SMS-204: Integrative marine sciences.

Chapter 5: The Reynolds number, low and high Reynolds number flows and swimming.

The Reynolds number (Re):

The Reynolds number is a non-dimensional number that represent the ratio between inertial forces and viscous forces acting in a given flow.

1. Inertial forces in a flow (per unit volume): $\rho U^2/L$

   {Force/Volume=ρ·acceleration=ρU(velocity) / (time=L/U) = $\rho U^2/L$}

where U is a characteristic velocity, L a characteristic length and ρ is the density.

2. Viscous forces in a flow (per unit volume): $\mu U/L$ (viscous shear stress) × L^2 (Area) / L^3(per unit volume) = $\mu U/L^2$

➔The ratio of these two forces IS the **Reynolds** number:

   $Re = \rho UL/\mu = UL/\nu$ (μ is the dynamic viscosity while $\nu=\mu/\rho$ is the kinematic viscosity nearly 1×10^{-6} m^2 s^{-1} for water).

When $Re \ll 1$ viscous forces dominate the flow while a $Re \gg 1$ indicates that inertia (dynamic) forces dominate the flow.

The great advantage of using non-dimensional numbers, such as Re, is that when we want to compare two flows, they are likely to be similar if we match their Re. Thus, when we want to study a design of an airplane we don't have to build an exact model. We can scale the model down (decrease L) while changing ν and U to match the Re of the full-sized airplane (care should be made to keep *all* relevant non-dimensional numbers similar, there is a whole bunch of these animals out there... For example, the Mach number, the ratio of U to the speed of sound, should be similar when supersonic effects are important).

Low Re flows are those that have $Re = UL/\nu < 1$. Since $\nu \sim 10^{-6}$ m^2/sec for water, this implies that $UL < 10^{-6}$ m^2/sec. For an organism that swims (or sinks) about one body-length per second, that means $L < 10^{-3}$m = 1mm.

Many marine organisms experience Low Reynolds number flows. These organisms include viruses, bacteria, phytoplankton and small zooplankton. It is therefore important that we understand the significance of these flows in aquatic environments.

In addition, near every boundary of the fluid (with bottom, surface, sides, and the surface of organism) there exists a viscous sub-layer in which viscous forces dominate over inertia called a viscous boundary layer connecting the fluid that does not move right next to the boundary (due to the no-slip condition) and the flow away from the boundary. This region is also characterized by a low Reynolds number flow.

Some important processes occur in this regime; the <u>sinking</u> of many marine particles to depth (with their carbon) is considered a low Reynolds number phenomena. <u>Swimming</u> by bacteria, ciliates and flagellates are low Reynolds number phenomena. <u>Feeding</u> by

small organisms has to be adapted to strategies in which inertia contributes little or not at all.

Sinking at low Re # regime:

The process of settling is governed by a balance between three forces: gravity, buoyancy, and drag.

Newton's 2nd law states: $ma = m\,dv/dt = F_{gravity} - F_{buoyancy} - F_{drag}$

Where m is mass, $a = dv/dt$ is the acceleration and F denotes force.

A settling particle will accelerate under gravity until it reaches a constant speed. At that point in time, there is not acceleration $(dv/dt = 0) \rightarrow F_{gravity} = F_{buoyacy} + F_{drag}$.

What is likely to affect the settling velocity of a particle?

    a. The particle's excess density to the fluid $(\rho_{particle} - \rho_{fluid}) \times g$ [(Kg/m³)(m/sec²)], same as the difference between the gravity and buoyancy forces.

    b. The fluid's viscosity, μ [kg/m/sec]

    c. The particle's surface area or cross sectional area, both scale as $\sim D^2$ [m²]

to a lesser degree:

    d. The particle's shape

    e. Proximity to other particles

From dimensional analysis alone we find that:

    $V_{settling} \propto (\rho_{particle} - \rho_{fluid})gD^2/\mu$ [m/sec].

    Additionally, a function of a non-dimensional variable may also be represented in the equation. The only relevant non-dimensional parameter is the Reynolds number, $Re = \rho_{fluid}DV_{settling}/\mu$.

So: $V_{settling} \propto func(Re)\,(\rho_{particle} - \rho_{fluid})gD^2/\mu$. ($\propto$ – denotes 'proportional to')

It turns out (and confirmed by experiments) that for spheres with Re <1:

$$V_{settling} = (\rho_{particle} - \rho_{fluid})gD^2/18\mu.$$

This equation was derived by Stokes in the middle of the 19th century. It implies that the drag force on a sphere at low Re is:

$$F_{drag} = F_{buoyancy} - F_{gravity} = 3\pi\mu DV_{settling},$$

linearly proportional to velocity ($V_{settling}$), diameter (D) and the viscosity coefficient (μ).

Feeding at low Re # regime:

In order to <u>capture</u> pray, feeding appendages of small marine organisms have to <u>encounter</u> it. Simplifying this problem by considering the encounter of a spherical particle with a long cylindrical appendage in low Re (computed from the relative velocity between appendage and particle, the diameter of the appendage and the fluid's kinematic viscosity), several mechanisms were identified (see Fig. 1):

    A. Direct interception, the particle moves with the flow and encounter the appendage.

B. Inertial impaction, the particle crosses streamlines due to its inertia and hit the appendage.

C. Gravitational deposition, the particle settles onto the appendage.

D. Diffusional deposition, the particle moves by Brownian motion (diffusion) towards the appendage.

E. Electrostatic attraction, the particle is attracted to the appendage by electrical forces (important only in fresh water).

