the beetles are short enough to be in the range where wavelength is mainly determined by surface tension rather than gravitational forces. Indeed, Tucker notes that there are no common whirligig beetles with lengths exceeding 17 mm, the point above which gravity waves begin to predominate. Again size enters in determining the practicality of a way of living, and again the underlying physical reality both raises opportunities and imposes constraints.

There's apparently a world of unfamiliar phenomena available to the fauna of liquid surfaces. Whirligig beetles seem to be able to "echolocate" through reflection of their ripples—it must be a queer sort of sense that requires body motion to send the signal. And Wilcox (1979) has shown that males of at least one species of water strider can tell one sex from the other by sensing surface waves—males add on a high-frequency flourish, a kind of tremolo, that conveys the message to the male receiver that they are not suitable mates for each other.

CHAPTER 6

Viscosity and flow

"Blood is thicker than water."
Sir Walter Scott on viscosity

The everyday meaning of "fluid" is that of "liquid"—the stuff we drink or use to fuel our cars. Properly, though, a fluid is any substance that flows, making the term a generic for both gaseous and liquid states. The lumping may seem odd just after a chapter that dwelled heavily on the differences between gases and liquids, but the two do have the important common quality of responding to unbalanced forces by flowing. Indeed, for problems involving flow the two are remarkably similar, more so than one has any a priori reason to suspect.

On account of their lower densities, gases are easier to push around—but that's a quantitative rather than a qualitative difference. One might worry about the vast differences in compressibility between gases and liquids—double the pressure on a gas and you almost exactly halve its volume; do the same to, say, water, and the reduction in volume is less than one part in 20,000. But it turns out that in the sorts of flows organisms encounter gases are functionally incompressible as well. Consider a wind of 20 m/s⁻¹ (45 mph) brought locally to a halt by hitting the beak of a flying bird—the increase in pressure will be 240 Pa (Chapter 7) at the upstream tip. This trivial increase (0.24%) over the ambient atmospheric pressure will cause only a comparably trivial compression. Compressibility becomes significant only when a gas encounters something at an appreciable fraction of the speed of sound (about 320 m/s⁻¹ or 720 mph).

Or one might worry about the different effects on liquids and gases of gravity and surface tension. These agents are certainly significant—they make waves, for instance—but their effects are almost entirely limited to fluid-fluid interfaces. So such effects can be ignored for natural flows that don't involve interfaces between fluids, which is to assert that they don't much matter for most situations of biological interest—again gases and liquids behave quite similarly.

Very young children really appreciate fluid flow—just watch a tot intensely absorbed by the transfer of a liquid from one container to another. But we (most of us, anyway) grow into a world dominated by the

¹ That is, unless the fluid is stratified by a density gradient as might result from temperature variation in an atmospheric inversion or to salinity variation in an estuary.
CHAPTER 6

more staid and apparently practical domain of solid mechanics, losing
sight of both the beauty of fluids in motion and the variety of their coun-
terintuitive behavior. I must admit, though, to a persisting infantile prej-
udice in favor of fluids, a partiality that has for many years supplied me
with notions to investigate and that abetted the predecessor to the pre-
sent book (Vogel 1981b). The beauty of flow, no mere intellectual appli-
cation, is nowhere better presented than in a book of photographs, An
Album of Fluid Motion by Van Dyke (1982).

We’ve already looked at the flow of fluids in several contexts. Chapter
2 introduced the very important principle of continuity and made the
point that one could derive forces just by measuring speeds of flow.
Chapter 3 casually mentioned that drag varied either with the first or the
second power of length, depending on the sizes and speeds involved.
Chapter 4 discussed the Froude number and introduced the drag coef-
ficient and the crucial notion of velocity gradients. And Chapter 5, of
course, took a brief look at surface waves.

SOLIDS VERSUS FLUIDS—VISCOITY

Gases and liquids share a property, viscosity, that is absent in solids and
lack another, stiffness (associated in popular usage with the idea of elastic-
ity), that is characteristic of solids. It’s worth emphasizing that the distinc-
tion we make isn’t just one of degree but a matter of fundamental appli-
cability of these analogous but clearly different properties. Solids resist
being deformed in shear—fluids simply don’t. Fluids, though, aren’t to-
tally indifferent to shear—what is different is how they respond to shear
stresses.

Consider (assume weightlessness, for convenience) rectangular blocks
of solid and fluid, each distorted in shear (Figure 6.1). For the solid, the
greater the force, the more the distortion. One can write a rough for-
mula for what the “shear stress” does—more stress means more strain
(distortion), and the ratio of stress to strain (what a biologist might call
the ratio of stimulus to response) is the “shear modulus,” a measure of
stiffness under shearing loads:

\[
\text{shear stress} = \text{shear modulus} \times \text{shear strain}. \tag{6.1}
\]

For the fluid, by contrast, it doesn’t take a greater force to produce
more distortion—the stuff is for all practical purposes capable of infinite
distortion at any force since it takes on any shape equally happily. But
what does depend on the force is the rate of distortion of the fluid cube—
the resistance of the fluid depends only on how fast it’s distorted. This
resistance to rate of shear is what we mean by viscosity; in short,
Fig. 6.1. Pushing across the top of a block whose bottom is fixed distorts the block—two faces of a rectangular solid become nonrectangular parallelograms as they are tilted to an angle Θ.

shear stress = viscosity \times shear rate. \hspace{1cm} (6.2)

Since the flow of a fluid along a solid surface inevitably involves shearing or distortion (I'll defend that bald statement below), viscosity comes down to a measure of the resistance of fluids to flowing across surfaces or through conduits. Thus, the more viscosity, the less "fluid" the fluid (which may seem backward, but that's how it's defined).

This notion of shear rate is worth a few more words. It amounts to a measure of how rapidly "layers" of fluid are sliding with respect to each other—as if you push across the top sheet of a pile of paper and each sheet moves a little faster than the one beneath it. It's thus a rate of change of velocity with distance—a velocity gradient, but one in which velocity varies, not in the direction of travel (as with acceleration), but at a right angle to flow. It's the gradient you'd experience when wading out into a creek through the quiet waters near shore toward the torrent in mid-stream. As mentioned in Chapter 4, the lack of "slip" of a fluid at a solid surface implies the presence of such a shearing region and velocity gradient wherever a fluid flows past a solid.

