CHAPTER 2 PRINCIPLES OF SWIMMING

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2.1 Introduction

The aquatic environment was the cradle of life on earth. Now, after $10^9$ years of evolution, there are more than 22,000 species of fish, which show a diverse variety of adaptations to meet the requirements of their environment. Although good swimmers are found in many other taxonomic groups, fish are masters of the art of propulsive movement through water. Chapters 2–4 of this book explore some of the ways in which fish swim and how they are suited to the habitats in which they occur. Chapter 2 deals primarily with the variety of swimming styles found in fish. It also focuses briefly on the hydrodynamic interactions that occur between fish and the surrounding water, and on the mechanisms involved in converting work done by muscle into a propulsive force in swimming. Chapter 3 looks at the different types of muscle used to power swimming and explores the relationships between muscle arrangement, physiology and function. The ways in which some fish maintain their position in water against a gravitational force is the subject of Chapter 4.

2.2 Modes of swimming

In all fish, the main body muscles are arranged as discrete segments of muscle, called myotomes, situated on either side of an inner spinal column which is incompressible but flexible. These adjacent blocks of muscle are separated by thin but stiff sheets of collagenous tissue called myosepta (which are similar to the collagenous fascia which link muscles to adjacent tissues in many invertebrates and vertebrates), onto which the individual muscle fibres are inserted. Even in primitive fish the myotomes have a complex shape (see Figure 2.1).

Figure 2.1 The arrangement of the myotomes in three groups of fish. (a) Lamprey (superclass Agnatha), (b) shark (subclass Elasmobranchii) and (c) trout (superorder Teleostei). For the shark (b) and the trout (c) the location of red muscle in the myotome is indicated.
Figure 2.1a and b shows several myotomes in the body of a lamprey and a shark. What we see in this view is the outer surface of the myotome, next to the skin. The three-dimensional structure of a single isolated myotome is shown to the right for each fish, with the surfaces that are normally adjacent to neighbouring myotomes shown in grey. In the trout (Figure 2.1c), several blocks of myotomes have been removed from three different locations to reveal their relationship with the surrounding muscle. To the right are two individual myotomes from the trunk and the tail in the fish body. You can see that, in such teleosts (a superorder which includes most of the bony fishes), the myotomes resemble a series of W-shaped overlapping cones. A single myotome spans many vertebrae between the tips of its anterior and posterior cones. The best way of visualizing the three-dimensional structure of fish muscle is to lightly boil a fish, for example a cod, so that the myotomes can be separated. Most of the muscle is white in colour and is used in burst swimming. The red or brown muscle, located as a small strip near the skin, is used at normal cruising speeds.

As a first step to understanding the role of the myotomes, it is useful to greatly simplify their shape, as shown in Figure 2.2. When the muscle fibres within several adjacent myotomes on one side of the body contract, the body is flexed in that direction. The eel (Anguilla anguilla) has a familiar style of swimming (Figure 2.3) but, even in this elementary form of movement, the body is not simply moved from side to side but is thrown into backward-moving waves which pass down the entire length of the body, increasing in amplitude as they do so. Some fish larvae, including herring larvae, swim in a similar way (Figure 2.4). Each locomotion wave is initiated by the contraction of a few anterior myotomes on one side, while the corresponding segments on the opposite side of the column are in a relaxed state and somewhat stretched—the body therefore bends towards the contracted side. The wave so formed then passes backwards, as the myotomal contractions on one side of the fish are propagated in progressively more posterior segments. In Figure 2.4, the crests of such backward-moving waves are indicated by the closed blue circles. Another wave of contraction is initiated anteriorly on the opposite side when the previously relaxed muscles contract and produce a bend in the reverse direction (indicated by the open blue circles) which also moves backwards. Because the bent portions of the body wall push against the water as the wave of contraction moves towards the tail, the fish is propelled forwards. The side-to-side movement of the tail is very pronounced and the ‘wasteful’ sideways movements at the head mean that this relatively inefficient type of swimming demands a high power output from the body musculature.

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Figure 2.2 A schematic and highly simplified diagram showing how bending of the fish is achieved. Sites of muscular contraction are shown in grey and the spinal column is shown in blue.

Figure 2.3 A mode of swimming typified by the eel (Anguilla anguilla). The black silhouette represents a dorsal view of the fish, and the other outlines show the position of the fish 0.3 seconds earlier (in grey) and 0.3 seconds later (in blue).

Figure 2.4 Swimming in the herring larva (Clupea harengus) at 0.02-second intervals. The series of black silhouettes shows the movement of a fish relative to a fixed position on the background, which appears as a broken line along the bottom. Movements of the snout and tail tip are indicated by black dots. The crests of the backwardly moving waves of myotomal contraction are indicated by the open and closed blue circles.
Backward-moving waves along the entire body are not evident in fast fish such as mackerel and tuna. These fish appear to generate thrust exclusively by the side-to-side movement of the large tail or caudal fin (see Figure 2.5). Their bodies are less flexible: in tunas, the major body muscles deliver the propulsive force to the tail by large tendons which pull the fan-like tail by moving it back and forth on a hinged joint. The great majority of fish have a mode of swimming intermediate between these two extremes.

Why do the myotomes of fish have such complex shapes?

In some fish, one reason is to transfer force efficiently from the mid-body section, where most muscular work is done, to the tail, where thrust is generated against the water. This consideration, however, does not explain why lampreys and eels, which do not have a well defined tail fin, should have complex shapes. Consider Figure 2.6a which shows muscle fibres running parallel to the spinal column (in blue). As the fish bends (Figure 2.6b), the inner fibres nearest the spine do not change length significantly, whereas the fibres near the skin show maximum length change. The parallel arrangement of fibres is therefore impractical since work is shared very unequally between different parts of the myotome. In fact, it has been shown that in order to share work equally, the muscle fibres should run at an angle to the spinal column, but parallel near the skin, with the angle increasing towards the spinal column. Various conical or helical arrangements of muscle fibres are found in different species of fish. They can be compared with the arrangement of fibres in a twisted rope. When a parallel-fibred rope runs round a curve such as a pulley, the outer fibres take most of the strain and are likely to break (Figure 2.6c). Twisted and plaited arrangements of fibres in ropes avoid this problem by ensuring that strain is equalized throughout the rope (Figure 2.6d). In fish, however, muscle fibres do not run throughout the length of the body. Fibres are short, and only run from one myoseptum to the next. The myosepta must be approximately at right angles to the local fibre direction, which means that to accommodate the necessary complex fibre trajectories (Figure 2.7), the myotomes must have a complex shape.
Figure 2.6  (a) and (b) Schematic diagrams of fish myotomes similar to that shown in Figure 2.2. As the fish bends, fibres *parallel* to the spinal column change length by different amounts according to their distance from the spine. (c) A parallel-fibred rope running round a pulley. The outer fibres are stretched the most and tend to break. (d) In a twisted-fibre rope, the fibres are all stretched by a similar amount and the work is shared between the strands.