These mechanisms are not exclusive and a combination of mechanisms can result in the particle being encountered by the appendage.
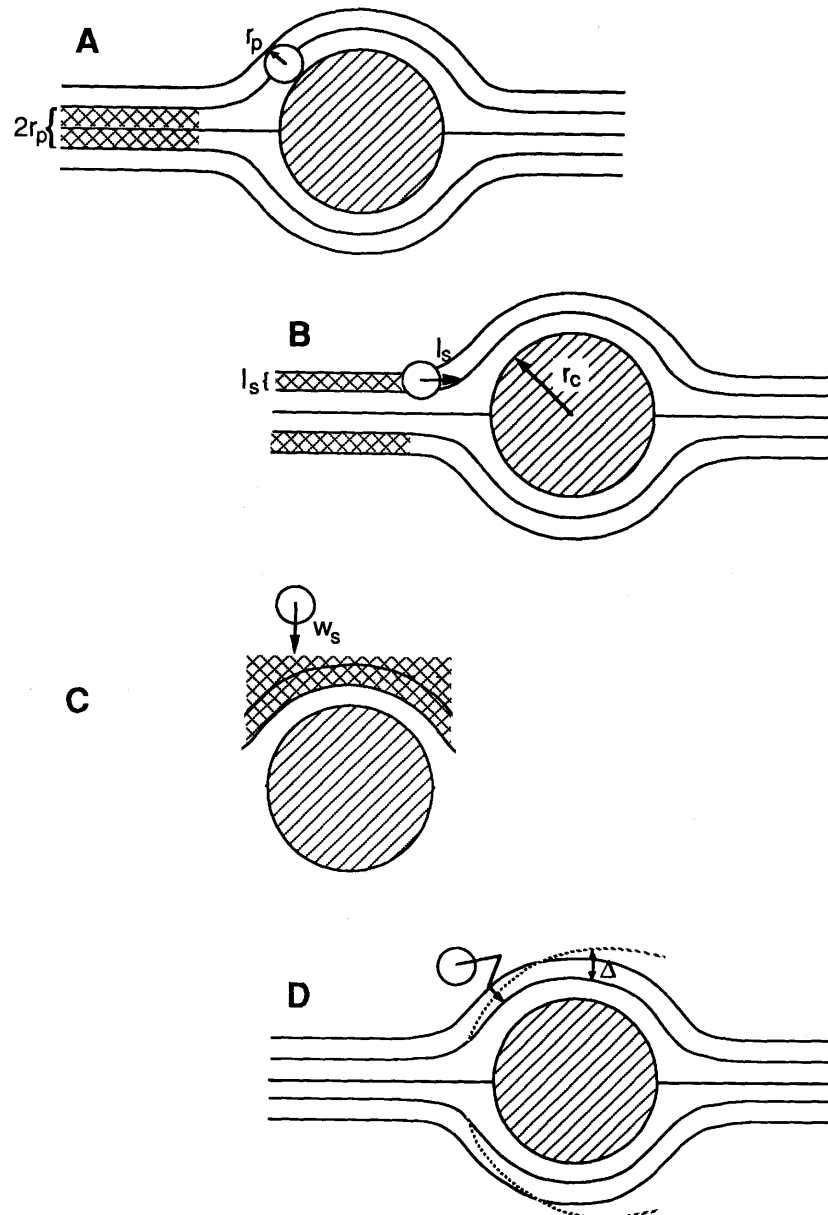
Figure 1. Mechanisms of capture of a particle by a large cylindrical appendage (seen in cross section). A. Direct interception, the particle moves with the flow and encounter the

appendage. B. Inertial impaction, the particle crosses streamlines due to its inertia and hit the appendage. C. Gravitational deposition, the particle settles into the appendage. D. Diffusional deposition, the particle move by Brownian motion (similar to diffusion) towards the appendage. From Shimeta and Jumars, 1993.

These mechanisms are also likely to be important in larger *Re* number flows in the viscous sub-layer (where the *Re* number is low) that exists around the collecting appendages. To learn about how different feeding at low *Re* number is, perform the following experiment: Try to capture beads immersed in Corn Syrup using a fork, a spoon and a knife. The Re will be similar to that of a feeding appendage, about 1.5 mm wide in water.

In low *Re* flows the disturbance created by moving an organ through the water extends many (tens to hundreds!) radii into the fluid. A settling sphere at low *Re* numbers (e.g. in a very viscous fluid) will not sink on the fork but flow around it (remember, inertia is very small). Approaching the fork or spoon to a particle will cause them to move away. The easiest way to approach a particle is with the knife, edge-on. That is because in that orientation the least fluid perturbation propagates towards the particle.

Laminar flows.

Laminar flows are flows in which the fluid is well organized in space and time. Adjacent layers of fluid flow smoothly flow on top each other. Low *Re* flows are laminar.

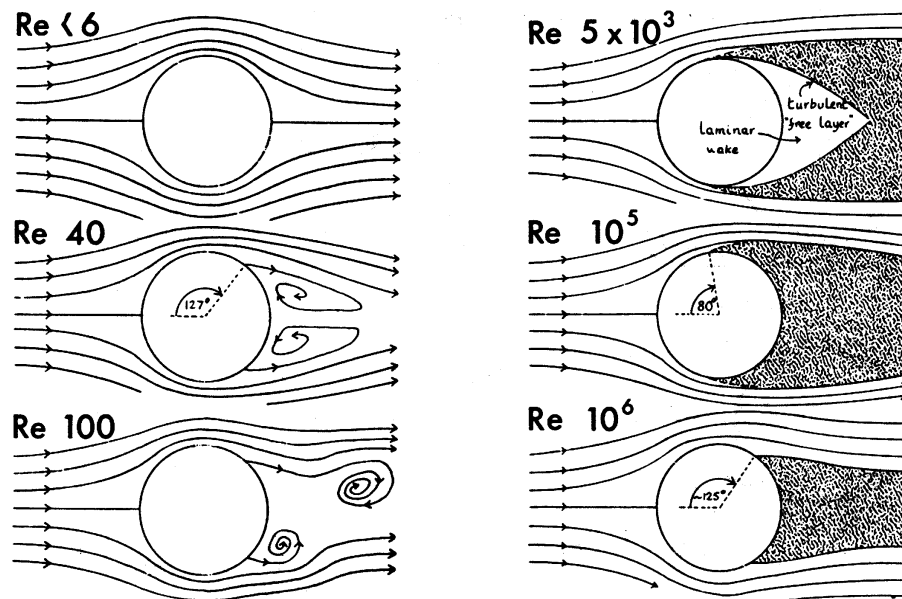## Increasing the Re: Flow at constant speed around a body.

Figure 4.3 Flow patterns around circular cylinders normal to the flow, for Reynolds numbers from less than six to about 10^6.

Figure 2, from Middleton and Southard, 1984.

Flows around a cylinder (Fig. 2):

At low Re (Re<6) the flow is steady and symmetric with respect to the cylinder. The flow accelerates towards the middle point where velocity is maximum (streamlines are closer together) and thus the pressure there is minimal (Bernoulli).

As we increase the Re (~40) fore-aft symmetry is broken and <u>flow separation</u> occurs. Fluid from the boundary layer separates away from the body. There are two counter-rotating attached vortices on the lee side of the cylinder.

At higher Re (~100) these vortices periodically break away from the cylinder and are shed down stream (known as 'Von Karman trail').

At higher Re (~1000) a turbulent (non-coherent, non-periodic, disorganized) wake exists at the back of the body with a laminar wake (where fluid is trapped) closer to the body.

At higher Re (~100000) the turbulent wake occupies a large portion of the back of the body.

Increasing the Re (~1000000) decreases the area of the turbulent wake.

