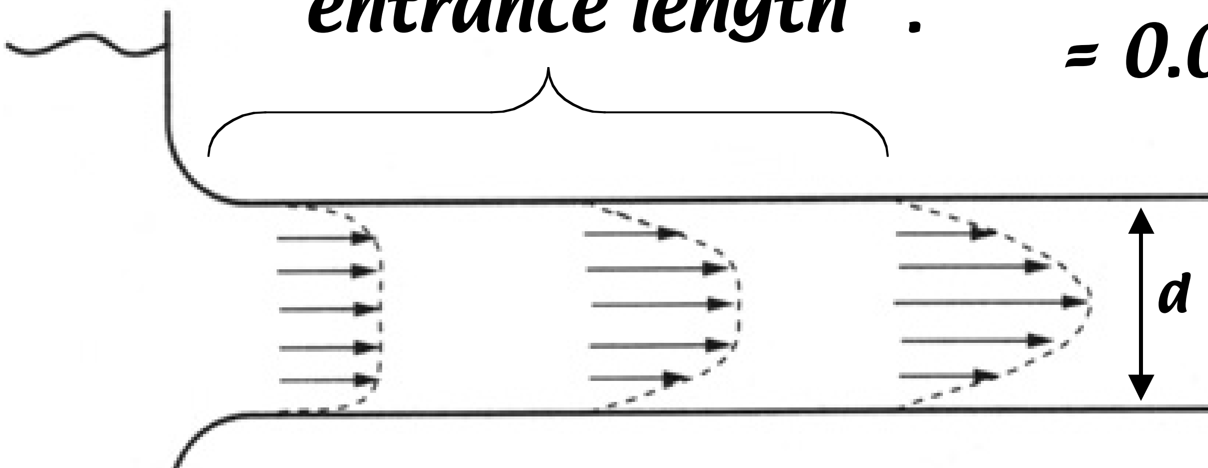
20% decrease in radius: A 59% increase in the pressure for a given flow

50% decrease in radius: A 94% increase in the pressure for a given flow

Laminar flow takes time to develop a parabolic velocity profile

"entrance length" : $l' = 0.058\ d\ Re$

$= 0.058\ \rho u d^2/\mu$



Many animals use short pipes
(i.e. insects that suck nectar, blood etc...)

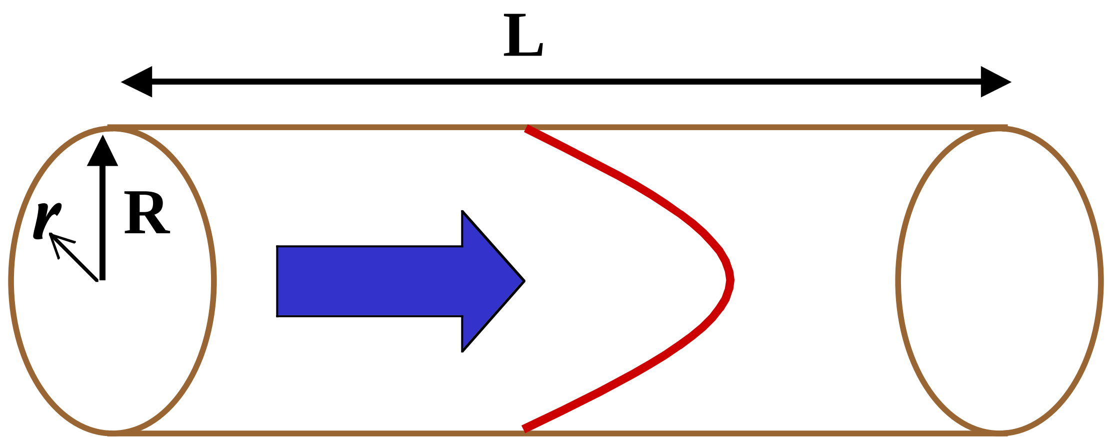
How does entrance length affect flow rate?

correction to Hagen-Poiseuille:
(Loudon and McCulloh, 1999)

$$\frac{Q_{real}}{Q_{calc}} = \frac{(l/l')}{(l/l') + 0.52}$$

- not much for most insects, but may have been important for extinct insects with larger mouthparts

How much power does it take to move fluid through a tube?



$$u(r) = \frac{\Delta P}{L}\frac{(R^2 - r^2)}{4\mu}$$

$$Q = \frac{\Delta P}{L}\frac{\pi R^4}{8\mu}$$

Recall work = F*d

Power = F*u

Flow work = $\Delta P\, dV$

$$\Delta P = \frac{Q\, 8\, \mu\, L}{\pi R^4}$$

Pumping power = $\Delta P\, dV/dt = \Delta P\, Q$

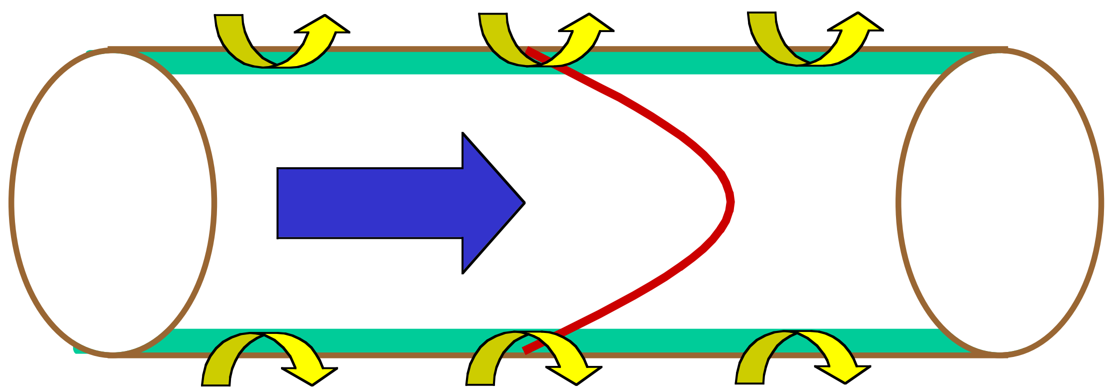
$$= \frac{Q^2\, 8\mu\, L}{\pi R^4}$$

low power: wide tube

high power: high flow rate, viscous fluid, long tube

Large tubes with circular cross-sections and laminar flow are good for some things

- fluid moves faster and costs less to pump.
- uses least wall material per volume
- resists failure better than other shapes



But....
the purpose of most circulatory systems is to exchange heat, respiratory gases, ions, organic molecules, etc....

Diffusion only occurs over short distances
→need to maximize surface contact with fluid

How do animals maximize fluid contact in circulatory systems?

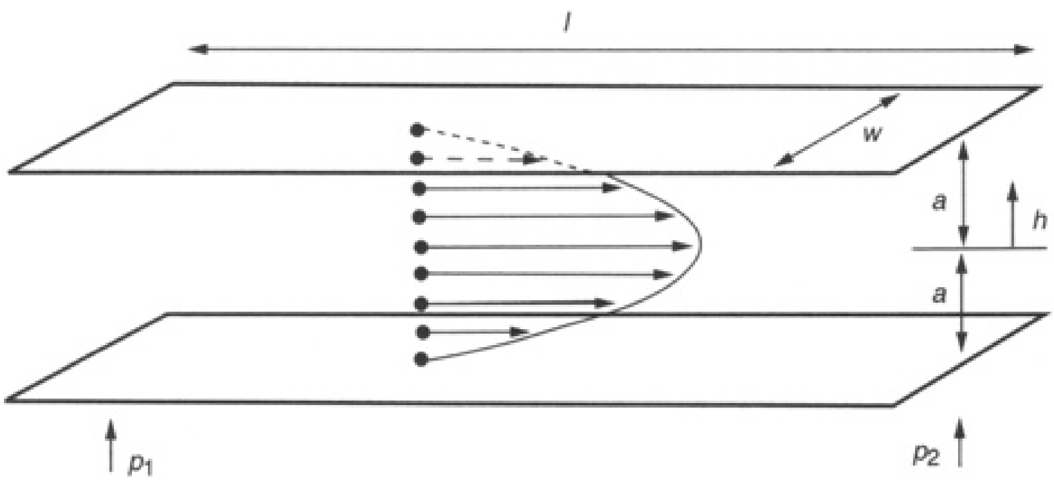
1. Move fluid between plates instead of inside tubes

- Gills of fish, invertebrates
- Book lungs of some spiders

parabolic velocity profile:

$$u(h) = \frac{\Delta P}{L} \frac{(a^2 - h^2)}{2\mu}$$

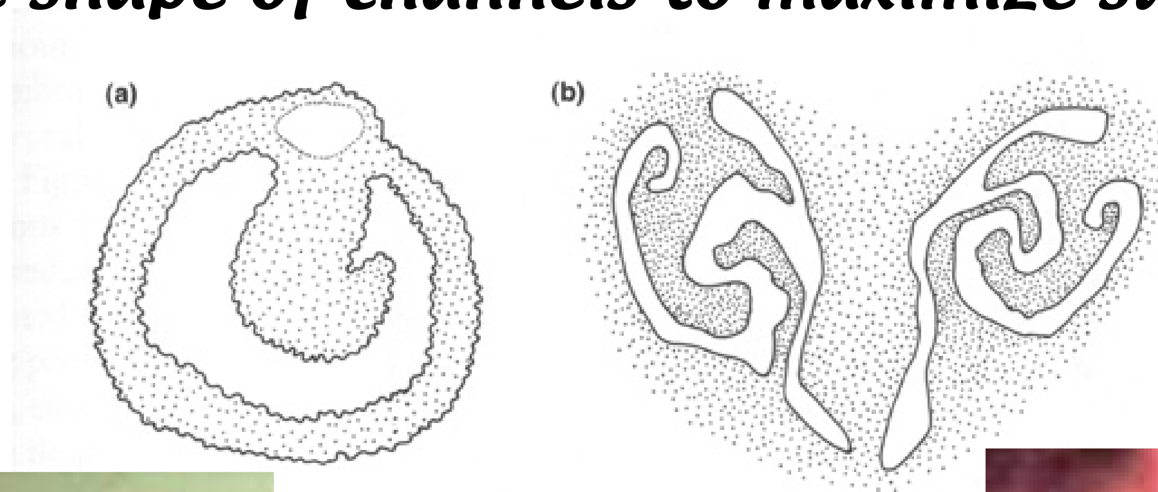
$$Q = \frac{\Delta P}{L} \frac{2wa^3}{2\mu}$$



*wide plates spaced close together have lots of surface area and low flow rate

How do animals maximize fluid contact in circulatory systems?

2. Change shape of channels to maximize surface contact



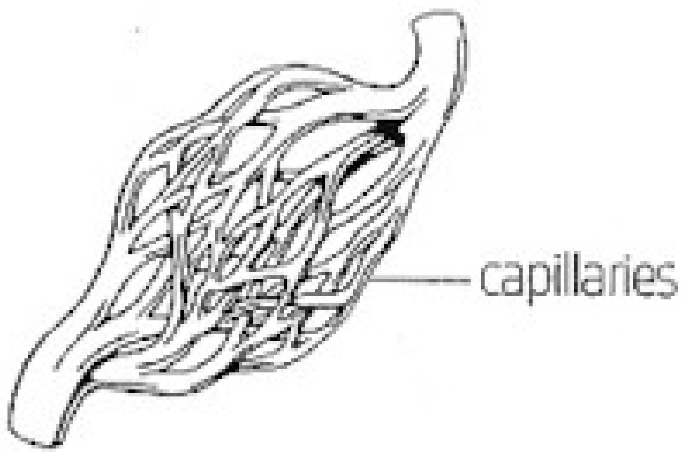
But costs more to pump fluid than in circular vessels!

U-shaped cross-section of earthworm gut maximizes surface contact for absorption of nutrients

complex cross-section of nasal passages maximizes contact for heat and moisture absorption

How do animals maximize fluid contact in circulatory systems?

3. Branch larger tubes into many smaller tubes



How should vessels branch to minimize these costs?

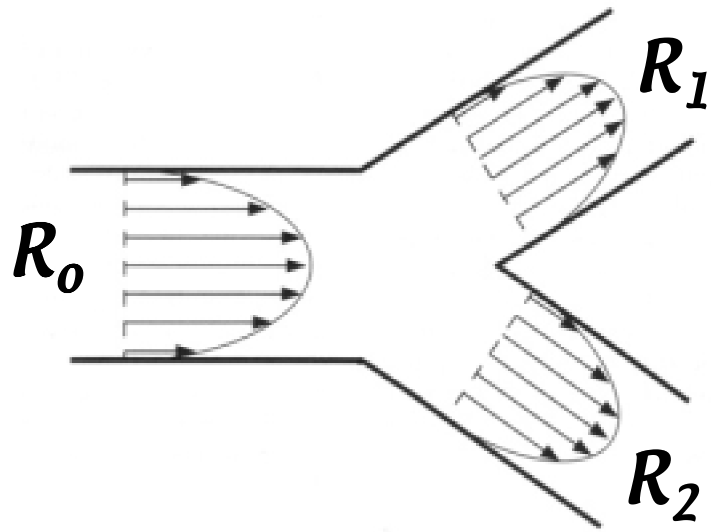
aorta x-s area: 6 cm^2
capillaries x-s area: 2000 cm^2

Costs in fluid transport systems:

- making vessels and blood - rises with contained volume, so favors small pipes
- pumping blood - inversely related to pipe size, so favors large pipes

How do animals maximize fluid contact in circulatory systems?

3. Branch larger tubes into many smaller tubes



How should vessels branch to minimize these costs?

Murray's Law (laminar flow):

$$R_0^3 = R_1^3 + R_2^3$$
$$= R_3^3 + R_4^3 + R_5^3 + R_6^3 \ldots$$

sum of cubes of vessel radii at any one level of branching should equal that at other levels.

For one vessel bifurcating:

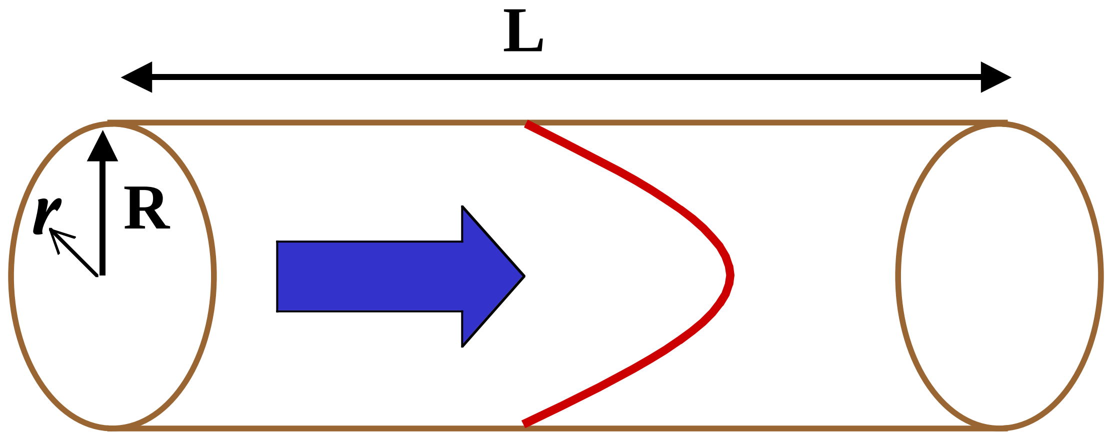
$R_{1,2} = 0.80\ R_o$

x-s $area_{1,2} = 0.63$ x-s $area_o$

x-s $area_{1+2} = 1.26$ x-s $area_o$

$u_{1,2} = 0.74\ u_o$

What is the shear stress caused by flow through tubes?



$$u(r) = \frac{\Delta P}{L}\frac{(R^2 - r^2)}{4\mu}$$

$$Q = \frac{\Delta P}{L}\frac{\pi R^4}{8\mu}$$

$\tau = \mu\, du/dr$ → $\tau = \Delta P\, r / 2L$

Where is shear stress maximum? $\tau_{max} = \Delta P\, R / 2L$

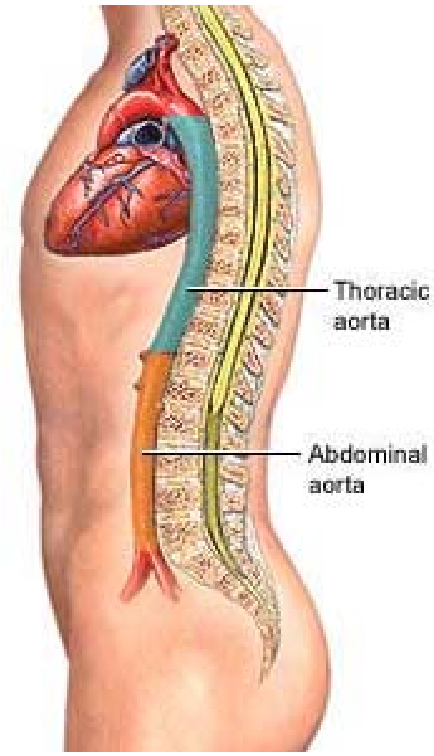
What is the total shear stress on the tube walls?

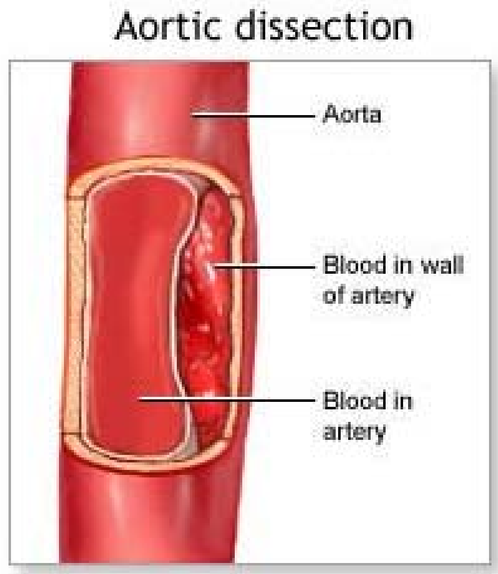
$\tau_{total} = \Delta P\, R / 2L\, (2\pi R L)$

$\tau_{total} = \Delta P\, \pi R^2$

Aortic dissection

- caused by shear stress on wall of aorta
- inner wall tears and blood flows between inner and outer walls of aorta
- fatal within 48 hrs if not fixed with surgery

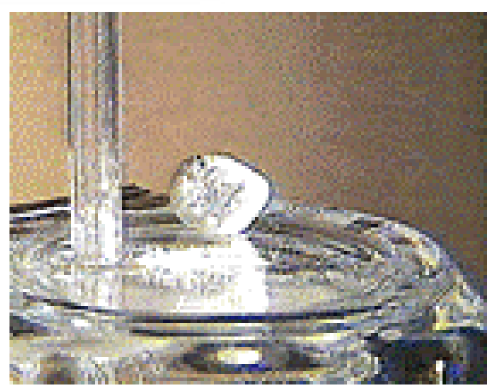




Risk factors:

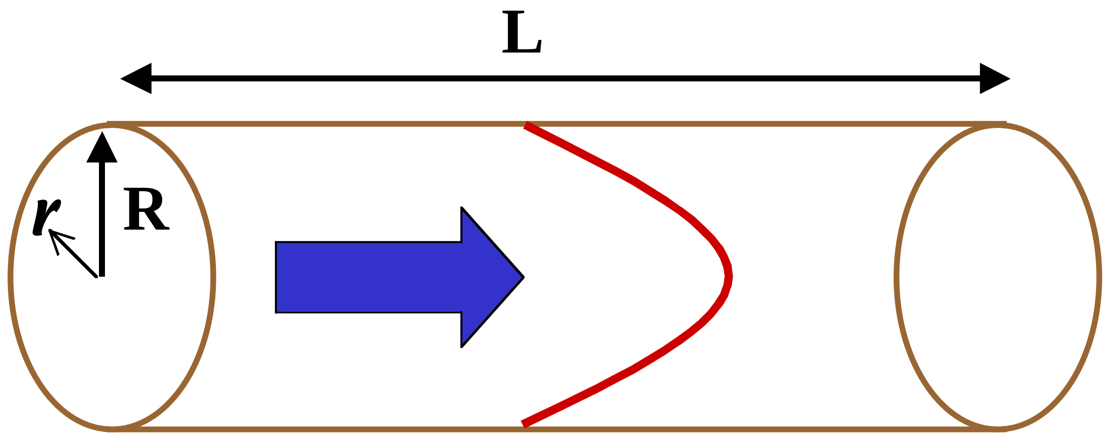
- ***high blood pressure***
- ***stiff vessel walls***
- ***crack cocaine?***

