CHAPTER 4  BUOYANCY AND DEPTH

Prepared for the Course Team by Mandy Dyson

4.1 Introduction

When a fish is totally immersed in water it displaces an amount of water equal to its body volume. If the weight of the displaced water is greater than the weight of the fish, the fish is said to be positively buoyant and will tend to float. If the weight of the water is less than that of the fish, the fish is said to be negatively buoyant and will tend to sink. If the weight of the displaced water equals that of the fish, the fish is said to be neutrally buoyant. So, underwater, the weight of an animal is counteracted by its buoyancy. This is the basis of Archimedes’ principle, which states that a body immersed in a fluid experiences an upthrust or buoyancy equal to the weight of the displaced mass of the fluid (water in this case).

Buoyancy is given by:

\[ A \text{ (buoyancy)} = V \rho_w g \]

where \( V \) is the volume of the animal, \( \rho_w \) is the density of water and \( g \) is the acceleration due to gravity (a constant).

The weight of the animal is given by:

\[ W \text{ (weight)} = V \rho_a g \]

where \( \rho_a \) is the average density of the animal.

So, an animal that is neutrally buoyant has a density \( (\rho_a) \) equal to the density of the water in which it is submerged \( (\rho_w) \). Under this condition, the upward force of buoyancy \( (A) \) will exactly balance the downward force of weight \( (W) \).

So if a fish or any other aquatic animal were made of materials that were of the same density (density = mass/volume) as the water in which it lived, it would not weigh anything in water, and would be neutrally buoyant (Chapter 1). Seawater has a density of around 1.03 g cm\(^{-3}\) and freshwater one of around 1.00 g cm\(^{-3}\) (at 1 atmosphere and 15 °C) but most animal tissues are of greater density. Muscles are full of contractile proteins with densities around 1.33 g cm\(^{-3}\), and skeletal tissues such as bone may be so loaded with calcium salts that their density is over 2.00 g cm\(^{-3}\). There are, of course, some less dense substances in most animals, such as fats of different kinds, and many marine animals (including bony fish) have body fluids that are more dilute than seawater (and are hence less dense). In general, one can assume that the densities of marine animals are around 1.06–1.09 g cm\(^{-3}\), i.e. they are some 5% denser than seawater and so tend to sink. In other words, these animals are negatively buoyant. For example, a mackerel that weighs 500 g in air weighs around 25 g in seawater, and in effect climbs a 1 in 15 hill all its life just to stay at the same depth in the sea and not sink. You can check this assumption yourself by weighing a fresh fish, e.g. a mackerel, in air, and then weighing it in water by suspending it from a small spring balance or bathroom scales. You can do this by putting a rod or a coat hanger across the scales and tying cotton to each end so that you can hang the fish from it (Figure 4.1). If you have weighed the fish in seawater you will find that the 5% difference in weight is about right, but if you do not live by the sea and so use freshwater, you will find the fish weighs about 7% of its weight in air.
Many scombrid fish (tuna, bonito, mackerel) have an average density greater than that of seawater. This means that the upward acting buoyancy force is not great enough to completely cancel the downward acting force of weight so that without an additional upward force, they would sink. One method of balancing these upward and downward forces is through the use of hydrodynamic lift (Section 2.3.3). Hydrodynamic lift is generated by the extended pectoral fins and, to a lesser extent, by the tail as the fish swims forward. Lift from the pectorals needs to be much greater than that from the tail because in most fish, the centre of buoyancy (determined by the distribution of volume along the body), and the centre of mass (determined by the relative densities of the different parts of the body), are usually nearer to the head than the tail due to the dense skull and jaws (Figure 4.2). In fish such as scombrids, which swim with the body horizontal, the two centres are always either in the same place, or just above each other. Lift from the tail therefore acts much further from the centre of buoyancy than does lift from the pectorals, and hence need not be so great.