The Re when the transition to turbulence occurs for a given body depends on the shape of the body and presence/size of perturbations in the flow (which can be initiated in smaller Re by the object being non-smooth, e.g. a golf ball).

<u>Flow separation</u> can occur in both laminar and turbulent flows. When the fluid in the boundary layer (the layer affected by viscosity) has exhausted its kinetic energy along the boundary (due to viscous dissipation) it detaches and continues along with the free flow.

Drag force on a body:

Two stresses (forces per unit area) act on bodies in flow. <u>Skin friction</u>, the stress parallel to the body, where the no-slip condition applies and a <u>form drag</u>, the stress due to the pressure (or normal stress) on the body. The sum of both integrated over the surface area of the body, is the drag, the force that needs to be applied to keep the body moving at a constant speed.

It is convenient to define a <u>drag coefficient</u>, C_D, a non-dimensional parameter defined as the ratio of the drag force to half the inertial force: $C_D = F_{drag}/\{0.5\rho U^2 A\}$, where A is the object's cross-sectional area.

Figure 7.13 Log–log plot of drag coefficient C_D as a function of Reynolds Number Re for spheres, transverse cylinders, and face-on discs. The broken straight line represents Stokes's law.
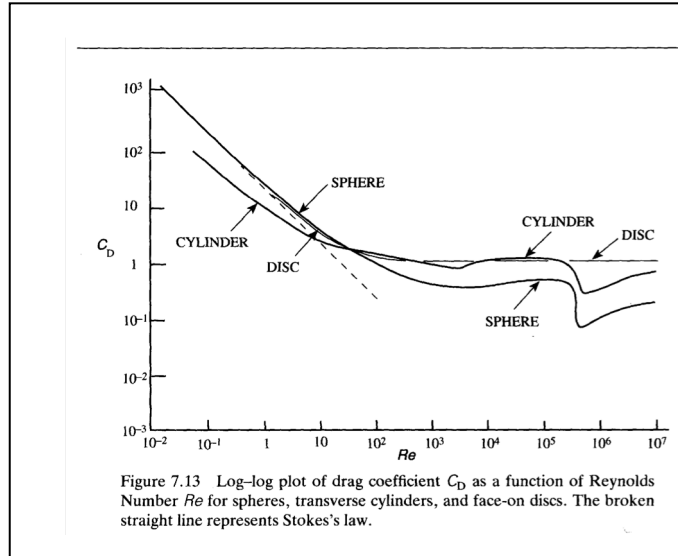
Figure 3. Change in drag coefficient as function of Re.

The change in the drag coefficient as function of the Re is depicted in Fig. 3. For low Re, the drag coefficient is proportional to $1/Re$ (which basically means the drag force is due to viscous forces). At $Re>100$ the drag coefficient becomes constant with Re. A sudden lowering of the drag coefficient occurs around $Re\sim1,000,000$ (termed drag crisis) due to a sudden reduction in the size of the turbulent wake around the body as seen in Fig. 2.

Drag force in a pipe:

Many flows also experience transitions as function of the Re. Flow in pipes (or rivers) change as function of Re. At low Re the flow is laminar and has a parabolic profile. At large Re the mean flow is much more homogeneous in the core and a boundary layer where velocity changes very rapidly is present near the walls (Fig. 4).
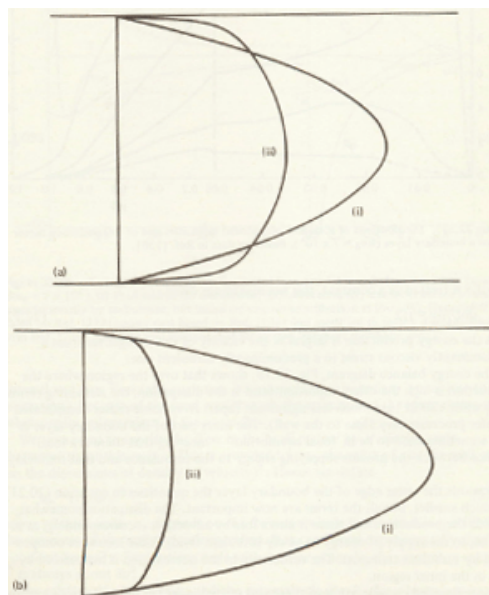
Fig 4. Comparison of laminar (i) and turbulent (ii) velocity profiles in a pipe for (a) the same mean velocity and (b) the same driving force (pressure difference). Figure 22.16 from Tritton, D.J. 1977. Physical Fluid Dynamics. Van Nostrand Reinhold, NY. p. 277.

When turbulence is present there is *more* drag on the flow (Fig 4b) for the same along-pipe pressure gradient due to exchange of momentum between fluid within the pipe and the boundaries. In laminar flows the momentum flux is molecular and thus much smaller.

A turbulent (high *Re*) flow is:
1. A flow, not a property of the fluid.
2. Unsteady and inhomogeneous.
3. Mixes momentum and solutes much faster than laminar flows.
4. Cannot be described simply by a steady velocity field.
5. A threshold phenomena. Below a critical *Re* it would not be turbulent.

Swimming

We cannot do justice to this topic in just one section. We therefore chose to concentrate on two extremes, the low Re range of microorganisms and the high Re flow of swimming fishes. If we assume the organism to be swimming at one body length per second in water, then $Re = L\text{U}/\nu$, which numerically (because $\text{U}=L$ s^{-1}) works out to be $Re = L^2/\nu \sim 10^6 L^2$ (L in m). Thus, a 1 μm bacterium has $Re = 10^{-6}$, a zooplankter of 1 mm length has $Re = 1$, and a 0.5-m fish a $Re = 2.5$ x 10^5. Size matters when it comes to swimming for marine organisms. Thus, in different life stages (sizes) different swimming strategies/efficiencies are expected for the same organism (larvae most often swim differently than adult organisms). Cod, for example, span five orders of magnitude in size from egg to adult and an even larger range in Reynolds number.

Newton's third law of motion is critical for swimming (remember, its state that ***All forces occur in pairs, and these two forces are equal in magnitude and opposite in direction).*** It means that if a body pushes the fluid a reactive force act on the body in the opposite direction.

Low Reynolds number (Re) swimming

As we learned above, at low Re inertia is negligible, so coasting or gliding is impossible. Organisms have to keep swimming in order to move. Another property of low-Re flows is that of reversibility, or symmetry in time. This means that if an organism pushes the fluid with a fin during a stroke to move forward when the fin is brought back before the next stroke the organism will go back exactly the same distance it moved forward. Many swimming strategies devised for high Re do not work at low Re.