Figure 2.7  Dorsal and lateral views of a typical teleost fish showing the course of muscle fibres along the body. Note the similarity to the arrangement of fibres in a twisted rope. The myotomes are complex because they must run approximately at right angles to these twisted helical fibre directions.

Summary of Section 2.2

Fish muscle is arranged into discrete segments called myotomes which, even in the most primitive species, are complex in shape. In the eel and some larval fish, backward-moving waves of muscle contraction pass down the length of the body. In fish such as mackerel and tuna, thrust is generated by the side-to-side movement of the large tail fin. The complex shape of the myotomes in these fish facilitates the transfer of force efficiently from the mid-body section to the tail.
2.3 Forces acting on fish

To understand how the work done by the myotomes is converted into a propulsive force in swimming, we first need to consider briefly the forces acting on a body surrounded by water. If the fish is not moving, then gravity (weight) acts in the downward direction and is opposed by buoyancy in the upward direction. In most fish the average density of the body tissue is close to that of water. Buoyancy is then roughly equal to the weight, a situation known as neutral buoyancy, and there is no tendency for the fish to rise or sink. Buoyancy is also known as static lift (Figure 2.8a).

![Diagram of buoyancy and forces acting on fish](image)

Figure 2.8 (a) In a neutrally buoyant stationary fish, e.g. a tuna, the upthrust from buoyancy exactly equals the weight of the fish. (b) A moving fish must generate forward thrust in order to overcome drag.

2.3.1 Overcoming drag

If the fish is moving, it experiences a force opposing the motion, known as drag. In order to move forward, the thrust must exceed the drag. Drag depends on the density and viscosity of the fluid medium. Compared with air, water is both dense and highly viscous and so, for swimming animals, overcoming drag is a serious problem. Drag increases with speed \(v\) in accordance with the square law.

- What are the consequences for drag of an increase in speed?

If speed doubles, the drag, and hence the thrust necessary, quadruples. Swimming fast therefore requires the ability to produce vast amounts of thrust in order to overcome drag.

The effects of the drag square law can be seen in Table 2.1. If we express speed in some arbitrary units, e.g. body lengths per second (BL \(s^{-1}\)), we can see that in order to travel at 10 BL \(s^{-1}\) requires 100 times the thrust (drag) and 1000 times the power needed for 1 BL \(s^{-1}\). Power is the rate of energy utilization (joules per second = watts) and the power required gives a good indication of the amount of muscle needed to achieve a given speed. Swimming at 10 BL \(s^{-1}\) requires 1000 times the muscle mass that swimming at 1 BL \(s^{-1}\) requires. Very large amounts of muscle are therefore needed to swim at very high speeds and the maximum speed of fish is limited by the total mass of muscle available in the body. As much as 60% of body mass can be muscle in some species.
Table 2.1 The drag, power and energy cost of swimming at different speeds.

<table>
<thead>
<tr>
<th>Speed, ( v )</th>
<th>Drag = thrust, ( \frac{v}{v^2} )</th>
<th>Power (drag × speed), ( v^3 )</th>
<th>Basal power, ( B )</th>
<th>Total power, ( v^3 + B )</th>
<th>Energy cost of transport, ( \frac{(v^3 + B)}{v} )</th>
</tr>
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<tr>
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<td>0.00</td>
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<td>1.00</td>
<td>10.01</td>
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<td>0.13</td>
<td>1</td>
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<tr>
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<tr>
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<td>65.00</td>
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<td>1001.00</td>
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This analysis seems to show that swimming in fish might be very difficult, but it should be noted that to swim at slow speeds requires very little power and hence very little muscle (remember the small quantity of red muscle present in most fish, as shown in Figure 2.1). Since the body weight is supported by buoyancy, underwater swimming at modest speeds by fish is the most economical form of transport known in the animal kingdom. The cost of transport is normally expressed in energy required per unit distance. In Table 2.1 we must first add basal or maintenance metabolism \( (B) \) to the power required for swimming to give total power. This sum divided by the speed then gives the cost of transport in the final column (arbitrary units are retained for simplicity).

- What does this final column show?

It shows that swimming very slowly is moderately costly and swimming very fast is very costly, but there is an optimum range of speeds at which cost is at a minimum.

- What is the optimum speed for most fish according to Table 2.1?

For most fish the optimum speed is approximately 1 BL s\(^{-1}\) and it is this speed that fish should adopt to achieve maximum distance with minimum energy expenditure. It should be noted that swimming at the surface (as humans do) wastes a lot of energy in wave-making and costs about five times as much as underwater swimming. The low energy cost of swimming only applies to submerged swimmers.

Overcoming drag dominates the swimming of fish and so any means of minimizing drag is beneficial and likely to be favoured by natural selection. Drag can be divided into two kinds of effect, pressure drag and skin friction drag. Pressure drag is the direct force experienced by the fish as it tries to push its way forward through the water. If you ride a motor cycle, you feel this as the
pressure of the air on your face and body if you try and sit upright. It is best avoided by crouching down on the motor cycle and minimizing your frontal area. If we imagine a hypothetical primitive spherical fish, it is obvious that drag could be reduced by changing the shape to that of a narrow cigar with minimum frontal area. This suggests that all fish should be long, thin and eel-like. However, increasing the length increases the skin area and therefore the friction drag caused by the water flowing over the body. There are also problems of flow over very elongated bodies. Shapes designed to minimize drag are known as streamlined. Minimum drag is experienced when the width \((w)\) to length \((l)\) ratio, i.e. the profile thickness, is 0.25 (Figure 2.9a).

This shape is found in most fast-swimming animals and many fish (Figure 2.9b). Drag is further minimized by reducing any protuberances on the body. In tunas, for example, all the fins (except the tail fin) can be folded into grooves or recesses on the body and even the eye is flush with the surface of the head and covered with a transparent layer of fatty adipose tissue.