We might suppose that because shark skeletons are cartilaginous, and cartilage is less dense than bone, sharks without buoyancy mechanisms that lower their density would be less dense and weigh less in water than similarly sized bony

Figure 4.1  How to weigh a fish in water with bathroom scales.
fish without buoyancy mechanisms. However, shark cartilage is strengthened by calcifications, and there are very dense denticles (tooth-like structures) in the skin. Shark skeletons are also more solidly built than the strutted girder-like bones of bony fish and, like most bony fish, weigh in seawater about 5% of their weight in air. Almost all sharks balance their weight in water by generating hydrodynamic lift with their outspread pectoral fins, and they also generate lift by setting their caudal fin at a slight angle as it sweeps from side to side (Section 2.3.3). The asymmetrical tail fins of sharks (where the upper lobe is supported by the upturned end of the vertebral column—the heterocercal condition) may have evolved because sharks are denser than seawater, and gain lift from the angle taken up by the more flexible lower lobe. However, there are sharks that are neutrally buoyant, and these too have heterocercal tails (Figure 4.3). In fact, in all sharks the angle of the lower lobe can be adjusted to give either lift or downthrust.

The density of air is so much lower than that of the materials from which animals are made that no flying animal can have the same density as air (as balloons and airships do). However, water is sufficiently dense for it to be possible for animals to store enough light substances to achieve neutral buoyancy. Neutral buoyancy is an advantage because it enables fish to save energy in two ways, and furthermore, to behave in ways that negatively buoyant fish cannot:

![Diagram of a fish with labels for buoyancy, weight, and lift](image)

**Figure 4.2** In this fish the centre of buoyancy (Cb) is situated just below the centre of mass (Cm). Because the density of the fish is greater than that of water, the weight is greater than buoyancy. Lift is generated by the tail (T) and the pectorals (P). Since lift generated by the tail acts further from the centre of buoyancy than does lift generated by the pectorals, it need not be as great.

![Diagram of a heterocercal tail](image)

**Figure 4.3** The neutrally buoyant deep-sea squaloid shark (*Centroscymnus*). Note that it has small pectoral fins that do not generate significant lift in level swimming.
Only neutrally buoyant fish can hover practically motionless in water. This ability is a great advantage for not only can such fish remain in position without expending muscular effort, but they can also hover or swim very slowly whilst seeking their prey. The John Dory (*Zeus faber*, Figure 2.13f), for example, is almost perfectly neutrally buoyant and sidles slowly to within range of unsuspecting small fish and crustaceans, whereupon it engulfs them by shooting out its protractile jaws. Similarly, deep sea angler fish hang in ambush in the water waiting for their prey to come within reach of their jaws. Marine fish without buoyancy organs have to generate an upward lift force (equivalent to 5% of their body weight) to stay at one level; to do this they have to move forwards all the time, and cannot remain stationary to lurk for their prey.

Neutral buoyancy saves a substantial proportion of the energy costs of forward movement. When a negatively buoyant fish swims at about 3–4 bodylengths per second, as much as 20% of the total power for movement is committed to overcoming the tendency to sink. As a result, a fish without a buoyancy mechanism needs a greater power output (and therefore an increased energy outlay, and a higher rate of oxygen consumption) to swim horizontally at a given speed, than does a neutrally buoyant fish.

These advantages appear so significant that it is at first sight rather surprising that there are many active fish which are not neutrally buoyant. As already mentioned, most scombrid fish are negatively buoyant. There are even some fish which seem to regulate their density carefully, not to that for neutral buoyancy, but to some density intermediate between that for neutral buoyancy and that for fish without any buoyancy mechanisms! We can easily imagine that for sluggish fish that spend most of their time resting on the bottom, such as dogfish or plaice, it would not be worth achieving neutral buoyancy, and in fact such fish are not neutrally buoyant. But why are many active fish, such as mackerel, not neutrally buoyant? To understand why, we need to examine the materials that provide fish with a source of static lift, namely lipids and gas.