(14 of 38 cases in 20 years at SF General were smokers who also used crack cocaine)



+

Flow in tubes is not always laminar.....



$$u(r) = \frac{\Delta P}{L} \frac{(R^2 - r^2)}{4\mu}$$

$$Q = \frac{\Delta P}{L} \frac{\pi R^4}{8\mu}$$

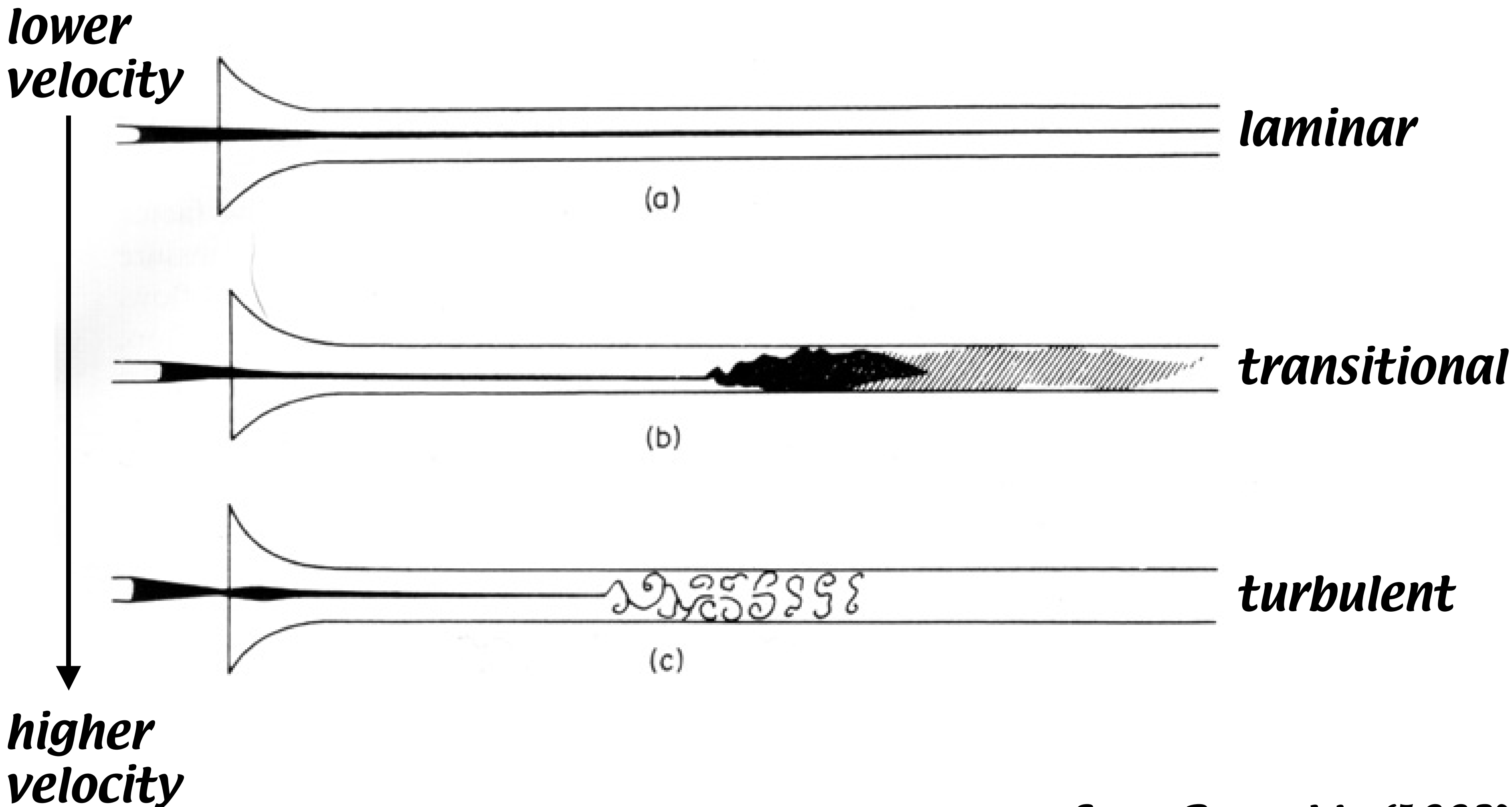
Hagen-Poiseuille law

Valid only as long when flow is laminar!

► Flow becomes turbulent at higher Reynolds numbers

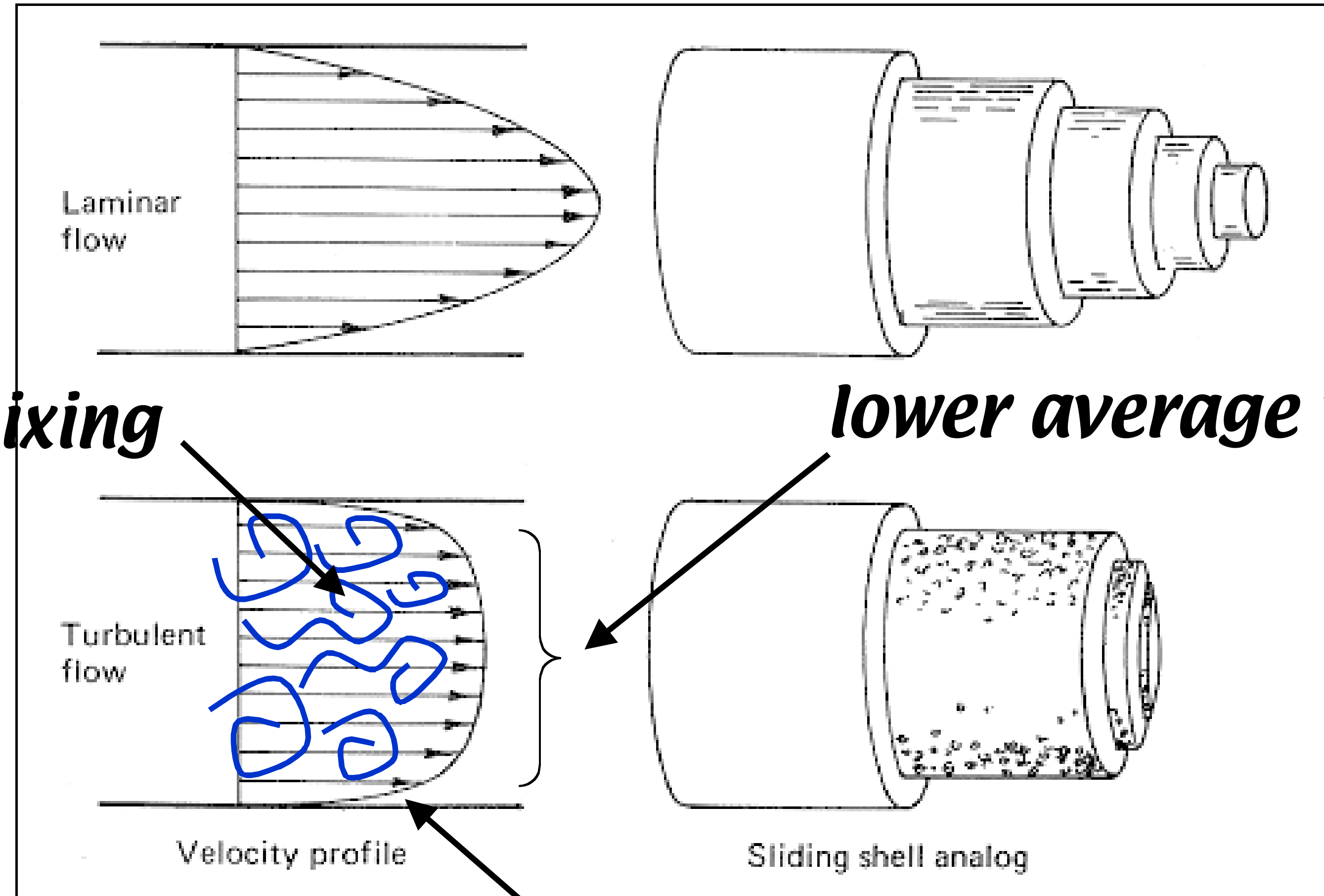
Turbulent flow in tubes and the Reynolds number

$$Re = \rho u D/\mu$$



from Reynolds (1883)

Turbulent flow changes the velocity profile



more mixing

lower average velocity

steeper velocity gradient near walls
(faster flow closer to walls on average)

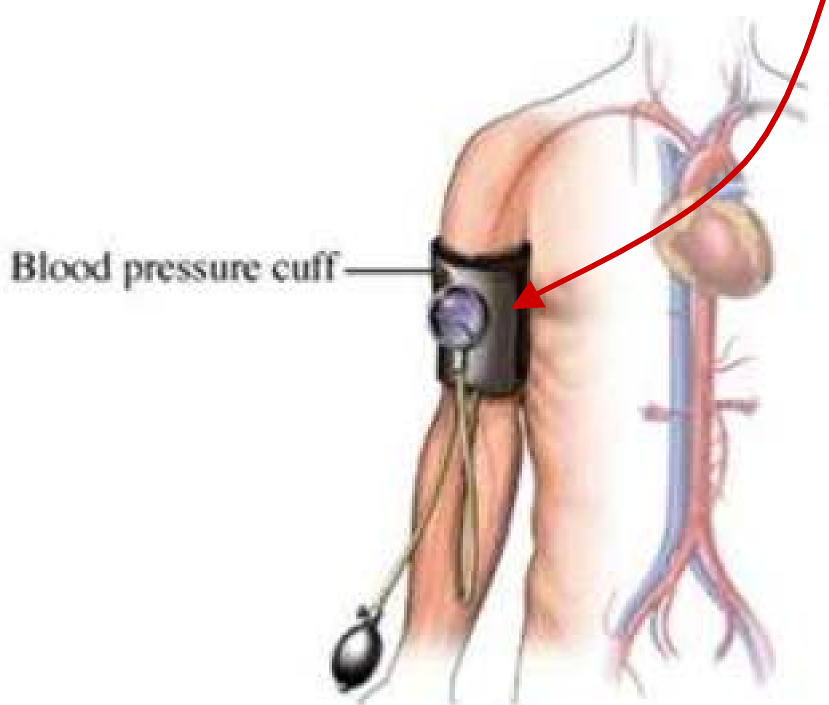
When does flow in tubes become turbulent?

Re ~ 2000

equivalent to 1-cm radius tube with 0.2 m/s flow
-most internal fluid transport systems are below this

turbulence sets in sooner with:

- roughness
- bending
- abrupt entry from reservoir
- changes in tube diameter....

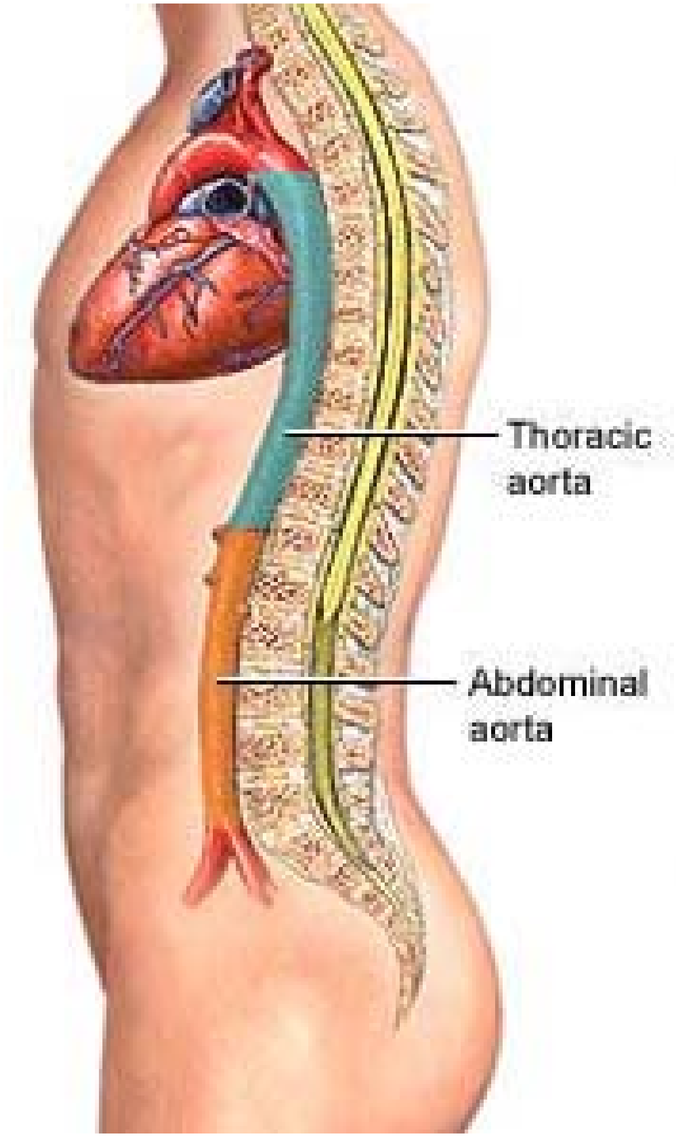


Blood pressure measurement

-cuff stops arterial flow
-pressure is slowly released
-when cuff P< systolic (max) P, some blood squeezes through artery
-abrupt entry causes turbulence (can hear with stethoscope)

Where might flow normally be turbulent in circulatory systems?

$$Re = \rho u D/\mu$$

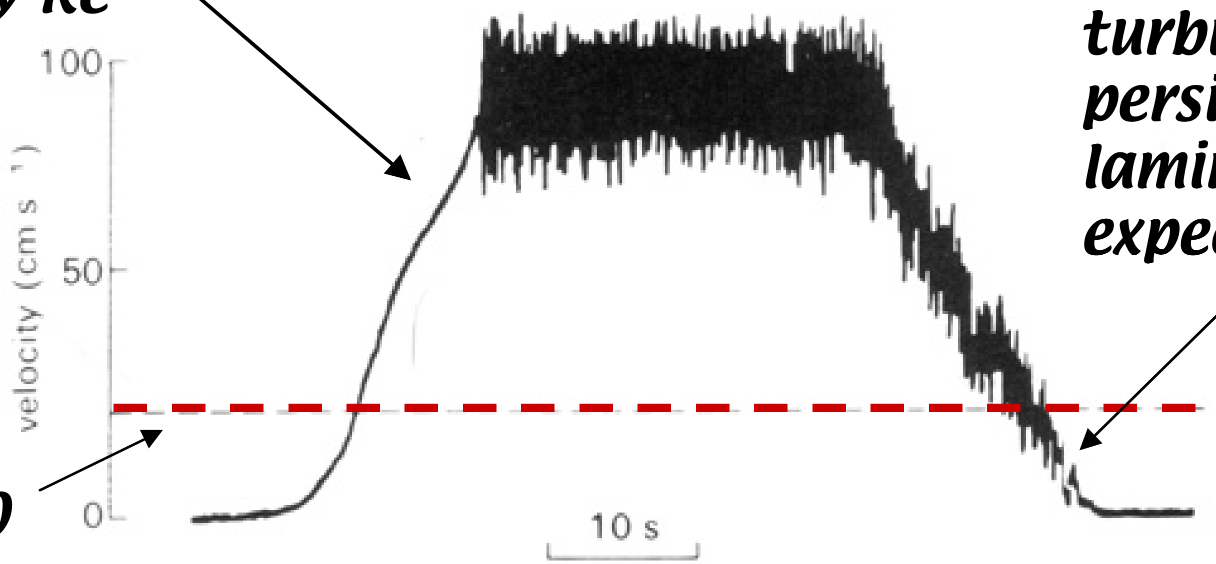


Aorta

- ▸*large diameter*
- ▸ *high velocity*
- ▸ *pulsed flow….*

How does pulsing affect turbulent flow?

turbulence does not develop as soon as expected by Re



turbulence persists after laminar flow is expected

Re ~ 2000

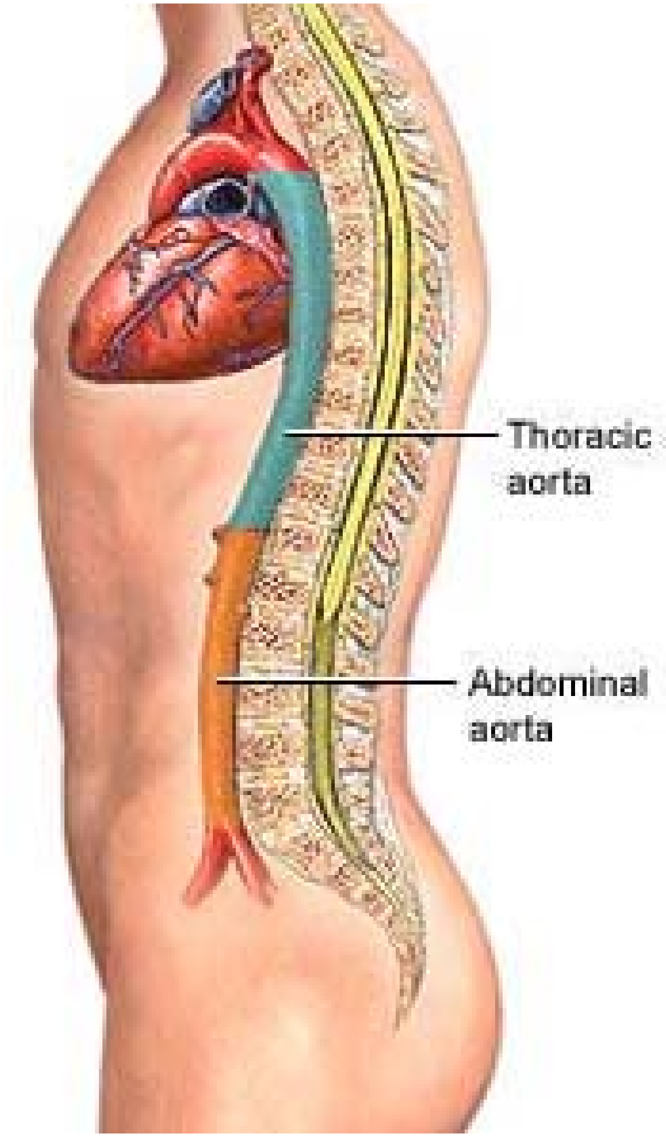
flow velocity changes with time

▸ accelerating fluid is more stable than steady flow and turbulence takes time to develop

▸ decelerating flow is less stable than steady flow and eddies that have developed take time to decay

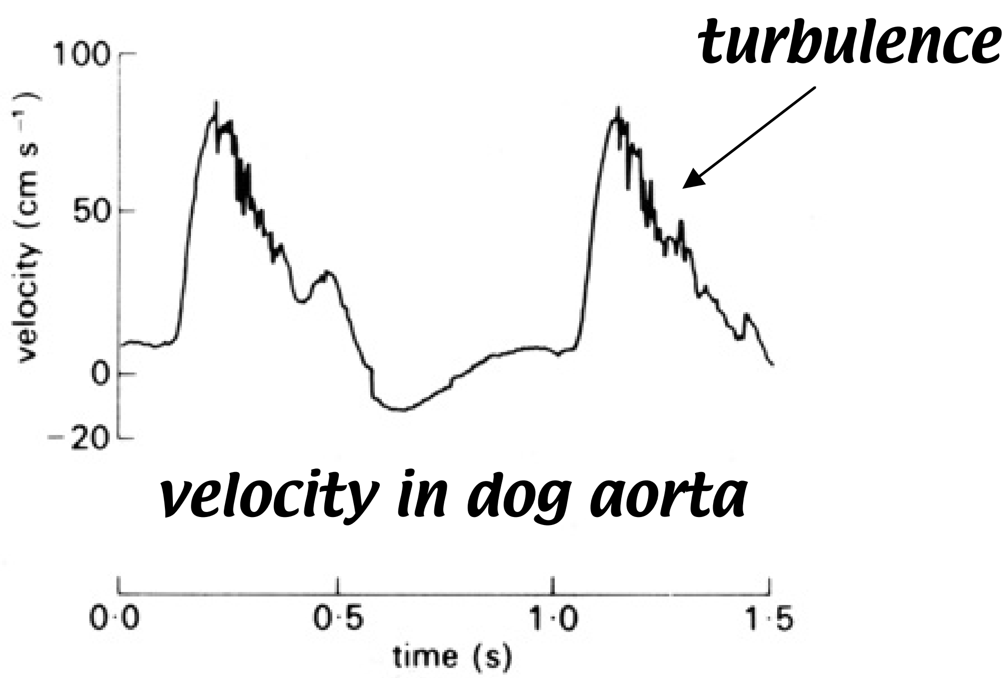
Where might flow normally be turbulent in circulatory systems?

