

Life in a Fluid Medium

Nothing is more fundamental about marine life than the medium of sea water itself. It is the purpose of this chapter to introduce some of the physical properties of sea water that affect the functioning of marine organisms. Many of the effects involve the movement of fluids or the movement of structures of marine organisms through the fluid. We should distinguish between primary and secondary effects of water movement. **Primary effects** are the direct results of the properties of the water and its motion, such as current speed. For example, water velocity and turbulence strongly influence the morphology and taxonomic composition of marine organisms and communities. Variation in water movement has **secondary effects** on food, nutrients, and oxygen availability. Stagnant waters will decrease in oxygen content and in the supply of planktonic organisms for suspension feeders. Sluggish currents will also be inefficient at dispersing pelagic larval stages of marine species (see Chapter 5).

* Whatever is part of the flow will not cross streamlines in a flowing fluid.

The movement of fluids can be readily diagrammed as a series of approximately parallel **streamlines** (Figure 6.1—but keep in mind that all is not usually so simple). Whatever is part of the flow will not cross the streamlines. One effect of this simple rule works is that fluids and entrained particles (e.g., protozoans, dye) move in the same direction. This helps greatly in tracing fluid motion because particles can be used to characterize flow (it's easier to watch dye, for exam-

ple, than to try to look at the movement of transparent water!). Thus, an important question is: Under what conditions will a particle be entrained in the flow? That is the subject of the next few sections.

Physical Properties: Density, Viscosity, and Velocity

* Water is relatively dense and viscous.

Water has physical properties far different from those of air. Sea water bathes marine organisms and protects soft moist tissues from drying. Oxygen can be obtained from solution. However, water is also a more supportive medium than air because it is denser. This eliminates the need for the strong supportive skeleton required by large terrestrial organisms. Water is also a **viscous** medium, and this poses some unique challenges. Imagine a frigatebird diving for fish through 10 meters of water, instead of through the same distance in air. The viscosity makes it far more difficult to move through the water. This chapter will serve as an introduction to some aspects of life in fluids, and as a resource for material to be presented in Chapters 7, 8, and 13.

The important properties of density and viscosity must be defined more clearly if you are to understand how flow affects marine organisms. **Density** is the mass per unit volume, and is expressed as g cm^{-3} . The salt content makes sea water somewhat denser than

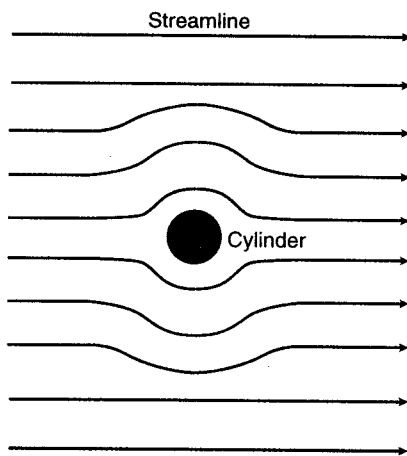


Fig. 6.1 Water flow can be visualized as streamlines, which indicate the path that individual particles would take. Particles move along, and not across, streamlines. In this illustration, water is flowing around a fixed cylinder, which is viewed in cross section.

fresh water. The density of sea water varies inversely with temperature. Dynamic viscosity is a measure of the molecular “stickiness” between layers of a fluid. Honey has greater dynamic viscosity than water, and water is more dynamically viscous than air. Dynamic viscosity decreases with increasing temperature.

* The Reynolds number is an estimate of the relative importance of viscous and inertial forces in a fluid.

In any fluid, there are two basic competing forces: **viscous forces** and **inertial forces**. Viscous forces are “sticky.” They keep the fluid together and flowing in smooth streamlines. In a fluid, particles affected by viscosity move, or stay still, depending upon the movement of the fluid. As viscosity increases, molecular stickiness keeps different parts of a fluid from separating easily, and any object in the fluid will be less able to move, unless the surrounding fluid is also moving. Inertial forces are those that relate to inertia, the tendency of a moving object to continue moving, when no force is applied to it. If you threw a steel ball through air, for example, it continues to move; that is an example of inertia. Inertial forces make a fluid break up into uneven streamlines, or allow an object to “drop” through a fluid like a stone in water—in other words to *not* go with the flow.