### 4.2 Lipids as a source of static lift

Lipids have virtually the same compressibility as water, so the static lift provided by lipids in a fish remains almost the same when the ambient pressure alters as the fish changes depth. This gives lipids a great advantage over gas in providing static lift, because the lift given by gas varies with ambient pressure unless it is stored in a strong rigid container. Indeed, many of the small myctophids (lantern fish), which make extensive daily vertical migrations to and from the surface of the sea, begin life by storing gas in a non-rigid, soft-walled container, the swimbladder, but as they grow older, gradually replace the gas with lipid. Ordinary fish lipids, such as cod liver oil, have densities of around 0.93 g cm$^{-3}$, but lipids used to give enough lift for neutral buoyancy are special lipids of lower density. Deep-sea sharks, basking sharks and a few teleosts store the hydrocarbon squalene, whilst many myctophids, together with the coelacanth (*Latimeria chalumnae*) and the castor-oil fish (*Ruvettus pretiosus*), store wax esters. Both of these special low-density kinds of lipid have densities of around 0.86 g cm$^{-3}$.

* Can you think of a disadvantage of using lipids to provide static lift?
Unlike gas, lipids such as squalene and wax esters have a density which is not greatly different to that of seawater, so neutral buoyancy is attainable only if relatively large deposits are accumulated. The metabolic cost of synthesizing these stores is substantial and more must be added as the animal grows. Lipid synthesis is not rapid enough to take account of short-term density increases such as occur after swallowing a large dense meal. However, many of the deep-sea sharks, e.g. the squaloid shark (*Centroscymnus*; Figure 4.3) attain neutral buoyancy because their enormous livers, which occupy 30% of the volume of the body, contain so much squalene (about 80%) that they provide just enough lift to compensate exactly for the weight in water of the denser parts of the body. Some of these neutrally buoyant deep-sea sharks store so much lipid (and are corpulent as a result) without reducing the dense components of their bodies that, if the liver is removed, they weigh in seawater just under 5% of their weight (less the liver) in air. Others, such as the bramble shark (*Echinorhinus*) have poorly calcified vertebrae and thin skins, and without their livers weigh in water only around 2% of their weight in air; hence they need to store relatively less lipid.

The large basking shark (*Cetorhinus*), which cruises slowly along with its mouth open, sieving plankton, also depends upon squalene in its huge liver to achieve near-neutral buoyancy, and a basking shark weighing nearly 2000 kg in air (measured with a 5-ton crane!) was found to weigh less than 2 kg in water. Basking sharks swim at around 1 m s\(^{-1}\) when feeding, which seems to be a good speed for filter feeding—the other huge elasmobranch filter feeders, the devil fish (*Mobula*) and the whale shark (*Rhincodon*), also swim at this speed. Basking sharks have to be close to neutral buoyancy because they cannot generate sufficient hydrodynamic lift at this slow swimming speed. The deep-sea squaloid sharks and the basking shark store sufficient lipid to attain neutral buoyancy, but the great majority of sharks do not. Bottom-living sharks such as the dogfish (*Scyliorhinus*) are inactive by day, resting on the sea bottom, and it is not necessary for them to achieve neutral buoyancy. However, most fast-swimming sharks like the spurdog (*Squalus acanthias*), or the blue shark (*Prionace glauca*) store lipid to reduce their density, but not in sufficient quantity to be neutrally buoyant. Some reduction in density is advantageous, because they can reduce the size of the pectoral fins used to generate lift (and so reduce the energy expended during swimming by reducing drag), but there is a limit to this reduction since the fins are used for manoeuvring and, unlike the fins of bony fish, cannot be furred.