$Re = \rho u D/\mu$



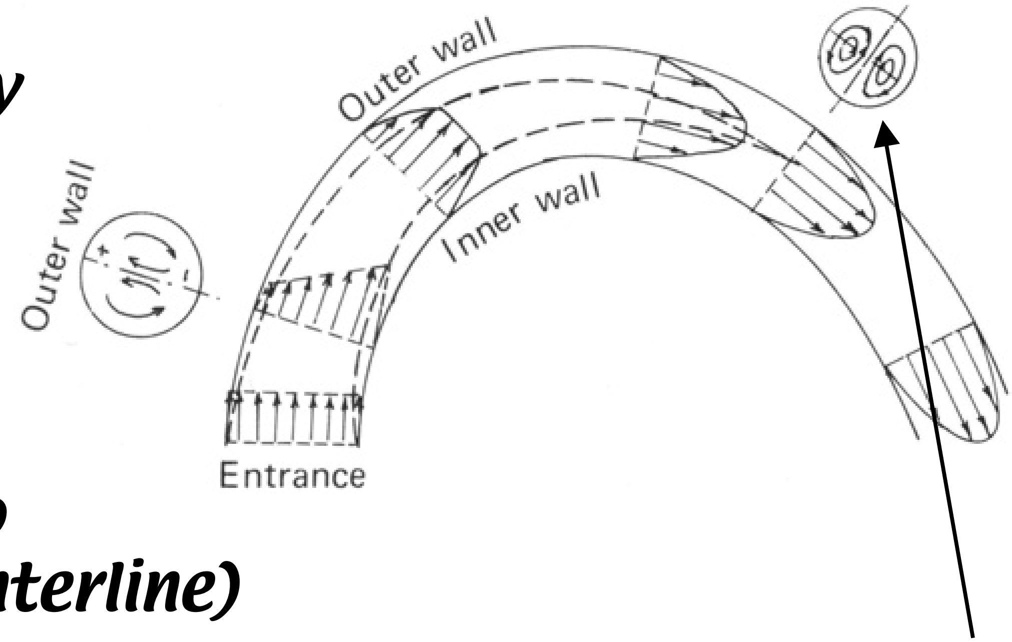
Aorta

- *large diameter*
- *high velocity*
- *pulsed flow*



velocity in dog aorta

Flow through curved tubes



▶*flow enters tube - velocity higher near inner wall*

▶*boundary layer grows*

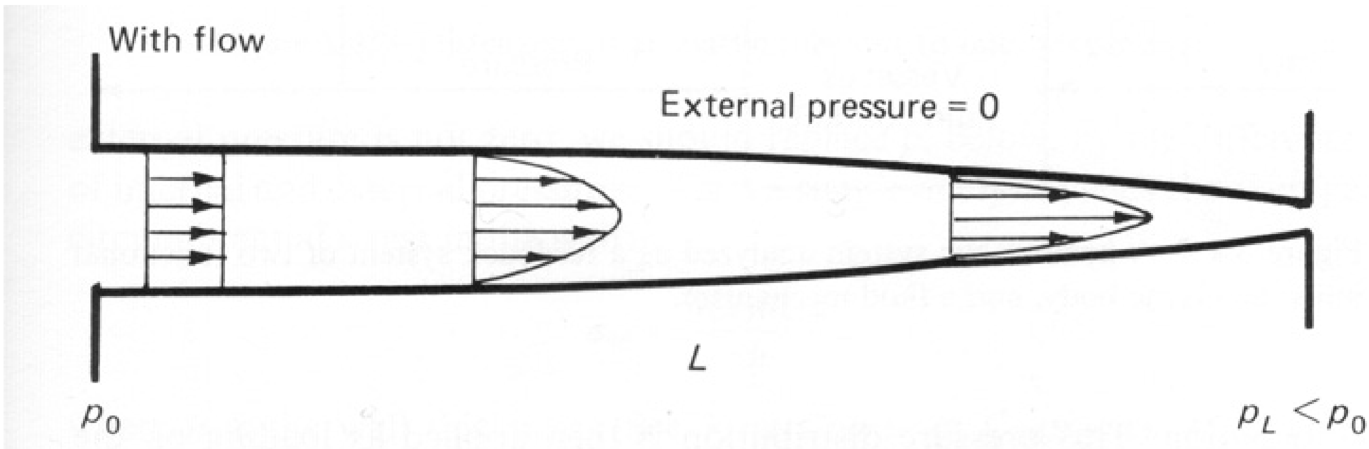
▶*centrifugal force pushes fluid towards outer wall (distorts velocity profile so peak velocity is beyond centerline)*

▶*pressure field is not uniform, so secondary flow develops*

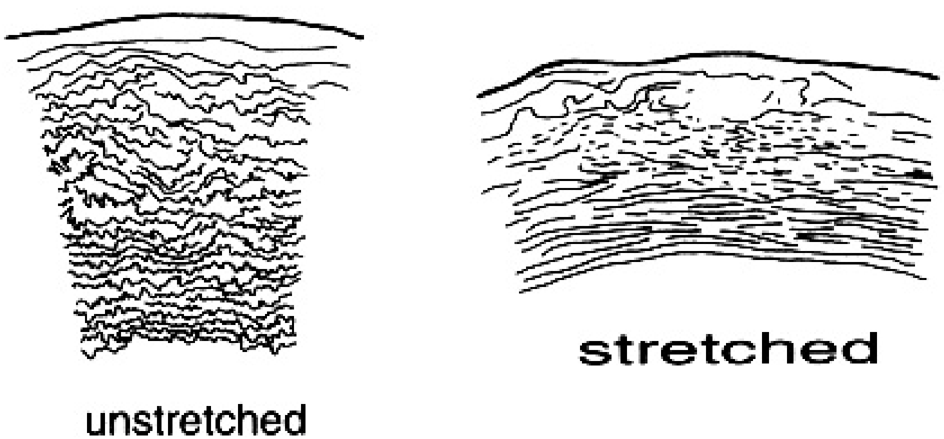
Curved tubes used in heart-lung machines to promote oxygenation of blood -> secondary flow promotes mixing of blood and faster oxygenation

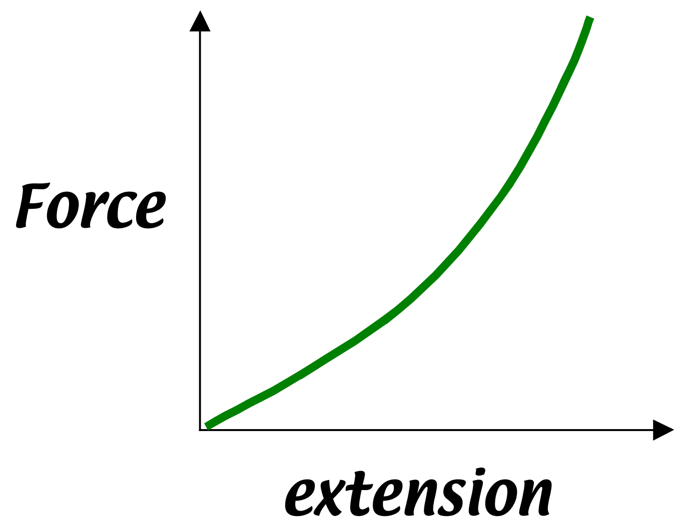
Flow in flexible tubes

cross-section varies with pressure along the length of the tube



- kinked collagen fibers prevent overextension

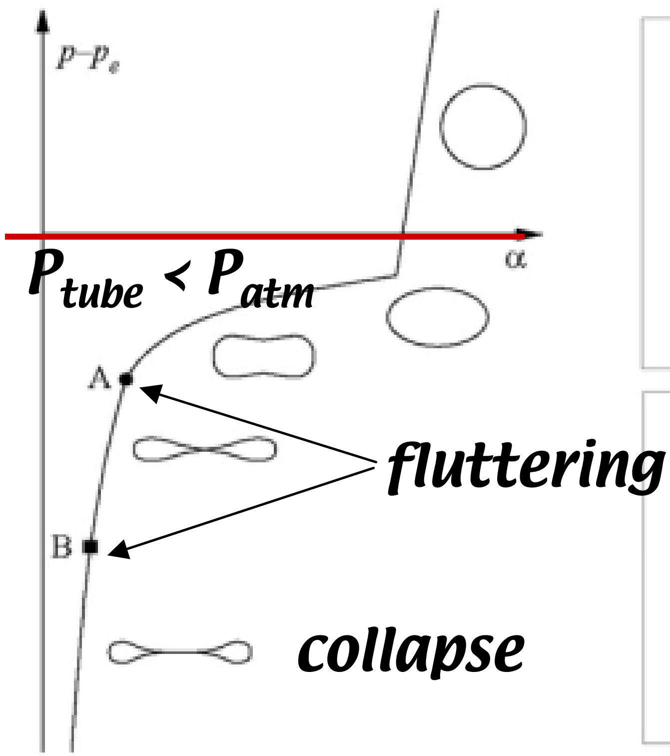


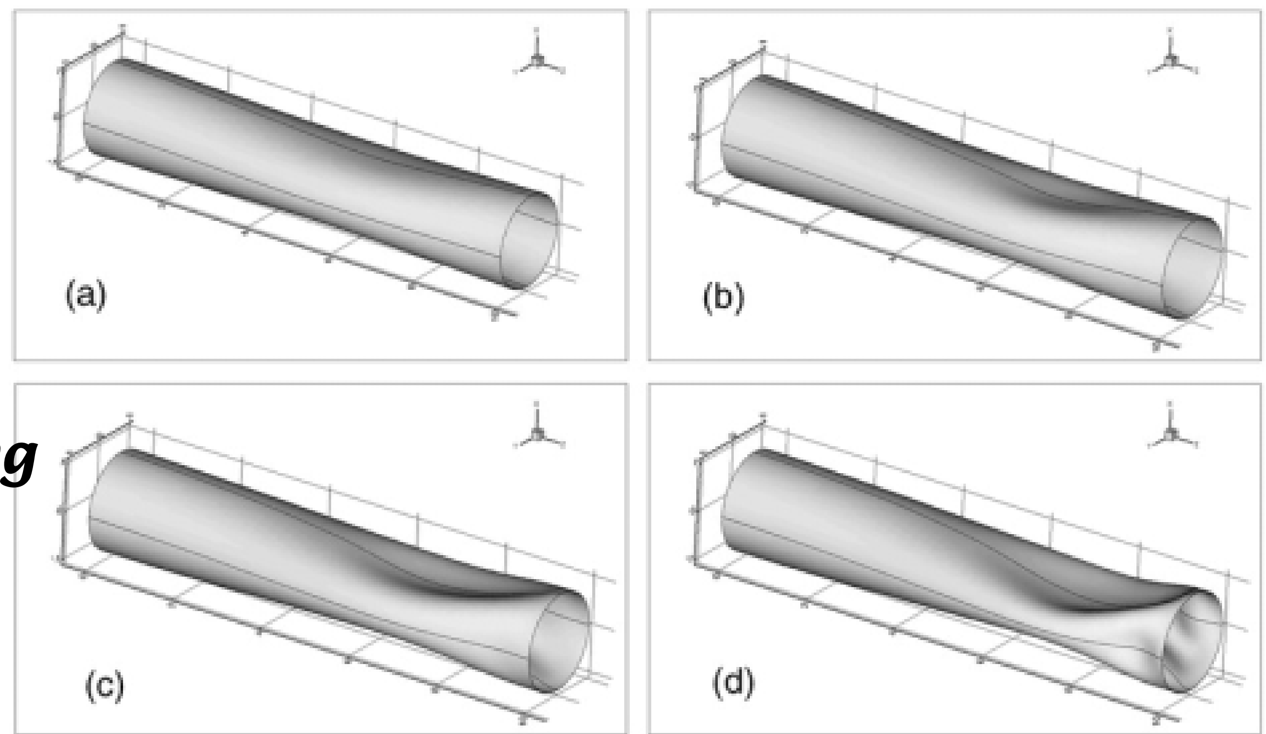


Flow in flexible tubes

Atmospheric pressure pushes in on flexible tubes

-> as pressure in tube falls below atmospheric, tube starts to flutter, and eventually collapses

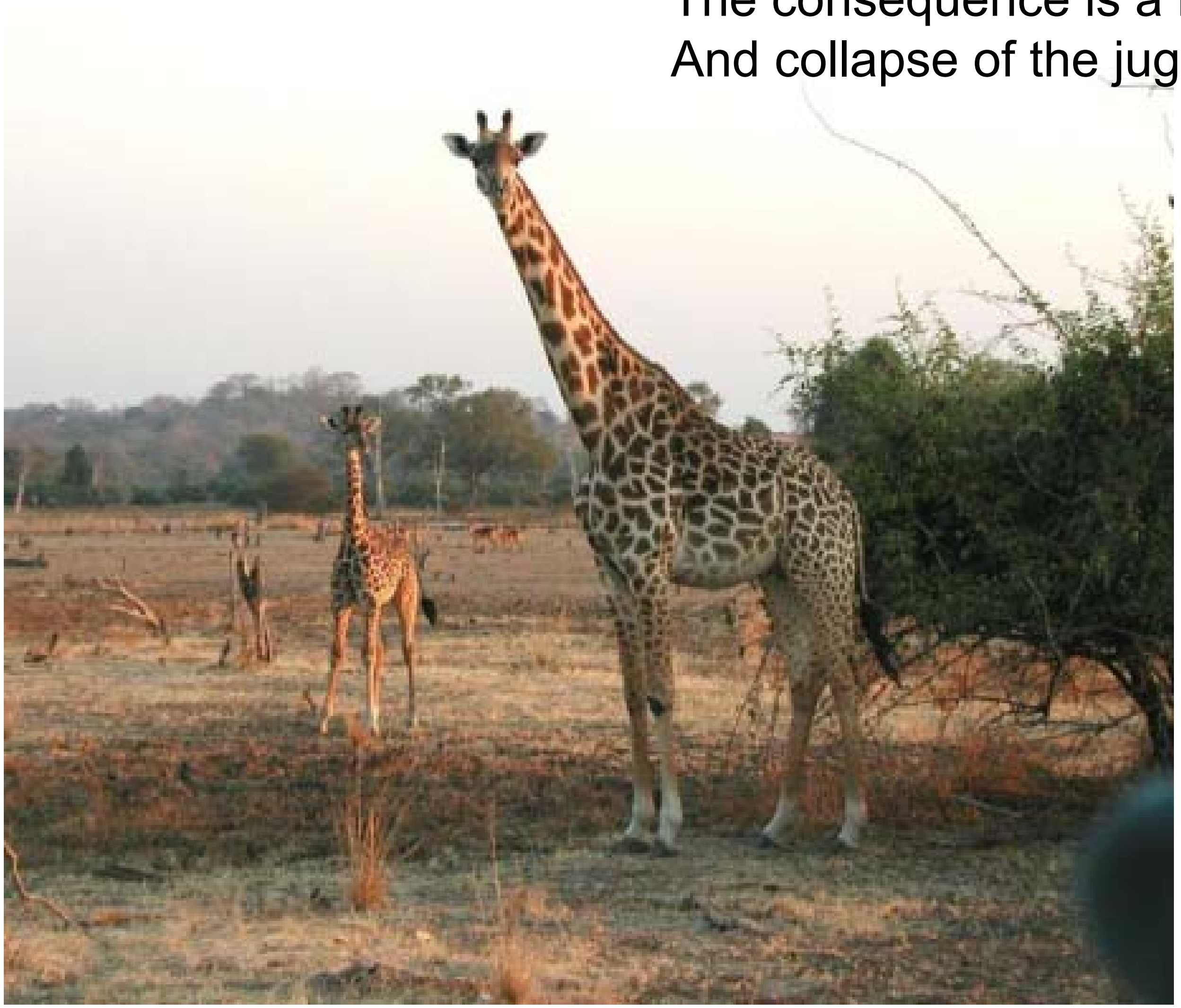




Flow in flexible tubes

The giraffe has a neck of phenomenal length,
Up which blood must be pumped to the brain.
The consequence is a heart of great strength,
And collapse of the jugular vein.

-T. Pedley



heart mass = 20 lbs
2% body mass
(vs. 0.5% in humans)

can pump 15-20 gallons blood/min

blood pressure 2.5X human BP

Flow in flexible tubes

- **Arteries of the lower extremities** experience extremely high pressures (high BP and effect of gravity)

Artery walls are thicker than normal and tight sheath of skin on legs maintains high extravascular pressure

- **Arteries of the head and neck** experience extremely high pressure when giraffe is bent down to drink

Arteries in neck are also reinforced, plus the rete mirabile (a complex of elastic arteries and veins) near the brain equalizes blood pressure when the giraffe bends down

Flow in flexible tubes

Does jugular vein collapse because of low pressure?

NASA project to study effect of gravity on circulation

-► placed pressure transducers in necks of South African giraffes

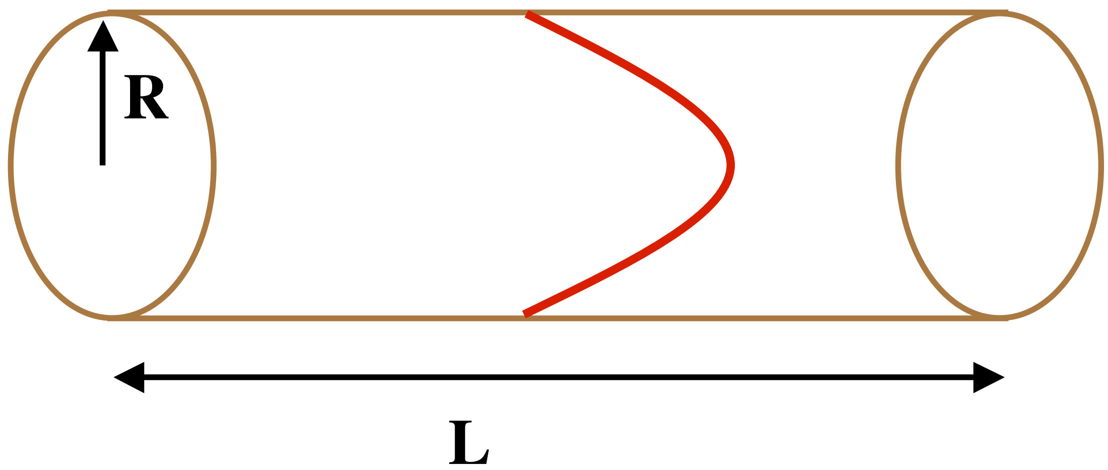
-► followed giraffe in jeep to receive pressure signal

-► showed that jugular vein is squeezed almost flat (!) because pressure is far below atmospheric

Biology 427 Biomechanics
Lecture 26. Internal biofluiddynamics II: blood flow.