**Figure 2.9** The effect of body shape on drag. (a) A width-to-length ratio of 0.25 with a circular cross-section gives minimal drag. (b) Some of the many fish and marine mammals that correspond closely to this shape.
In streamlined fish swimming at low speeds, the flow of water around the body is ordered into layers. A thin layer of water, known as the boundary layer, adheres to the skin and successive layers away from the body are influenced less and less by the movement of the fish. This condition is known as laminar flow and results in relatively low drag. As swimming speed increases, the flow around the body tends to break down and the boundary layer becomes turbulent. The onset of turbulence causes an approximately three-fold increase in drag, which could impose a maximum speed barrier on some species. However, there are several ways in which fish can delay the transition to a turbulent layer. The onset of turbulence usually begins in the tail region and it is thought that, in tunas, the little finlets on the peduncle (Figure 2.5b) help delay the onset of turbulence as speed increases. In fast-swimming fish, lateral movements of the body are reduced—only slow swimmers have body movements of large amplitude. Mucus exuded from fish skin can also reduce the friction and promote laminar flow. Tests on mucus of the Pacific barracuda (*Sphyraena sp.*) suggest that frictional drag might be reduced by almost 66%, but there is no means of verifying this estimate in a living fish. Calculations indicate that reduction of friction by mucus is likely to be most effective at slow speeds. The effect of turbulence, however, can be reduced by deliberately roughening the skin to generate microturbulence. The microturbulent layer next to the skin acts as a sort of lubricating layer reducing frictional drag and delaying the onset of fully developed turbulence. The scales of some fish such as sharks are equipped with little teeth or protuberances 0.05–0.20 mm high that may help promote microturbulence. In some racing yachts it has been found that deliberately roughening the hull may reduce drag.

Some marine fish have a ‘porous’ skin, with a ‘canal’ system filled with seawater just under the outer surface, which may help sustain laminar flow. Among the most interesting is the castor-oil fish, *Ruvettus pretiosus*, examined by the British physiologist Quentin Bone. Here, pointed ctenoid scales project above the skin surface and act as ‘vortex generators’, producing tiny vortices from the tips of the scales which stabilize the boundary layer (Figure 2.10). In addition, this complex skin has sub-dermal spaces that may aid stabilization by sucking in and squirting out seawater as the body moves.

**Figure 2.10** The castor-oil fish (*Ruvettus pretiosus*) and the structure of the skin. (a) The ctenoid scales (shown as white dots). (b) Three-dimensional representation of the pores which are irregularly scattered between the ctenoid scales, and their connection to the relatively large water-filled sub-dermal spaces. (c) A vertical section which suggests how the ctenoid scales might operate as vortex generators. Blue arrows indicate water movement.
2.3.2 Generation of thrust

The basic undulating-body swimming motion of fish can be understood by comparing it with a snake crawling through grass. However, this analogy is an oversimplification since water does not remain static as the fish moves forward. In reality, water must be accelerated backwards to generate a force (thrust) propelling the fish forward. Thus, as a fish swims through the water, it leaves a jet of backward-moving water behind it.

If we compare the fish to a toy submarine, it can be seen that the total momentum imparted to the jet of water from the propeller is equal to the thrust force (Figure 2.11a). In fact, wakes of propellers are more complex and fish certainly do not generate a steady jet flow from their tails. Rather, a series of spinning vortices is shed from the tail (Figure 2.11b, c). Each vortex can be regarded as a packet of water propelled backwards by the sweep of the tail. The direction of the vortex is anti-clockwise during the tail beat to the right and clockwise during the tail beat to the left. The amount of thrust developed depends on the number of vortices shed per second and their magnitude. A single to-and-fro sweep of the tail sheds two main vortices known as a stride. The stride length of most normal fish corresponds to about 0.7 body lengths, i.e. the fish moves forward a distance of 0.7 body lengths for each to-and-fro beat of

![Figure 2.11](image)

- **(a)** The thrust in a toy submarine is equal to the momentum imparted by the propeller to the water.
- **(b)** A two-dimensional view of the wake behind a swimming fish viewed from above. The bound vortices, released at the end of every stroke to the left or to the right, are shown. The arrows indicate the direction of rotation, and their length the relative velocity of the vortices.
- **(c)** An impression of the three-dimensional vortex flow system behind a saithe (*Pollachius virens*). The tail blade is shown in the middle of a stroke to the left, i.e. towards you. The thickness of the arrows indicates relative velocity. The velocity decreases and the diameter of the vortices increases with increasing distance from the tail.
the tail. There is, therefore, a simple linear relationship between the tail-beat frequency and the speed of a fish. A further limitation to the maximum speed of fish is the minimum contraction time of the muscles.

The amount of water propelled into the vortex wake is clearly dependent on the size of the tail. The aspect ratio (AR) of a fin is defined as the square of the span of the fin (i.e., the square of the distance between the tips of the lobes, $s^2$) divided by the surface area of the fin (Figure 2.12). A tail with a high aspect ratio (AR), projecting to a maximum distance above and below the mid-line of the body, will produce the maximum thrust. High-aspect-ratio tails (Figure 2.12a) are found in fish such as mackerels and tunas that swim at a constant high speed. The tails of tunas have an AR of about 6, which is about as high as can be achieved without sacrificing strength. If you imagine such a tail as in Figure 2.12a beating very slowly, the water simply flows around it without having any effect and no thrust is generated because the lower viscosity limit of the tail fin has been reached. In other words, the tail has no 'grip' on the water and it 'stalls'. One solution to this is a broader, low-aspect-ratio tail such as is found in salmon and cod (Figure 2.12b). Such tails are better at slow speeds and for acceleration from a standing start. The tail fin is supported by flexible rays which enable the aspect ratio of the tail to be adjusted as the speed changes. However, at very low speeds the tail fin becomes completely ineffective and the 0.7 body lengths per stride relationship breaks down. The lower viscosity limit of a low-aspect-ratio tail is reached when oscillating at one beat per minute.

The solution for generating thrust efficiently at low speeds is to use rapid undulations of smaller fins accelerating a smaller mass of water. Thus many fish swim by undulating either the pectoral, ventral or dorsal fins or a combination of these.