But we need a more quantitative view of viscosity. Imagine our previous cube now transformed into two thin, flat plates with fluid between (Figure 6.2). The lower plate is fixed, a force moves the upper one horizontally, and the no-slip condition applies to both inner faces. As a result, the fluid between them shears, producing a smooth variation in flow rate, that is, a constant velocity gradient. With this diagram we can put equation 6.2 in more formal terms, using the Greek μ (µ) for viscosity (sometimes called the "coefficient of viscosity" or "dynamic viscosity"):

\[ F/S = \mu \omega/l. \hspace{1cm} (6.3) \]

From this equation one can figure out the basic dimensions of viscosity—they come out to ML\(^{-1}\)T\(^{-1}\), a combination that has no obvious intuitive
CHAPTER 6

Figure 6.2. Flat plates with fluid between. With the no-slip condition applicable to both plates, a constant velocity gradient develops between them; the viscosity of the fluid determines how much force it takes to give the top plate a given velocity for a certain area of plate and distance between them.

significance. The SI unit is the kilogram per meter-second or, shorter, the “pascal-second” (Pa·s).

Looking up viscosities isn’t especially difficult but is rarely necessary, since two materials, air and water, dominate the biological scene. Table 6.1 gives their viscosities at a temperature of 20°C, along with the densities and the ratio of viscosity to density, the latter called the “kinematic viscosity” (problems involving viscosity very often involve density as well). Notice that the substances have very different viscosities and densities but the ratio of the two properties differs only fifteenfold. It’s surprising (and will prove a considerable convenience) to find such a similarity between two such different materials.

Boundary Layers

Since the no-slip condition is universal, so are velocity gradients adjacent to surfaces—that’s why viscosity is so important. Pipes and arteries develop deposits on their walls, it takes a strong wind to remove a spore resting on a leaf, and water without suspended grit has no erosive action

Table 6.1. Viscosities and densities

<table>
<thead>
<tr>
<th></th>
<th>Viscosity, μ (Pas)</th>
<th>Density, ρ (kg·m⁻³)</th>
<th>Ratio, μ/ρ (m²·s⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Air</td>
<td>1.81 × 10⁻⁶</td>
<td>1.20</td>
<td>15.0 × 10⁻⁶</td>
</tr>
<tr>
<td>Water</td>
<td>1.00 × 10⁻³</td>
<td>1.00 × 10³</td>
<td>1.00 × 10⁻⁶</td>
</tr>
<tr>
<td>Seawater</td>
<td>1.07 × 10⁻³</td>
<td>1.02 × 10³</td>
<td>1.05 × 10⁻⁶</td>
</tr>
</tbody>
</table>
on rock. If a fluid is very resistant to (rate of) shearing, then the velocity gradients in it will tend to be gentle, and there will be a relatively great distance between the stationary surface and the region of moving fluid where the motion is at full speed (the so-called free-stream velocity). If, conversely, the effects of viscosity are slight, then the gradients will be steeper and the distances shorter. Figure 6.3 graphically depicts how speed changes within the gradient region for flow parallel to a flat plate at moderate speeds.

Even more useful than a measure of the steepness of the gradient would be a figure for the thickness of the whole gradient region, from zero speed at the surface to the final free-stream speed. There’s a difficulty, though. While the inner limit (zero speed) presents no problems, the outer one is, strictly speaking, indefinite—the local speed of flow approaches the free-stream speed asymptotically. So if we are to quote a figure for the thickness of such a gradient region we must arbitrarily define the outer limit. The classical definition was established early in this century by Ludwig Prandtl (Von Karman 1954 gives an engaging historical account) who set the outer limit where the speed achieved 99% of the final free-stream value, so we can speak of the gradient region defined by that convention as the “Prandtl boundary layer.”

Perhaps the clearest way to show how the thickness of a boundary layer varies is by citing Prandtl’s formula for its thickness in the simplest possible case—a flat plate oriented parallel to the direction of flow (Prandtl and Tietjens, 1934). Thickness here is designated by the Greek lower case delta (δ):

\[ \delta = 5 \sqrt{\mu x/\nu} \]  \hspace{1cm} (6.4)

![Figure 6.3. The velocity gradient on a flat plate oriented parallel to flow; the length of each arrow above the plate is proportional to the velocity at its base. The thickness of the gradient region has been grossly exaggerated for the purpose of illustration.](image-url)
The thickness of the layer increases with the square root of $x$, which is
the distance behind the upstream edge of the plate—thickness increases
parabolically (Figure 6.4), that is, rapidly at first and more gradually far-
ther downstream. It is thicker, as we’d expect, if the viscosity is greater;
and it’s thinner for greater values of density and free-stream speed. It
should be noted that the formula, taken strictly, refers to a rather specific
geometry rarely encountered in nature—surfaces aren’t commonly rigid,
smooth, just parallel to flow, and with sharp upstream edges.$^2$

The arbitrary element in the definition should be emphasized. The fig-
ure of 99% has biological, not physical, roots—the exact value is an acci-
dent of our bipedal and pentadactyl anatomy. Prandtl wanted a gener-
ous definition—he was interested in calculating drag and wanted to omit
no region where viscosity might be doing anything significant. If, instead,
one is interested in whether the spore-bearing stalk of some fungus ex-
tends out into substantially full wind, one might pick a value of 90%
rather than 99% of free-stream speed for the outer limit. The resulting
boundary layer will be only 3/5ths as thick—a constant of $3$ will replace
the $5$ in equation 6.4.

People sometimes ignore the picture given by Figure 6.3 and focus in-
stead on a diagram such as Figure 6.4. They thus retain a fuzzy notion
that the boundary layer is a discrete region of nonmoving fluid rather
than the discrete notion that the boundary layer is a fuzzy region in
which there is a strong velocity gradient. Gradients, again, are all impor-

![Diagram of wind flow over a flat plate with boundary layer thickness marked as $\delta$.]