Bacteria

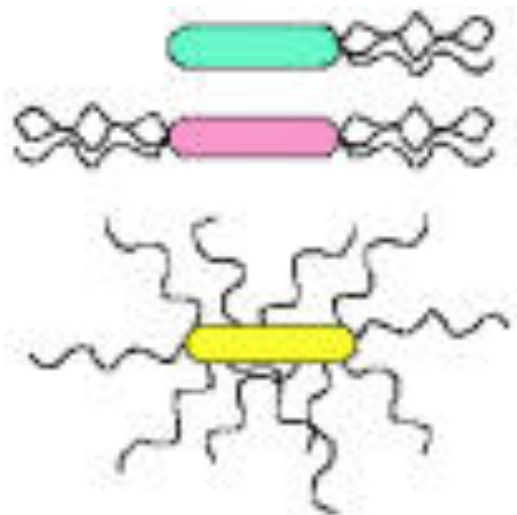Many types of prokaryotic cells (single-celled organisms that lack a nucleus) have one or several flagella.

Figure 5: Cartoon depicting different arrangement of flagella around bacteria. From: http://www.slic2.wsu.edu:82/hurlbert/micro101/pages/Chap3.html

The flagella of bacteria are made of a single protein called flagellin. Each flagellum is driven by a molecular 'motor' that is attached to the bacterium and rotates the flagellum, much like a propeller or a dough hook (Fig. 6). Typical bacteria (such as the well studied *E. coli*) advance in a sequence of 'runs' and 'tumbles.' During a 'run' the flagellum (one) or flagella (more than one) turn in a given direction only and the cell advances in a nearly straight line. After the 'run,' the cell 'tumbles,' changing direction, because the motor reverses and the flagellum or flagella turn in the opposite direction (as if unwinding from the twist they accumulated during the run). Due to the tumble, the next 'run' will take a different direction. By changing the length of 'runs', to be longer when conditions improve and shorter when they don't, bacteria can move towards an attractant (a behavior termed 'chemo-taxis').

Flagellar motion is controlled from the base and looks much like a wave superimposed on a corkscrewing motion. The unidirectional rotation of the flexible flagellum during the run does not have the symmetry problem of beating back and forth of a rigid appendage and results in net movement forward. The motion itself can be explained by the different forces acting in parallel and perpendicular direction on a flagellum moving in the fluid (the drag force parallel to the flagellum is nearly half the perpendicular drag force). The change of amplitude along the flagellum results in an asymmetry of drag force along the flagellum resulting in a linear motion (much like the movement of a corkscrew into or out of a cork, where a rotation is translated into a linear forward motion).
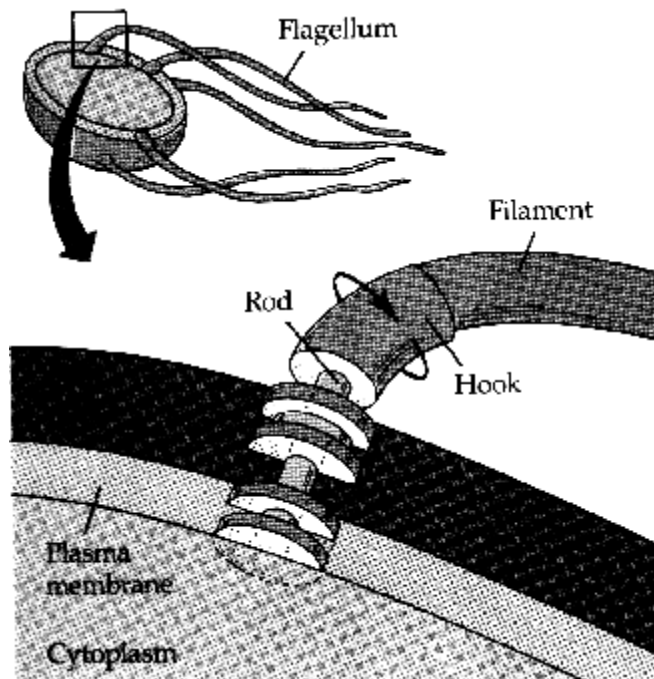

Figure 6. Schematic of the rotary motor which drive prokaryotic flagella.
http://home.att.net/~creationoutreach/pictures/flagella.htm

Eukaryotic cilia and flagella

Eukaryotic cells (cells having a nucleus) have evolved a different swimming appendage than prokaryotic cells. The appendage is made out of pairs of microtubules (9 on the

outsides and 2 at the center) which can slide relative to each other (Fig. 7). Thus, eukaryotes can control the shape of the swimming appendage at every part of it. In the case of cilia, much of the cell is covered by these tiny hairs beating together (Fig. 8). The flexibility of the appendage breaks the symmetry compared to a rigid appendage, resulting in a net force on the fluid and thus providing propulsion to the cell (Fig. 9).
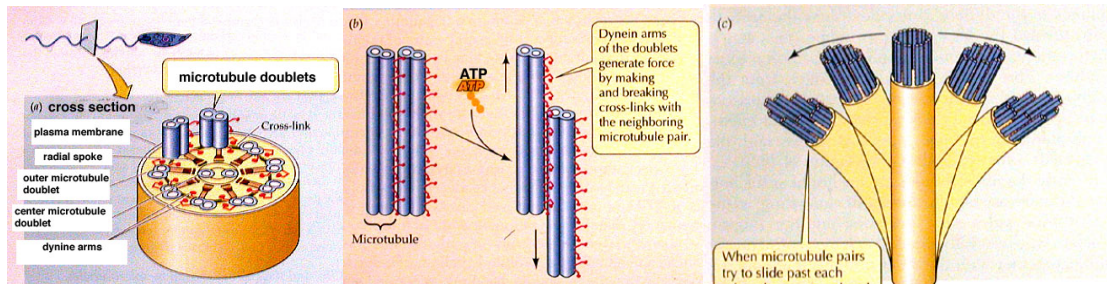

Figure 7. Structure of swimming appendages of eukaryotic cells. Left-cross section of the appendage, center-movement of microtubule pairs relative to each other is achieved by energy (ATP) and dynine arms (a motor molecule) resulting in deformation of the swimming appendage (right).
http://academic.brooklyn.cuny.edu/biology/bio4fv/page/flagella-movement.html