The **Reynolds number** (Re) is a measure of the relative importance of inertial and viscous effects of a fluid and on objects in a fluid. As the Reynolds number increases the inertial forces come to dominate. Un-

der high Reynolds number, objects in a fluid are dominated by inertia, that is, they tend to keep on moving when a force is applied to them. Under low Reynolds number, objects do not move unless a force is applied, because viscous forces dominate.

Reynolds number, Re , is simply the product of the velocity, V , size, l , and density, ρ , divided by the viscosity, ν . As long as we are dealing with sea water, we can take the density and the dynamic viscosity to be constants. We therefore must measure the remaining two variables, velocity, V , and size of the object, l . Reynolds number increases with an increase of either velocity or size.

There are two different situations in which we can measure the velocity that is needed to calculate the Reynolds number (Figure 6.2). First, if we place an object in a moving fluid, and keep it fixed to the bottom, we can measure the fluid’s velocity past the object (for example, water flowing past a coral). As an alternative method, we can take a non-moving fluid and measure the velocity of motion of an object through the stationary fluid (for example, measuring the swimming speed of a fish).

Table 6.1 gives Re for a range of organism sizes and swimming velocities. Empirical research has shown that when Re is less than about 1,000, viscous forces predominate. If Re is much greater than 1,000, inertial forces predominate. The threshold (actually a broad band of transition) makes all the difference in terms of how organisms move in and react to their environment. Because the viscosity of seawater can be

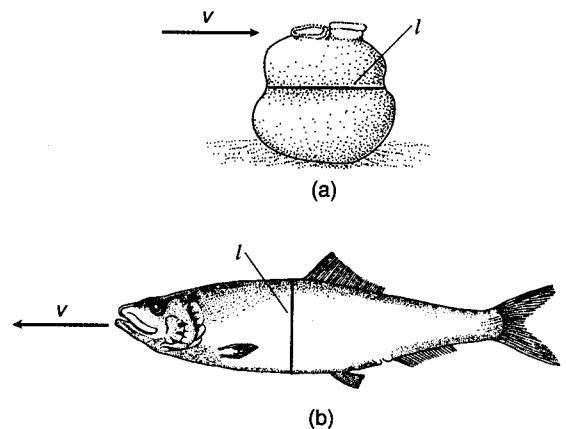


Fig. 6.2 Two different situations in which one can find the size and velocity parameters necessary to determine the Reynolds number: (a) an object (a sea squirt) is stationary in moving water; (b) an object (e.g., a fish) is moving through the water. (Note that l = size; V = velocity.)

Table 6.1 Reynold number for a range of swimming organisms of different sizes and swimming velocities. (Data from Vogel, 1981.)

Animal and velocity	<i>Re</i>
Large whale swimming at 10 m s ⁻¹	300,000,000
Tuna swimming at 10 m s ⁻¹	30,000,000
Copepod swimming at 20 cm s ⁻¹	30,000
Sea urchin sperm swimming at 0.2 mm s ⁻¹	0.03

assumed to be constant we need worry only about velocity and size. A small object traveling at a relatively low velocity is dominated by viscous forces; in other words, it is living in what amounts to a sticky medium. That is why a *Paramecium* swimming through still water can stop seemingly instantaneously. The instant the protozoan ceases to move its cilia, it is entrained in the still water and stops. By contrast, a supertanker may require several miles to come to rest from full speed. The supertanker operates at high *Re*, is only modestly affected by viscosity, and its inertia must be overcome in order to bring it to a stop. The protozoan, by virtue of its minuscule size and low velocity, lives in a world completely different from that of a ship, or of a fast and large fish, even though all live in the same fluid. If a protozoan ceases movement, it stops instantaneously, because,

at low Reynolds number, inertia is unimportant relative to viscous forces. To swim, a protozoan must therefore continuously exert a force against the surrounding medium; it cannot depend upon inertia for movement. Measured in terms of body lengths per unit time, *Paramecium* should have a better reputation for being an excellent swimmer, at least in relation to its body size. A protozoan can sustain swimming speeds of 100 body lengths sec⁻¹, whereas a tuna cannot swim much faster than 10 body lengths per second.