**Figure 6.4.** The variation of the thickness of the boundary layer on a flat plate with distance from the upstream edge. Note that the velocity gra-
dient gets less steep as one moves downstream. While the shape of the
curve is real, the line as drawn is somewhat arbitrary; it certainly repre-
sents no physical discontinuity in the flow.

$^2$ The formula is limited, as well, to Reynolds numbers between about 500 and
500,000; more about these numbers in a few pages.
tant; boundary layers are just regions of velocity gradients and thus places where viscosity exerts its pernicious effect on flows and forces.

These boundary layers provide both trouble and assistance to organisms. Getting down near a surface provides protection from the forces of fast flows of air or water (although nothing is so flat as to have no drag at all—at the surface itself the velocity may be zero, but the all-important velocity gradient is not). Conversely, an organism feeding from the water passing by must somehow raise its feeding equipment or intake pipe up high enough to encounter adequate flow speeds. In short, there’s lots of biology here, enough for an entire book.

A moth’s antenna

The gentle velocity gradients at low speeds are no small matter even where the geometry of the situation precludes using tidy formulas such as equation 6.4. For example, consider the problem of male saturniids (giant silkmoths). Females draw males for mating by releasing a volatile attractant chemical, but these moths typically live at very low population densities. Males have equipment to smell out females at distances of miles—large, feather-shaped antennae (Figure 6.5) on which some 70% of the sensilla are sensitive to nothing other than the females’ perfume—truly an olfactory sensation. A nineteenth-century French entomologist, Fabre, did a few experiments on the phenomenon but simply could not believe that any sense of smell could work so well (Teale 1949).

In order for an odorant to be picked up from the airstream, air must be made to pass through an antenna. The tacit presumption among people interested in olfaction has commonly been that air directly upstream

Figure 6.5. A male Luna moth and one of its antennae.
from an antenna would pass through it. But gases as well as liquids have
viscosity, and passing through a dense array of sensilla involves shearing
and velocity gradients, so the air might well prefer to go around an ant-
tenna as if it were a solid plate. The moth thus faces an odd problem in
design—more sensilla would give more sensitivity to odorant but at the
same time would reduce the passage of odorant-laced air. For another
investigation I had built a very tiny device to measure airspeeds, so I
looked at the speeds immediately behind antennae, where air had just
passed through (Vogel 1983). Comparing these speeds to the free-stream
gave figures of from 8 to 18% for the fraction of the air approaching an
antenna that went through and not around—for the “aerodynamic trans-
missivity.” The exact figure depended on the particular free stream
speed. Lower speeds gave lower transmissivities, as one would expect
from the presence of velocity in the denominator of equation 6.4—lower
speeds mean thicker boundary layers even where that equation doesn’t
precisely apply. The figures are far below the generally assumed 100%
and well below even the antenna’s optical transmissivity of 43%. With less
air passing immediately by them, the sensilla must be even more sensitive
than previously imagined—such are the vicissitudes of viscosity.

The moth’s problem is only an instance of something quite wide-
spread—a great number and diversity of organisms, creatures such as
sponges, barnacles, some sea anemones, and various aquatic worms, live
by separating edible material from large volumes of water. The game is
called “suspension feeding” and almost always involves some sort of fil-
tration mechanism and thus the attendant difficulty of getting out tiny
particles without excessively discouraging the flow of the water in which
the particles are suspended. But the rules and possible moves in the game
are complicated—simple sieving is only one way of doing the necessary
separation (Rubenstein and Koehl 1977).

Stirring the substratum

One occasionally notices snow swirling around on the downwind side
of a tree or smoke vortices behind a chimney. The same phenomenon
occurs on a much smaller (but not microscopic) scale behind small cyl-
drical organisms protruding from a solid substratum into a flow. But
here there’s a second component of the motion. Near the top of the pro-
trusion the local speed of flow is greater than it is near the bottom (sub-
stratum)—the cylinder is, of course, sticking up through a boundary
layer. Fluid, as repeatedly mentioned, doesn’t like to shear rapidly, and
the fluid behind the top of the cylinder is subjected to more shear from
the faster-moving fluid passing by it than is the fluid near the bottom. So
fluid behind the top is drawn, essentially by its viscosity, into the passing
flow; and that fluid is replaced by fluid moving up behind the cylinder from the bottom. In short, there is a net upward flow behind a protruding vertical cylinder—the effect is occasionally referred to as “viscous entrainment.” It is sometimes misattributed to Bernoulli’s principle (Chapter 7); the principle, though, doesn’t apply to velocity differences due solely to position within a boundary layer.

Protruding vertical cylinders are extremely common in nature—all sorts of plants grow that way. They occur, as well, as attached animals sticking up into moving water. Until recently it was assumed that arrays of cylinders inevitably had a stabilizing effect on any erodible substrate, that they caused what is termed “skimming flow” in which the cylinders shelter the water between them from the current which then “skims” over the top. But it’s now clear that skimming requires a very dense array of cylinders, and that lower densities have the opposite effect of eroding sediment by creating the vertical aftercurrents just described (Eckman et al. 1981). The protruding tubes of several kinds of marine worms effectively resuspend detritus—edible dirt, loosely speaking (Carey 1983)—one worm switches from feeding on detritus to suspension feeding with its pair of tentacles when the water velocity increases (Taghon et al. 1980).

Some black fly larvae that live in shallow, rapid streams have an interesting variation on the device. They are attached at their posteriors and have a pair of food-trapping fans on their anterior ends. A larva twists lengthwise so one fan is uppermost and feeds from material suspended near the outer edge of the boundary layer (Figure 6.6). The other fan is then lower and a bit downstream; it feeds on material resuspended in the vortices rising behind the body. Upward flow of water in the vortices is further encouraged by a downstream tilt of the body as a whole. Groups of larvae, positioned as they are in nature, don’t compete for food but instead enhance each other’s feeding efficiency (Chance and Craig 1986). There’s more than sex to being social; sometimes it’s just a way to stir up some dirt!