Figure 8. A cartoon of a ciliated (left) and a flagellated eukaryotic cell. From:
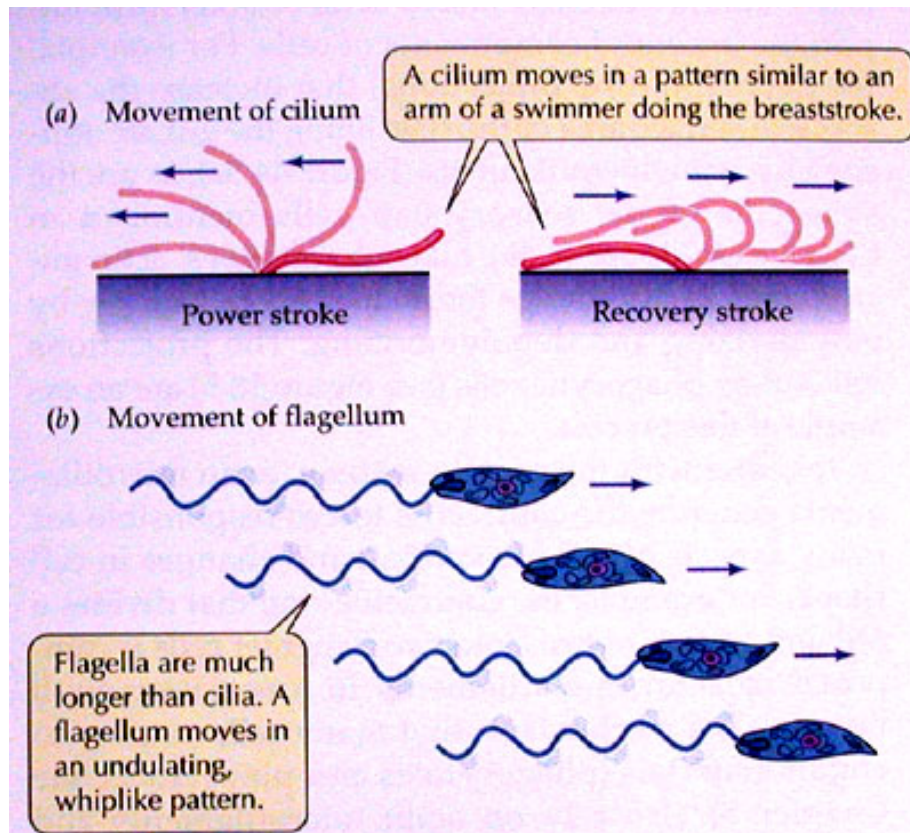*http://www.world-builders.org/lessons/less/les4/details.html*

Figure 9. The beat pattern of a cilium (A) and a flagellum (B). In both cases a net force is generated, propelling the cells in the opposite direction. From: http://academic.brooklyn.cuny.edu/biology/bio4fv/page/flagella-movement.html

As for prokaryotic cells, the net force is due to the asymmetry in the drag force exerted on the appendage in the perpendicular and parallel directions. The eukaryotic flagella motion is not necessarily rotational. Flexibility of the appendage and wavy motion along it (a propagating wave along the flagellum) are sufficient to result in a net force forward.

Eukaryotic cells do not tumble. A hypothetical comparison of the two different swimming trajectories towards an attractant is shown in Fig. 10.
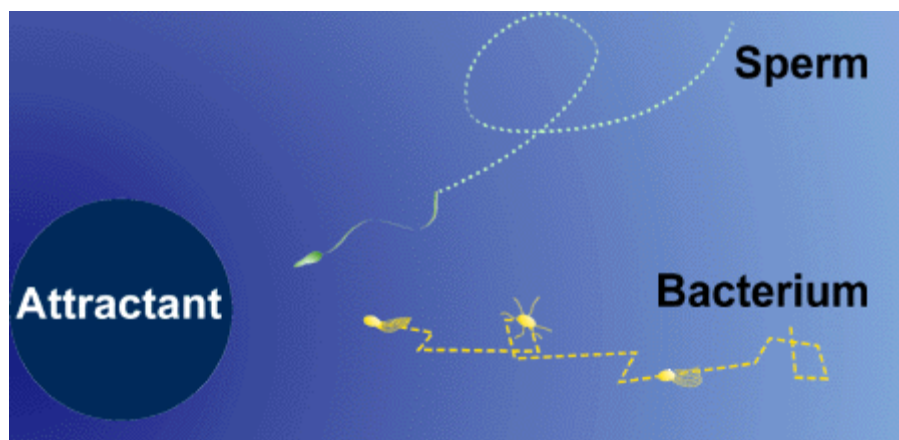
Figure 10. A cartoon of the trajectories of a eukaryotic cell (sperm) and a prokaryotic cell (bacterium) while moving toward an attractant (both have sensors that provide information about the environment.

One way to learn about swimming of organisms is to build an analogue model (a robot). Such a model (driven by a walkman's motor!) of a low-*Re* organism moving by corkscrew motion of an appendage is presented in Fig. 11. The low *Re* is achieved by having a high-viscosity fluid (such as corn syrup) for a robot that is much bigger than the organism we are modeling, so that the *Re* stays in the same range as the organisms whose swimming we wish to model.

Figure 11. A low Re # swimmer.

High Reynolds number (*Re*) swimming

At low *Re* gliding or coasting are not practical. A cell the size of a bacterium will stop practically immediately when it stops swimming (it will glide less than a small fraction of its body length). In contrast, at high *Re* inertia dominates and coasting or gliding is observed in the swimming of many organisms covering that range. In addition, at high *Re,* repeated motion such as flapping back and forth of a *rigid* appendage can result in net forward motion. Propulsion is achieved because the fluid pushed does not stay next to the appendage (as it does in low *Re*) but rather is pushed far back into the fluid and away from the body and is replaced by new quiescent water. This pushing is accompanied by shedding of vortices; little rotational blobs of fluid that propagate away from the body, and generate (with the vortices shed in the previous swimming stroke) a linear current pattern that assists the organism in its swimming.