* Laminar flow is regular, whereas turbulent flow is irregular.

We can distinguish between two main types of flow. **Laminar flow** is regular, and lines describing movement of water molecules characterized by such flow are parallel (Figure 6.3). By contrast, **turbulent flow** is characterized by lines that are very irregular, and the overall direction of flow can be determined only as an aggregate of individual irregular motions. The famous hydrodynamicist O. Reynolds (for whom the Reynolds number is named) discovered that flow in a pipe became irregular (i.e., turbulent) if velocity, pipe diameter, or fluid density increased beyond a certain point. These factors contribute to increasing the Reynolds number. (In this case, *l* is equal to the pipe diameter.) These same principles can also apply in open water. When the Reynolds number is high, a fluid encountering an object may change velocity rapidly and inertia may cause the fluid to break up into complex vortices and wakes behind the object.

Water Moving Over Surfaces and Obstructions, Such as Organisms

* As a fluid moves over a solid surface, velocity steadily decreases with depth, the water reaching a standstill at the solid surface.

Consider water moving over a perfectly smooth-surfaced bottom. It is a hydrodynamic necessity that water velocity will decrease to zero at the bottom (Figure 6.4). This is called the **no-slip condition**. In effect, the grab of the bottom is perfect at the surface, but rapidly loses hold as you go into a **mainstream**, where the current velocity is not affected by the solid surface. The exact decline of velocity is complex but it is determined in large measure by the velocity of the fluid, and by the dynamic viscosity.

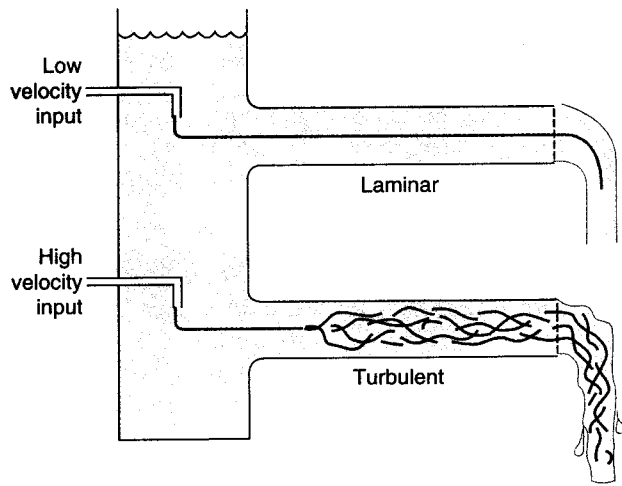


Fig. 6.3 Laminar and turbulent flow. Green lines represent paths of flow. (After Vogel, 1981.)

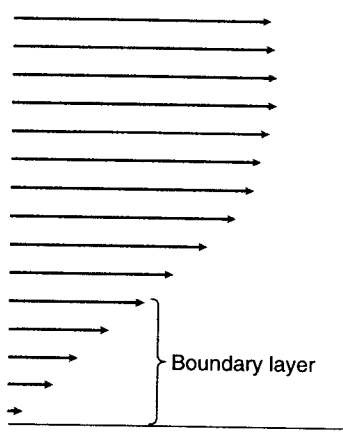


Fig. 6.4 Flow over the bottom. Water velocity maintains an average mainstream velocity well above the bottom, but velocity decreases to zero at the bottom surface. Near the bottom is a thin boundary layer, where velocity is relatively low but increases linearly from the bottom surface. (Not to scale: boundary layer is often less than a centimeter thick.)

If the flow is regular and the bottom is level, very close to the bottom there is always a **boundary layer**, where velocity declines approximately linearly with decreasing distance to the bottom surface. Outside this boundary layer, velocity increases asymptotically toward the mainstream current. The border of the boundary layer is more of a transition zone than a precise depth. Within the boundary layer, viscosity must be factored into studies of flow. The thickness of the boundary layer, relative to the size of an object, decreases with increasing Reynolds number. When Re is small, the boundary layer is relatively thick, making it something of a barrier to exchange of materials and energy. A microscopic organism, such as a protozoan, lives enmeshed in a relatively viscous environment. It used to be believed for example, that cilia on the gills of bivalves or setae on the feeding appendages of copepods trapped food particles between the fibers, much like a sieve, as the particles drifted by on currents and impacted on the cilia or setae. The boundary layer prevents this, however. As the particles approach the feeding microstructures, they may even be deflected off of the boundary layer. If they are trapped within the boundary layer, the cilia must reach out and touch or grab the particles, or the particles must collide directly with the cilia or other collecting fibers. The new understanding of this process has changed the way we look at suspension feeders, or animals that collect particles as food from sea water (see Chapter 13).