Many of the fish living in the depths of the sea avoid the difficulties of lipid storage by greatly reducing their dense components, so that they need little lipid to achieve neutral or near-neutral buoyancy. They have watery muscles, there are often large subcutaneous sinuses and pockets containing a lymph less dense than seawater, and in the skeleton only the jaws are well calcified. Such fish have an extremely high water content: the angler fish (*Melanocetus*) is 95% water, the gulper eel (*Eurypharynx*) 94% and the bristlemouth (*Gonostoma*) 90%. In contrast, fish that use gas for static lift (see Section 4.3.1) can afford to support the dense components of their bodies without difficulty, and the lantern fish and the curiously flattened hatchet fish are much less watery and have fully calcified skeletons. The buoyancy balance sheets in Figure 4.4 show the differences between the bristlemouth (*Gonostoma*), a fish that stores lipid and hence has greatly reduced dense components, and a shallow-water wrasse (*Ctenolabrus*), which uses gas for static lift and hence can afford to support much more dense body components.
Summary of Section 4.2

Fish composed of materials that are more dense than seawater weigh more than the volume of water they displace, i.e. they are negatively buoyant. Such fish can avoid sinking when swimming by generating hydrodynamic lift, mainly by using their outstretched pectoral fins as hydrofoils. For fish that normally rest on the sea bottom, negative buoyancy may be an advantage, but when fish are free-swimming, generating lift hydrodynamically represents a substantial drain on the resources for locomotion because it demands an increased expenditure of energy. Except for very fast-moving fish, a better solution is to acquire static lift and become weightless in water by accumulating light materials, particularly lipid and gas but also, in the deep sea, dilute body fluids. Lipid has the advantage that it is virtually incompressible and offers a constant amount of lift irrespective of depth, but it is also inconveniently bulky, because relatively large amounts are required.

4.3 Gas as a source of static lift

Animals that use gas for buoyancy face a quite different set of problems, and some of the most remarkable adaptations in the whole animal kingdom have resulted from the need to overcome them. If the animal is ‘designed’ to float at the surface, then gas is an excellent source of lift, for little is required and, moreover, it is not difficult to confine or secrete gas against atmospheric pressure. Several of the remarkable planktonic siphonophores (a specialized group within the phylum Cnidaria, including the Portuguese man-of-war, Physalia) float in this way at the surface. Most aquatic animals, however, do not use gas for floating, but to achieve neutral buoyancy; these animals are subject to changes in ambient pressure when they move to different depths. For every
10 metres of increased depth in the sea, hydrostatic pressure increases by 101.3 kPa. So any animal that uses gas in this way faces considerable problems. In some animals, the gas is confined within a rigid box, so that when they change depth the volume of the box always remains the same (and hence the lift generated by the contained gas does not vary). This solution is adopted by the cephalopod molluscs (especially the cuttlefish *Sepia* and *Nautilus*) and was probably used by the abundant fossil ammonites. It works well within certain depth limits but, just like deep-sea diving suits, the box containing gas has to be very strongly constructed to withstand the ambient pressure. Cuttlefish, for example, cannot go below 200 m without their buoyancy organ, the cuttlebone, imploding. As we might guess, they live in shallower water! Here we concentrate on fish where the gas is held in a non-rigid soft-walled container, the swimbladder.

### 4.3.1 Buoyancy from elastic gas-filled swimbladders

Most (but not all) teleosts have elastic gas-filled swimbladders that are approximately oval and located above the abdominal cavity beneath the vertebral column (Figure 4.5).

![Vertebral column and swimbladder](image)

Because gases have low densities, only quite small amounts of gas are necessary to match the density of the fish to the surrounding water. Suppose that a fish without a swimbladder has an overall density of 1.07 g cm⁻³. If the fish weighs 107 g in air it displaces 100 cm³ of water. Knowing the relative densities of seawater (1.03 g cm⁻³) and freshwater (1.00 g cm⁻³), we can calculate that the fish weighs 4.0 g in seawater (107–103) and 7.0 g (107–100) in freshwater. If the volume of the fish is increased by only 4.0 cm³ in seawater or 7.0 cm³ in freshwater by a swimbladder filled with ‘weightless’ gas, the fish is neutrally buoyant. By accumulating gas, the fish is increasing its volume without changing its mass and so its overall density is reduced. In fact, although the shape of swimbladders varies a good deal (partly because they may be involved in functions like sound production and hearing as well as in buoyancy), their volume in marine fish is usually about 5% of the total body volume. In freshwater species the swimbladder (as we would expect) is larger, usually some 7% of the body volume. However, there are some freshwater fish, such as the primitive garpike (*Lepisosteus*) of the Americas, which are covered with thick heavy scales and their swimbladders are as much as 12% of their total body volume.