- Recap tube flow
- Blood flow and hematocrit variations
- Farheaus-Lindqvist effect
- Blood viscosity in the microcirculation
- Murray's law

Rigid circular vessel of constant radius R



$$u(r) = \Delta P\, R^2(1 - (r/R)^2)/4\, \mu\, L$$

$$Q = \pi\, R^4\, \Delta P/8\mu L$$ Hagen-Poiseuille law

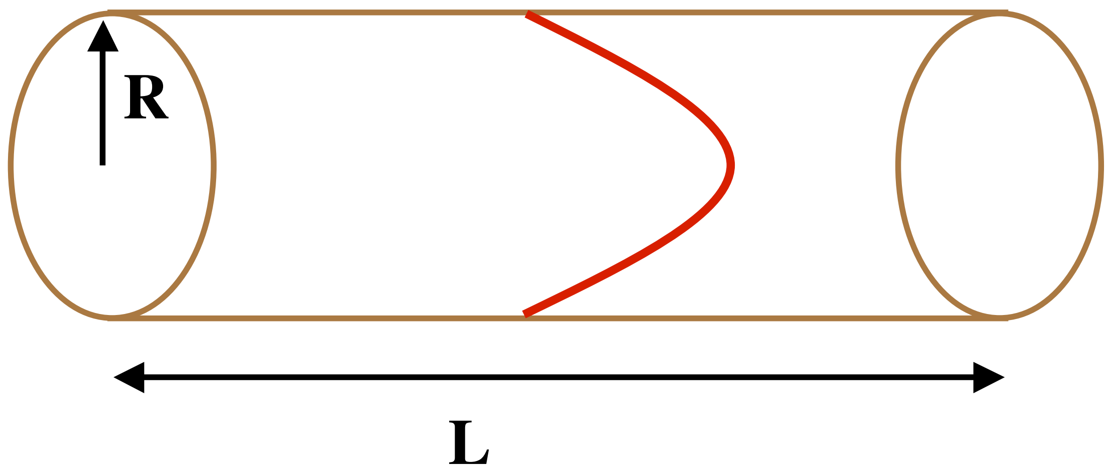
Recall flow work = $\Delta P\, dV$

Pumping power = $\Delta P\, dV/dt = \Delta P\, Q$

$= \pi\, R^4\, \Delta P^2/8\mu L$ or

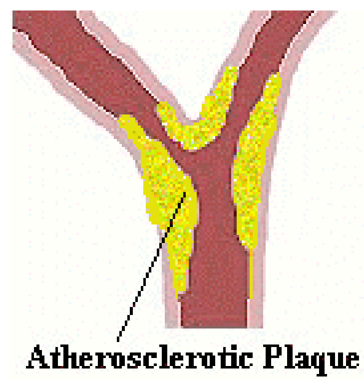
$= Q^2\, 8\mu L/\pi R^4$

Rigid circular vessel of constant radius R

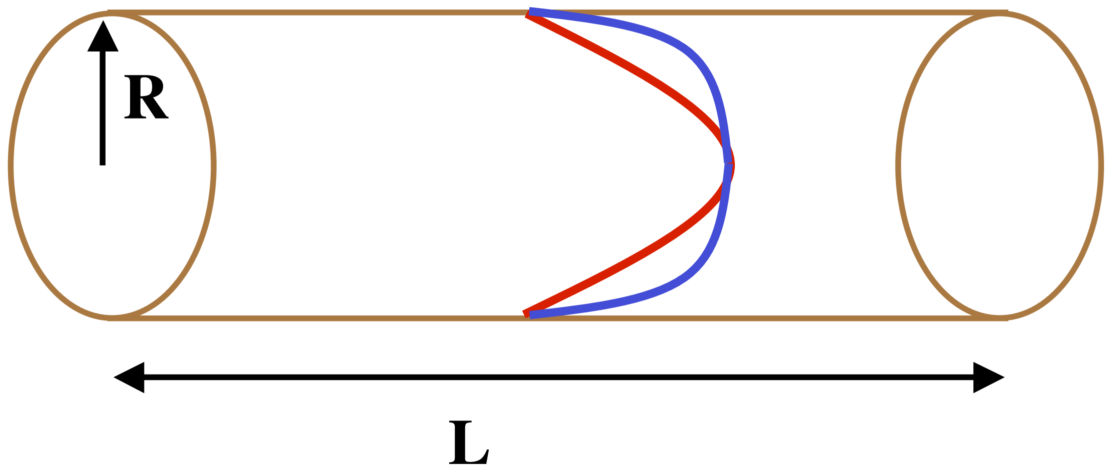


$Q = \pi R^4 \Delta P / 8\mu L$ Hagen-Poiseuille law

What happens with a 5% decrease in the radius?

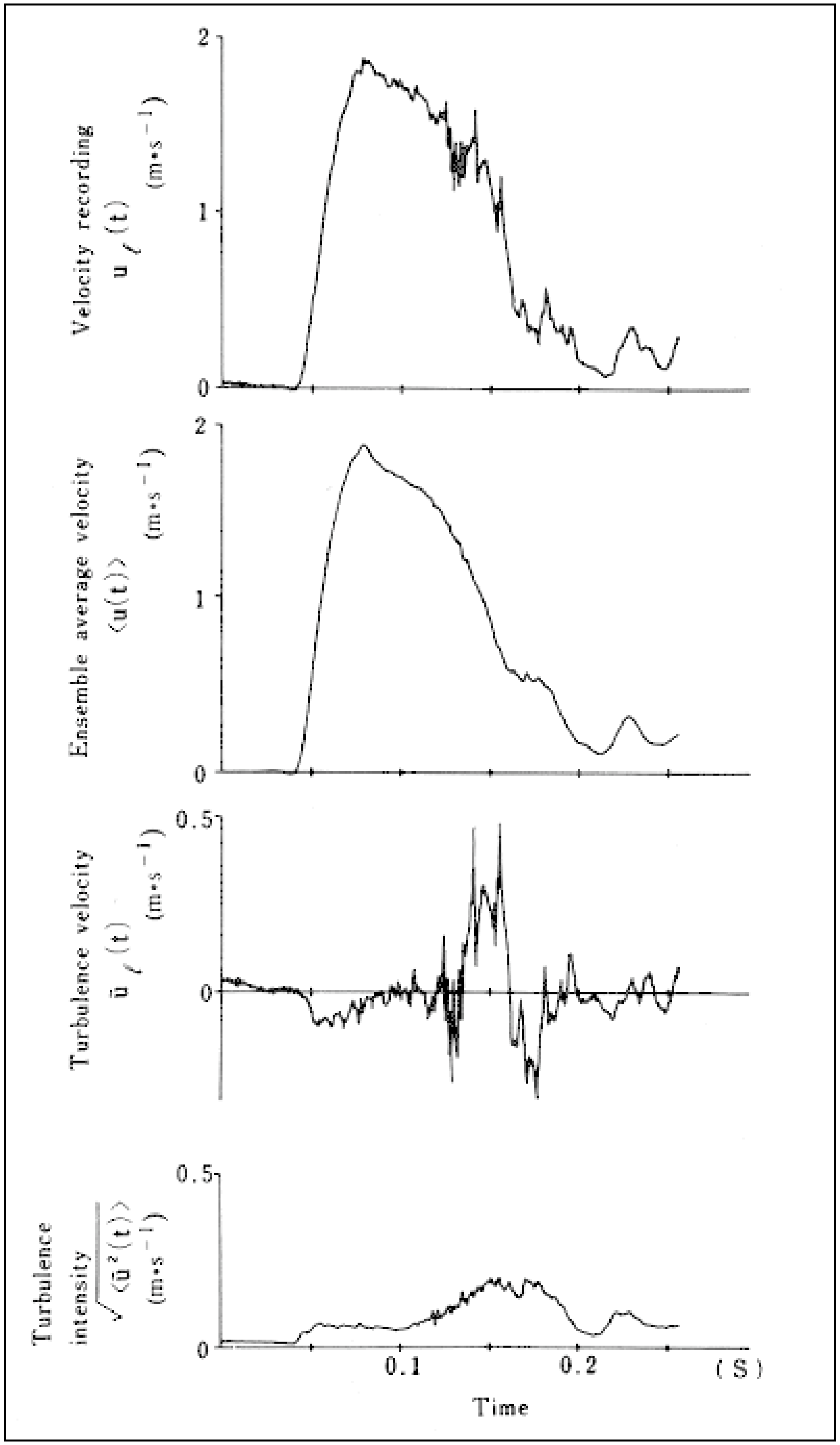


Rigid circular vessel of constant radius R



$Q = \pi R^4 \Delta P / 8\mu L$ Hagen-Poiseuille law

Valid until the flow is turbulent!
$Re = UD/\nu$
($Re > \sim 2000$)



Turbulence and unsteadiness

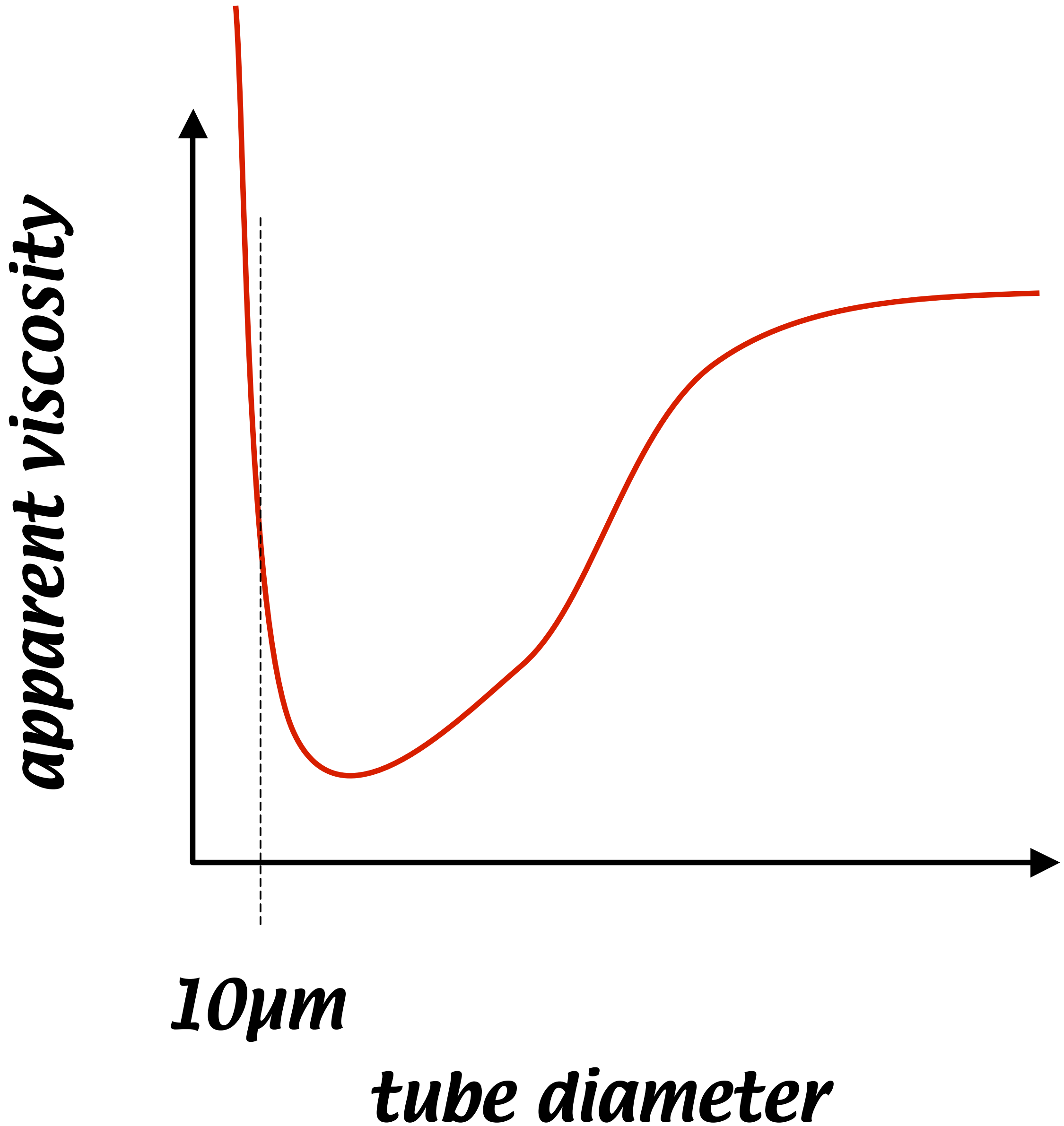
Womersely Number

$Wo = 2 \pi f D/U$

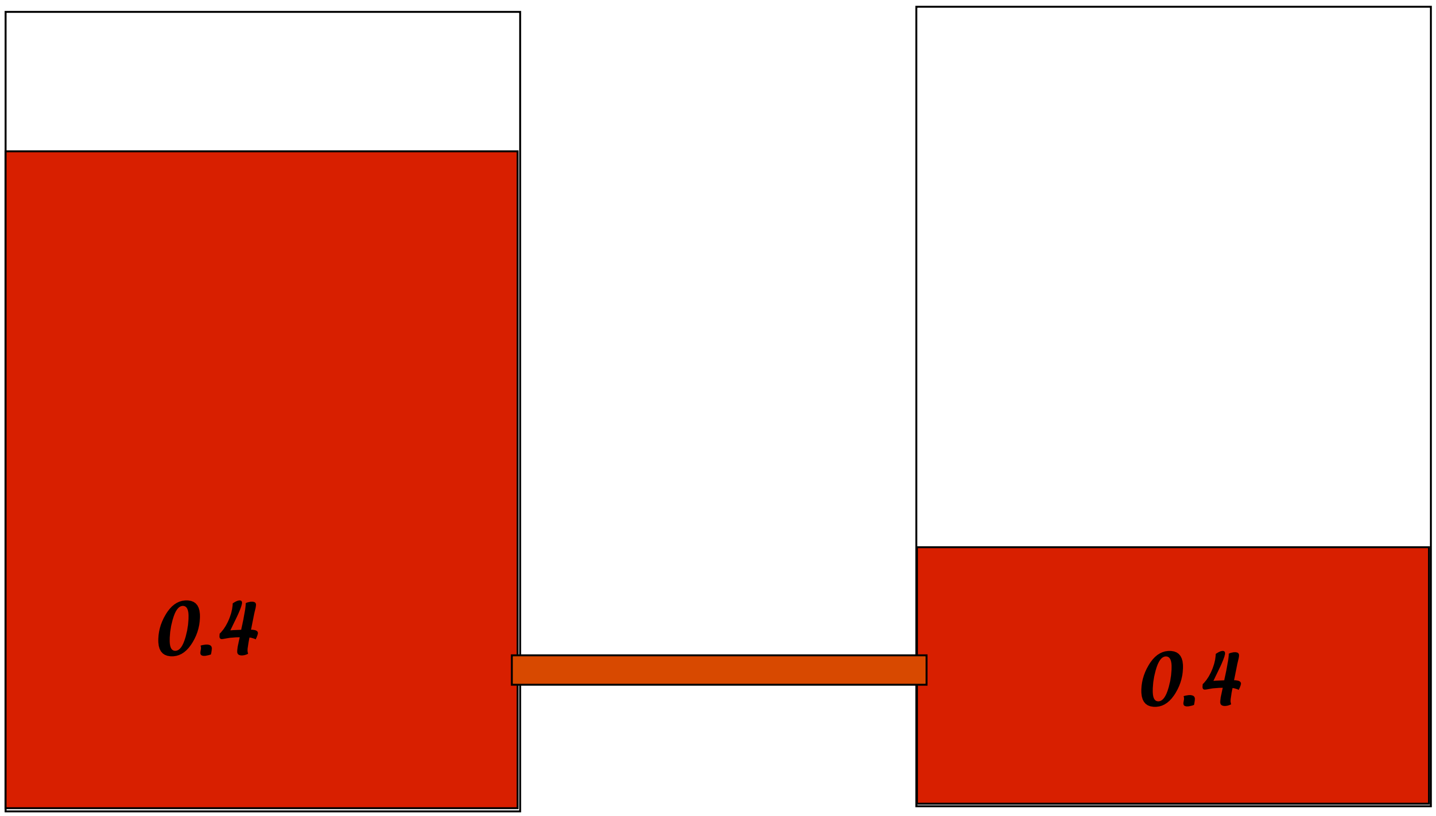
when large, acceleration effects are important

Pulse pressure is a function of accelerations and: bends (a 180 bend acts like a doubling in the length of tube

The Farheaus-Lindqvist effect



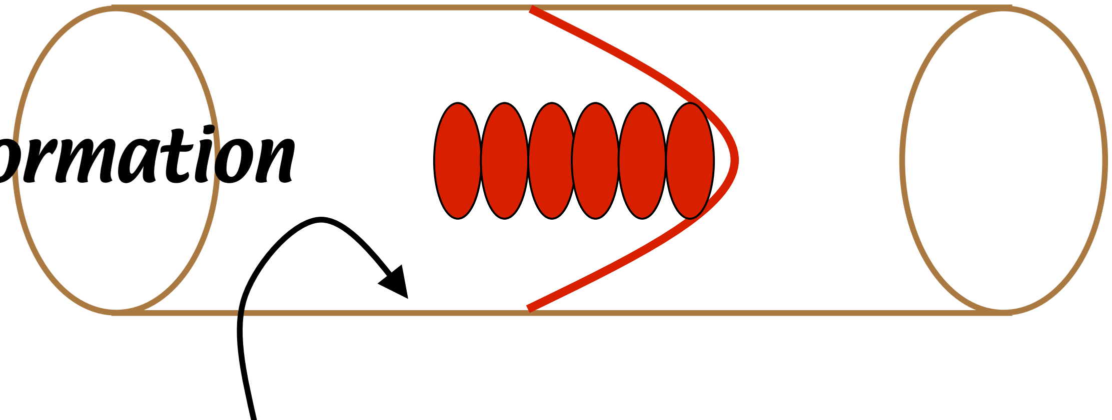
Factors underlying the effect.



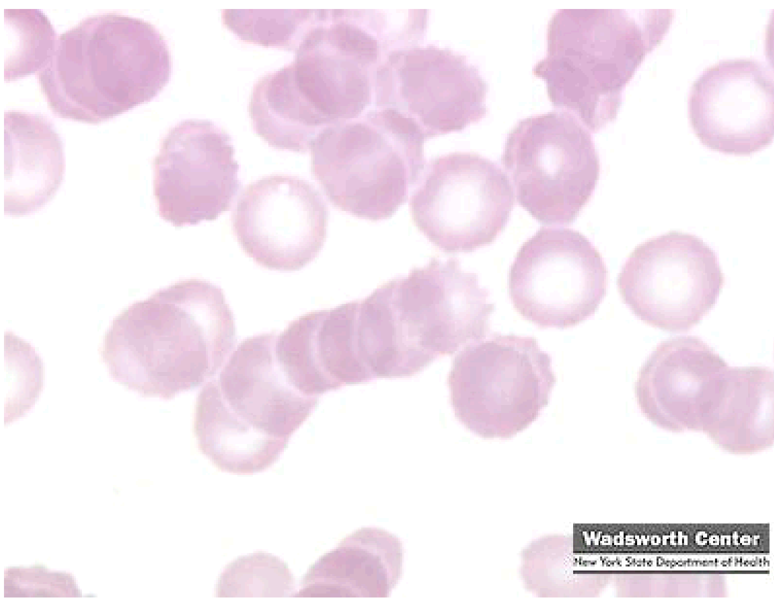
what is the hematocrit in the tube? (0.3)
why?