* The principle of continuity allows one to calculate flow velocity in a biological circulatory system.

Consider a unit volume of fluid flowing through a rigid pipe. Assume that the fluid is incompressible; therefore, if a liter volume enters at one end, an equal volume will leave at the other. The product of the velocity and the cross-sectional area always remains constant (neglecting friction). If the fluid is then forced to flow through a pipe of half the cross-sectional area, its velocity will be doubled (Figure 6.5). This principle of **continuity** applies equally to changes in cross section of a single pipe or a case in which a pipe splits into several smaller pipes. If, for example, a pipe splits into several equal subsections, the product of the velocity and cross-sectional area of the main pipe will equal the sum of the products of the velocity and cross-sectional areas of the smaller pipes.

The principle of continuity permits organisms to regulate water velocity. The principle can be applied, for example, to understand flow through a simple sponge (Figure 6.6). Sponges consist of networks of chambers, each of which is lined by flagellated cells known as choanocytes. The chambers are all connected to one or several main water expulsion channels, which guide wastewater from the sponge. If you dive, an application of food coloring to a sponge will quickly show you that the velocity of these excurrent openings is great, on the order of 10 cm s^{-1} . How can a choanocyte, that each can produce a water velocity of only $50 \text{ } \mu\text{m s}^{-1}$, manage to produce such a rapid exit speed together? The total cross-sectional area of choanocyte chambers adds up to several thousand times the cross-sectional area of the excurrent canal. The velocity through the excurrent canal must increase proportionally. Suspension-feeding polychaetes and mollusks employ a similar principle to drive water at fairly high speeds through interfilamen-

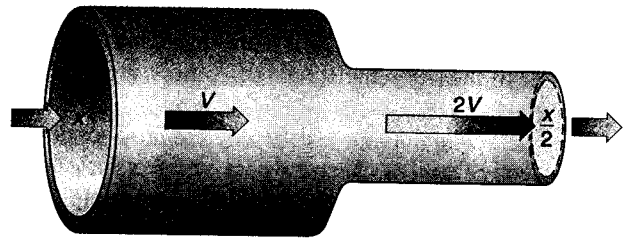
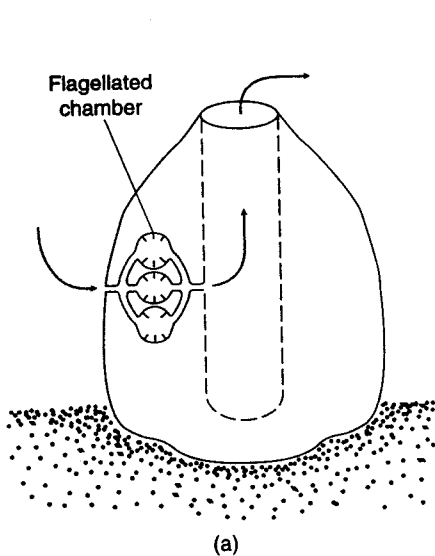
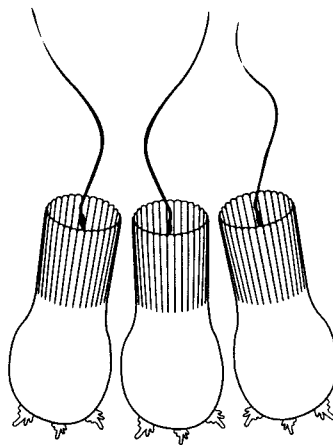


Fig. 6.5 Flow velocity through a pipe. The product of cross-sectional area and velocity is constant. Therefore, if cross-sectional area x decreases by half, the velocity doubles.