Although fish using gas for neutral buoyancy need to store relatively little gas compared with the sharks and other fish which have to store large amounts of lipid, gas storage involves some serious difficulties.
Swimbladders are compliant and elastic, and not rigid boxes like the buoyancy organs of cephalopods, so if the ambient pressure changes when the fish swims up and down in the water, the swimbladder changes its volume. In general, when fish are subject to transient small-scale changes in pressure, the swimbladder gas obeys Boyle’s law* reasonably well (Figure 4.6).

It is easy to see that obeying Boyle’s law produces a major problem for fish using gas to achieve neutral buoyancy, unless they swim only at one depth. Suppose that a fish swimbladder is filled with a fixed mass of gas and that the fish is neutrally buoyant.

What happens when it changes depth?

If it swims deeper, where the surrounding hydrostatic pressure is greater, the pressure change is transmitted through the body, the swimbladder is compressed and the overall density of the fish increases. The fish will tend to sink further and unless it wants to continue to go deeper, has to generate hydrodynamic lift by swimming actively to remain at this new greater depth. This requirement is not too serious because, even if the swimbladder were to be fully compressed, the difference in density between the fish and water is relatively slight, and in any case the fish is no worse off than other fish which do not have swimbladders! But suppose that the fish swims upwards, perhaps in pursuit of prey, or to escape from a predator. The fish is now in a much more risky situation. Because the external pressure decreases, the swimbladder expands and so the density of the fish decreases. This increased buoyancy sweeps the fish nearer the surface, increasing the swimbladder volume even more and making the fish even more buoyant. Although for small positive changes in buoyancy the fish could actively swim downwards, this process of positive feedback may increase the buoyancy of the fish to such a degree that it cannot swim downwards hard enough and so rises helplessly to the surface. Experiments with cod have shown that they can cope with reductions of 25% below the pressure to which they were originally adapted. When fish are brought up on deep-sea long lines, their swimbladders have expanded to such an extent that when they are brought to the surface they float. In fact, their swimbladders have often burst. Fish are of course not designed to be fished at depth, and then brought rapidly to the surface!

*At a constant temperature, the volume (V) of a given mass of gas is inversely proportional to the pressure (P). The product PV is therefore constant.
So fish with swimbladders suffer from **vertical instability**, because any movement away from buoyancy equilibrium at one depth produces accelerated upward or downward displacement.

- How might fish maintain neutral buoyancy during variations in ambient pressure caused by changes in depth?

The obvious solution is to maintain a constant gas volume despite changes in depth. Remember that density is mass/volume, which means that fish have to change the mass of the gas within the swimbladder. This conclusion may be obvious, but it is not a simple matter, for fish need mechanisms for inflating and deflating the swimbladder in a controlled way, and at the same time the swimbladder has to be impermeable or the gas would soon diffuse out of it. To remain neutrally buoyant, fish have to decrease the mass of gas within the swimbladder as they ascend in the water and increase it as they descend. Such adjustments present formidable difficulties and fish such as cod or swordfish, which undertake large vertical movements, cannot maintain neutral buoyancy throughout their depth range and, indeed, may be neutrally buoyant only at the top of this range. What is more, because the swimbladder is elastic, the total pressure of the gases inside is normally identical to the ambient hydrostatic pressure, and yet there are fish which manage to use gas-filled swimbladders even at the greatest depths of the oceans. As we shall see, the ways in which fish have solved the problems inherent in using elastic gas containers may justly be regarded as being among the greatest feats of biological engineering. Most of our knowledge comes from studies of shallow-water marine species, but the swimbladders of freshwater fish, and of deep-sea fish (where the problems are most acute) are of essentially the same design, and are likely to function in much the same way.