The rays swim by means of greatly enlarged pectoral fins. Figure 2.13a is a lateral view of a manta ray swimming from left to right. Waves of undulations (in a vertical plane) pass backwards along the fin margins, and a superficial similarity with the mode of flight in birds is striking. Other fish move by the undulations of the dorsal fins. For example, the bowfin (Figure 2.13b) uses only its dorsal fin for gentle forward locomotion, though it can undulate its body for rapid movement during feeding or escape. The knifefish (Figure 2.13c) swims by undulation of an extremely long anal fin. The sea-horse (Figure 2.13d) uses both its dorsal and pectoral fins to generate thrust. The swimming function of the tail has been lost and it has become a grasping organ enabling the fish to hold onto seaweed. The thrust produced by undulating fins can often be reversed or changed in direction, something that is difficult to achieve using the caudal fin. Many fish 'row' themselves or they oscillate small dorsal or pectoral fins. Often such fins are rounded and paddle-like, and beat very rapidly and synchronously, for example, those of the stickleback (Figure 2.13e). The John Dory (Figure 2.13f) moves forward by wave-like movements of the dorsal and anal fins, with the pectoral fins mainly used to provide stability during any manoeuvre. Many of the tropical coral reef fish move exclusively by fins and steer with the caudal fin. The ocean sunfish is a remarkable species, because much of the body musculature has been lost. The tail is a rudder-like hinged flap, and forward locomotion depends on the side-to-side movement of the extraordinarily high dorsal and anal fins (Figure 2.13g). The aspect ratio of the fins is very high and movement in this fish has properly been described as 'a bird flight mode turned through 90°, with high-aspect-ratio wings displayed in a vertical plane'.
Figure 2.13  Fish that use undulating fins for locomotion grouped according to the fins concerned — see left-hand side of the figure. The relevant fins are shown in blue.

2.3.3 Hydrodynamic lift

Many fish are heavier than water and the static balance diagram shown in Figure 2.8a does not apply. Such fish must create hydrodynamic lift to compensate for the net negative buoyancy. Lift can be generated by extending the pectoral fins like wings on either side of the body (Figure 2.14a, b). Viewed from the side, the pectoral fins of a swimming dogfish are slightly inclined to the horizontal, with their leading edge higher than their trailing edge. Under these conditions the fins act as a hydrofoil. If a hydrofoil is to generate lift, it must be inclined, i.e. it must operate at an angle of incidence, \( \alpha \), otherwise the pressure above and below the foil will be equal. With an inclined fin, water moves faster over the upper surface, and this produces a difference in the pressures above and below the foil that lifts the fish upwards. This mechanism is shown schematically in Figure 2.15, where the pressure at the various sites shown in blue on the upper and lower surface of a hydrofoil is indicated by the height of the blue fluid in the manometer tubes. The lift force on a wing or hydrofoil increases with the velocity squared, so that at very low speeds the resulting upward force is small and may not be sufficient to counterbalance weight. Because of this, there is a minimum speed below which a shark or tuna cannot swim without sinking. Mackerel avoid sinking at low speeds by tilting their body upwards. The tilted body provides some extra lift, and swimming forces from the tail are no longer directed horizontally but slightly upwards along the direction of the vertebral column. The tilt angle can be varied in order to increase or decrease speed (Figure 2.16). In sharks and dogfish, lift is also generated by the asymmetric tail, which has a relatively longer, stiff, upper lobe (Figure 2.14a). The tail twists as it moves from side to side, and so generates an upward force as well as forward thrust. Sharks and dogfish therefore do not have to tilt their bodies to create lift.
Chapter 5 looks at how birds’ wings act as aerofoils and generate lift for flight.

Figure 2.14 The forces that act on swimming fish for (a) the dogfish (*Scyliorhinus* sp.) and (b) tuna (*Thunnus* sp.), both of which are denser than the seawater in which they swim.

Figure 2.15 The distribution of pressure around a hydrofoil at a positive angle of incidence (α) in a water tunnel. The height of the blue fluid indicates the pressure at the corresponding position on the upper or lower surface of the hydrofoil. Ambient pressure is indicated by the blue lines.

Figure 2.16 The relationship between tilt angle and speed in the mackerel (*Scomber scombrus*).
To create lift efficiently it is better to have pectoral fins with a high aspect ratio. Figure 2.17 shows examples of both elasmobranchs and teleosts that are heavier than water and have high-aspect-ratio pectoral fins.

Figure 2.17  The shape of the pectoral fins of a variety of fish, viewed dorsally. The shaded fins to the left are of teleosts: (a) mackerel (*Scomber scombrus*); (b) swordfish (*Xiphias* sp.); (c) carangid (*Trachurus* sp.); (d) longfin tuna (*Thunnus alalunga*). The fins on the right are of elasmobranchs: (e) blacktip shark (*Carcharhinus limatus*); (f) dogfish (*Scyliorhinus* sp.); (g) basking shark (*Cetorhinus* sp.).

In most fish that are adapted to fast and prolonged cruising, the ARs of both the caudal and pectoral fins are high and many such fins are elliptical. However, such fins are not appropriate for rapid acceleration or swift manoeuvring when the angle of incidence must be high—tall thin hydrofoils with a high AR are particularly prone to stalling when the angle of incidence is large. The result is that fish that rely upon rapid acceleration or high manoeuvrability, e.g. salmon, pike, barracuda and cod, have shorter pectoral and large ‘spoon-like’ caudal fins with lower ARs, which are less susceptible to stalling. You will see in Chapter 5 that the same design principles are relevant to flight: large birds requiring rapid acceleration at take-off (for example, the pheasant) tend to have stubbier wings than birds that are adapted for prolonged cruising (for example, the albatross).

So far we have only considered lift as force acting vertically upwards. Strictly, lift is any force acting at right angles to the direction of motion. Figure 2.11c shows vortices being shed by the tail in generating thrust. The tail can be thought of as an undulating wing generating lift in the sideways direction, first one way and then the other. Since the body of the fish is shaped so as to not move sideways, by appropriate adjustments of the angle of incidence of the fin, a forward component of lift is expressed as thrust.

Summary of Section 2.3

There are several forces that act on a fish surrounded by water. When a fish is stationary, gravity in a downward direction is opposed by buoyancy in an upward direction. In most fish, the average density of the body tissues is close to that of water and the fish is said to be neutrally buoyant. The forward movement of a fish is opposed by drag and so in order to move forward, fish must generate
thrust that exceeds drag. There are several means by which fish overcome drag. One of these is by streamlining, another is by reducing protuberances on the body. Thrust is generated by a series of vortices shed from the tail, and the amount of thrust generated depends on the number of vortices shed per second and on their size. This in turn depends on the size of the tail. Tails with high aspect ratios produce maximum thrust and are found in fish that swim at constant high speeds. Low-aspect-ratio tails are better at slow speeds and for acceleration from a standing start. Some fish are heavier than water and so must generate hydrodynamic lift in order to compensate for net negative buoyancy, and there are several ways in which this is achieved.