Fish swimming

A swimming fish relies on its skeleton for framework, its muscles for power, and its fins for thrust and direction. The skeleton of a fish is the most complex in all vertebrates. The skull acts as a fulcrum, the relatively stable part of the fish. The vertebral column provides levers that operate for the movement of the fish. The muscles provide the power for swimming and constitute up to 80% of the fish itself. The muscles are arranged in multiple directions to allow the fish to flex in any direction. A sinusoidal wave passes down from the head to the tail. The fins provide a platform to apply the force from the muscles to the water (Fig. 12), which in turns applies force on the fish (Newton's 3rd law). The Thrust is the resultant force (from all forces applied on the body) that causes the fish to move in the direction it is.
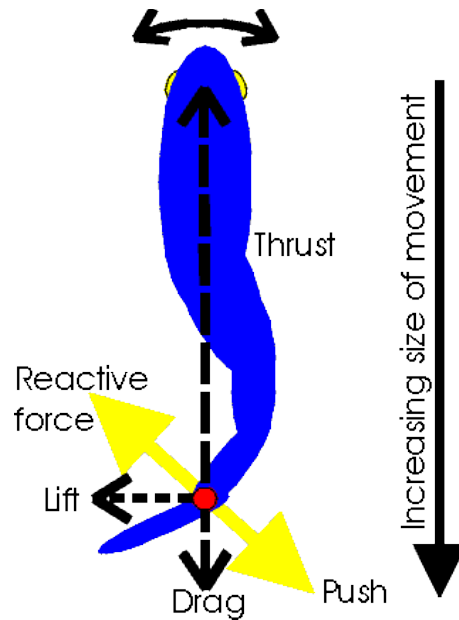
Figure 12. Diagram of forces when a fish swims. Thrust- force in animal's direction of movement. Lift- force is at right angles to the thrust. Drag- force is opposite the direction of movement. All lift forces cancel out over one complete tail stroke (otherwise the fish would drift sideways).

Form drag is greatly reduced by the streamlined shape of the fish and skin friction is reduced by a special slime that fish excrete from their skin to maintain laminar (smooth) flow of water near the fish (no slip stills apply). Three major roles have been suggested for the function of the helically-wound fiber lattice found in fish skin, which may not be mutually exclusive:

(1) **fiber-wound hose** - the skin may provide a flexible container that allows easy bending of the animal's body without buckling, much like the action of helical reinforcing in many garden hoses.

(2) **rope** - the skin may act as a rigid linkage system that serves to transfer muscular forces generated in the anterior portion of the fish, backwards to the tail where the majority of the propulsive thrust is generated.

(3) **spring** - the skin may act as an elastic system that captures energy from the stretch applied to it at one stage of the swimming cycle and then pays back this energy through elastic recovery at a later stage, in a process that might improve efficiency or enhance performance.
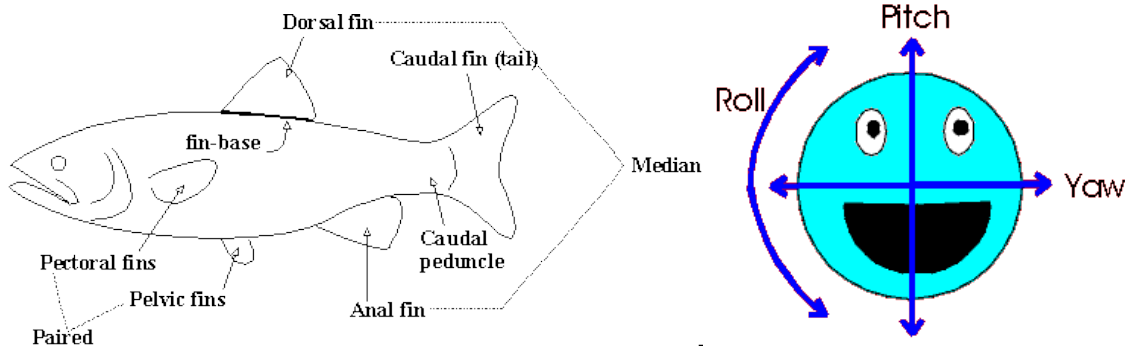
Figure 13. Fish fins give a fish control over its movements by directing thrust, supplying lift and even acting as brakes. A fish must control its pitch, yaw, and roll. Caudal fin-- provides thrust, and control the fish direction. Pectorals-- act mostly as rudders and hydroplanes to control yaw and pitch. They can also act as very important brakes by causing drag. Pelvic fins-- mostly control pitch. Dorsal/anal-- control roll. From: http://www.ece.eps.hw.ac.uk/Research/oceans/projects/flaps/swim.htm

In order to increase swimming speed, some large, fast-swimming fish have a mechanism to increase their temperature relative to that of the water surrounding them. The higher the body temperature, the greater the muscular power produced. Thirty or so degree Celsius is the optimum temperature for muscle speed. With increased speed, the tuna can capture the slower, cold-blooded fish it preys upon. Tunas have been clocked at record speeds of 50-70 mph!

Bony fishes have swim bladders to help them maintain buoyancy in water. The swim bladder is a sac inside the abdomen that contains gas. This sac may be open or closed to the gut. If you have ever caught a fish and wondered why its eyes are bulging out of its head, it is because the air in the swim bladder has expanded (air expanded in the bladder when brought to surface) and is pushing against the back of the eye. In order to avoid such problems, some fish that migrate extensively vertically have developed means to "burp" some of the air out of the bladder. Other fish, particularly deep-sea fish, have filled the bladder with lipid (fatty material) instead of air.

Swimming classifications:
Fish can be divided based on to two types of swimming defined by their method of living, and reflected in their physiology:
A. Cruisers: These are the fish that swim almost continuously in search for food, such as the tuna. Red Muscle- richly vascularized (blood-carrying capacity), rich in myoglobin (oxygen holder and transferor into the muscles active sites) able to sustain continuous aerobic movement.
B. Burst Swimmers: These fish usually stay around the same area. Examples are rock and reef fish.

Most fish generate thrust by bending their bodies into a backward-moving propulsive wave that extends to the caudal fin, a type of swimming classified as Body and/or Caudal

Fin (BCF) locomotion. Additionally, a number of fish have developed swimming mechanisms using their median and pectoral fins, termed Median and/or Paired Fin (MPF) locomotion. It is estimated that about 15% of the fish families use non-BCF modes as their routine propulsive means, while a much greater number that typically rely on BCF modes for propulsion employ MPF modes for maneuvering and stabilization (for example hovering by coral reef fish).

A further distinction made for both BCF and MPF propulsion is on the basis of the movement characteristics: *Undulatory* motions (Fig. 14) involve the passage of a wave along the propulsive structure, while in *oscillatory* motions (Fig. 15) the propulsive structure swivels on its base without exhibiting a wave. The two types of motion should be considered as a continuum, since oscillatory movements can eventually be derived from the gradual increase of the undulation wavelength. Within the basic grouping into MPF and BCF propulsion, further types of swimming (often referred to as *modes*) can be identified. They are presented in detail in the following sections.

Fish exhibit a large variety of movements that can be characterized as swimming or non-swimming. The latter include specialized actions such as jumping, burrowing, flying and gliding, as well as jet propulsion. Swimming movements have been classified into two generic categories on the basis of their temporal features:

Periodic (or steady or sustained) *swimming* is characterized by a cyclic repetition of the propulsive movements. Periodic swimming is employed by fish to cover relatively large distances at a more or less constant speed.