In general, fish living near the surface have swimbladder gas that resembles air in composition (i.e. about 80% nitrogen, and 20% oxygen), but the proportion of oxygen in the swimbladder is greater in species from greater depths (Figure 4.7).
This fact was discovered in dramatic style in 1803 by the French physicist, Jean-Baptiste Biot, whose primary interest was the composition of the atmosphere. He placed samples of air in a delicate glass gas analyser, added excess hydrogen and sparked the mixture. By weighing the resultant water, the oxygen content of the sample could be established. Perhaps bored by the constancy of atmospheric oxygen, he introduced a sample of swimbladder gas from a deep-sea fish—the resulting explosion wrecked his apparatus! Realizing that this observation meant that the swimbladder gas contained more oxygen than did air, he was able to show, using a new gas analyser, that the proportion of oxygen in swimbladders increased with depth and that the swimbladders of deep-sea fish contained almost pure oxygen. In contrast, it was later found that the gas in the swimbladder is almost entirely nitrogen in some freshwater salmonids (*Coregonus*).

Neutral buoyancy can be achieved at different depths by varying the amount of gas in the swimbladder in such a way that the gas volume is held constant, regardless of external hydrostatic pressure. Fish therefore face two problems: decreasing the mass of gas within the swimbladder as they ascend in water and increasing the mass of contained gas as they descend. Such adjustments present formidable difficulties: because the swimbladder is elastic, the total pressure of gas inside is normally identical to ambient hydrostatic pressure. To see how formidable a task the fish faces with a gas-filled swimbladder when the ambient pressure is high, think of the oxygen-filled swimbladder of deep-sea fish that live at 4 000 m below sea level (some may live at 7 000 m—a depth of over 4 miles!). Remember that for every 10 m of increased depth in the sea, hydrostatic pressure increases by 101.3 kPa. At a depth of 4 000 m, the external pressure will therefore be about $400 \times 10^2$ kPa and the total gas pressure within the swimbladder must be the same. The partial pressure of oxygen ($P_{O_2}$) in the swimbladder is also about $400 \times 10^2$ kPa; if 5% of the gas was nitrogen, the partial pressure of nitrogen ($P_{N_2}$) would be about $20 \times 10^2$ kPa and the $P_{O_2}$ would be $380 \times 10^2$ kPa. The $P_{O_2}$ and $P_{N_2}$ in the ambient water at this depth would be no greater than about 20 and 80 kPa, respectively, and the partial pressures of these gases in the blood would be about the same. On descent, and even at constant depth (because there may be some slow loss of gas from the swimbladder), fish therefore may have to add oxygen to the swimbladder against the huge partial pressure gradient of no less than $2 000:1$ ($400 \times 10^2 : 20$ kPa)! Remarkably, this inward movement of oxygen does not occur by active transport of oxygen but by free diffusion of the gas, although the process is somewhat misleadingly called *oxygen secretion*.

A third major difficulty faced by such deep-water teleosts is that the swimbladder wall must be impermeable to prevent the contained gas at high partial pressures from diffusing out into the surrounding tissues.

### 4.3.2 Structure of the swimbladder

In development, the teleost swimbladder forms as a pouch from the roof of the foregut, and in some more primitive bony fish such as herring, eels and salmonids, the connection between the oesophagus and the swimbladder remains as an open pneumatic duct in the adult (Figure 4.8a). In the majority of teleosts with swimbladders, however, this connection is lost during development, and the adult swimbladder is a closed sac (Figure 4.8b). It is not known why the open duct to the oesophagus has been abandoned in the great majority of the advanced teleosts. There are a number of obvious advantages for shallow-water fish in
having an open duct—for example, the swimbladder can easily be emptied, and filled again at the surface by gulping air. As herring ascend in the water towards the surface, they release gas from the anus and so keep swimbladder volume (and hence their density) the same. Fish such as cod, have closed swimbladders and cannot swim near to the surface. Presumably there are greater advantages in sealing off the swimbladder since the great majority of fish have this arrangement, but we have no idea what these may be!

