bending over in strong flow, much as palm fronds conform to a strong wind.

When currents and drag are too strong, some animals, such as 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 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 5.9). Many seaweeds simply bend over, and this allows their long axis to be nearly parallel to the current, which reduces cross section exposed to the flow and, therefore, reduces pressure drag.

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, the mobile invertebrates such as drilling snails and limpets found on exposed coasts are much smaller than members of the same species inhabiting 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 Judge 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 time means fewer resources for growth, which may also explain the smaller size of the exposed shore limpets. The interaction of seeking food and dealing with drag is discussed in Hot Topics in Marine Biology 5.1.

![Flow patterns around a cylinder](image)

**Figure 5.8** Flow patterns around a cylinder (view is down the axis of the cylinder, looking at the cross section). Note the irregular flow in the wake of the cylinder.

Pressure drag is mainly the result of inertial forces in the fluid, and it dominates total drag at high $Re$. 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 stream effectively pushes along the object. Pressure drag increases proportionally to the cross-sectional area exposed to the current and to 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 flat surface of the plate is parallel to the current. This principle also applies to objects moving through a fluid, such as air or water. Anyone who has driven an old van or a big truck knows that its flat front creates sufficient drag to increase fuel 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 with the long axis parallel to the current and 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 Koehl 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

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4 See Koehl, 1976, in Further Reading.

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Fish form and streamlining to allow fast swimming must mainly reduce pressure drag but also skin friction.

In Chapter 8, the form of fish is discussed. However, it is worthwhile 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 drag 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 5.10). If a fish is short and squat, there is a very steep pressure gradient from front to rear, and this leaves a large and irregular 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

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5 See Judge, 1988, in Further Reading.
drag is reduced greatly. That is why fast- and continuously swimming fish exhibit some variation of the classic shark or tuna shape, which creates the smoothest wake. Fast-swimming sharks also have adaptations to reduce skin friction, including arrangements of scales that present surface irregularities. Fish surface slimes also reduce skin friction and some rib-bearing fish scales may be adaptations to hold onto the slime.

**Conflicting Hydrodynamic 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 a blade of sessile eelgrass. It projects upward from the bottom and thereby is able to capture light and nutrients. However, this upward projection causes a significant pressure drag. There is a conflict of different functional requirements. The size and velocity scaling of hydrodynamic effects create additional conflicts. As an organism grows in length, the $Re$ increases. Consider Figure 5.11, which shows patterns of flow downstream of a cylinder under conditions of varying $Re$. 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 as the current increases 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.

**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 for 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 study the behavior of very small creatures at low $Re$. In moving waters, flumes of various types are used to study the effects of flow. A flume is a device that includes a source
Flow Is a Drag, but It Sure Can Smell Good

The first thing that we usually learn about organisms is that they are rarely controlled by only one factor in nature. Not only are several different effects usually at work (e.g., temperature, salinity, and water flow), but also the organism has numerous needs (e.g., to find food, mates, and a proper substratum). This complexity is readily illustrated by a study of the effects of flow on marine epifaunal invertebrates such as predatory crabs and prey bivalves.

Consider the carnivorous blue crab *Callinectes sapidus* (see Figure 13.20c), which is a common coastal crab on the east and Gulf coasts of North America. Its favored prey is the infraunal eastern hard clam *Mercenaria mercenaria*, which is found in soft intertidal and shallow subtidal bottoms. The crab walks actively about and can locate its prey by means of chemosensory hairs on the antennules that recognize molecules carried to it in bottom currents. Where do these molecules come from? They are propelled through the hard clam's exhalant siphon and become entrained in the flow, creating an odor plume that eventually reaches the crab (Box Figure 5.1).

The crab's problem is as follows: How can it locate the origin of the detected molecules (even clams have a scent, which must be explained by various excretory products such as peptides and urea)? It can walk randomly until the scent (or, more properly, rate of stimulus of the chemosensory hairs) becomes stronger, but this would be rather inefficient. It helps that the sensory hairs are on both the right and left antennules. As the crab moves, it is able to judge whether to move left or right, depending on the relative strength of the signal that reaches the sensory hairs. (The sensory hairs are quite small, and a viscous boundary layer of water develops around them. That's why crabs and lobsters often flick their antennules to reduce the boundary layer and to allow flowing water and the entrained molecules to impact upon the chemosensory hairs.)