(a)



(b)

Fig. 6.6 How a sponge generates a relatively high exit velocity through its excurrent channels. (a) The low velocity of the water from flagellated cells in flagellated chambers is compensated by the far greater total cross-sectional area of the flagellated chambers, relative to the excurrent opening of the sponge; (b) diagram of flagellated sponge cells. (After Vogel, 1981.)

tal openings or siphons. The action of tens of thousands of cilia may operate at low individual velocity, but the total cross-sectional area is great, relative to (for example) the exhalent siphon of a bivalve mollusk.

Bernoulli's Principle

* Bernoulli's principle states that pressure varies inversely with fluid velocity.

Bernoulli's principle applies the principle of conservation of energy to pressure changes in pipes and burrows, or along surfaces. If total energy must be constant, then **pressure will vary inversely with the velocity of the fluid**. The simplest case is represented by a pipe whose diameter changes somewhere along its length. If the diameter decreases (Figure 6.7), then velocity in that section of the pipe will increase, as discussed above. Pressure, however, will decrease in this section. If you punctured a pipe of this sort filled with flowing gas and then lit a match, the flame would be higher in the thick section of the pipe, owing to the higher pressure.

This principle has broad biological applications. The design of a cross section of a wing is based directly on an application of Bernoulli's principle. The lower surface is flat, whereas the upper surface is curved. As air encounters the wing, it moves more rapidly along the upper surface and the pressure is thus lower than along the lower surface. The pressure difference creates lift. The same principle applies to a

flatfish (Figure 6.7). As the fish pushes through the water, its flatter bottom has greater pressure than on the curved top, and lift develops.

Pressure differences on either side of a tube can also be used by an organism to create a current. Consider a U-shaped tube in the mud, where one entrance to the tube opens to a small rise, higher than the adjacent entrance. Because the entrance in the rise is probably exposed to a slightly higher current speed, the pressure will be lower than at the other entrance. As a result, water will flow passively through the tube. This principle also reduces the work needed to drive water through worm tubes or through sponges, because a moving current above the sponge reduces the pressure at the exit.

Drag

* Water moving past an object creates drag, a force that operates differently at different Reynolds numbers.

Consider a blade of eelgrass sticking up into the water from the bottom. The flow will be disrupted and will exert a force, or drag, upon the blade. Drag can be dissected into two components, either of which may dominate alternately depending upon the Reynolds number. At low Reynolds numbers (more sticky, or viscous, situations), **skin friction** dominates. It is a force resulting from the interlayer stickiness of the fluid, and acts parallel to the surface of the object and in the local direction of fluid flow. The more surface is exposed to the flow, the more skin friction there is.

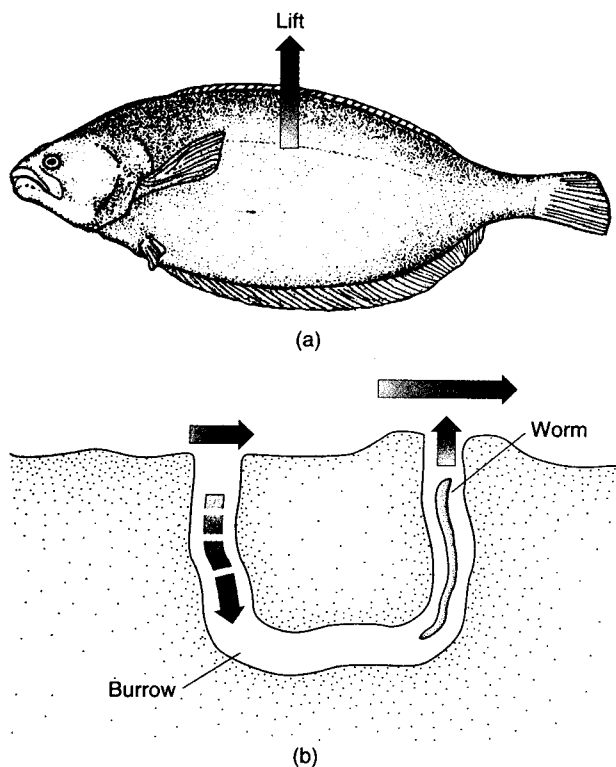


Fig. 6.7 Bernoulli's principle. (a) Differences in pressure above and below a moving flatfish creates lift (after Vogel, 1981); (b) a raised mound on one end of a U-shaped tube places it in a slightly higher current velocity, relative to the other opening, which is flush with the sediment. Water moving past the two holes creates a pressure difference, with lower pressure on the raised area, and this drives water through the tube. (Length of arrows proportional to water velocity.)