2.4 Energy expenditure during swimming

Although it is possible to measure the swimming speeds of fish in the wild using telemetry, energy expenditure estimates are generally derived from basic measurements made on fish that are exercised at known speeds in the controlled environment of a swimming chamber—the aquatic equivalent of a treadmill. There is a wide variety of ingenious swimming chamber designs, but an arrangement in which the fish swims against a water current within a stationary chamber known as a water tunnel, is most widely used (Figure 2.18). The water current is generated by gravity flow or a pump. The practical problems of their design are considerable: minor currents and excessive turbulence have to be avoided, friction can warm up the water of the chamber and the fish have to be confined to a limited section. (A light source can act as a visual cue and mild electric shocks can restrict the fish). If the total volume of water in a swimming chamber is fairly small, changes in the concentration of dissolved gases can be accurately monitored by an oxygen electrode and the rate of oxygen consumption by the fish gives us measurements of metabolic rate and energy expenditure at various swimming speeds.

Figure 2.18 A tunnel respirometer used to measure oxygen consumption in sockeye salmon (Oncorhynchus nerka). The fish swims ‘upstream’ against a water flow that can be varied. If the fish moves slower than the flow of water, it slips back onto an electrically charged screen. Water temperature can be varied and, when the system is closed and a fixed volume of water circulated, the reduction in oxygen content of the water can be calculated.
Figure 2.19 shows the relationship between oxygen consumption and swimming speed in Pacific sockeye salmon. The data were obtained over 30 years ago by John Brett using this apparatus. The fish used had been kept at the experimental temperature for a long time beforehand and so were acclimated or adapted to it. Oxygen consumption is shown as the continuous blue line and the ‘at rest’ metabolic rate by the dashed black line. It is clear that metabolism increases approximately exponentially with increased swimming speed (Figure 2.19a). This is because the power required for swimming increases with velocity in an approximately cube law relationship (Table 2.1). Maximum oxygen consumption is about 630 cm$^3$O$_2$ kg$^{-1}$ h$^{-1}$ when the salmon swims at about 4 BL s$^{-1}$. This high level of energy expenditure can be sustained for long periods and is the greatest metabolic rate that can be fully supported by aerobic metabolism. So, 630 cm$^3$O$_2$ kg$^{-1}$ h$^{-1}$ represents the aerobic capacity of the fish which, as we shall soon see, is of great interest to physiologists concerned with animal performance.

So far we have talked only of sustained swimming in the salmon, supported by aerobic metabolism. However, during brief bursts, speeds well in excess of 4 BL s$^{-1}$ are attainable and the extra energy is supplied anaerobically. After such bursts, additional oxygen, known as recovery oxygen, is taken up to complete the oxidation of substrates only partially oxidized by anaerobic metabolism. The amount of recovery oxygen taken up for the salmon can be estimated from Figure 2.19a. By extending the continuous blue line (the dashed section), we can estimate the theoretical demand for oxygen at swimming speeds greater than 4 BL s$^{-1}$. However, the amount of oxygen actually consumed at these speeds is at the maximum level (about 630 cm$^3$kg$^{-1}$h$^{-1}$). The blue area shown in Figure 2.19a represents the difference between the total energy needed and the smaller amount supplied by aerobic means at speeds above 4 BL s$^{-1}$. As Figure 2.19a implies, the amount of recovery oxygen required is very modest at speeds less than 4 BL s$^{-1}$ and not sufficient to interfere seriously with the fish’s performance.
At high speeds, the utilization of the limited stores of glycogen restricts the length of burst swimming, and the duration of bursts decreases as their speed increases. Speeds of about 5–6 BL s\(^{-1}\) can be maintained for only a few minutes. The time taken for the uptake of recovery oxygen can be estimated by measuring oxygen consumption after the completion of burst swimming; when O\(_2\) consumption returns to pre-exercise levels, and when muscle glycogen and lactate are restored, sufficient oxygen has been taken up. During recovery in the sockeye salmon, the fish rests quietly on the bottom with little visible movement, other than pronounced hyperventilation, for as long as 2–3 hours (see Figure 2.19b). Uptake of sufficient recovery oxygen may take more than 5 hours, although spontaneous movement may begin again after 3 hours. Recovery from intense burst swimming in mackerel may take up to 24 hours. We are unsure why recovery from burst swimming is so slow. In the wild, prolonged inactivity would be a serious handicap because exhausted fish are vulnerable to predation. This probably explains why fish are extremely reluctant to move at high speed unless the motivation is strong and, under natural conditions, intense burst swimming is probably a rare event.

The most significant environmental factor influencing the metabolic activity of fish is temperature, though the precise effect differs from species to species. To show this, the data in Figure 2.19a can be replotted on semi-logarithmic coordinates, so they now appear as a straight line. In Figure 2.20 the blue line labelled ‘sockeye 15 °C’ simply replots the values shown in Figure 2.19a and the other lines give data at different temperatures (5 °C and 20 °C for the salmon) and for a number of different species.

- What does the graph show?

Within a single species, for example the sockeye salmon, the differences in the slope of the lines at various temperatures show that the extent to which oxygen demand is raised as swimming speed increases, varies with ambient temperature. It also shows that when both basal and maximum rates of metabolism are measured at the same temperature, there are considerable differences between species. For example, compare bass and salmon at 20 °C: the bass has a maximum oxygen consumption less than half that of the salmon, and at this point could reach speeds of only 2.4 BL s\(^{-1}\) as compared with 3.6 BL s\(^{-1}\) for the sockeye salmon.

Two further points emerge from Figure 2.20:

1. Because the salmon is a poikilotherm its metabolism increases as the animal is warmed, resulting in greater oxygen demand (compare basal metabolism at 5, 15 and 20 °C). However, at elevated temperatures, water holds less dissolved oxygen so warm fish must ventilate a much greater volume of water over their gills. When salmon migrate from the oceans to what may be warmer rivers for migration upstream, their energy expenditure must increase substantially.

2. *Tilapia* is a poikilothermic warm-water species. If fish showed a simple relationship between metabolic rate and temperature, then the basal metabolic rate of *Tilapia* at 25 °C would be considerably greater than that of the salmon at 20 °C, which is not the case. Indeed, the oxygen demand of a *Tilapia* swimming at 1 BL s\(^{-1}\) at 25 °C is about the same as that of the sockeye salmon swimming at the same speed at 15 °C. We are very uncertain of the biochemical basis of such differences in poikilotherms.
2.4.1 Aerobic metabolic scope

So far, we have used the data on salmon in Figure 2.19 to identify a basal rate of metabolism (about 42 cm$^3$O$_2$·kg$^{-1}$·h$^{-1}$) and a maximum rate of O$_2$ consumption—the aerobic capacity (630 cm$^3$O$_2$·kg$^{-1}$·h$^{-1}$). The difference between these two values reflects the maximum amount of energy that is available to support work or activity over and above that necessary for normal ‘routine’ energy requirements (for example, growth and reproduction) and is termed the aerobic metabolic scope. It gives an indication of the capacity of an animal to support activity by aerobic methods. If we are concerned with the total energy that an animal can make available for work or activity, we have to add a second component, anaerobic metabolic scope, which is limited by the size of the muscle store of glycogen and by the maximum rate of lactic acid formation by glycolysis.