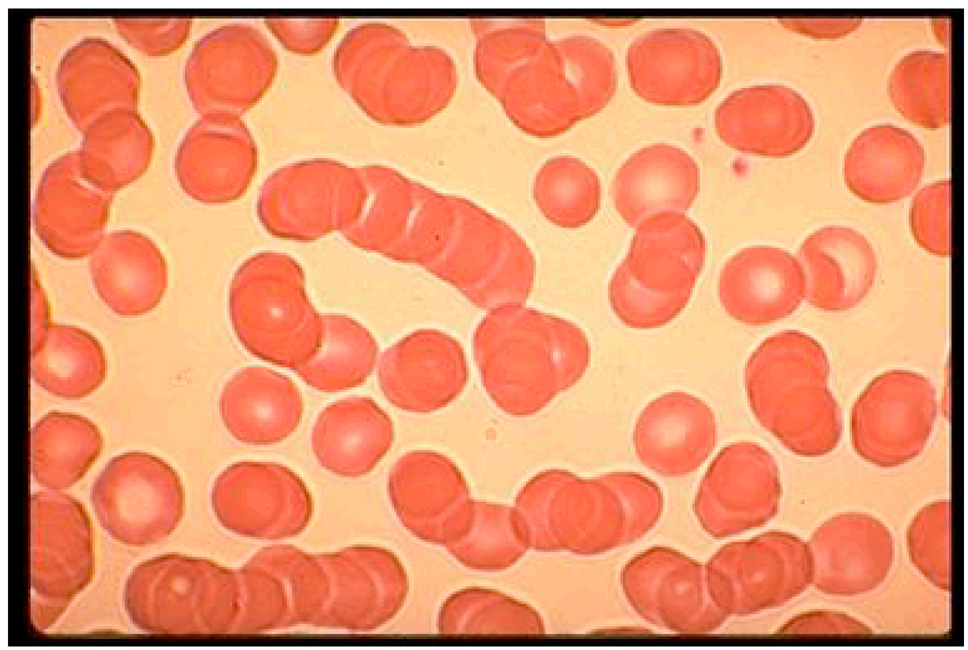
cell migration towards core

rouleaux formation

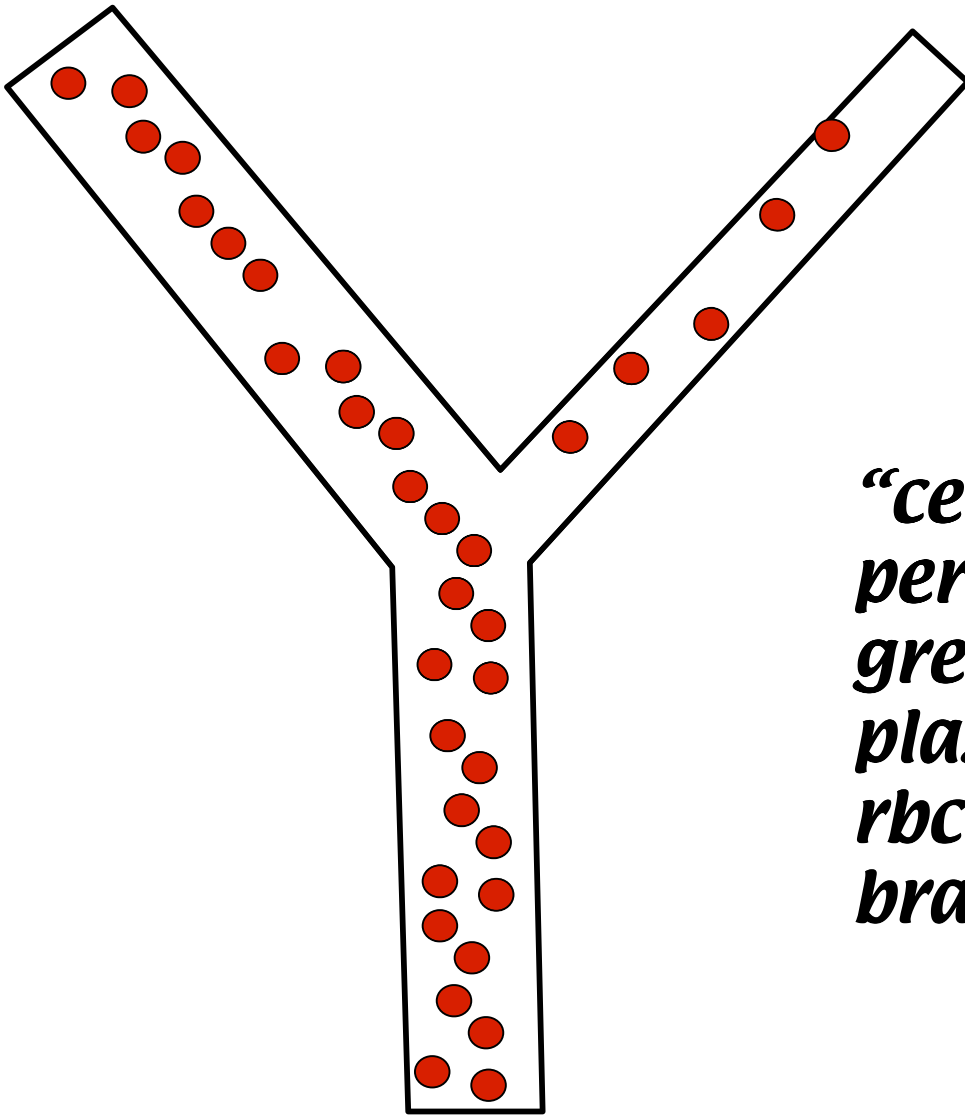


slower flow and fewer cells per volume of fluid



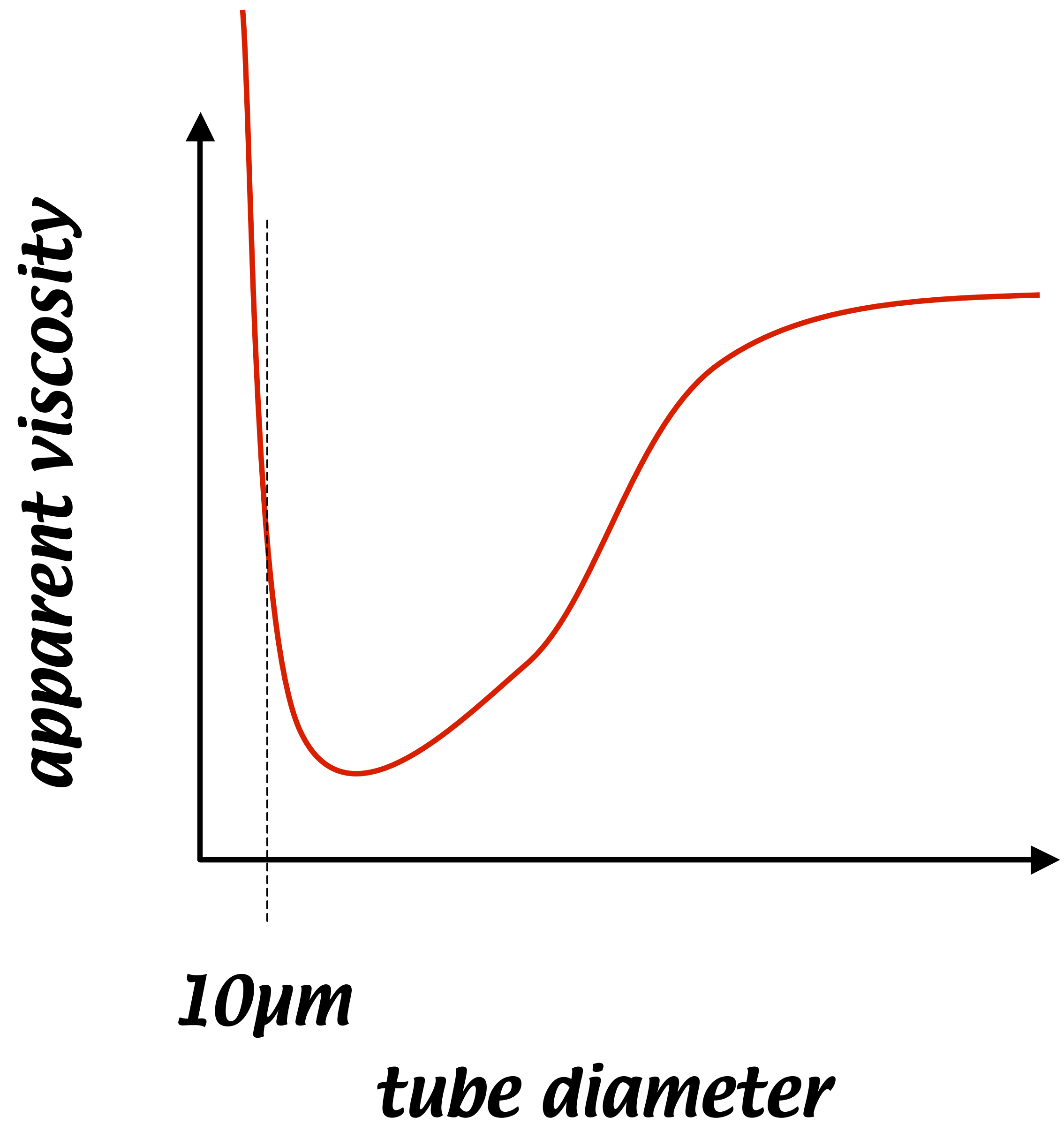


Entrance effects/plasma skimming

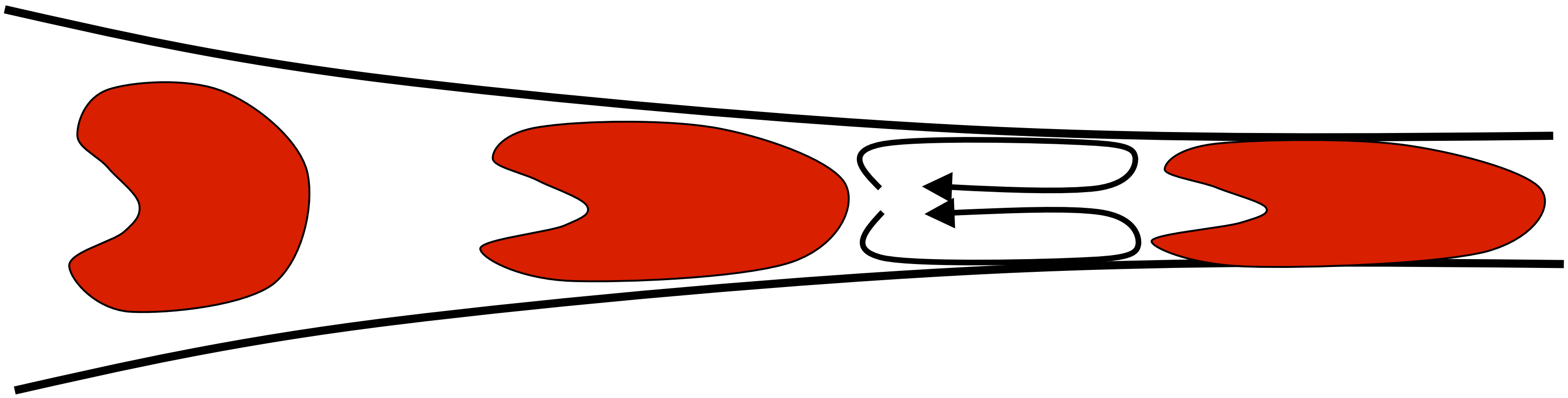


"cell free" layer near perimeter leads to greater plasma/volume (fewer rbc/vol) in asymmetric branching vessels.

The Farheaus-Lindqvist effect

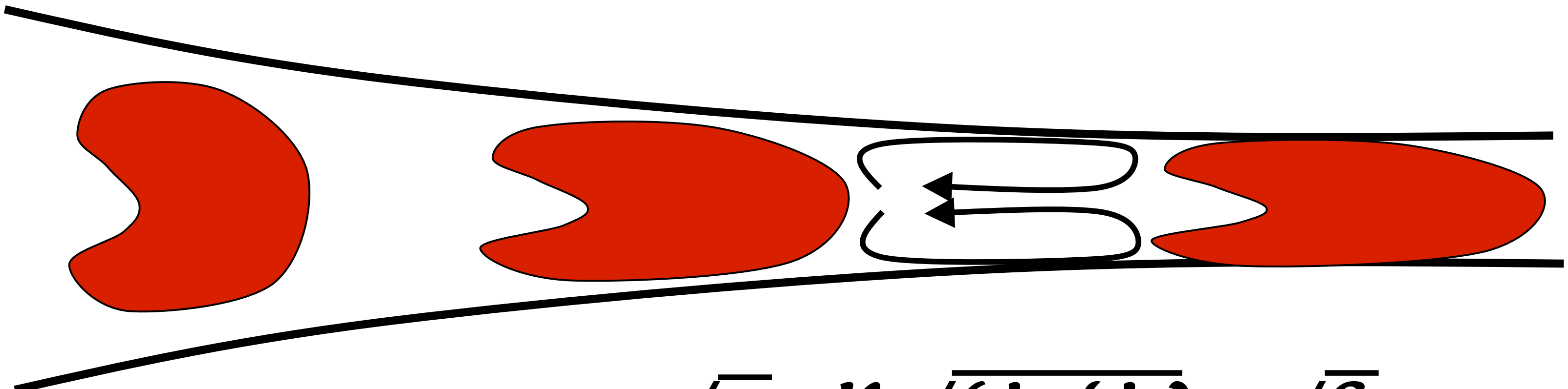


Cell deformations and secondary flows underlie significant increases in apparent. viscosity



These deformations and flows may also underlie augmented flux of nutrients and gases!

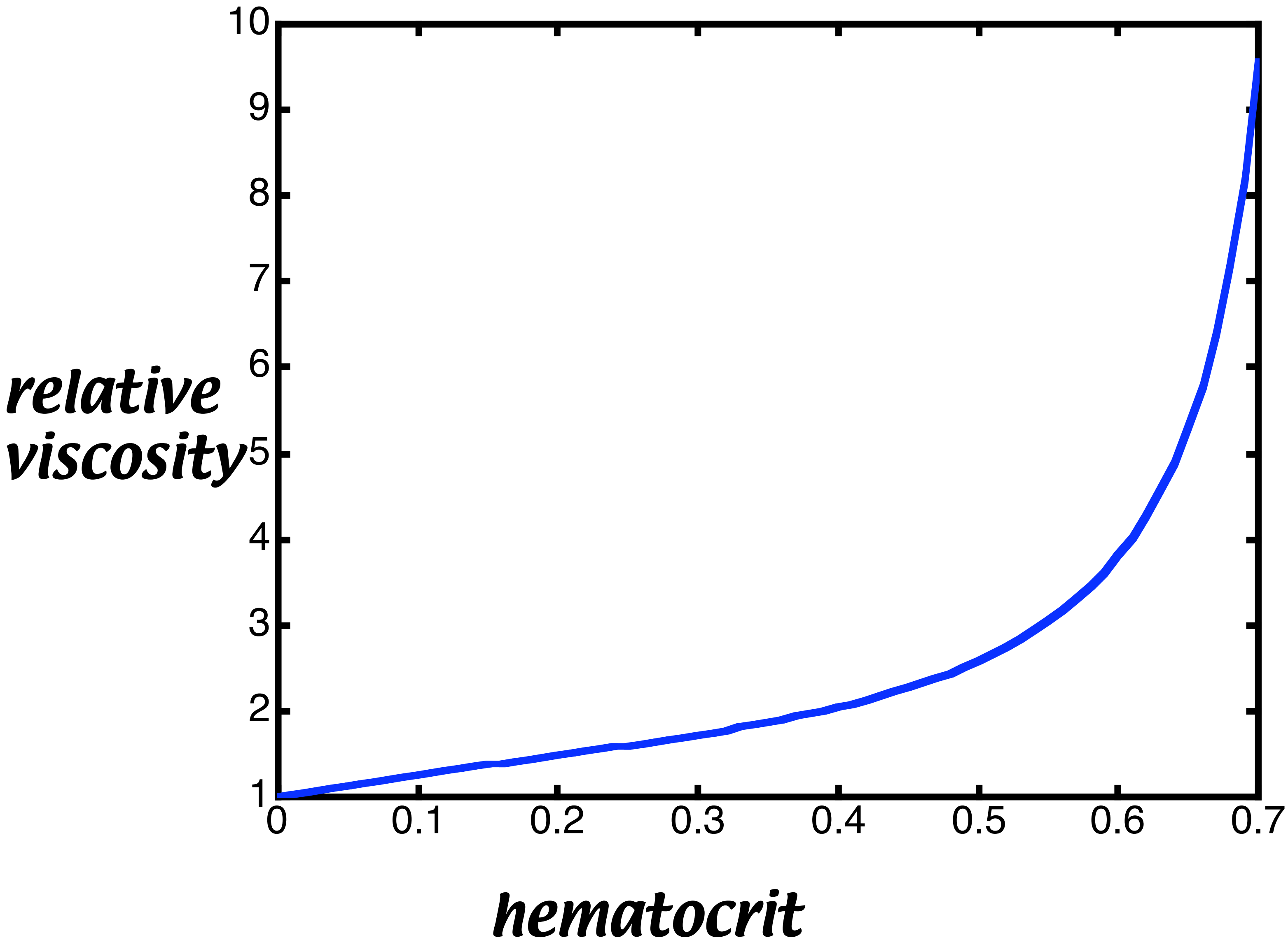
Blood viscosity varies with the shear stress



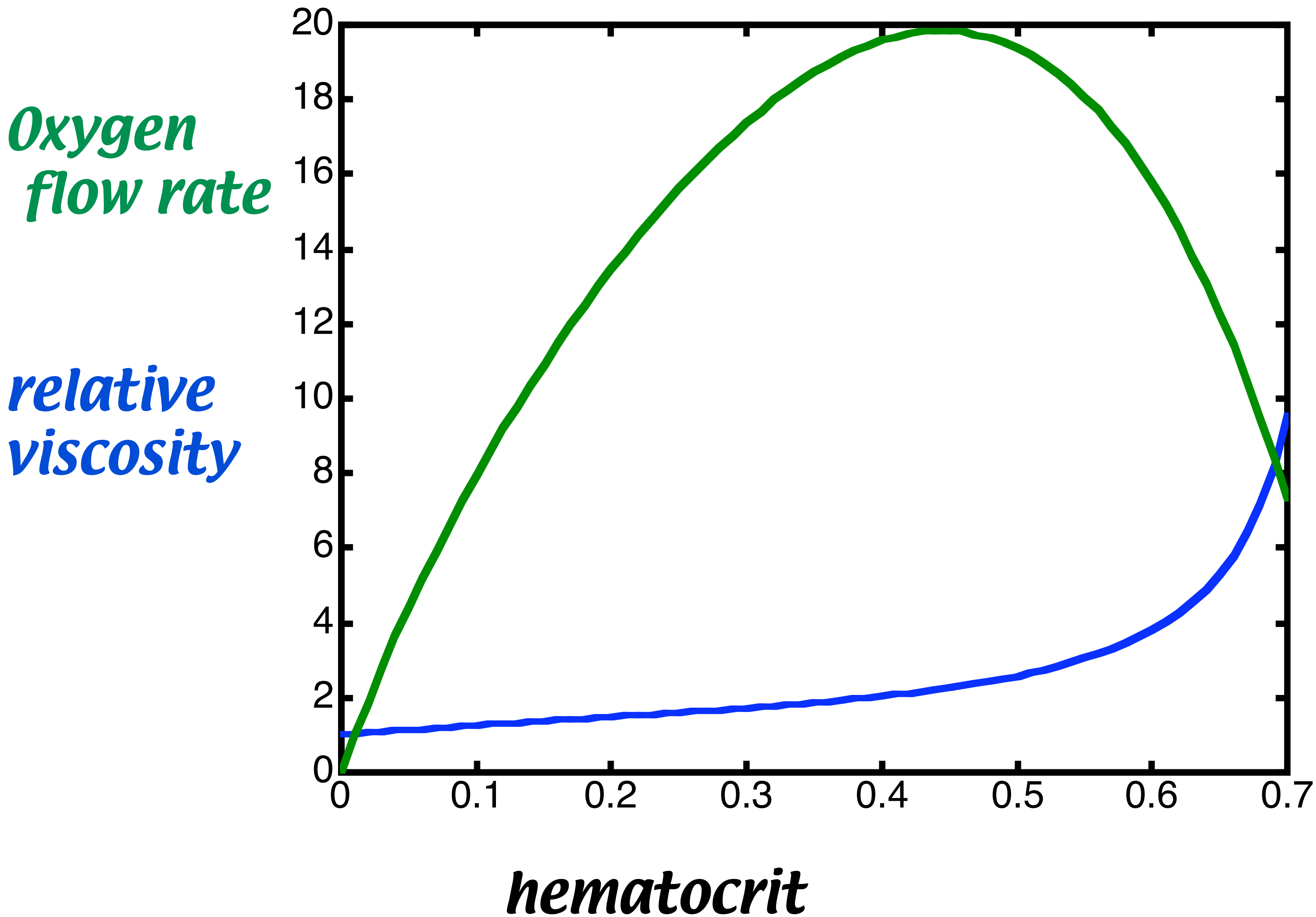
$$\sqrt{\tau} = K\sqrt{(du/dr)} + \sqrt{C}$$

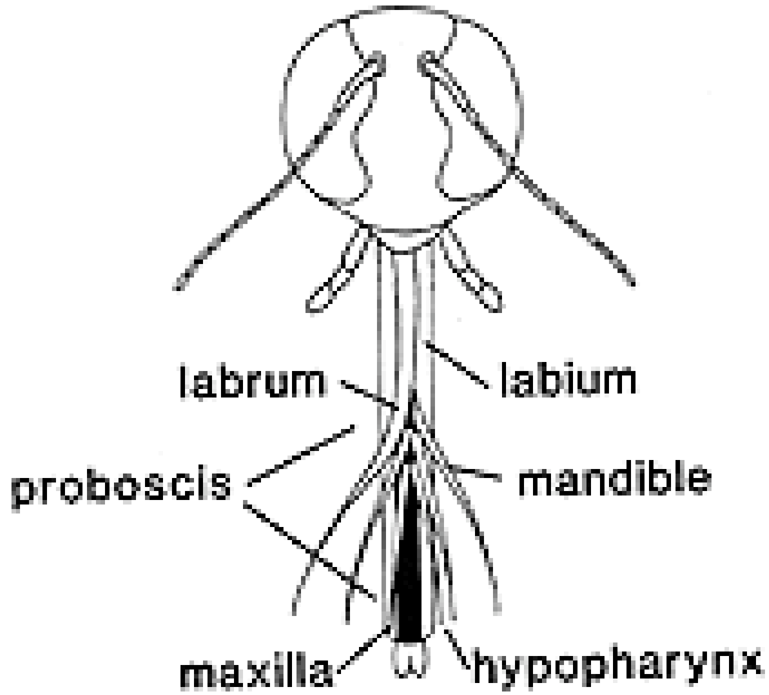
$$K^2 = \mu_p/(1 - \alpha\phi)$$

$$\alpha = 0.07\exp\{2.49\phi + 1107\exp(-1.65\phi)/T_K\}$$


relative viscosity
10
9
8
7
6
5
4
3
2
1
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
hematocrit