Although skin friction never disappears, it becomes far less important at higher Reynolds number.

Pressure drag is mainly the result of inertial forces in the fluid, and it dominates total drag at high Reynolds numbers. It occurs because pressure exerted on the upstream part of the object (e.g., a stationary coral in a current) is not exactly counterbalanced by an equal pressure on the downstream side. The object is effectively pushed along by the stream. Pressure drag increases proportionately to the cross-sectional area exposed to the current, and with the square of the current velocity. For example, a flat plate oriented perpendicular to a current exerts a maximum amount of pressure drag; the pressure drag is minimized when the plate is parallel to the current. Anyone who has driven an old van knows that its flat front creates suf-

ficient drag to increase gas consumption. Modern vans have much more streamlined shapes to reduce drag, but it's still more efficient (and fun) to drive a highly streamlined vehicle, such as a Ferrari.

The best way for an engineer to minimize pressure drag is to orient elongated objects parallel to the current, and to give them a long tapering tail on the downstream side. This allows the fluid, after passing over the front of the object, to decelerate gradually in the rear. The object is pushed forward by the closure of the fluid around the object toward the rear. This principle explains the streamlined teardrop shape of fast-swimming fish, such as skipjack tuna, and the shape of submarines. (See further discussion in Chapter 8.) Many organisms are fixed to the bottom, and pressure drag on them may be considerable. Seaweeds, corals, sea pens, and sea anemones all project into the flow from the bottom. The work of Miriam Koehl¹ has contributed much to our understanding of how flexible organisms can reduce drag, both by the structure of their body wall and by alteration of their behavior. Drag can be reduced by flexibility, and by bending over in strong flow, much the way leaves of a palm tree conform to a strong wind. When currents and drag are too strong, some animals, such as anemones and feather stars, either contract the body, or retreat to a crevice (see Chapter 13). The sea anemone *Metridium senile*, for example, normally protrudes its tentacles into the flow in order to feed, but this creates drag. When the current increases and pressure drag is too great, the animal withdraws its tentacles, which greatly reduces drag (Figure 6.8).

Let's consider a specific example of how pressure drag may affect an organism. If we visit an exposed rocky shore, we immediately see waves crashing against the organisms attached to the rocks. In many cases, mobile invertebrates such as drilling snails and limpets are much smaller on exposed coasts relative to their size on protected rocky shores. It is possible that larger animals would simply be swept away by the waves. Larger animals project above the surface to a greater degree and are simply more exposed to the drag effect of passing waves. Michael Judge² tested the latter idea, by gluing vertical copper plates to the west-coast rocky shore limpet *Lottia gigantea*. The limpets with the plates spent less time moving around than those lacking plates, which gave the plated limpets less time to feed. The loss of feeding

1. See Koehl, 1976, in Further Reading.

2. See Judge, 1988, in Further Reading.

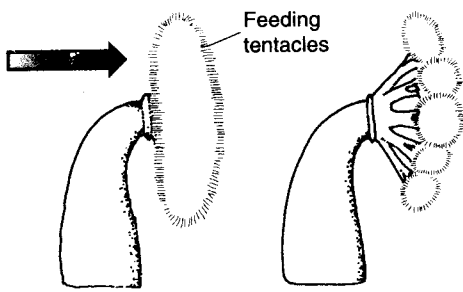


Fig. 6.8 Changes (left to right) of the sea anemone *Metridium senile* as the current increases.

time means fewer resources for growth, which may also explain the smaller size of the exposed shore limpets.

* Fish streamlining is a compromise between drag and skin friction.

In Chapter 8 the form of fish will be discussed. However it is worth it at this point to think about how the characteristics of a fluid contribute to influencing the swimming efficiency of a fish. Most fast-swimming fishes move by rhythmic contractions, which pass through the body as a wave. At any one time, part of the fish body is pushing against the water, propelling the fish forward.