Aerobic metabolic scope is a useful idea but it is not as simple as it seems, and one major limitation is evident from work with fish. Measuring capacity for work in the way just described assumes that the energy-requiring processes that occur when the fish is resting do not increase in magnitude once the fish becomes active. This assumption is clearly untrue—the ventilatory and circulatory systems increase their work output and, at maximum swimming speeds, they may account for as much as 40% of the increased oxygen uptake.

The necessity of accounting for such ‘maintenance’ costs is one of many reasons why we should view aerobic metabolic scope only as an indicator of the extent to which animals can increase aerobic metabolism and not as an indirect measure of an animal’s capacity to perform work. However, when we look at a single species, or at a group of closely related species, the maximum oxygen consumption can be closely linked with maximum performance and here differences between species in aerobic metabolic scope do parallel differences in the capacity of different fish to perform work.
The type of diagram shown in Figure 2.21 is useful if we want to compare oxygen consumption at different states of activity and at different temperatures. Basal metabolism and aerobic capacity have been measured in the sockeye salmon at a variety of water temperatures. The upper line shows the maximum $O_2$ consumption at peak sustainable speeds after acclimation at different ambient temperatures. The scope for aerobic metabolism is indicated by the vertical distance between the two lines. Figure 2.21 shows clearly that in the salmon the scope is greatest at 15 °C. The highest temperature that the salmon can tolerate is the upper lethal temperature—25 °C. The general features shown in Figure 2.21 for the sockeye salmon are evident in many other fish species. In particular, the maximum aerobic metabolic scope is exhibited at some optimum temperature (15 °C for the sockeye salmon) above and below which the scope is smaller. Many poikilothermic animals have a ‘preferred’ body temperature, which is normally maintained by behavioural means in the wild and which may conform to the temperature at which aerobic metabolic scope is maximal.

It is very instructive to compare the aerobic capacities and scopes of different groups of animals, though any generalizations must be framed cautiously. Ideally we should compare species of approximately similar size because differences in body mass alone have a major effect on metabolism. In general though, more active fish have higher aerobic metabolic scopes and higher aerobic capacities than less active fish. It is even more interesting to compare teleosts with reptiles. For example, Figure 2.22 shows the maximum and minimum $O_2$ consumption at various temperatures for three species of lizard, together with the now-familiar data for the sockeye salmon (shown in blue). The most striking feature here is that despite the lizards’ air-breathing habit, their aerobic capacities and scopes are not greatly different from those of the fish. In fact, the salmon has a higher capacity and scope than either the bearded dragon or the iguana. Some reptiles normally maintain by day a body temperature quite close to that of homeotherms, and such animals tend to live at a higher metabolic rate than most fish. Nonetheless, most lizards display short bursts of activity supported mostly by anaerobic glycolysis, separated by longer bouts of rest and relative quiet, when metabolism is largely aerobic. Of the lizards shown in Figure 22.2, the monitor lizard is large and predatory and has an aerobic
metabolic scope that increases with temperature; it is distinguished among
reptiles because it can maintain long periods of sustained activity. Figure 2.22
implies that much of this activity may be supported aerobically. In
homeotherms, the story is different. Birds and mammals have a much higher
resting oxygen consumption than that of poikilotherms. For example, the basal
metabolic rates of birds and mammals are approximately five to ten times higher
than the resting rates of similarly sized lizards at a body temperature of about
40 °C. The aerobic capacities of fish and reptiles are usually lower than the basal
metabolic rates of similarly sized birds and mammals. As is evident from Table
2.2, not only is the basal metabolic rate of homeotherms higher than those of
fish and reptiles, but the aerobic metabolic scope of mammals is usually greater.

What differences between poikilotherms and homeotherms do these figures
highlight, with respect to energy needs and consumption of oxygen?

Most poikilotherms have much lower aerobic metabolic scopes than
homeotherms but, for short periods, their burst activity can equal that of some
homeotherms by relying on anaerobic mechanisms. An aquatic type of

<table>
<thead>
<tr>
<th>Table 2.2</th>
<th>The minimum oxygen consumption (basal metabolic rate) and maximum oxygen consumption (aerobic capacity) in homeotherms and poikilotherms, comparing animals of equal mass.</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Salmon</td>
</tr>
<tr>
<td>Body mass/g</td>
<td></td>
</tr>
<tr>
<td>Optimum temperature at which maximum O₂ consumption occurs/°C</td>
<td>15</td>
</tr>
<tr>
<td>Basal metabolic rate/ cm³ O₂ kg⁻¹ h⁻¹</td>
<td>50</td>
</tr>
<tr>
<td>Aerobic capacity/ cm³ O₂ kg⁻¹ h⁻¹</td>
<td>500</td>
</tr>
</tbody>
</table>
respiration ties the body temperature of most fish to that of the environment and the metabolic rate is usually comparatively low. Living in water allows neutrally buoyant fish to ‘rest’ economically after exertion and to utilize surplus oxygen as recovery oxygen. Lower vertebrates such as reptiles enjoy the benefit of a superior respiratory medium, but they are still tied to relatively inefficient anaerobic mechanisms that accumulate lactate, although large amounts of energy can be made available on demand. The ability of animals to increase maximum oxygen consumption (aerobic capacity) by a great amount evolved along with the development of homeothermy. Rather surprisingly, this condition is detectable in some exceptional fish (which we shall discuss in Chapter 3) but it is only fully developed in birds and mammals. These higher vertebrates have aerobic metabolic scopes that are many times greater than those of poikilothermic vertebrates, and this capacity for sustained aerobic metabolism has no doubt contributed to their great success.

2.4.2 Measuring swimming performance of fish

In studying performance of fish the following questions are often asked regarding swimming speeds:

- (a) What is the maximum speed?
- (b) What is the maximum sustainable speed?
- (c) What is the average speed normally used by fish in the wild?