**Regimes of flow and the Reynolds number**

Even with fixed geometry of the solid elements across or through which fluid passes, flows vary widely in character. Sometimes fluid moves smoothly, with each bit following a course nearly parallel to adjacent ones. Under other circumstances fluid moves less regularly, with the overall direction of flow mainly a statistical matter and the individual bits tracing all sorts of erratic courses. We speak of these situations as “regimes” of flow—“laminar” (smooth) and “turbulent” (irregular) in these
particular cases. You surely have had experience with both—syrup pours in a laminar fashion, water emerges turbulently from a nozzle, and deliberately induced turbulence disperses the cream in the coffee.

The consequences of the existence of such distinct regimes underlie most of the apparent complexity of the phenomena attending flow—the definition of viscosity and the Newtonian laws may not change, but the manner in which they apply to particular situations is certainly variable.

The first systematic investigation of the phenomena seems to have been that of Osborne Reynolds (1883). He knew that flow through pipes was sometimes laminar but could abruptly become turbulent, so some queer discontinuity clearly existed. Using a variety of pipes, fluids, and flow speeds, he was able to show that the transition from laminar to turbulent flow happened at about a certain value, 2000, of a dimensionless, composite variable to which we now give his name—the Reynolds number. This proves to be an extraordinarily useful quantity, perhaps the best single index to the character of flow, not just in pipes but in streams, lungs, ocean currents, blood vessels, or industrial vats, in fact just about everywhere that real fluids flow steadily at substantially subsonic speeds reasonably far from fluid-fluid interfaces. Which includes most biologically interesting flows—without mention of Reynolds numbers, no sensible treatment of flow in living systems is possible.

What the Reynolds number does is give an indication of the importance of viscosity—actually the unimportance, since low Reynolds numbers are associated with very viscous situations. One might expect that
the value of viscosity would suffice, but other factors have equal influence in determining its relative role. We've noted that what viscosity does is to oppose the existence of steep velocity gradients, so viscous force (as in equation 6.3) measures what one might term the "groupiness" of a fluid, the tendency of bits of fluid to flow coherently, in unison. What does the opposite, promoting gradients? Recall that these gradients are across the direction of overall flow, not along the flow. The inertia of a bit of fluid will keep it moving steadily in the face of the retarding or accelerating effects of adjacent bits of fluid. Thus, inertial resistance to acceleration, the need of a force to change speed, opposes viscous forces and reflects the "individuality" of a bit of fluid.

We thus have two opposing sorts of forces, loosely called "inertial" and "viscous." The Reynolds number is simply the ratio (dimensionless, of course) between these two. It is entirely analogous to the Froude number, which you may recall is the ratio of inertial to gravitational forces. Inertial force is represented by the familiar \( F = ma \), although disguised a bit into a form useful for steady flow of fluids. Mass is replaced by density times area (across the flow) times length (with the flow), and acceleration is replaced by velocity over time. Since length/time is velocity,

\[
F_i = \rho S v^2 \text{ or } \rho S v^2. \quad (6.5)
\]

For viscous force, we adjust equation 6.3, introduced earlier to define viscosity:

\[
F_v = \mu S v. \]

The result is surprisingly ordinary, without even an exponent to challenge the calculator:

\[
\text{Re} = \frac{F_i}{F_v} = \frac{\rho v}{\mu}. \quad (6.6)
\]

None of the factors in the Reynolds number presents much of an evaluation problem for practical situations. Density and viscosity refer to the fluid and (if not found in Table 6.1) are usually matters of public record. Notice that the ratio of the two appears in the Reynolds number—the ratio matters more than the individual values. For a given size and speed, then, flows of water have Reynolds numbers fifteen times greater than those of air—flows of water are, oddly, less viscous in character. Velocity is that of the mainstream fluid relative to the object, or substratum, or the wall of a pipe. Length is another "characteristic length" of an object chosen largely by convention—maximum length in the direction of flow for flows across solids, or the diameter of pipe or channel for internal flows. As with scaling rules (which the Reynolds number is), one is dealing with wide-ranging situations and a fairly crude index. In fact, one
almost never cites a Reynolds number with more than two significant figures, and one can't compare the Reynolds numbers for different shapes to even that rough level of precision. It's a ballpark business.

And organisms encounter an especially wide range of values (Table 6.2). The extreme range results from the fact that small creatures typically move slowly or encounter slow flows deep within boundary layers; large creatures experience more rapid flows; and the formula includes the product of length and speed. The main consequence is that a good shape for one organism may be quite inappropriate for another if the two operate at substantially different Reynolds numbers, even if they are engaged in what seem similar activities.

At low Reynolds numbers (roughly 10 and lower), flows across solids are laminar and orderly; if vortices occur at all, they are relatively large and distinct. Velocity gradients are gentle and, in general, drag is proportional to the first power of velocity and doesn't depend very strongly on shape. As we'll explain shortly, streamlining is almost without value as a scheme for reducing drag at low Reynolds numbers.

As Reynolds numbers rise (from roughly 100), flows become increasingly disordered, with turbulent chaos setting in, first in one situation or location and then in others. Velocity gradients are increasingly steep, and drag may be proportional to the square of velocity (but the relationship is rarely tidy) and becomes strongly shape-dependent. For instance, total drag may be reduced as much as fiftyfold by shifting from a sphere to a well-streamlined form where both have the same frontal area perpendicular to flow.

Incidentally, the identity of most of the factors of equation 6.4 with those of equation 6.6 is neither accidental nor irrelevant. For the range of Reynolds numbers over which equation 6.4 applies, the thickness of a boundary layer relative to the length of a flat plate varies quite systematically with changes in the Reynolds number—thickness is inversely proportional to the square root of the Reynolds number. Thus, the higher the number, the thinner, relatively, the boundary layers. There's an agreeable consistency to these matters.