Figure 4.8  (a) An open swimbladder, as in the eel (Anguilla anguilla). Note that the herring, which also has an open swimbladder, lacks the gas gland and the pneumatic duct opens into the stomach, so the swimbladder of the eel should not be thought of as a ‘typical’ open swimbladder. (b) A swimbladder of the closed type as, for example, in the perch (Perca fluviatilis). Arterial vessels in both (a) and (b) are shown in blue.

In both types (though not in herring, which can only fill their swimbladders by gulping air at the surface) there is a special region, the gas gland, where gas is ‘secreted’. We know this is the site of secretion because when actively secreting swimbladders are cut open, the gas gland is covered with foamy mucus. The foam contains bubbles of oxygen, and experiments with oxygen isotopes have shown that molecular gas moves into the swimbladder from the blood. The blood supply to the gas gland is peculiar in that the incoming capillaries form an elaborate network with the outgoing capillaries that lie close to them. This rete mirabile (seen in Figure 4.8, and in more detail in Figure 4.9a) consists of a staggeringly large number of capillaries running parallel to each other. In the eel, it has been estimated that there are no fewer than 116 000 arterial capillaries closely apposed to 88 000 venous capillaries! The precise relationship between the rete and the gas gland (where the blind-ending loops of the capillaries lie) varies, but the essential point is that arterial blood moving towards the swimbladder and returning venous blood are in intimate contact (see the cross-section of the rete, Figure 4.9b), forming a **counter-current exchanger**. A
similar counter-current exchanger (used for a different purpose) is found in the muscles of warm-bodied tuna and sharks (see Section 3.3.1). The total surface area of the capillary wall in the rete of the eel is about 105 m² although the volume of blood in the rete is less than a drop—only 0.064 cm³. So there is a very large ratio of diffusion area to blood volume in the rete; around 1700 m² : 1 cm³, nearly 20 times greater than that in human lungs.

The general blood (systemic) circulation is linked to the swimbladder at the gas gland via the rete (see Figure 4.8a), but there is also a second connection without the intervention of a rete. In closed swimbladders (Figure 4.8b), this second connection is at a special region which can be sealed off from the rest of the swimbladder by sphincter muscles. Because of its shape, this region is known as the oval. Sometimes (as in wrasse) a transverse septum with a hole surrounded by a sphincter muscle divides the portion of the swimbladder connected with the systemic circulation from the main region. In some open swimbladders (as in the eel, Figure 4.8a), this connection is found on the pneumatic duct.

### 4.3.3 Operation of the swimbladder

Let us now consider the way in which fish solve the three problems they face when changing depth.

1. How is gas lost from the swimbladder as the fish ascends?

This problem is the easiest to solve. Because the blood in the systemic circulation will have a $P_{O_2}$ of around 20 kPa, all that is required to lose gas from the swimbladder is to arrange a connection between the swimbladder and the circulation, and to ensure that this connection can be shut off when no more gas is to be lost. As we have seen, in closed swimbladders, this connection is provided by the oval (Figure 4.8b), and in open swimbladders, by the pneumatic
duct (Figure 4.8a). In fish such as conger eels, a decrease in ambient pressure first causes the swimbladder to swell, which opens the sphincter to the pneumatic duct and gas diffuses into the systemic circulation at the network of vessels that connect with the wall of the duct. If the ambient pressure decreases further, gas is belched out via the oesophageal sphincter.