Casual observation of fish leaping out of the water indicates that very high speeds are possible but obtaining clear measurements of the exact speed through the water is extraordinarily difficult. One indirect approach is to measure the height to which fish jump. Then by applying Newtonian mechanics, the take-off velocity from the water surface can be calculated. Salmon have been observed to jump 5 m to clear a waterfall. Such feats require a take-off velocity of 10 m s\(^{-1}\) or 12.5 BL s\(^{-1}\) for an 80 cm-long fish. We suspect this performance represents approximately the maximum burst speed of a salmon, but such jumps may be aided by water flow at the base of the waterfall. Scombroid fish (tunas and mackerel) are probably the fastest fish. A yellowfin tuna (Thunnus albacares) hooked on a line, with a recorder on the reel, was clocked at 20.7 m s\(^{-1}\) or 18 BL s\(^{-1}\). Video recordings of mackerel (Scomber scombrus) in a large enclosure revealed maximum burst speeds of 5.5 m s\(^{-1}\), which for a 30.5 cm-long fish is equivalent to 18 BL s\(^{-1}\). Such high-speed bursts generally last less than one minute and, after a burst, there is an enforced period of relative inactivity before burst swimming can recommence. This type of ‘sprint’ behaviour is linked with prey capture and/or pursuit from predators and, as in salmon, in the negotiation of obstacles and rapid currents. The body size of the fish has a major effect on the speed of burst swimming; small fish (10 cm) can achieve 30 BL s\(^{-1}\) (at 14 °C) with very high tail-beat frequencies. Even fairly poor swimmers like the carp and the wrasse are briefly able to achieve about 7–8 BL s\(^{-1}\).

Tag and recapture programmes have shown that a number of species of fish are capable of transoceanic journeys covering thousands of kilometres. One spiny dogfish tagged off the American west coast turned up over 8 700 km away near Japan. Two large bluefin tuna (Thunnus thynnus) crossed the Atlantic from Florida to Norway (6 700 km apart) in less than 120 days. Tagging of the longfin tuna (Thunnus alalunga) suggests that the fish migrate in schools on an extraordinary two-way trip from California to the mid-Pacific (or Japan) and
back again. One such school apparently covered 420 km in one day, equivalent to an average speed of 486 cm s\(^{-1}\) or 5.7 BL s\(^{-1}\) assuming a body length of about 85 cm. Other tagging studies indicate that average 'cruising' speeds of migrating fish are much lower. Such tagging studies, however, can only give an estimate of the average speed along a straight line between the release and recapture positions.

Fish can be directly tracked in the sea by tagging individuals with acoustic transmitters that emit an ultrasonic signal which can be picked up remotely by receiving equipment on board a boat. Kim Holland has tracked yellowfin tuna (*Thunnus albacares*) in this way off Hawaii. The fish swam continuously, generally near the surface at night, at 0–30 m depth, and deeper during the day, diving to 200 m. The average speed varied between 1.2 and 2.4 BL s\(^{-1}\). The measurements, however, are hampered by the fact that the speed was calculated between hourly position fixes and might have missed convolutions in the path taken. Barbara Block and colleagues, therefore, attached a speedometer transmitter to a blue marlin (*Makaira nigricans*) (Figure 2.23). The transmitter encoded information on the rate of rotation of a propeller towed by the fish and thus gave precise information on swimming speed. Figure 2.24 shows the distribution of speeds observed. The highest speed recorded was 2.25 m s\(^{-1}\), or approximately 1.5 BL s\(^{-1}\). In fact, this species is capable of high-speed bursts, having been recorded to take baits trolled at 8 m s\(^{-1}\).

Figure 2.23 A speedometer transmitter tag (not to scale) as used to measure the swimming speed of blue marlin. The tag is attached to the back of the fish as shown. It transmits a coded acoustic signal to a boat carrying receiver equipment, enabling the exact speed of the fish to be recorded at any particular instant.

Figure 2.24 The frequency distribution of speeds observed in the blue marlin.
Atlantic salmon (*Salmo salar*) have been tracked during their return migration to Scottish rivers from feeding grounds in the North Atlantic. The data showed that the fish swam continuously in a south-eastward direction at a speed of 0.65 BL s⁻¹. Thus, salmon, although capable of much higher speeds, use quite modest speeds for their transoceanic phase of migration. The reason can be seen in Figure 2.25, in which the cost of transport has been calculated by Gordon Smith of Aberdeen using the data of Brett (assuming that swimming metabolism is similar in Atlantic and Pacific salmon species). The speed for minimum cost of transport is at the minimum of the curve (as already shown in Table 2.1) and it seems that during their migration salmon are swimming continuously at close to the theoretical optimal speed.

Many species of fish, however, do not spend all their time swimming. Figure 2.26 shows the track of a pike (*Esox lucius*) in Loch Kinord near Aberdeen. Over a period of 90 hours it moved a total straight line distance of 750 m, a distance typical of many species of fish. The mean swimming speed along the track was 0.011 BL s⁻¹. Swimming was not continuous but was made up of short bursts with resting periods in between. The fish was patrolling a reed bed and feeding on young perch (*Perca fluviatilis*) that were emerging from the weeds at this time. The acoustic transmitter in this case telemetered the heart rate and muscle activity. Interference from the electromyograms (EMGs) gave an indication of the frequency of occurrence of bursts of swimming (Figure 2.27). Whenever the fish moved, as indicated by the EMGs, the heart rate increased but quickly fell to normal levels after the burst of activity, which indicated that
the fish did not incur a need for any recovery oxygen; during repayment of recovery oxygen we would expect the heart rate to remain high. The heart rate can be used as an approximate indicator of metabolic rate with 30 beats per minute as basal rate and 80 beats per minute as the aerobic capacity. Note the aerobic capacity was only reached for two minutes during the whole day. Uptake of recovery oxygen persisted for no more than 10 minutes. Most of the energy expenditure of the fish was associated with the digestion of the perch it was feeding on each day.

Studies on fish captured in trawls and on lines have caught the imagination of scientists who have been impressed by the swimming abilities and anaerobic capacity of fish. Telemetry studies in the field, however, show that most fish, even the continuous swimmers, spend most time at slow aerobic speeds. Most fish rarely exceed their aerobic limit. Most other animals probably do the same. We all know that human athletes can achieve phenomenal speeds but most of us rarely make use of our anaerobic sprint capacity! The small volume of red muscle in fish is therefore very important, as it is responsible for most of the swimming activity when the fish is likely to be cruising at its optimum speed.
Figure 2.27  The heart rate and electromyogram record of the pike from Figure 2.26 during the third day. The heart rate has been divided into the basal rate (grey area at the bottom of the graph), a rate arising from feeding and digestion (the shaded blue area), and a rate arising from bursts of swimming activity. Note that the spikes indicating swimming activity correlate well with the EGM recording at the top of the graph.