<table>
<thead>
<tr>
<th>Table 6.2. Reynolds numbers—examples</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bacterium swimming</td>
</tr>
<tr>
<td>Pollen grain falling, or sperm swimming</td>
</tr>
<tr>
<td>Fruit fly (fuselage) in flight</td>
</tr>
<tr>
<td>Small bird flying</td>
</tr>
<tr>
<td>Squid fast jetting</td>
</tr>
<tr>
<td>Large whale swimming</td>
</tr>
</tbody>
</table>
Modeling

Like the Froude number, the Reynolds number provides a useful tool for making models. For two geometrically similar situations, equality of Reynolds numbers assures equality of patterns of flow, whatever the individual values of length, speed, density, and viscosity. We biologists seem always to be dealing with extremes of size so a good scaling rule is a big boon, although it must be admitted that biologists are often skeptical of its legitimacy—those \( \mu \)s and \( \rho \)s look like Greeks bearing gifts.

I’ve had recourse to the use of the Reynolds number for scaling experiments on quite a few occasions. At one time I was interested in induced air flow through the burrow systems of prairie dogs at low ambient winds (Vogel et al. 1973). A burrow in nature is 3 m deep, 15 m long, and about 0.1 m in diameter—quite an awkward item to bring into (or reproduce in) a laboratory. But tenfold reduction of lengths permitted use of a simple model made of copper water pipe beneath a plywood “ground” that would fit in the local wind tunnel. In compensation for the reduction in size \( (l) \) all I had to do was increase speed \( (v) \) by the same factor, so 1 m s\(^{-1}\) became 10 m s\(^{-1}\). As a bonus, the internal speeds were raised to a more easily measured range. More recently, I felt I needed to know how pressures varied along the length of a rapidly swimming squid (Vogel 1987). My best pressure-measuring device works only in air, and I wanted to get up to rather high speeds. The local engineers kindly loaned me a wind tunnel that went up to 75 m s\(^{-1}\) (170 mph), and I made my model half again as large as life. As a result I could simulate a squid jetting at nearly 8 m s\(^{-1}\) in water, as the reader can easily verify.

For such modeling it’s only necessary that the conditions for applying the Reynolds number be met—no fluid-fluid interfaces, decency subsonic flow—and that any shift from, say, air to water not cause abnormalities (due to the change in forces) in the shape of the organism or model. The changes can be extreme—use of corn syrup instead of water permits more than a thousandfold increase in size and thus macroscopic modeling of microorganismic phenomena. By contrast, modeling surface ships with the Froude number is far messier—ships protrude downward from the surface, so the Reynolds number matters as well. Comparing equations 4.6 and 6.6, it’s easy to see that an alteration in size or speed cannot be made without changing either one dimensionless index or the other, so serious compromises are inevitable.

Streamlines

The principle of continuity, presented in Chapter 2 in terms of flow through pipes, states that the rate at which volumes of fluid enter a rigid
system of pipes must exactly equal the rate at which volumes of fluid leave the system or pass any cross section of it. For an incompressible fluid, that requires that the product of velocity and cross-sectional area must be the same for all cross sections of the system.

The principle turns out to be quite as useful for flows across objects and surface—open fields of flow—where there are no rigid pipes to provide boundaries. Fluid (for our purposes) is still incompressible, and mass is still conserved. But to apply the principle, it is necessary to provide some analog of the walls of pipes; in practice the scheme is a simple one. Consider a two-dimensional (to fit on paper) field of flow (Figure 6.7) where the speed of flow varies from place to place but does not, at a given place, vary from time to time. (This condition defines "steady flow," which, somewhat confusingly, may involve acceleration and is thus not analogous to "steady motion.")

Assume that you have some device to tell the direction of flow at any point (a thread on a stick, a stream of dye, a time-exposed photograph of a particle passing through the field, etc.). The directions of flow can be mapped by drawing short lines that follow the local flow directions—lines bits of fluid will pass along as they flow. With enough points mapped, the short lines can be connected into longer ones running completely across the field in the directions of flow. Mapped this way, fluid is automatically prohibited from crossing the lines, so the lines amount to nonmaterial partitions and play exactly the same role as the walls of rigid pipes! Between any pair of lines, the principle of continuity must hold. If a pair of lines diverges, the fluid must be slowing down; if a pair converges, the fluid is accelerating. The lines are called "streamlines" since

![Image of streamlines]

**Figure 6.7.** Streamlines (dotted lines in the center) connect upstream points with others successively farther downstream with respect to the local directions of flow.
they follow the stream of fluid at all points. In three dimensions the set of lines just takes the form of a set of tubes, and the principle applies as well. "Streamlining" in the popular sense means shaping something so fluid flows smoothly around it and causes a minimum of drag; it's only indirectly connected with these streamlines.

Armed with streamlines, we can take a more physical view of the way the Reynolds number delineates flow regimes. Figure 6.8 gives the streamlines for flow around a cross section of a long circular cylinder—the real messiness of the world with which fluid mechanics must deal is immediately obvious, but so also is the way the Reynolds number at least orders the mess.

The world of very low Reynolds numbers

The orderliness of flow at low Reynolds numbers is evident, if unremarkable, in Figure 6.8. Flow undergoes no further awkward transitions below $Re = 10$, not just around spheres but around practically any shape at all. Such simplicity doesn't imply familiarity, though. Perhaps nowhere else do our experiences and prejudices as big animals who move rapidly distance us further from immediate reality than in the world of low Reynolds numbers—a new domain of intuition must be cultivated to deal with this novel regime of flow. A few general examples ought to point up the strangeness.

Flow without inertia

We normally and uncritically regard flow as a disordering process—even linguistic conventions reflect the view, as someone "stirs up trouble." At Reynolds numbers below unity, flow is not necessarily disordering—it's very hard to mix two viscous fluids, such as corn syrup and molasses or the two components of epoxy glue, in terms of both the work it takes to stir and the amount of stirring needed to have much effect. With a little care one can demonstrate in such syrupy combinations the phenomenon of stirring without mixing—the effect of three turns clockwise with a spoon can be pretty well undone by three turns counterclockwise.

And turbulence is simply unimaginable—turbulence is associated with high rates of shear and steep velocity gradients. Sustaining the velocity gradients of turbulent vortices is beyond the poor power of the fluid's inertia as it pales before the militance of viscosity. While vortices have been made at $Re = 0.01$, they were created with difficulty and could be sustained only by continuously doing work.