The crab also derives information directly from the flow. The molecules are moving downstream, and so it makes sense to use water flow information to aid in locating higher concentrations of those molecules. That is why crabs also have mechanoreceptor hairs on the antennules.

Armed with both chemosensory and mechanosensory hairs, the crab's prey location problem appears to be solved, and it might seem that any nearby clams are doomed. Or are they? The odor plume emitted by a clam can provide useful information only if there is a regular decline of concentration with distance of the material in the plume responsible for the strength of the odor. That occurs if there is a well-developed boundary layer. Then water is propelled through the clam's exhalant siphon and moves regularly up into the mainstream. From an initial position downstream, the crab walks upstream toward the source of the odor and eventually finds its way to the exhalant siphon by successively encountering increasing odor intensity, much as a heat-seeking missile might find its way down a warm chimney. Work by Richard Zimmer demonstrated that the flux of material (molecules per unit time) flowing past an odor-detecting animal is what matters: a low-velocity current with high concentration of odor has the same effect as a high-velocity current with low concentration of odor.

**Box Figure 5.1** Dye traces of odor plumes. The blue crab *Callinectes sapidus* must locate the odor plume emanating from the exhalant siphon of the clam *Mercenaria mercenaria*. (a) If the current is relatively weak, the flow is laminar and the odor plume maintains its integrity. (b) If the current is strong, or if the bottom is rough, the boundary layer becomes turbulent and the crab will have trouble following the odor to its source. (Courtesy of Marc Weissburg.)

If, on the other hand, the bottom is irregular or the near-bottom water current is very fast, the water flow near the bottom will be turbulent and there will be a poorly developed boundary layer. Under these conditions, clams often fail to locate the odor plumes generated by the clams. In the natural estuarine habitats of the crabs, such as Chesapeake Bay, the current velocities are often in the range at which a boundary layer is well developed, and recent research shows that the plumes are regular enough to permit the crabs to follow them to the source.

How do the crabs detect the odor? Detection is chemical, and it is done by receptors on the claws, legs, and antennules. Leg sensors help control steering as the crab moves toward the odor plume's source and antennule sensors help control upstream movement. The claw, leg, and antennule sensors are located on the right and left sides of the crab, so the crab gets its best information by facing directly upstream to get orientation information from both left and right sides. But there is a major problem: with an odor source often comes a water flow, which is sometimes a challenge to the crab. Imagine yourself standing in the surf facing directly into an oncoming wave: you will be knocked down! If you turn 90 degrees you will be a bit more streamlined; this is a natural response of people facing the surf. The same goes for a blue crab. Its drag is much less if...
**BOX Figure 5.2** (a) Experimental design to study the spread of odor plumes. Dye and odor chemical are both released at the same location in a flume. Water currents carry both downstream, and flow is characterized by a laser-light source that induces fluorescence and is detected by high-speed video. (b) Drag on crabs is measured by attaching crab in flume to a strain-detecting device; (c) blue crabs have maximum sensory detection but also maximum drag when facing current, as shown by larger downstream wake in left crab photo, where crab faces current frontally. (d) Drag caused by crabs placed at different angles to the flow. They rotate to minimize drag when current strength increases. (Courtesy of Marc Weissburg.)
it does not directly face the flow. So, a conflict arises: if the current speed is fast, maximal information needed for moving upstream and steering in the direction of the odor plume is in conflict with minimizing drag.

Weissburg and colleagues' used a complex apparatus (Box Figure 5.2a) to characterize the odor plume in moving water in a flume. Both an odor and a fluorescing dye were released upstream of a crab under different conditions of flow. A laser light source produced planes of light that could be integrated to characterize the flow. Crabs were placed in the moving water and, when they were impacted by moving water, their motion rotated a device that could estimate the drag on the crab (Box Figure 5.2b). By this mechanism they could show that drag was maximal when the crabs faced directly into the current and minimal when the crab rotated 90 degrees (Box Figure 5.2d). When flow was very low, crabs faced into the current but rotated when the current increased. The researchers used dye to visualize the flow around crabs in different orientation, and crabs facing the current head-on had a dead spot of water eddies downstream of the body, showing how a localized low spot of pressure downstream would greatly increase drag in this orientation (Box Figure 5.2c).