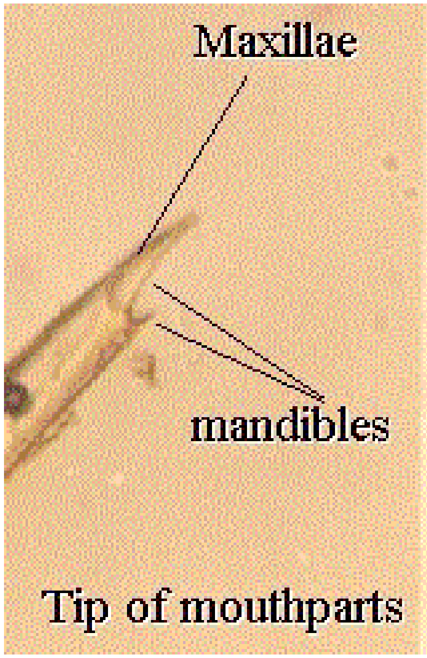
Oxygen flow rate ~ $Q\phi = \pi \phi r^4 \Delta P/(8 \mu L)$



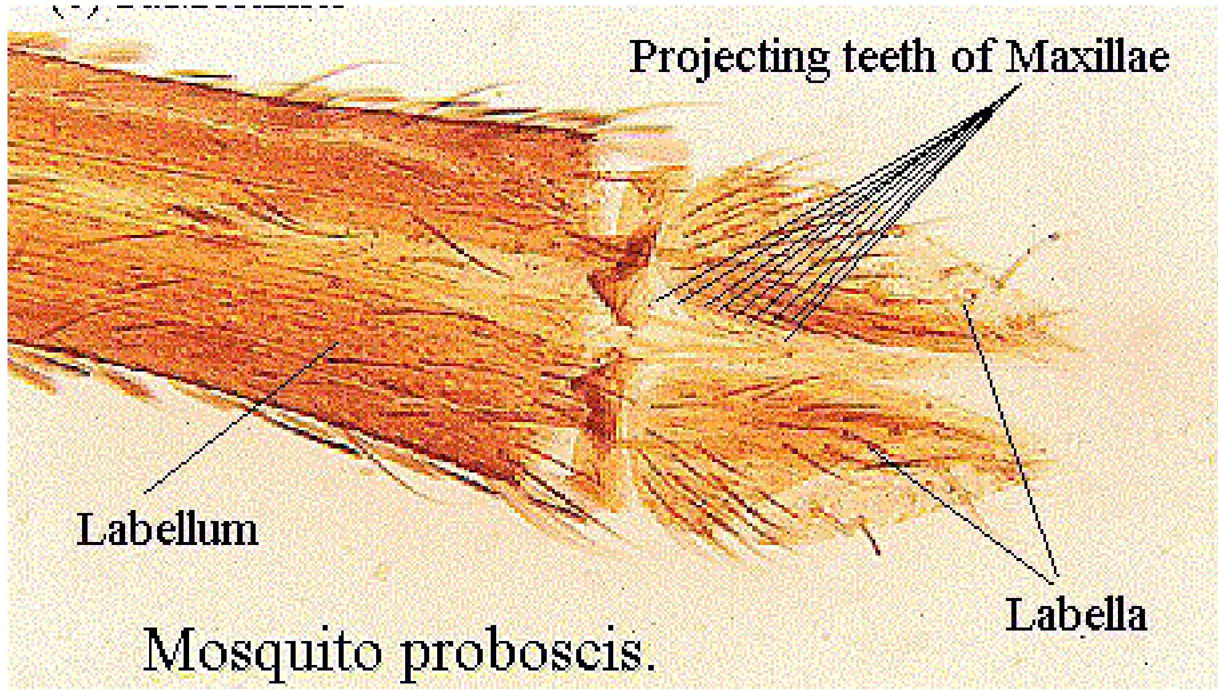


PIERCING-SUCKING

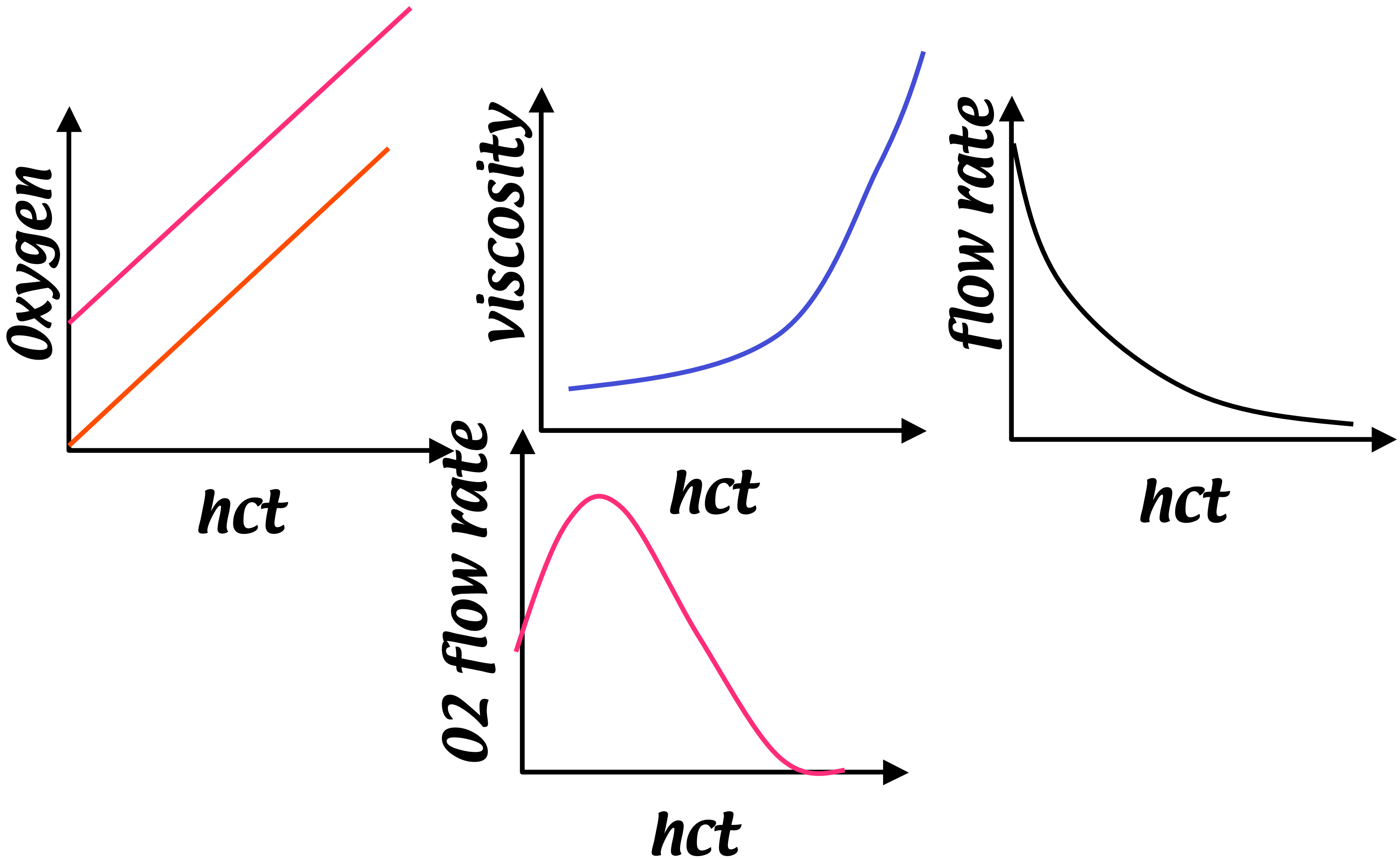
Mosquito



Tip of mouthparts



Mosquito proboscis.


Oxygen
hct
viscosity
hct
flow rate
hct
O2 flow rate
hct

Biology 427 Biomechanics 2004
Lecture 28. Coupled flow problems: waves and size limits to intertidal organisms.

- Recap dispersion and mass transport
- Laminar vs. turbulent boundary layers
- Environmental flows and size limits on creatures in wave-swept shores
- Evaluations

Dispersion depends strongly upon flow

$$\partial C/\partial t = D\nabla^2 C - U.\nabla C$$

change in concentration per time

diffusion of substance

convection of substance by flow

Dispersion depends strongly upon flow

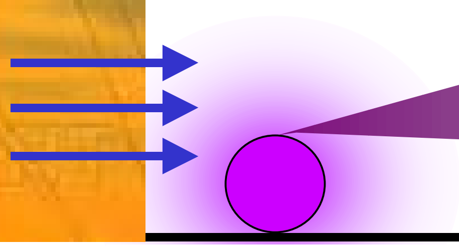
$$\partial C/\partial t = D\nabla^2 C - U.\nabla C$$

change in concentration per time

diffusion of substance

convection of substance by flow

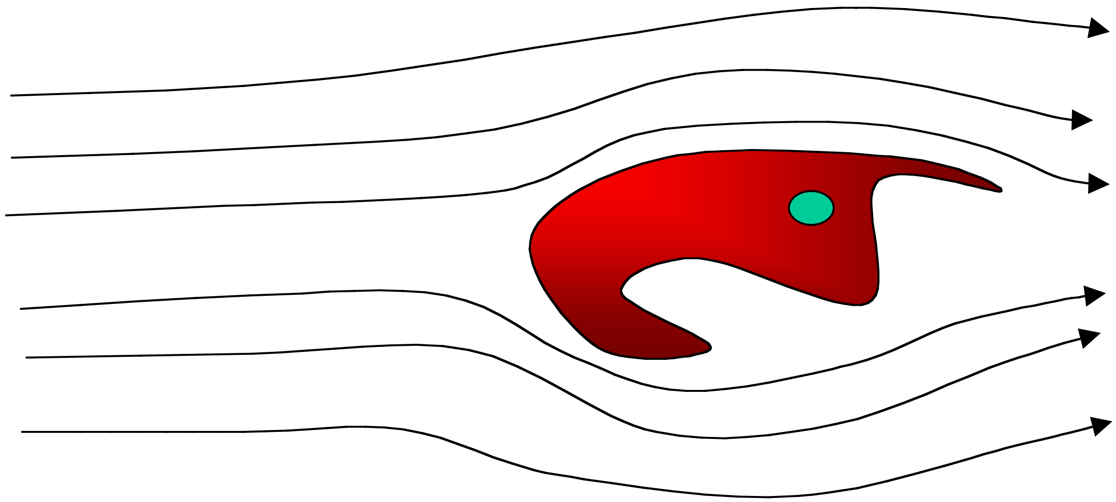
D ~< 0.000002, so U dominates



	Water	Air
ν	$1\ 10^{-6}$	$15\ 10^{-6}$
D_H	$1\ 10^{-7}$	$22\ 10^{-6}$
D_V	xx	$24\ 10^{-6}$
D_{O2}	$2\ 10^{-9}$	$20\ 10^{-6}$
D_{CO2}	$2\ 10^{-9}$	$14\ 10^{-6}$

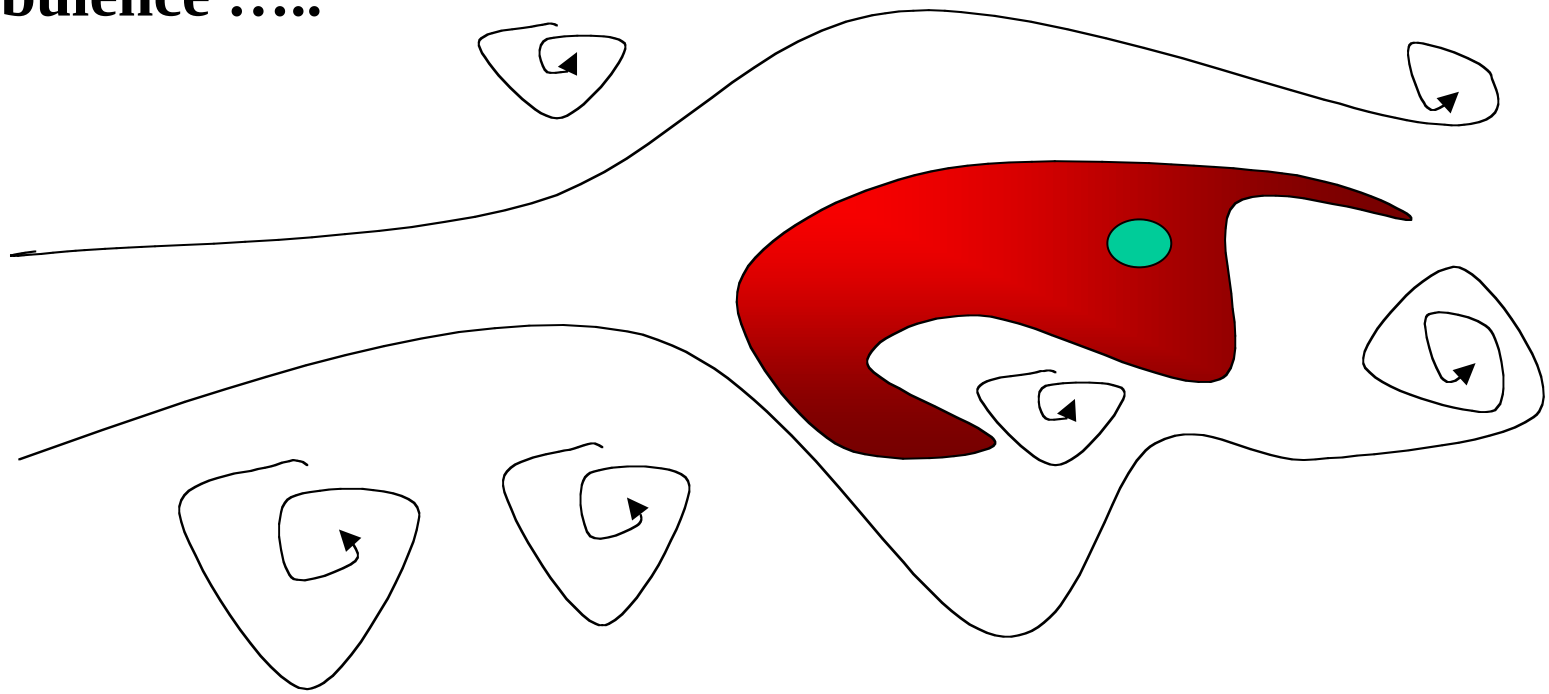
The nature of the flow also has a strong effect on mass transport….

The nature of the flow depends upon Reynolds number, shape, turbulence …..



The nature of the flow also has a strong effect on mass transport….

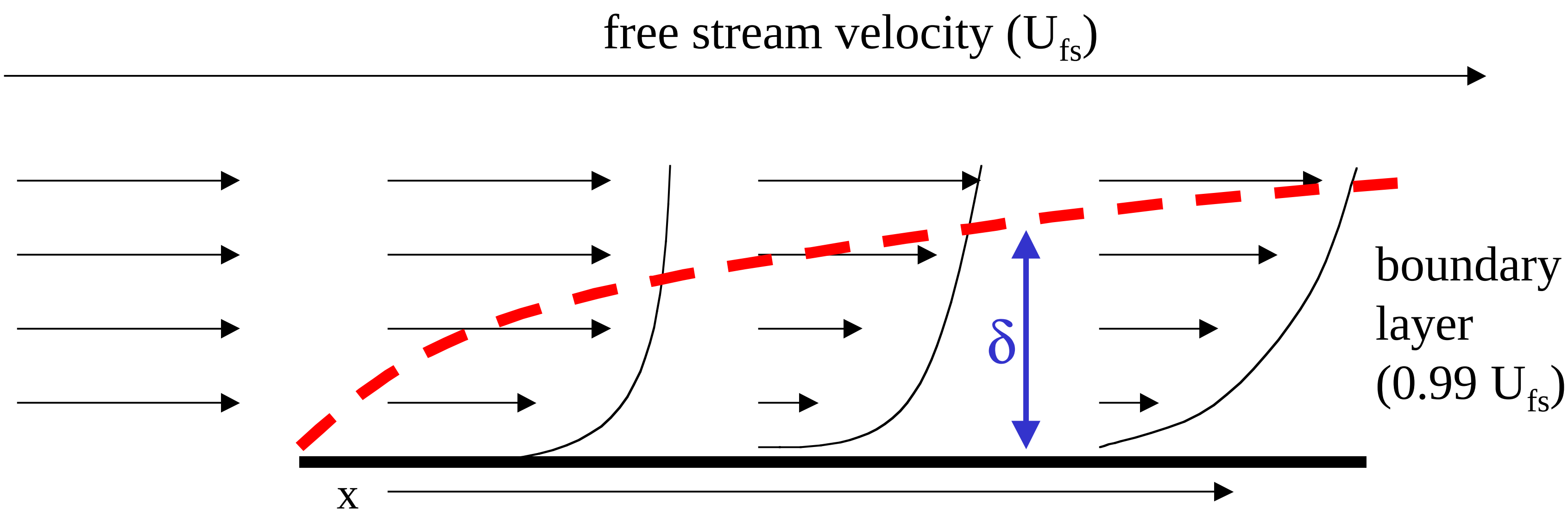
The nature of the flow depends upon Reynolds number, shape, turbulence …..



Complex flow fields confound easy predictions of U and tubulence creates an additional "diffusive" mechanism

How can we understand these phenomena?

A boundary layer of slower flow develops over an object due to the "no-slip" condition



For laminar flow:

$$\delta = 5\sqrt{\frac{x\,\mu}{\rho U}}$$

Closer to front of object (small x) -> thinner boundary layer

Faster flows (big U) -> thinner boundary layer

But, environmental flows are often turbulent

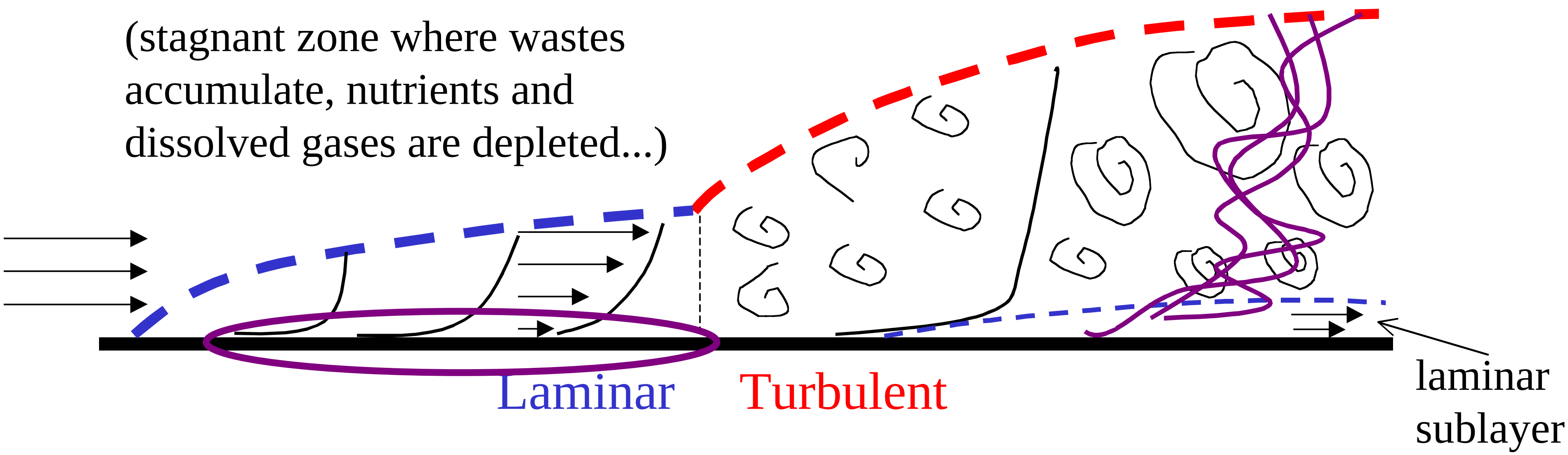
Turbulence enhances mixing in boundary layers. It thus leads to thicker boundary layers (but very steep gradients at the surface)

$$\delta_L = 5\sqrt{\frac{x\,\mu}{\rho U}}$$

$$\delta_T = 0.376\,x\sqrt[5]{\frac{\mu}{\rho x U}}$$

No cross-flow transport (vertical mixing)
-barrier to exchange of heat and materials
(stagnant zone where wastes accumulate, nutrients and dissolved gases are depleted...)