This reversibility of flow extends as well to the forces involved. At higher Reynolds numbers one can get a net force (and thus propulsion)
Figure 6.8. The character of flow around a circular cylinder (shown in cross section) depends very strongly on the Reynolds number, from orderly flows at low values through several transition regimes—attached vortices and periodically shed vortices—to thoroughly disorderly flows at high values.
VISCOSITY AND FLOW

by moving a fluid with a rapid stroke in one direction and a slow one in reverse. The total “impulse” of the force (the product of force and time) differs for the two directions, and so there can be “power” and “recovery” strokes. The difference traces to the fact that the force of drag for each stroke varies (very roughly) with the square of its speed, whereas the time for each stroke varies inversely with speed to the first power—the product of time and force is therefore different for the two strokes. By contrast, at low Reynolds numbers drag is proportional to the first power of speed, and time is still inversely proportional. While a faster stroke may still mean more drag, the time is proportionately shorter, so the magnitude of the impulse is always the same for two strokes that cover the same distance. Each stroke, whatever its speed, always just cancels the effect of the other.

Nor can one do terribly well by “feathering” a paddle for a recovery stroke. Drag no longer depends very much on shape, and it turns out that a paddle broadside to flow (for a power stroke) has only about 50% more drag than the same one edge on to flow (for a recovery stroke). About the best arrangement possible along these lines involves the use of a cylinder, oddly enough. The drag of a cylinder with its axis perpendicular to flow is nearly twice that with the axis parallel to flow, so some progress is possible by erecting a cylindrical paddle for a power stroke and then folding it down for a recovery stroke. And folding down gets the cylinder further from the mainstream. This arrangement is just what is used by the cilia of many tiny organisms (Figure 6.9). It’s not wonderfully efficient, but it does work, and there are few alternatives.

Low Reynolds numbers may create an orderly world, but the dominance of viscous forces makes it a gooey one. Howard Berg views a tiny organism in motion as like a person “swimming in a sea of asphalt on a summer afternoon.” Inertia has no practical meaning—Berg calculated (Purcell 1977) that if a bacterium could instantaneously stop spinning its

![Diagram of cilia](image)

**Figure 6.9.** The stroke of a cillum, progressing from left to right, consists of a short (fast) power stroke and a longer (slower) recovery stroke. For a cillum beating as is this one, the liquid above will be pushed from right to left.
CHAPTER 6

flagellum it would almost as instantaneously stop moving through water—it would coast a distance equal to only the diameter of a hydrogen atom! To move is to distort the fluid, not just immediately around you but to a remarkable distance away. Among other consequences, the difficulty of moving is affected by the presence of walls far from the immediate vicinity of the mover. As an extreme example, the drag on a cylinder dropping in a viscous fluid at Re = 10⁻² is doubled by the presence of walls five hundred cylinder diameters away (White 1946). Biologists have not been au courant with these small-scale, slow flows even though we ordinarily work with small items—our standard icon is a microscope. We describe the motion of microorganisms abnormally crowded between glass slide and cover slip; we have tables of falling speeds for spores obtained by watching them descend within unreasonably tiny capillary tubes.

Attention has recently returned, beginning with Strickler and Twombly (1975), to the long-neglected consequences of the wide field of disturbance caused by the passage of an object or organism. For a small creature such as a microcrustacean to swing its appendages and swim, in effect, to announce “here I am.” A nearby predator can easily sense its presence. Conversely, it is at least theoretically possible that simply by monitoring the forces needed to propel itself, such an organism might detect walls, food, or even predators. Even an object settling under gravity announces its passage. An analysis by Wu (1977) suggests a partial evasion of the problem. An organism (a paramecium, for instance) swimming by means of a coating of cilia must make far less “noise” than even an inert object falling at the same speed. To work, the cilia must extend from the organism’s surface out into fluid not moving with the organism, so the velocity gradient region on the surface of a ciliated creature cannot be thicker than the length of its cilia. Thus the region of distortion of flow is greatly reduced compared with that associated with swimming with great paddles or even with sinking passively. There’s perhaps some indirect benefit from the inefficient system of ciliary locomotion!

In general, though, movement of an organism or an appendage carries with it a lot of the adjacent fluid and anything in the fluid as well. That’s a good thing if you’re a paddle made of bristles on a power stroke, and many small creatures swim or even fly by moving paddles that lack any continuous membrane over their bristly struts. As we’ve mentioned, it’s a bad thing if you’re trying to filter out molecules or edibles. The problem of filtering described for a silkmoth’s antenna occurs with a vengeance when a tiny crustacean tries to capture food with its appendages, as studied in detail by Koehl and Strickler (1981). This functional goodness of water also has other peculiar consequences. A tiny attached protozoan on a contractile stalk can contract the stalk when a small but voracious pred-
ator is about to bite off its head, but contraction might just draw the predator forward at the same time—the predator's inertia is consequential. If only the Reynolds number were higher! Faster contraction has just this effect, and, as it happens, the most rapid contraction of any bit of animal is that of the so-called spasmoneme of the stalked, colonial protozoan *Zoothamnium* in Figure 6.10 (Weis-Fogh and Amos 1972). On the other hand, a predator also has to get to its prey, not push the prey forward while still out of reach. Again a burst of speed does the deed—one predatory microcrustacean, a millimeter long, can briefly get up to $Re = 500$; to do so, though, it must move at the remarkable speed of 200 body lengths per second (Strickler 1977).

*Stokes' law*

If, as at low Reynolds numbers, drag depends on viscous and not on inertial forces, it's possible to do a simple dimensional analysis to get the suggestion of a formula for drag. Assuming that the relevant variables are the size and relative speed of an object and the viscosity of the fluid, it turns out that drag ought to be proportional to the product of the three, each raised only to the first power. (Ignoring inertial forces has the

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**Figure 6.10.** Contraction of the spasmoneme of *Zoothamnium*—the straight stalk through which the spasmoneme passes hunkers down into a tight helix.
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effect of removing density from consideration—if density is included, the
analysis is no longer so simple, as you can easily verify.) As usual, there's
a numerical constant about which the analysis is silent; it turns out to
depend on shape and orientation. For a sphere, George Stokes (1819–
1903) long ago showed that the full formula (Stokes' law) can be given
simply as

\[ D = 6\pi \mu a v, \] (6.7)

where \( a \) is the radius of the sphere.