Transient (or unsteady) *movements*, that include rapid starts, escape maneuvers and turns. Transient movements last milliseconds and are typically used for catching prey or avoiding predators.

Periodic swimming has traditionally been the center of scientific attention among biologists and mathematicians. This has mainly been because, compared to sustained swimming, experimental measurements of transient movements are difficult to set up, repeat and verify.

AXIAL UNDULATORY PROPULSORS

PERIODIC SWIMMING PATTERNS

ANGUILLIFORM   SUB-CARANGIFORM   CARANGIFORM   THUNNIFORM   OSTRACIFORM

A1

A2   S2   C2   T2   O2

A3

A4
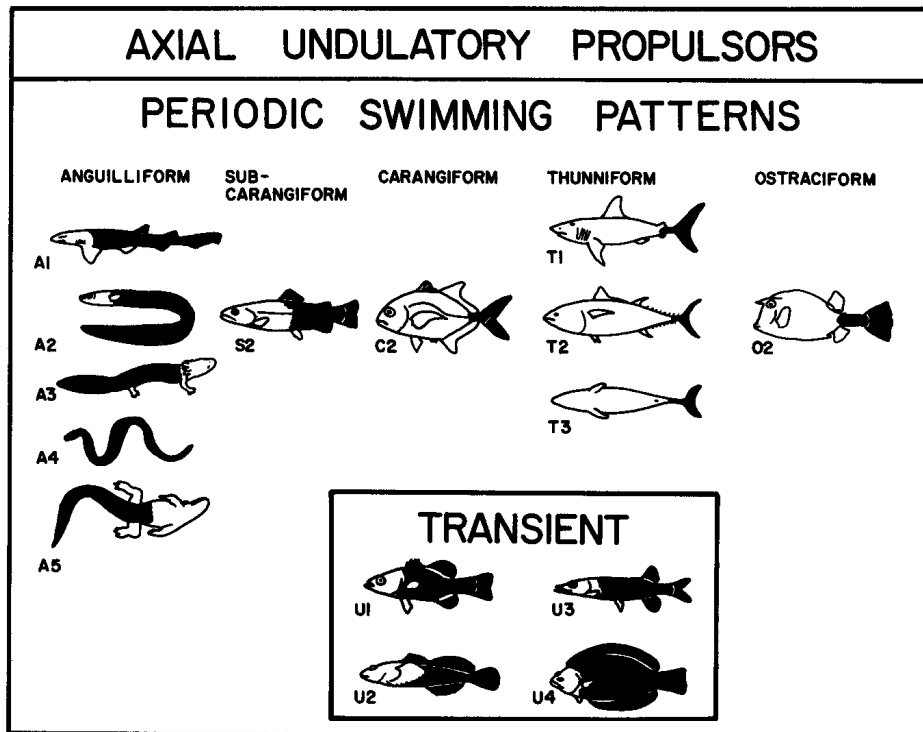
T1

T3

A5

TRANSIENT

U1   U3

U2   U4

Figure 14: Basic classification of undulatory fish swimming. Transient are between the undulatory swimmers and the appendage swimmers of Fig. 13. See text for details. Image from: http://www.comprehensivephysiology.com/WileyCDA/CompPhysArticle/refId-cp130103.html

We can generalize that fish swim by pushing water away behind them, although fish swim by various methods. As the well-known categories for the swimming fish, a zoologist, C.M. Breder classified into the following three general categories based on length of a tail fin and strength of its oscillation (see Fig. 14).

In **anguiliform (eel-like) locomotion** waves of contraction go down each side of the fish causing waves of flexion of the body to travel from head to tail of the fish. If the fish is long and slender (an eel), an obvious sinusoidal-like wave will migrate from head to tail, exerting a force on the water. The forces cancel side to side but sum to a backward force exerted on the water, pushing the eel forward. The eel appears to wiggle itself forward through the water.

In **sub-carangiform locomotion** a fish, like a trout, exhibit waves of contraction from front to back are still there, but less extreme than in the eel, and the increase in amplitude from head to tail is much more obvious. Forward flexions start the adjacent water moving to the rear; as it goes back each segment, having greater amplitude, adds to the acceleration. The last edge of the caudal fin provides the greatest thrust, determining the final acceleration given to the water. The broader the span of the caudal fin, the greater the mass of water that will be affected by swimming. As the water is accelerated backwards the fish moves forward (Newton's 3rd law).

In **carangiform locomotion** the body is almost rigid, but still waves of contraction pass from head to tail. The amplitude increases toward the rear but seldom exceeds 20 % of

the body length. Because of the small displacement, many more waves of contraction can be traveling down the body at a time. Consequently, the tail moves back and forth very rapidly, 10 - 25 times per second and provides essentially all the force. The relative rigidity of the body permits maximum streamlining, and the short, fast caudal strokes maintain nearly constant thrush. Carangiform swimmers are fast (at sustained swimming) but, because of their relative rigidity, can neither turn nor accelerate as rapidly as anguiliform or sub-carangiform swimmers.

In **ostraciiform locomotion** the body is does not move laterally or sinusoidally while the tail fin oscillates for forward movement and pectoral fins flex and scull for hovering, like the boxfish and other puffers.

In **thunniform locomotion** the body is stiffened still more, but two joints, one at either end of the caudal peduncle, permit flexion of the peduncle and the caudal fin. Nesting of the myomeres is extreme, and the myosepta are extended into powerful tendons which insert either on peduncular vertebrae or the caudal fin itself, allowing the peduncle to be oscillated rapidly while keeping the angle of attack of the caudal fin optimized. Thunniform swimmers are the fastest fishes (at sustained cruising) but are not well designed for rapid starts or turns.

Carangiform and sub-carangiform locomotion methods are good for pursuing relatively large prey for relatively long distances.