![Creeping flow](image1)

![Somewhat turbulent wake](image2)

![Attached vortices](image3)

![Fully turbulent wake](image4)

**FIG. 5.11** Different types of wake downstream of a cylinder, at different Reynolds numbers. (After Vogel, 1994.)

of moving water, a working area where the organism and flow field are characterized, and a drain-return system (Figure 5.12).

Most flume designers seek two objectives: maintenance of laminar flow and maintenance of scaling by Re (and there are also other parameters beyond the scope of this text). A long flume is desirable because it takes awhile 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 Re is also essential to keep the proper ratio of inertial to viscous forces. This refinement 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.

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See Weissburg and colleagues' 2003, in Further Reading, Hot Topics in Marine Biology.

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*See Hot Topics in Marine Biology 5.1 to see a flume application.*
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 mainstream 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 the siphon difficult to control, and it is withdrawn. The animal then 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. Using a flume with a video recording device can carry out such qualitative observations quite easily.

7 See Levinton, 1991, in Further Reading.

CHAPTER SUMMARY

- Water is relatively dense and viscous. Dynamic viscosity measures the molecular stickiness of a fluid, whereas kinematic viscosity is dynamic viscosity divided by the density.

- The Reynolds number is the product of velocity, size, and density divided by dynamic viscosity. When $Re < 1$, viscous forces dominate fluid properties; when $Re > 1,000$, inertial forces dominate. Small and slow-moving organisms operate in a very viscous world, whereas large fast-moving organisms are dominated by inertia.

- If an object is entrained in moving water, it will move along with streamlines. Laminar flow is regular and occurs under relatively slow flow and low $Re$. Turbulent flow is irregular and occurs under higher velocities and high $Re$.

- Turbulence on the scale of meters occurs at high $Re$. On a smaller scale, it involves shear, which allows new water to arrive more quickly to the surface of small organisms.

- Water moves in a free stream above a surface, but its velocity is zero at the surface (the no-slip condition). A boundary layer of lower velocity and low $Re$ exists at the surface, even if water is moving some distance away. Cells in the middle of the water column also have no velocity at the cell surface and very low $Re$. Shear due to cell motion can move materials toward the cell surface.

- The principle of continuity states that velocity is inversely proportional to cross-sectional area. If the area doubles, velocity is cut in half.

- Organisms can propel water at low velocities with thousands of tiny structures called flagellae. Water velocity through an exit channel is increased when the total cross-sectional area over which many flagellae act is much larger than the exit.

- Bernoulli’s principle states that pressure varies inversely with fluid velocity. Organisms use differential velocity to create pressure gradients, which can create lift and also drive water through burrows.

- Drag is produced when pressure differs upstream and downstream of an object. Drag can be reduced by streamlining, by reducing the presentation of flat surfaces perpendicular to a water current, or simply by bending over (as in seaweeds and soft corals). Streamlined form in fast-swimming fishes minimizes pressure drag and also minimizes skin friction.

FURTHER READING


**Going Deeper References**


**Hot Topics in Marine Biology**


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**REVIEW QUESTIONS**

1. What is dynamic viscosity? Give an example of a fluid that is more dynamically viscous than water.

2. What information does the Reynolds number provide?

3. In seawater, what are the principal factors that vary to determine the Reynolds number?

4. Why can a ciliate stop nearly instantaneously, whereas a large swimming fish takes much more time and a higher number of body lengths to stop?

5. What is the no-slip condition?

6. What conditions are different within the boundary layer, relative to mainstream flow conditions?

7. Marine larvae try to find a place to settle and metamorphose into an adult. If the larvae are hovering a meter or so above the bottom, what must they do to find a clue that a member of their species is present in the bottom?

8. How can a sponge have an exit velocity through its exhalant siphon that is orders of magnitude greater than the intake velocity?

9. How might an attached organism reduce drag, even when it protrudes into the mainstream flow?

10. How might a burrowing worm take advantage of the Bernoulli principle to enhance the flow of water through its burrow?

11. What are the advantages and disadvantages encountered by a sessile marine organism that projects its body into the mainstream flow?

12. Consider a fish swimming in moving water. What creates drag on this fish?