The formula is tidy and useful, at least up to \( \text{Re} = 1 \)—it gives the drag
on a fog droplet or a spore sinking in air or on a buoyant algal cell rising
in the ocean. Since drag is not strongly dependent on shape, the formula
gives a decent approximation of drag for shapes other than spheres (al-
though formulas for other ordinary shapes are available). Several cau-
tions are necessary in connection with its use—first, as should be clear by
this point, it doesn’t work when a wall is nearby; second, it is unlikely to
be useful for locomoting organisms, for which the production of thrust
complicates the local flow; finally, it assumes no slip at the surface of
the object. For a droplet of gas rising in a liquid, the liquid induces motion
in the gas, and their joint motion has the effect of a slipping surface—
the factor of 6 in the formula should be replaced by a 4, according to
Happel and Brenner (1965).

The most common use of Stokes’ law is in the derivation of a formula
for the terminal velocities of spheres. At terminal velocity, you’ll recall,
the upward forces (here drag and sometimes buoyancy) equal the down-
ward force of gravity. So one just sets the Stokes formula for \( D \) equal to
\( mg \) and solves for \( v \). Where buoyancy is significant, or if it’s handier to
use densities than masses, there’s a minor additional complication—for
mass one substitutes the product of the volume of the sphere and the
difference in densities between sphere and fluid medium, to get

\[ v = \frac{mg}{6\pi \mu a} = \frac{2a^2\rho g (\rho_s - \rho_f)}{9\mu}. \] (6.8)

It’s important to emphasize that equation 6.8 gives no universal
scheme for calculating terminal velocities, even for spheres. All of the
limitations on the use of Stokes’ law apply, in particular, the limitation to
Reynolds numbers not substantially above 1.0. On the other hand, one
ought to recognize that the rule refers to sinking or rising with respect to
the local fluid and is applicable whatever the larger-scale downdrafts or
upwellings.

The formula for terminal velocity provides a scheme for measuring
viscosity—it isn’t always applicable but is far more practical than the imaginary apparatus of Figure 6.2. One just releases a ball that is sufficiently small or has a density near enough to that of the fluid to ensure a sufficiently low Reynolds number. The density and size of the ball and the rate of ascent or descent go directly into equation 6.8. I once got a rather surprising result with this technique. I had filled a small recirculating tank with corn syrup and wanted to know the viscosity. So I timed the fall of a plastic sphere. Looking up the viscosity of a saturated glucose solution, I found that my calculated viscosity was fully two orders of magnitude higher—a hundredfold error is hard to explain away as inaccuracy of balance, ruler, or stopwatch. But an answer emerged after a bit more investigation, working from the density of the corn syrup and the calorie content on the label. It turned out that commercial corn syrup is mainly supersaturated glucose that just doesn’t crystallize, so the viscosity I had looked up was inappropriate. In the process I found out why the stuff is used in cooking. Table sugar (sucrose) crystallizes readily—if you want sticky frosting or fudge, use lots of corn syrup; if you want solid stuff, use mainly dissolved table sugar; read a recipe and anticipate its result.

LAMINAR FLOW THROUGH PIPES

Let us turn from flow around an object such as a sphere to the opposite, an object around a flow, in particular, flow through a pipe. Drag isn’t the most useful quantity any longer, but the drop in pressure per unit length as a fluid flows down a pipe is completely analogous. Again we’ll consider a situation in which the only force resisting flow is that due to viscosity. It ought to be mentioned that so far we’ve talked a lot about velocity gradients but only once had a decently straightforward one, the constant gradient between the two plates used in defining viscosity (Figure 6.2 and equation 6.3). The gradient in the boundary layer was nearly constant (“linear”) near the surface, but velocity asymptotically approached that of the free stream, giving something quite messy mathematically. And we silently stepped over the complexity of the gradients adjacent to spheres in the so-called creeping flows of low Reynolds numbers.

For laminar flow through circular pipes circumstances are nicer. At least, once fluid gets well downstream from the entrance to a pipe, from a bend, or from any abrupt change in bore, the gradient of velocity across a pipe turns out to be quite thoroughly ordinary. Each bit of fluid proceeds at an unchanging distance from the walls; resistance is entirely a consequence of the no-slip condition and viscosity; and, since it’s then just as hard to force fluid through one part of the pipe as another, the
pressure loss per unit length remains unchanged down the pipe. A simple derivation to be found in almost any textbook of fluid mechanics shows that the “velocity profile” takes the form of a paraboloid (Figure 6.11) with, naturally, the highest speed in the middle and zero speed at the walls. The equation describing the profile is

\[ v_r = \frac{\Delta p (a^2 - r^2)}{4\mu} \]  \hspace{1cm} (6.9)

where \( a \) is the radius of the pipe, \( r \) is the distance of some position on the radius from zero at the center, and \( v_r \) is the speed at that position.

From the velocity profile it is a minor step to get a well-behaved equation giving the relationship among total volume flowing per unit time, \( Q \), pressure drop per unit length, \( \Delta p/l \), the radius of the pipe, and the viscosity of the fluid. In fact, integration of speed (dimension \( LT^{-1} \)) over the cross-sectional area of a pipe (\( L^2 \)) to get volume flow rate (\( L^3T^{-1} \)) was mentioned near the end of Chapter 4. In terms of equation 6.9 (or a graph of it), we’re integrating from \( r = 0 \) (the middle) to \( r = a \) (the wall). The result is straightforward:

\[ Q = \frac{\pi \Delta p a^4}{8\mu} \]  \hspace{1cm} (6.10)

The only difficulty is in pronouncing its name, “Poiseuille’s equation,” or the “Hagen-Poiseuille equation.” (The name of the old unit of viscosity, the poise, was a merciful truncation.)