As a fish moves forward, the forces on the fish surface include pressure and frictional effects. As water in streamlines passes over the fish, friction causes the water to lose some kinetic energy. This loss prevents the water from penetrating the steep pressure gradient behind the fish and the water that leaves the surface behind the fish forms a wake (Figure 6.9). If a fish is short and squat, there is a very steep pressure gradient from front to rear, and this leaves a large wake as the fish moves along. The difference in pressure creates drag. In effect, the fish is being pushed back to an extent as it swims. Through streamlining, the wake is diminished and the drag is reduced greatly. That is why fast and continuously swimming fish are shaped in some variation of the classic shark or tuna shape.

The question arises: If length and slenderness reduce drag, why aren't fast-swimming fish not much longer and more slender than they actually are? Why don't they have an eel shape? The answer has to do with the skin friction caused by the surface of the fish in contact with the water. The longer and narrower the fish, the more fish surface there is over which the water must move, and the greater is the friction for a given body weight. The shape of a shark or a tuna is therefore a compromise between considerations of drag and skin friction minimization.

The Use of Flumes

* Flumes are useful for studying the effects of moving fluids on organisms, although flumes must be scaled carefully.

It is usually quite tricky to study the effects of flow in the marine environment. Some clever investigators have devised field current meters, and have been able to characterize the flow field around an organism. Because of inaccessibility, this becomes impractical when studying the streamlining of a tuna, or the flow about a deep-sea organism. Even in accessible habitats, it is very difficult to measure flow on the smallest of scales. Electronic devices, such as flow meters based upon thermistor sensors, are usually difficult to use accurately in the field.

In still waters, microcinematography allows us to

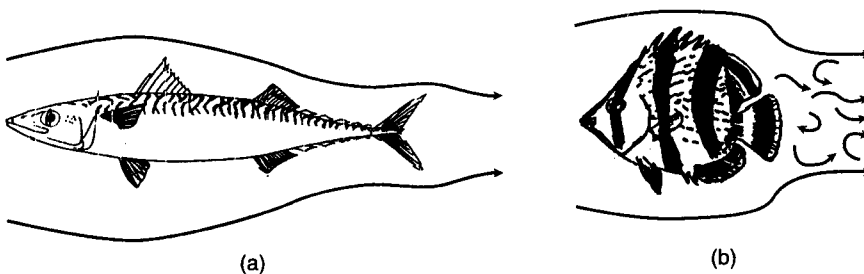


Fig. 6.9 Drag on a fish is affected greatly by streamlining: (a) if a fish is well streamlined, the wake is reduced, streamlines are maintained behind the fish, and the drag is much reduced; (b) if a fish is poorly streamlined, a wake is created at the rear, producing a pressure gradient and drag.

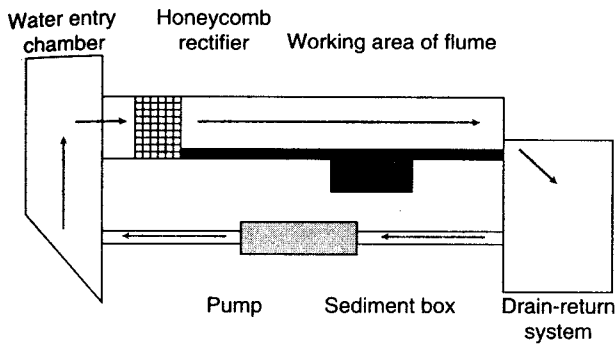


Fig. 6.10 A flume designed to study the effects of flow on small epibenthic animals. In this design, water is recirculated by means of a pump. Water enters a honeycomb-like material to rectify the flow, and then enters the working area of the flume, where organisms are placed. Water leaves the working area and drains into a sump, from which it is pumped to the water entry chamber.

study the behavior of very small creatures at low Reynolds numbers. In moving waters, various types of **flumes** are used to study the effects of flow. A flume is a device that includes a source of moving water, a working area where the organism and flow field are characterized, and a drain-return system (Figure 6.10).