Ambush Predators
Flexibility sufficient to bend the body into a strong arc provides a power thrust from a standstill. Large dorsal and anal fins, located far back on the body (pike style) maximize the force exerted on the water for such a jump-start. In a pike or barracuda, the long body provides lateral resistance to prevent the head end from swinging too far out of line. Shorter ambush predators (for example small-mouth bass) often have a relatively large, spinous dorsal fin fairly well forward to stabilize lateral movement. The spinous dorsal is lowered to reduce resistance as soon as the fish is well in motion.
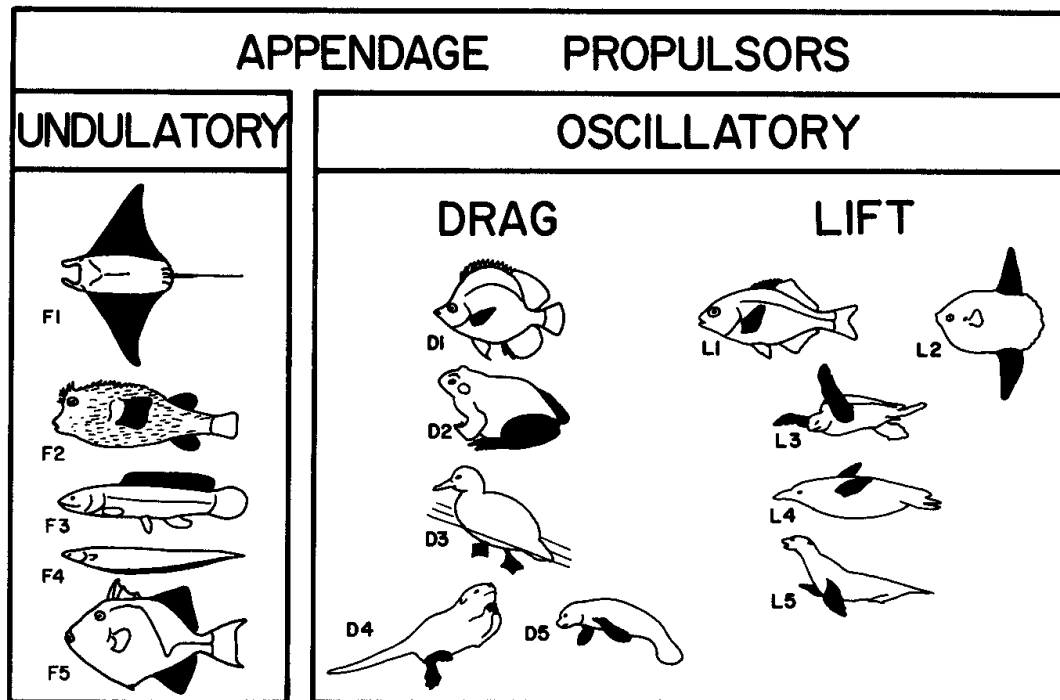
Figure 15. Appendage swimmers. See text for details. Image from http://www.comprehensivephysiology.com/WileyCDA/CompPhysArticle/refId-cp130103.html

Maneuverability Specialists
Small-item resources are overall much more abundant than large prey. Small items don't move fast, but require delicate, focused movements for capture. Accordingly, many species of fish are specialists for maneuverability rather than speed. A short, rounded body with sculling or undulating fins nearly all the way around it maximizes maneuverability. Compressing the body laterally provides a wide surface to exert force on the water for quick escape movements. The pumpkin-seed or disk shape is one of the most common in the fish world.

Additional notes on fin (appendage) swimming:
Pectoral fins are handy for braking or steering, but can also be employed in a powerful "breast stroke" as an aid in jump starts (sculpin). Many slow-cruise, precise maneuvering, fishes employ elongate, somewhat diamond shaped pectorals in a vertical, figure-eight sculling (Examples include bluegill and surfperch).

Elongated dorsal and/or anal fins can provide propulsive force through an undulating wave traveling their length. While much less powerful than body-flexion swimming, it provides measurable advantages. The body can remain rigid to improve sensory systems such as electrical detection, or facilitate sneaking up on prey. Movement can be equally facile in either direction (knifefish, bowfin).

Vortex shedding

Vortex shedding is the phenomenon by which rotating fluid (a vortex) is shed from a moving object (or from an object held in a flow). This phenomenon is central to swimming at high *Re* as it provides lift and is observed in the wake of all swimming organisms. An opposite vortex is formed in the opposite phase of its stroke preventing the swimming organism from changing orientation. Note the jet at the center of the two vortices in Fig. 15-4 which is indicative of thrust in the opposite direction.
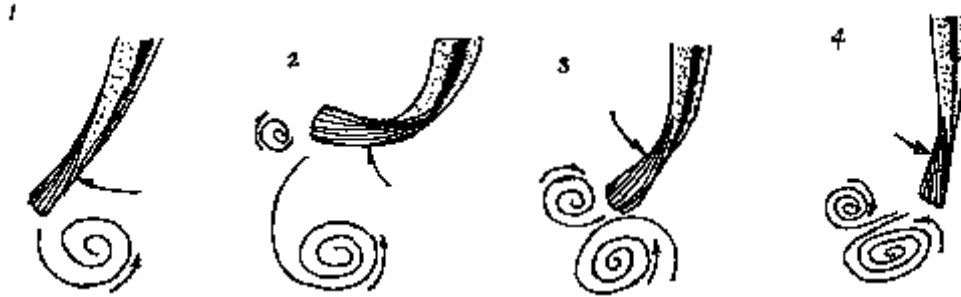

Figure 15: Production of vortices by an undulating tail. The backward movement of the water counters (and produces) the forward movement of the fish.

Fish robots

There are several labs around the world that are building fish robots for different purposes from learning about propulsion and control to mine detection. It is well known that propulsion with propeller is much less efficient energetically than the methods used by fish. It may happen, in the not too far future, that submarine will be propelled using artificial appendages rather than the current propellers.

Figure 16. An example of a fish robot built by the Draper Corporation (http://www.draper.com/).

Jet propulsion

Jet propulsion is achieved by pumping fluid rapidly, often through an orifice, opposite the direction of swimming. This is an inertial swimming method that can only function at high *Re*.
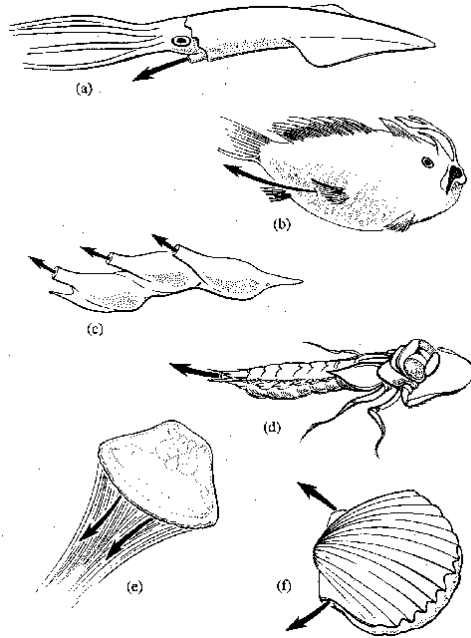

Figure 17: Jet-propelled animals: (a) squid, (b) frogfish, (c) salps, (d) dragonfly nymph, (e) jellyfish, and (f) scallop. Figure 4.14 in Vogel, 1994.

References and additional reading

http://en.wikipedia.org/wiki/Fish_locomotion

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