Summary of Section 2.4

Many fish can maintain a steady cruising speed of approximately 0.1–6.0 BL s\(^{-1}\) for prolonged periods, depending on the species. Some migrating fish swim more or less continuously over relatively long distances, as revealed by acoustic tags. Burst swimming is much faster (about 20 BL s\(^{-1}\) in the yellowfin tuna) but can be maintained for only very brief periods, and recovery is often prolonged (up to 24 hours in captive mackerel). In sockeye salmon, oxygen consumption increases approximately 10-fold from a basal, resting level to swimming at 4 BL s\(^{-1}\). At this speed, oxygen consumption is at a maximum level (termed the aerobic capacity) and faster swimming is sustained for short periods by increased anaerobic metabolism.

Temperature has a major effect on basal metabolism and aerobic capacity in fish, though differences between species are apparent. An approximate but sometimes unreliable measure of the ability of a fish to perform work is the aerobic metabolic scope, which also varies with temperature. More active fish tend to have higher aerobic metabolic scopes than less active fish species. In general, the aerobic capacities of many reptiles fall into approximately the same range as those of many fish, when measured at the same temperature. Bursts of intense activity in both reptiles and fish are fuelled almost exclusively by anaerobic mechanisms. Compared with reptiles, birds and mammals of about the same mass usually have a much higher basal metabolic rate and aerobic metabolic scope at the same body temperature. The combination of the air-breathing habit with homeothermy led to the development of a greatly improved ability to sustain activity exclusively by aerobic metabolism.
2.5 Conclusion

Fish swim with such apparent ease that it is hard for us to realize just how difficult it is to move rapidly through water. Unlike rigid structures such as submarines, which generate thrust with propellers, fish generate thrust by changing their shape as they move through water. Various fish have adopted unique methods of locomotion, using paired or unpaired fins to row, flap or undulate themselves along, but the great majority of fish propel themselves using a combination of two processes—the backward passage of transverse waves along the body and lateral movements of the caudal fin. In general, the fastest-swimming fish rely on the oscillation of a high-aspect-ratio caudal fin, which is attached to the body by a narrow caudal peduncle; slow-swimming fish undulate through the water like eels. The flexible method of thrust generation makes it impossible to apply directly hydrodynamic data from the performance of rigid bodies (such as submarines) to the analysis of fish swimming. Nonetheless, research into the hydrodynamics of fish swimming has made good progress over the last decade, particularly in the areas of obtaining kinematic and respirometric data from swimming fish set up in water tunnels and in working out suitable mathematical models of fish swimming. As a consequence, we can now make reasonable estimates of the power needed for swimming and of the efficiency of the process.

Objectives for Chapter 2

After completing Chapter 2 you should be able to:

2.1 Define and use, or recognize definitions and applications of, each of the bold terms.
2.2 Describe the arrangement of fish muscle and give reasons why myotomes have such complex shapes.
2.3 Draw a diagram illustrating the main forces acting on the body of a fish when the fish is (a) stationary and (b) moving forward.
2.4 Outline the concept of drag and describe the mechanisms used by fish to overcome drag.
2.5 Describe the morphological and functional differences between high- and low-aspect-ratio tails.
2.6 Outline the concept of hydrodynamic lift and describe the ways in which fish generate lift.
2.7 Explain what is meant by the aerobic capacity of a fish.
2.8 Describe some differences between poikilotherms and homeotherms with respect to aerobic metabolic capacities and scopes.
2.9 Give examples of the kinds of swimming speeds attainable by different species of fish, and the distances over which they travel.
Questions for Chapter 2

(Answers to questions are at the end of the book.)

Question 2.1 (Objectives 2.1, 2.2, 2.3, 2.4, 2.5 and 2.6)
Classify the following statements (a–i) as true or false and explain why.

(a) The pectoral fins of all fish provide substantial hydrodynamic lift.

(b) Bending of the body in fish is initiated when the myotomes on both sides of the spinal cord contract simultaneously.

(c) The main locomotor muscles in tunas are confined to the peduncle, and they move the caudal fin from side to side.

(d) In general, fish such as salmon and pike, which are highly manoeuvrable and can accelerate rapidly, have caudal and pectoral fins with a low AR.

(e) In some fish, the backward-moving waves of muscular contraction are initially of relatively small amplitude and only the posterior portion of the body normally shows pronounced side-to-side movement.

(f) In order to accelerate, a fish must generate a thrust force equal to and opposing the drag force.

(g) When buoyancy is roughly equal to the weight of the fish, there is no tendency for the fish to rise or sink and the fish is said to be neutrally buoyant.

(h) Fish that are denser than water, and do not utilize static lift, must maintain a minimum forward cruising speed to generate enough lift to prevent themselves from sinking.

(i) The castor-oil fish has a complex skin that appears to be specialized for maintaining a turbulent boundary layer. Both the ctenoid scales and the subdermal spaces help prevent flow separation.

Question 2.2 (Objective 2.9)
Calculate the average swimming speed (in BL s\(^{-1}\)) of a 72 cm salmon that is observed to swim for 8 h and to cover a distance of 16 km. Make the rather unlikely assumptions that the fish is unaided by currents and swims at a constant speed.

Question 2.3 (Objective 2.9)
Classify the following swimming speeds as typical of burst or cruise swimming:

(a) 20 BL s\(^{-1}\) in a 1 m yellowfin tuna;

(b) 6 BL s\(^{-1}\) in a longfin tuna;

(c) 30 BL s\(^{-1}\) in an unidentified 10 cm teleost;

(d) 4 BL s\(^{-1}\) in a year-old sockeye salmon.

Question 2.4 (Objectives 2.7 and 2.8)
Classify the following statements (a–f) as true or false and explain why.

(a) In natural conditions, swimming by salmon at a rate in excess of 4 BL s\(^{-1}\) is likely to leave them exhausted for several hours.
(b) Data for salmon (and bass) reveal that the basal metabolic rate of fish increases as the acclimation temperature increases.

(c) Aerobic metabolic scope is a measure of the extent to which oxygen consumption can be increased by activity; in fish this scope is a function of temperature.

(d) The duration of burst swimming is not likely to be influenced by the amount of stored glycogen in the muscle.

(e) Air-breathing poikilotherms have a much greater aerobic metabolic scope than water-breathing fish of comparable size.

(f) Compared with birds and mammals, reptiles and fish generally place a greater reliance on anaerobic metabolism to fuel intense activity.