This equation asserts that volume flow rate and pressure drop per unit length are mutually proportional—it takes more pressure to push fluid along faster—and that volume flow rate is inversely proportional to viscosity—stickier fluids flow more slowly. All this is nicely intuitive. But it says something more startling as well. Volume flow rate varies with the \textit{fourth} power of the radius of the pipe, which is pretty extreme stuff. Part of the latter is obvious—if the radius is doubled, cross-sectional area is

**Figure 6.11.** The paraboloid of revolution formed by the local velocities in laminar flow through a circular pipe.
quadrupled, so even without viscosity, volume flow rate should be proportional to the square of the radius. In addition, though, a bigger pipe has less wall relative to its area (recall the reasoning in Chapter 3), so it has (relatively) much less resistance to flow on that account as well. Thus, if a big pipe is divided into a pair of small ones without change in total cross-sectional area or pressure drop, the overall volume flow rate is halved. Or if, to save material, you halve the diameter of a pipe in a plumbing system, you need sixteen times as much pressure to keep the flow rate the same. These matters of scale will prove decisive in explaining many features of the plumbing within organisms (Chapter 8).

Some other useful relationships come out of these equations. From equation 6.9 comes the maximum speed of flow—just look at the center by setting \( r = 0 \). From equation 6.10 comes the average speed of flow—just divide volume flow rate by the cross-sectional area of the pipe, \( \pi r^2 \). Then something else spills into our laps. Maximum flow speed is just twice as fast as average flow speed, independent of the values of any of the specific variables. How nice! Sometimes it’s handy to measure the maximum, using the time of first arrival of some tracer substance such as a dye. At other times it’s easier to measure the average, catching and timing the discharge, say, with beaker and stopwatch. No matter—one can always convert one into the other.

Still, you may ask, just how useful is all this talk about laminar flow in pipes? After all, laminar flow around spheres as described by Stokes’ law is good only up to \( \text{Re} = 1 \), which corresponds to rather small-scale operations, to an object a millimeter in diameter going a millimeter per second in water or a little over a centimeter per second in air. But recall Reynolds’ original observation. Laminar flow in pipes extends up to \( \text{Re} = 2000 \), where the length in the expression for Reynolds number is taken as the diameter of the pipe. That corresponds to a pipe of 1-cm bore carrying water at 0.2 m/s. It may not be much of a piece of commercial plumbing, but it includes virtually all internal fluid transport systems in organisms. We approach the limit in our aortae, but their careful design normally ensures the absence of turbulence with its resulting higher pressure drop. Turbulence makes noise, and the character of this pathological noise, audible with a stethoscope, is a useful diagnostic tool.

*Manipulating the parabolic profile*

For many purposes a pipe of circular cross section and laminar flow is just fine. Its construction uses less wall material relative to its inside volume than does any other shape, and it withstands internal pressure with less bulging or cracking. (We’ll examine the mechanics of such cylinders in Chapter 11.) No other shape gives as low a pressure drop per unit
length for a given flow. The pressure drops in laminar flow are usually
less than those associated with any amount of turbulence. And flow is
minimally sensitive to the texture of the inner pipe walls—small bumps,
scratches, and minor bends make little difference.

For functions that depend on having a lot of surface relative to volume
there may be no worse shape than a pipe with a circular cross section. In
particular, flow through pipes and channels within organisms is com-
monly associated with exchange processes. Heat, dissolved respiratory
gases, ions, and organic molecules pass back and forth between internal
fluid and external material, going through the walls of the pipes—this
exchange is the main reason for pumping liquids and gases around
within organisms. Exchange, obviously, is facilitated by the most exten-
sive contact between fluid and walls, and a combination of geometry and
fluid mechanics that minimizes this contact is clearly a disability. The sin-
gle most effective way to increase contact is through a proliferation of
small pipes; the point was made in connection with surface areas in
Chapter 3. But an organism can play various games with the profile of
flow itself.

If flow is between parallel plates instead of in circular channels, there
is more wall and less channel; on the average, a bit of fluid flows closer
to the wall relative to the overall thickness of the channel (Figure 6.12).
Gills of many aquatic organisms, both vertebrate and invertebrate, are,
arranged in the form of parallel flat plates, as are the so-called “book
lungs” in spiders. The nasal passages of mammals are extensive and flat-
tened in cross section—contact between air and wall serves a variety of
functions even beyond the exchange involved in olfaction. In small mam-
mals and birds, heat from an exhalation may be used to warm the walls;
the same heat then warms the subsequent cold inhalation instead of
being lost to the atmosphere. And in the same process water vapor from
the lungs may condense out on the cold walls where it can be used to

\begin{figure}[h]
\centering
\includegraphics[width=\textwidth]{figure6.12.png}
\caption{The parabolic distribution of velocities from flow in the
narrow gap between two very wide flat plates parallel to each other.}
\end{figure}
moisten the next inhalation as another conservation device (Schmidt-Nielsen 1972). Interestingly, adult humans exhale air only slightly below body temperature, but infants exhale air closer to ambient temperature (at least my son did so)—their different surface-to-volume ratios within the air passages probably make the difference.

Other schemes also promote intimacy between flowing fluid and channel wall. Blood is transported from heart to capillaries in large vessels with a nearly parabolic velocity profile. (Some distortions arise from the pulsatile flow, from branching, and from the peculiar irregularities of blood viscosity.) In capillaries the flow is far from parabolic—red blood cells just squeeze through (Figure 6.13), so the plasma between successive cells has to flow faster near the walls than it would otherwise. Thus the blood cells, whatever else they may accomplish, must passively enhance exchange between plasma and capillary walls.

Recall that the parabolic profile comes about because the resistance to flow is entirely due to the presence of the material walls of a pipe. What if the walls provide propulsion instead of resistance? A ciliated surface does just that, greatly increasing the steepness of the local velocity gradient. We're a bit big to make much use of the device (or so one guesses)—cilia in our respiratory passages move surface mucus, not the air itself. But lots of invertebrate gills have ciliated surfaces as the basic pump, and the digestive tubes of many small creatures are lined with cilia, so the arrangement is really quite widespread. Such ciliary propulsion ought to facilitate exchange between fluid and walls of the conduits.

**Figure 6.13.** Red blood cells flowing through a capillary. The fit is sufficiently tight so the retarding effect of the walls on adjacent flow ends up distorting these normally disc-shaped cells into something closer to deflated basketballs.