Most flume designers seek two objectives: maintenance of laminar flow, and maintenance of scaling by Reynolds number (and there are also other parameters beyond the scope of this text). A long flume is desirable, because it takes a while for the flow over the bottom surface to stabilize and produce a predictable boundary layer and velocity profile above the bottom. A wide flume, relative to water column

height, prevents effects of the walls on flow. Scaling by Reynolds number is also essential to keep the proper ratio of inertial to viscous forces. This has an advantage, however, in that you can study a very small object, such as a copepod, by making a larger model and placing it in a more viscous medium.

Using a flume, one can study the hydrodynamic forces at work on a biological object. For example, I have studied the reaction of the siphon of a sediment-ingesting bivalve mollusk, *Macoma secta*, which feeds much like a vacuum cleaner. At low current velocity, the siphon is protruded into the water, and swirls around, picking up sand grains. If the current increases to about 15 cm s^{-1} , the pressure drag on the siphon makes it difficult to control, and the siphon is withdrawn. The animal feeds on sediment within the burrow. At velocities above 35 cm s^{-1} , the bottom sediment is stirred up and the bottom is very unstable. At that point the animal ceases to feed. Such qualitative observations can be carried out quite easily using a flume with a video recording device.

Conflicting Constraints

* Hydrodynamic forces often present conflicting constraints.

Hydrodynamics may suggest simple rules for both behavior and morphology, but many marine organisms find themselves having to live with conflicting needs. Consider the sessile eel grass leaf discussed earlier. It projects upward from the bottom and thereby is able to capture light and nutrients. However, this same upward projection causes a significant pressure drag. There is a conflict of different functional require-

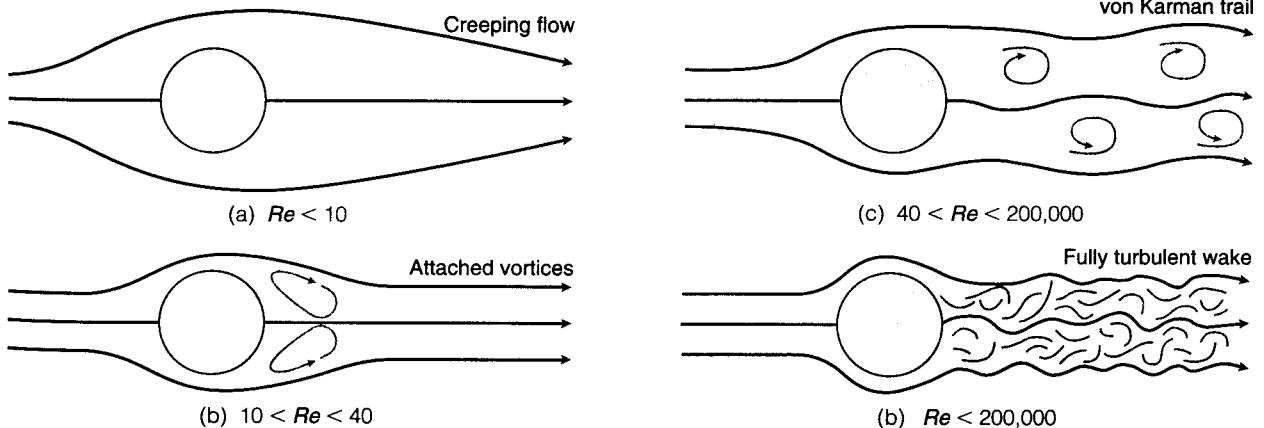


Fig. 6.11 Different types of wakes down current of a cylinder, at different Reynolds numbers. (After Vogel, 1981.)

ments. The size and velocity scaling of hydrodynamic effects create additional conflicts. As an organism grows in length, the Reynolds number increases. Consider Figure 6.11, which shows patterns of flow downstream of a cylinder under conditions of varying Reynolds number. When Re is about 30, a pair of attached vortices reside just downstream of the cylinder. This might give a small coral the “opportunity”

of feeding on particles that are relatively stationary. As the coral grows larger (or the current increased in velocity), these vortices become more erratic, however, and food may not be held in a predictable pattern. Size and velocity can increase together; as an organism grows larger, it often projects into a rapid “mainstream” current.