More mixing and cross-flow transport
-but, less of a refuge from forces of the free-stream flow

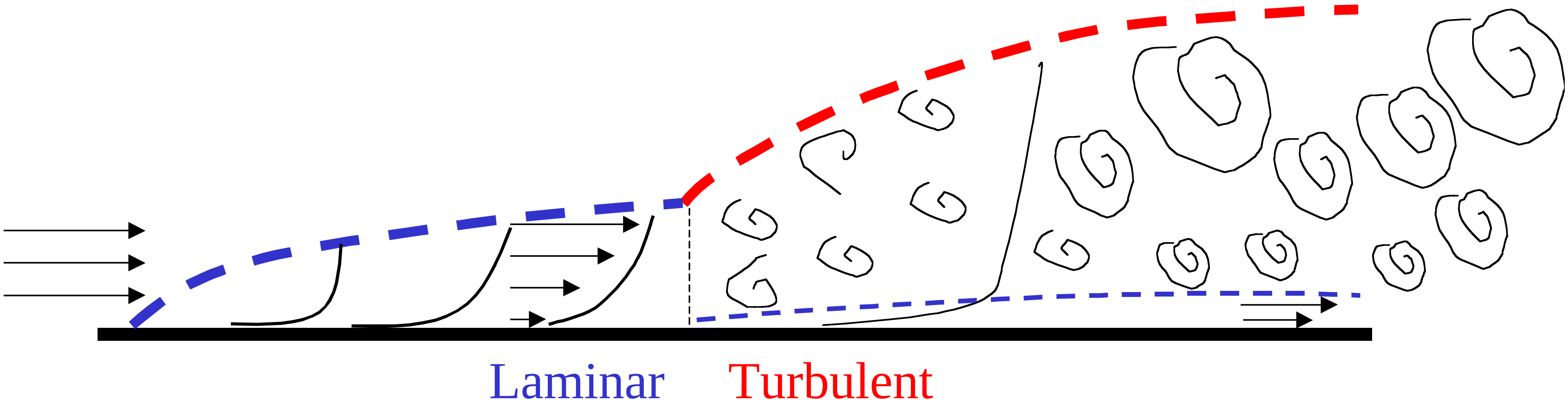


Momentum transport is mediated by vortical mixing:

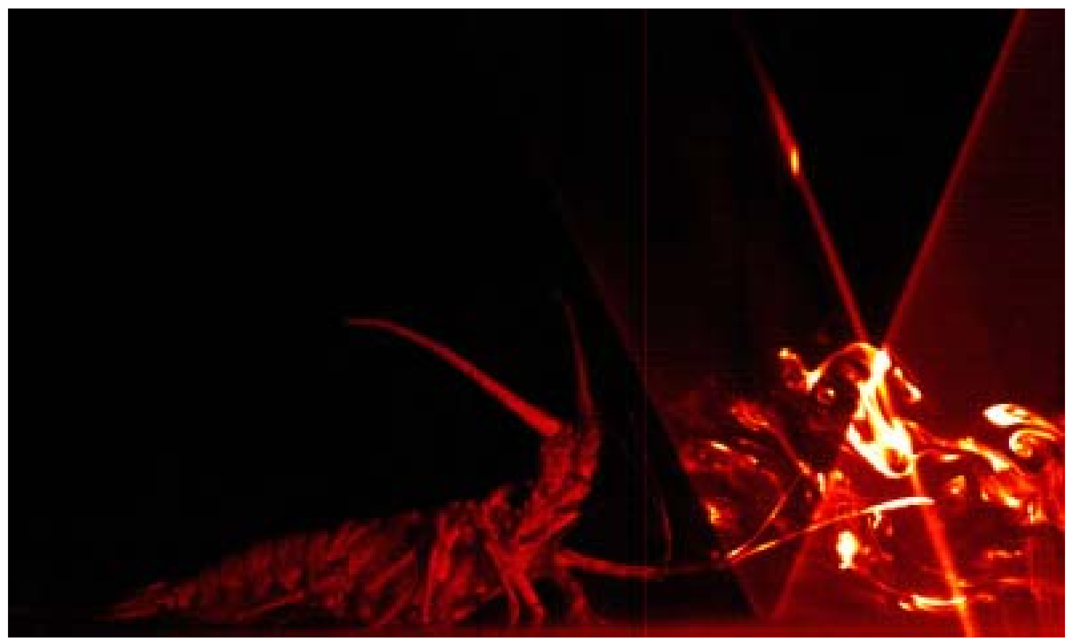
$$\tau=\varepsilon\ d(\rho u)/dz$$

ε is the eddy diffusivity.

Vortex size (ε) generally increases with height (z) above the surface. Thus the diffusivity of momentum mediated by vortical mixing increases with height.



Flow of materials, chemical signals, etc. will be vastly different in turbulent environments



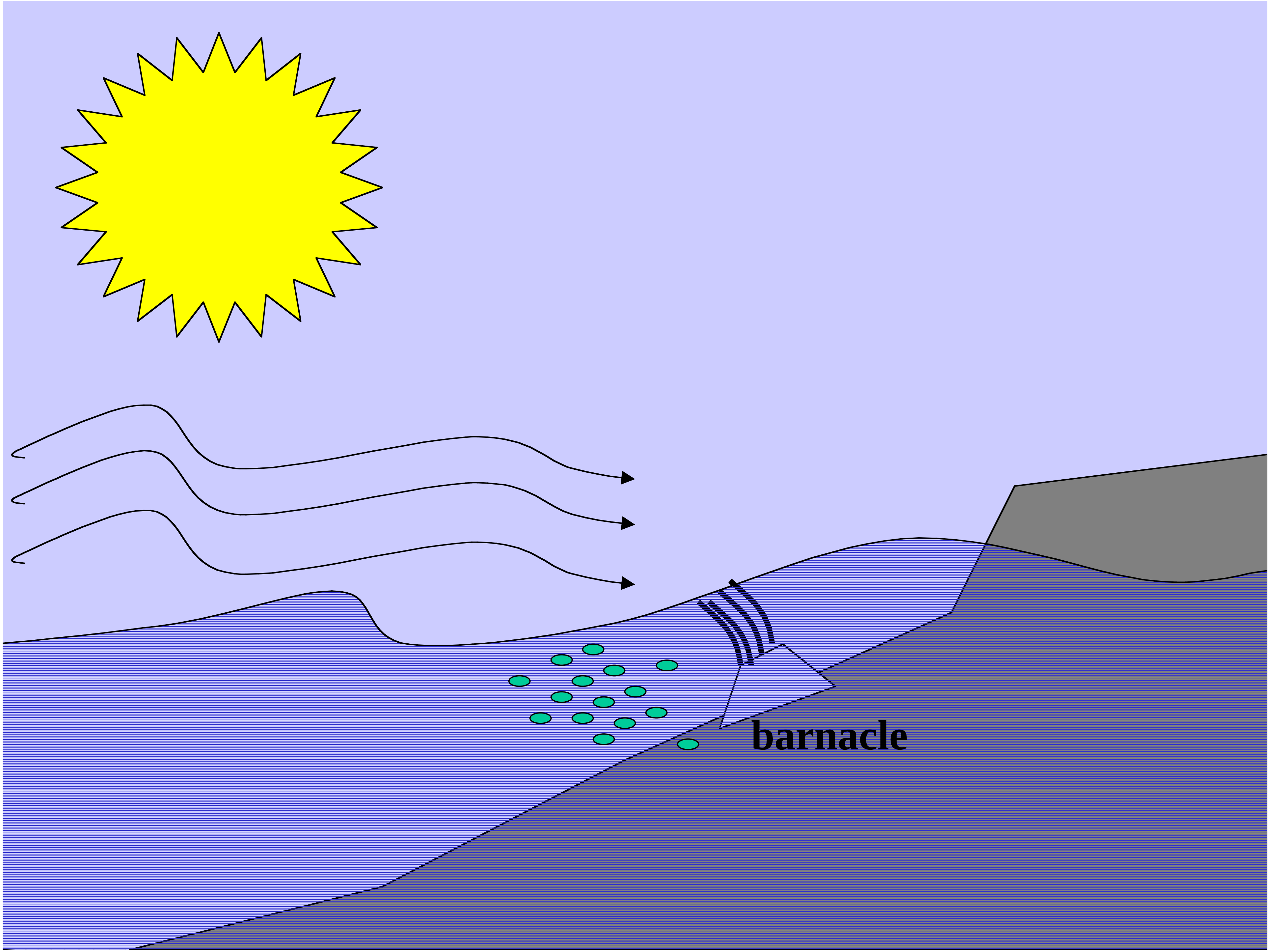
In many environments, flows are not only turbulent, but also unsteady

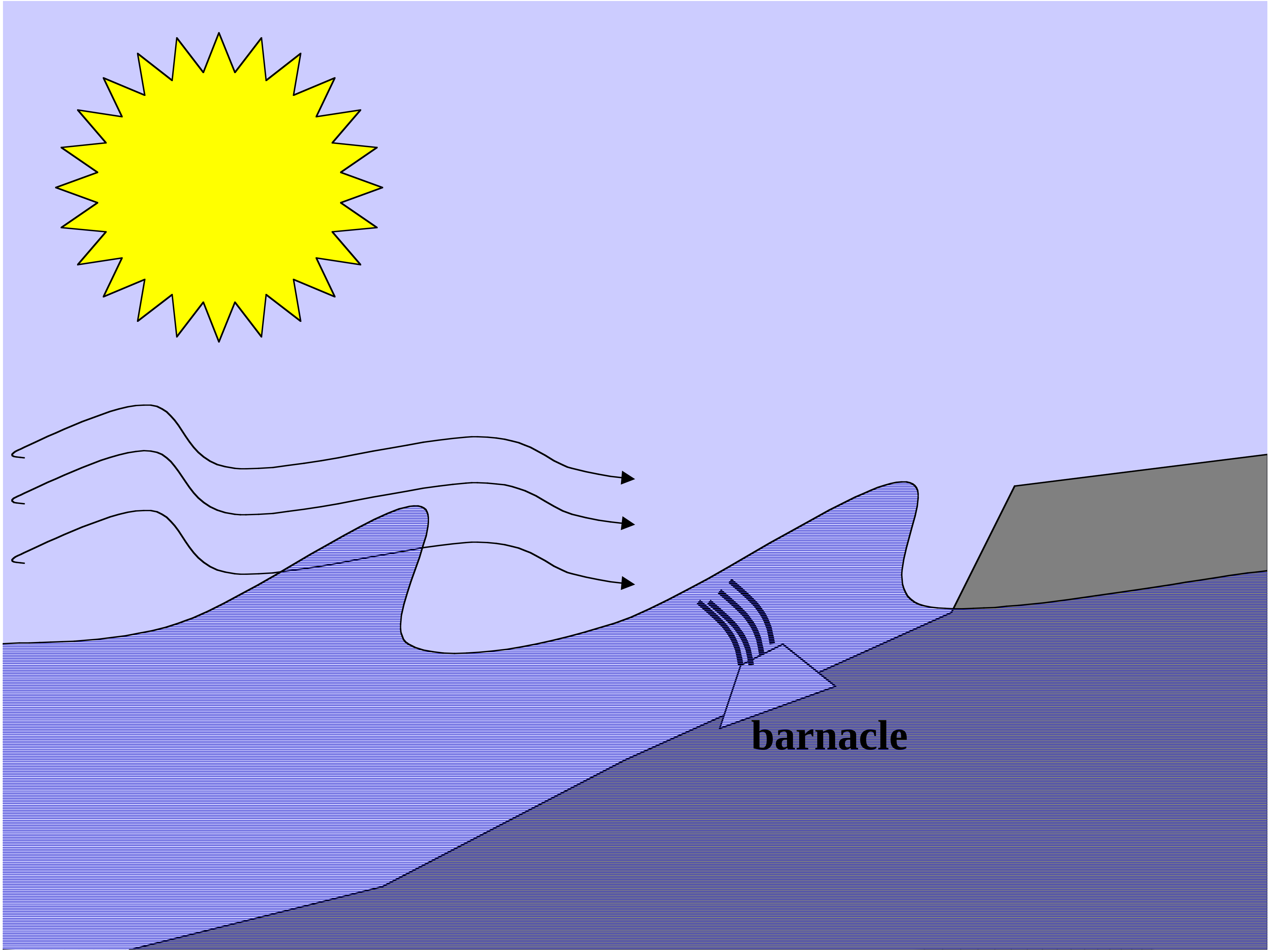
(Rocky intertidal zones, shallow reefs.....)

High velocities, huge accelerations

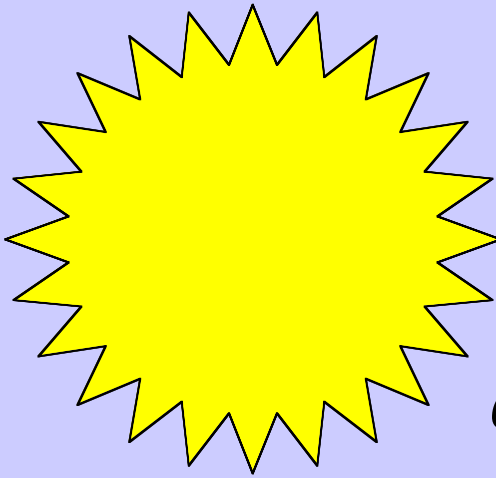
Many creatures that live on wave-swept shores are not as large as creatures that live in more protected habitats

Do the forces imposed upon wave-swept organisms limit maximum body size?

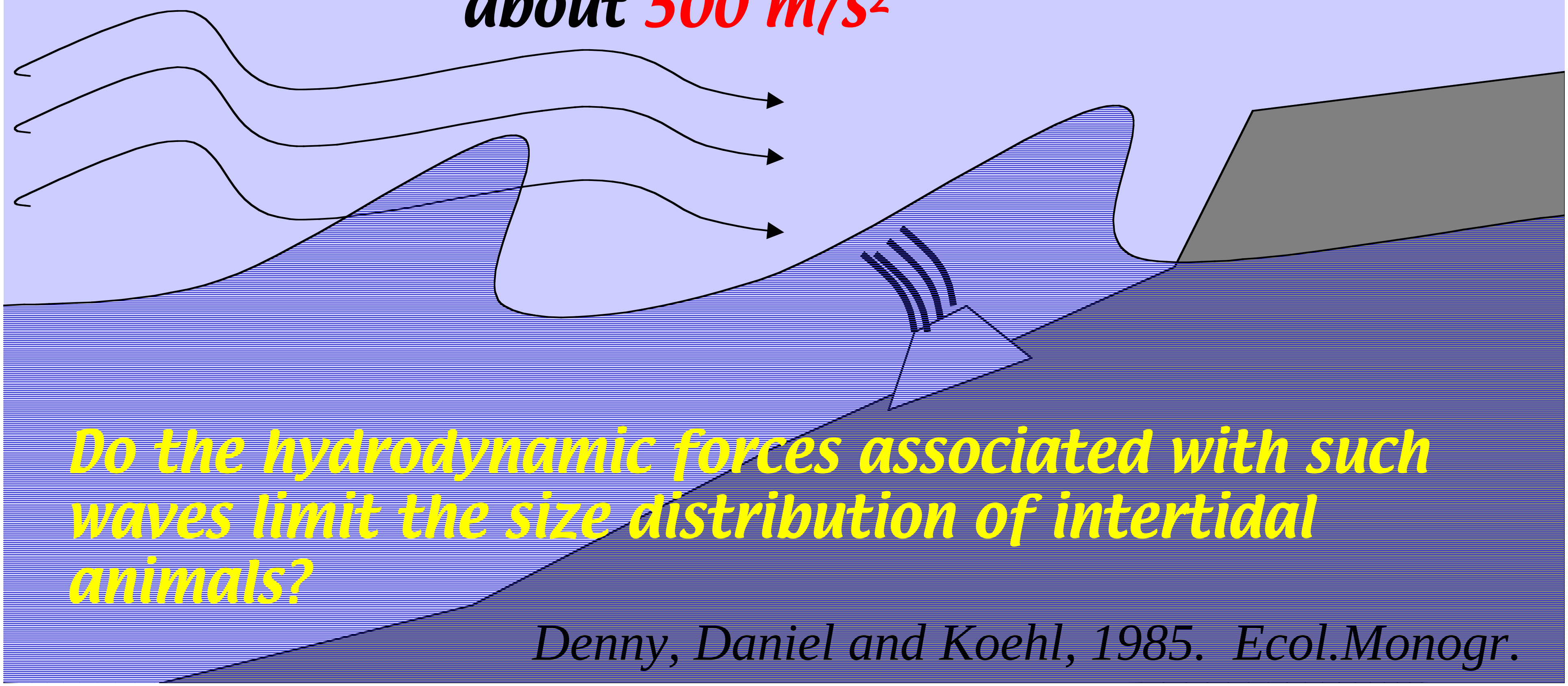

barnacle


barnacle

Wave dynamics in intertidal environments are impressive

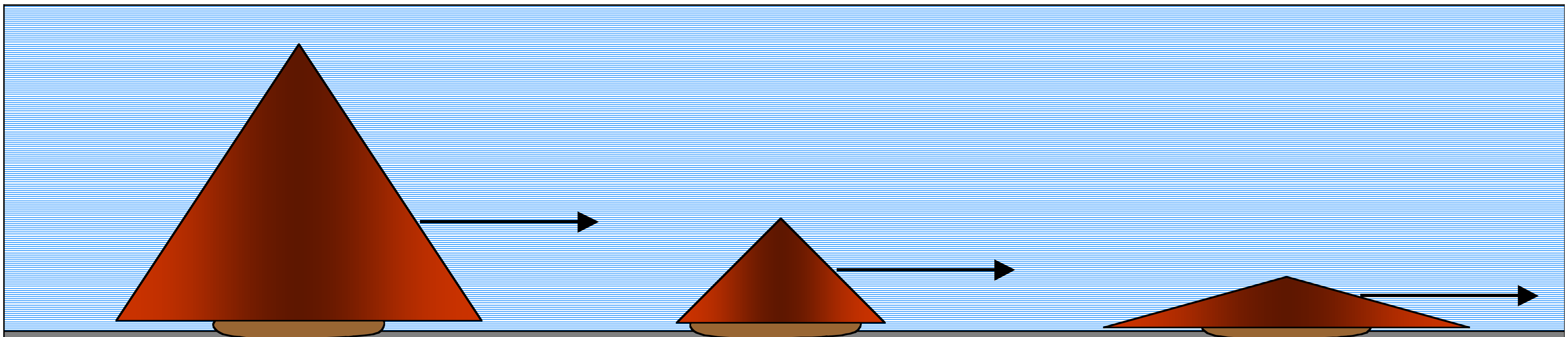


- Wave heights of 2 - 4 m (up to 20 m!)
- With such wave heights, we can expect crest velocity at breaking to be about 15 m/s with accelerations of about 500 m/s^2



Do the hydrodynamic forces associated with such waves limit the size distribution of intertidal animals?

Denny, Daniel and Koehl, 1985. Ecol.Monogr.



*One key observation: for a host of intertidal creatures, their strength does not depend on size -> only attachment area

Strength (σ_{br}) = Dislodgement force/attachment area

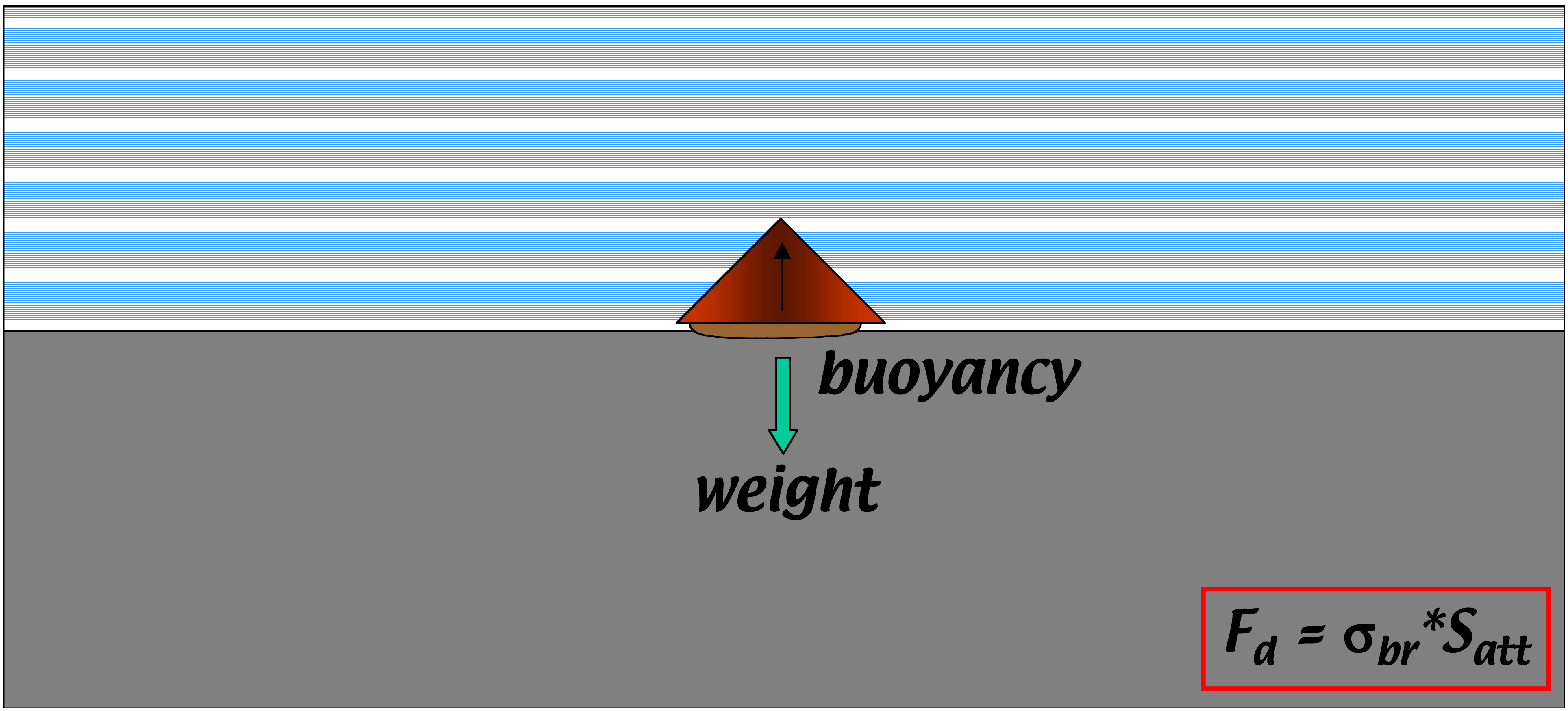
What is the force resisting dislodgement?

$$F_d = \sigma_{br} * S_{att}$$

What are the forces acting on this limpet?

weight = $m\,g$

buoyancy = $\rho\,V\,g$

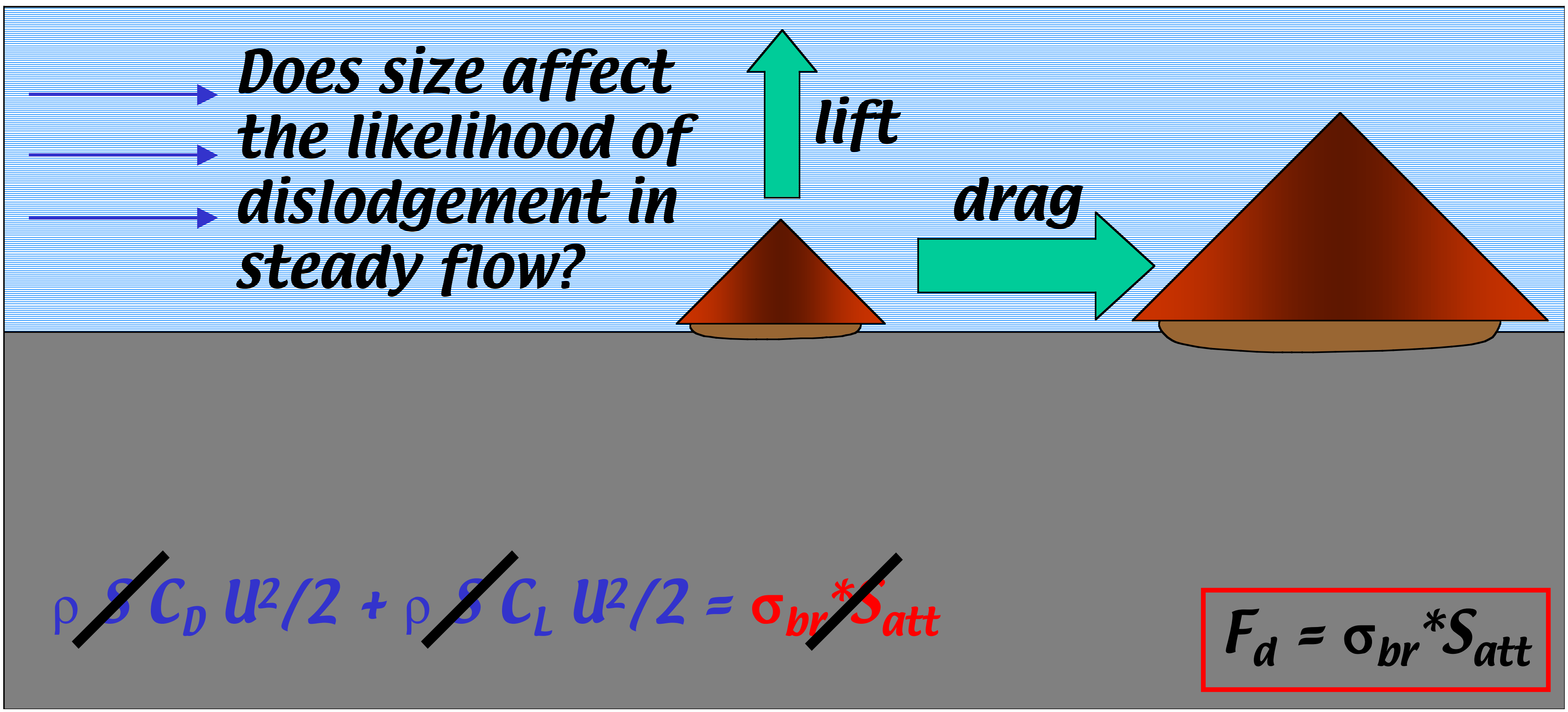


What are the forces acting on this limpet?

$drag = \rho\ S\ C_D\ U^2/2$

$lift = \rho\ S\ C_L\ U^2/2$

Geometrically similar creatures in steady flow cannot explain a size limit!



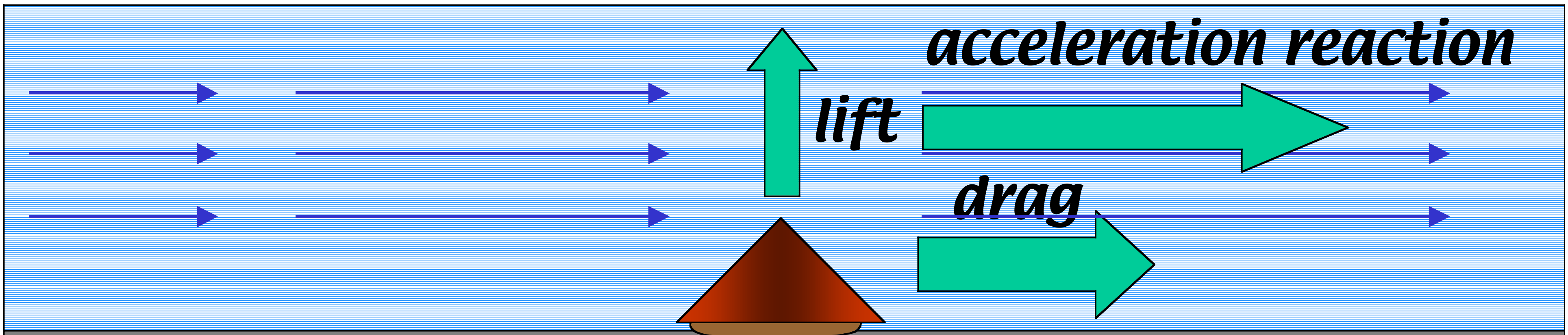
What are the forces acting on this limpet?

drag = $\rho\, S\, C_D\, U^2/2$

lift = $\rho\, S\, C_L\, U^2/2$

acceleration reaction = $\alpha \rho\, V\, dU/dt$

Does size affect the likelihood of dislodgement in unsteady flow?



$$\rho\, S\, C_D\, U^2/2 + \rho\, S\, C_L\, U^2/2 + (\alpha+1)\rho\, V\, dU/dt = \sigma_{br} {*} S_{att}$$

$$\rho\, \cancel{S}\, C_D\, U^2/2 + \rho\, \cancel{S}\, C_L\, U^2/2 + (\alpha+1)\rho\, \cancel{S} {*} L\, dU/dt = \sigma_{br} {*} \cancel{S}_{att}$$

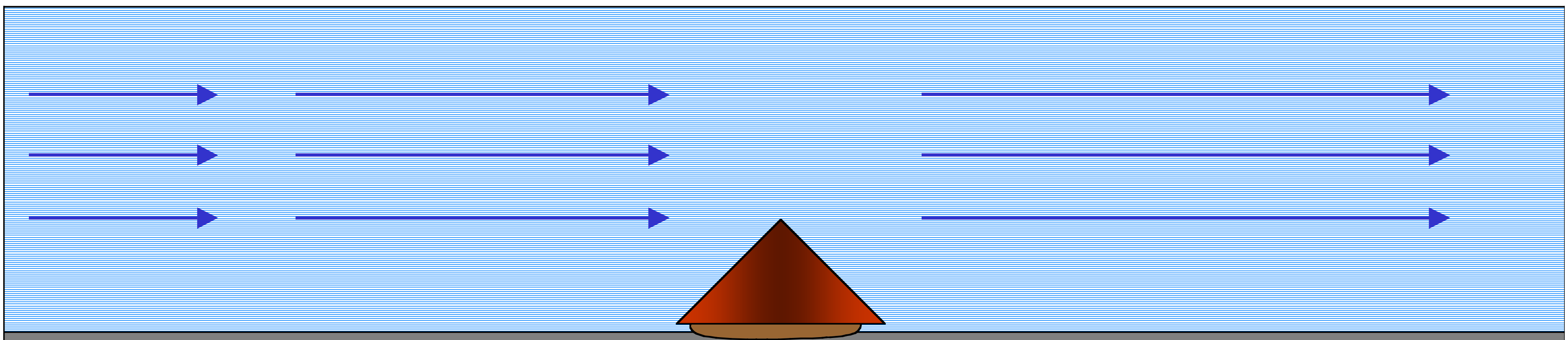
*Forces caused by acceleration scale with size!

$F_d = \sigma_{br} {*} S_{att}$

Why be bigger?

$$\rho\, S\, C_D\, U^2/2 + \rho\, S\, C_L\, U^2/2 + (\alpha+1)\rho\, V\, dU/dt = \sigma_{br} * S_{att}$$

volume ∝ reproductive output!



May help:

- *-ward off predators*
- *-overgrow competitors*
- *-survive drying/heating (less surface area/vol)*
- *-survive damage from projectiles, etc.*
- *-be more efficient metabolically*

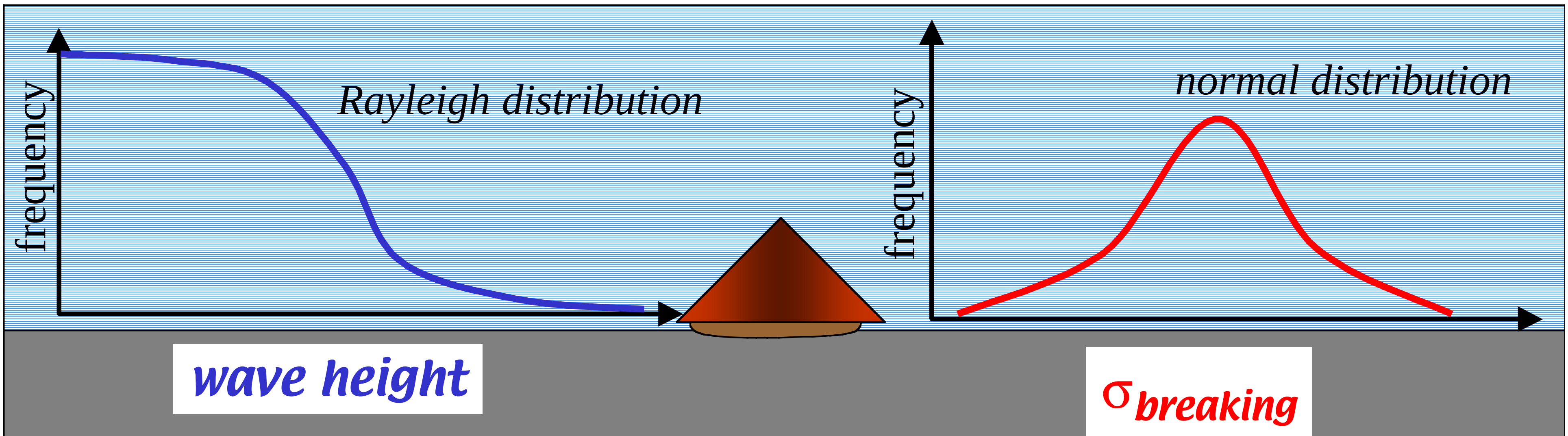
What is the probability of survival?

$$\rho\ S\ C_D\ U^2/2 + \rho\ S\ C_L\ U^2/2 + (\alpha+1)\rho\ V\ dU/dt = \sigma_{br}{}^{*}S_{att}$$

*left hand side cannot exceed right hand side

Probability of survival depends on time and these distributions

$$P_s = f(time, distributions)$$



Wave velocity and acceleration are correlated with wave height.

Normal distribution of adhesive strengths in a population

What is the probability of survival?

$$\rho\, S\, C_D\, U^2/2 + \rho\, S\, C_L\, U^2/2 + (\alpha+1)\rho\, V\, dU/dt = \sigma_{br}{}^{*}S_{att}$$

*Measured velocities and accelerations, coefficients of lift and drag, and added mass coefficients of several creatures

P_s = f(time,distributions)

stribution

normal distribution

correlated

dis

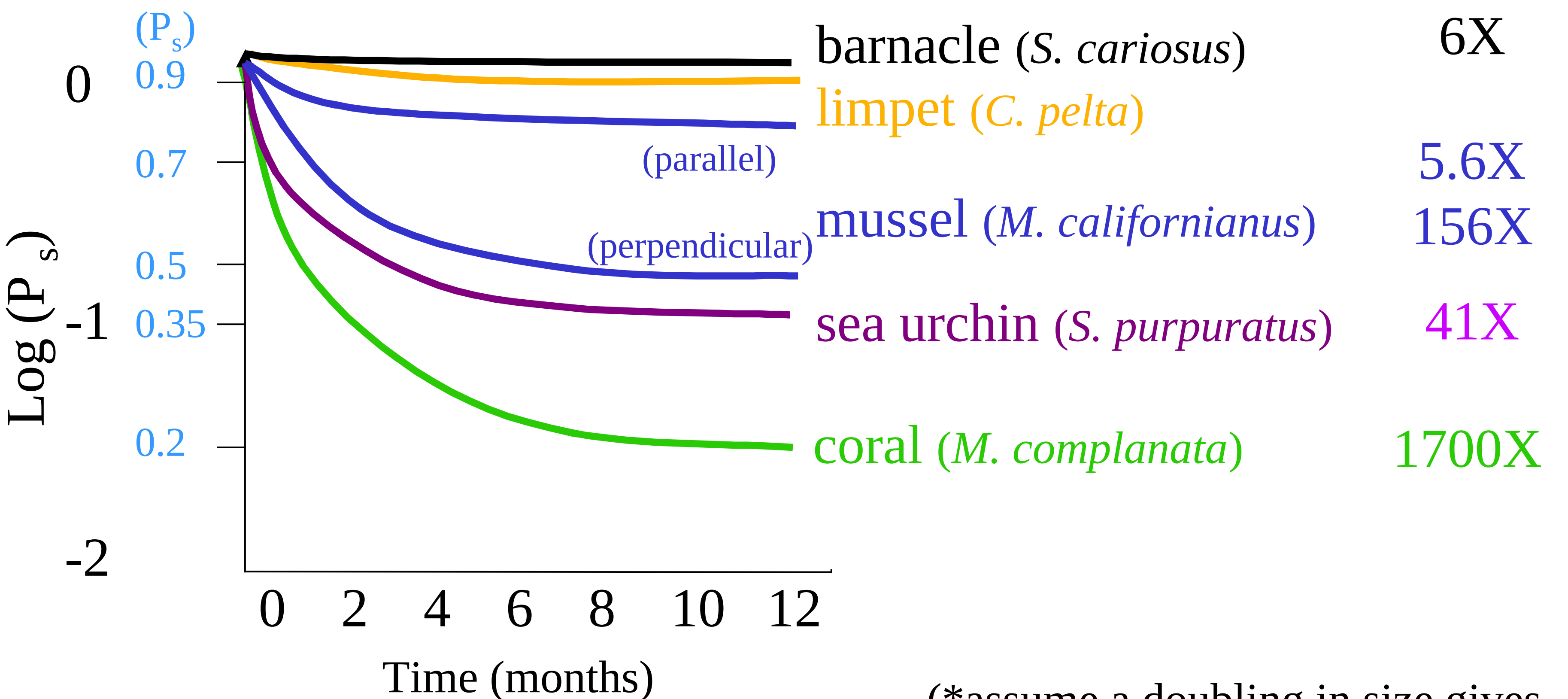
adhesive st

a population

*Denny, Daniel and Koehl, 1985. Ecol.Monogr.

What is the probability of survival?

How much less likely to survive 12 months if twice as big?

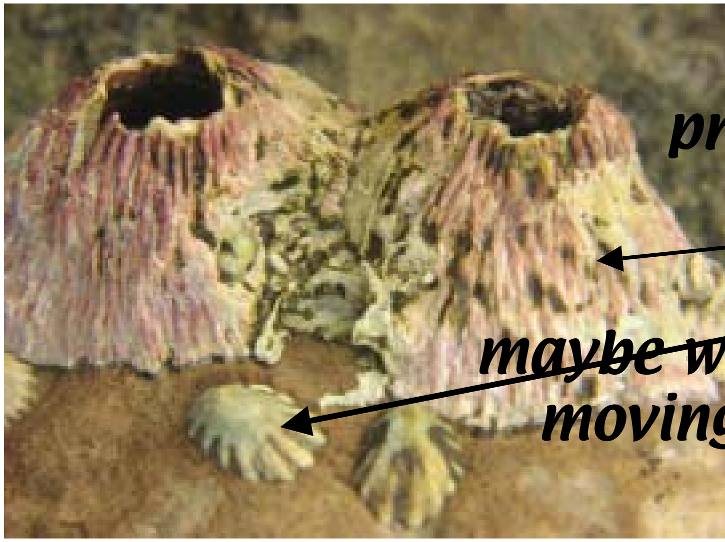


(*assume a doubling in size gives 8X reproductive capacity per year)

Hand-drawn recreations from
Denny, Daniel and Koehl, 1985. Ecol.Monogr.

Which animals may be mechanically size-limited?

How much less likely to survive 12 months if twice as big?



probably not

maybe when moving

barnacle (*S. cariosus*) 6X

limpet (*C. pelta*)

5.6X

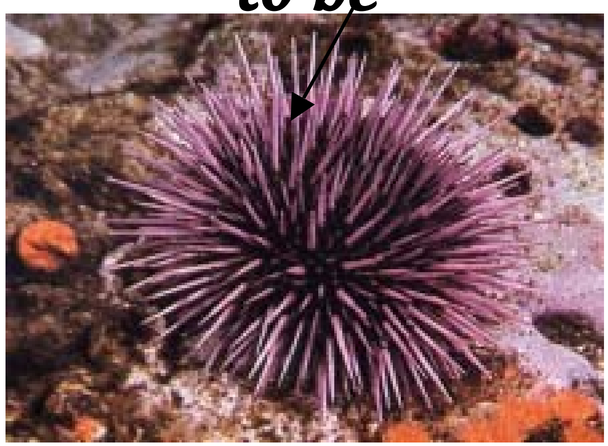
mussel (*M. californianus*) 156X

sea urchin (*S. purpuratus*) 41X

coral (*M. complanata*) 1700X

maybe when solitary

appears to be



uses breakage for dispersal

Denny, Daniel and Koehl, 1985. Ecol.Monogr.