There is, however, a definite limit to the rate at which fish with closed swimbladders can lose gas as they ascend in the water. For example, experiments on cod which had been adapted to different initial pressures and then subjected to reduced pressures, showed that they can lose 12–36 cm$^3$ gas kg$^{-1}$ h$^{-1}$. The greater the pressure to which the cod was adapted beforehand, the greater was the rate of loss of gas from the swimbladder. After reading the next section, you should be able to see why the initial pressure to which the cod were adapted made a difference to the rate of loss of gas.

2 How is gas prevented from diffusing out of the swimbladder?

This second problem is solved in a most ingenious way. Next time you buy a fish (not a mackerel or a flatfish such as plaice) for supper, open the visceral cavity and expose the internal organs; the swimbladder is usually conspicuous because it is silvery even if it is not full of gas. The silvery layer on the swimbladder is formed by a series of thin overlapping platelets of guanine about 3 μm thick which make the bladder impermeable. Eric Denton of the Marine Biological Association Laboratory at Plymouth showed (using an isolated swimbladder from a conger eel) that if the silvery layer was removed there was a rapid loss of gas from the bladder. This loss of gas takes place by diffusion, and the impermeability of the silvery layer results from the great length of the diffusion pathway from the inside to the outside, which is formed by the overlapping, impermeable, guanine platelets. This is a beautiful solution to the problem of constructing an elastic impermeable bladder from natural material because, provided that the platelets are numerous and of sufficient size, they remain impermeable even if the walls of the swimbladder are stretched and shrunk as the fish alters its depth in the water. Conger eels do not live at great depths, and the swimbladder is made sufficiently impermeable by a relatively thin layer of guanine crystals. However, in deep-sea fish, where the problem of preventing gas diffusing from the swimbladder is much greater, the guanine platelet layer is about ten times thicker, and the swimbladders look much more silvery than those of shallow-water fish.

At the gas gland, systemic blood must be brought into contact with the swimbladder to enable the secretion of gas, so a potential leak must exist here. Why does gas not diffuse out of the swimbladder into the circulation at this point as it is arranged to do at the oval? The answer to this question is that it does and it doesn’t! Consider the arrangement of the rete mirabile, with its incoming and outgoing capillaries closely apposed in parallel. If there is any difference in $P_O_2$ between outgoing and incoming capillaries, oxygen diffuses across from one to the other. Suppose that oxygen diffuses out of the swimbladder into the outgoing venous capillaries at the gas gland and raises the blood $P_O_2$. Oxygen will then diffuse from the venous capillaries across into the incoming arterial capillaries along the length of the rete, so that blood finally leaves the rete (if the rete is long enough) with a $P_O_2$ very nearly the same as that of the incoming blood at the beginning of the rete. In other words, the $P_O_2$ along the outgoing capillary drops while that in the incoming capillary rises; little, if any, oxygen would be lost from the swimbladder. This ingenious counter-current arrangement effectively prevents any loss of gas from the swimbladder, as summarized in Figure 4.10.
Figure 4.10  How the rete mirabile prevents loss of gas from the swimbladder. Oxygen dissolves in the blood passing through the gas gland but very little of it escapes from the swimbladder because it is 'short-circuited' by the counter-current system of the rete.

The greater the depth at which the fish normally lives, the greater is the difference in partial pressure between the swimbladder gases and the gases in the surrounding seawater and systemic circulation. It is not surprising then that not only the thickness of the guanine crystal layer, but also the length and complexity of the retial system (Figure 4.9c, d) is greater when this partial pressure gradient is greater. The longest retia yet found occur in the deep-sea fish; in some cases they are 60 mm long. This length is amazing—normal capillaries in muscle are only around 0.5 mm long.

3 How is gas secreted into the swimbladder as the fish descends?
This problem proved to be much more of a puzzle to physiologists than the two we have already considered. It had long been obvious that the retia were involved, and that there must be some change in the blood as it flows through the gas gland into the wall of the swimbladder. What is needed is a way of reducing the amount of gas in the venous blood leaving the rete to a level that is lower than that in the arterial blood entering the rete. The reduction (i.e. the difference in the amount of gas between the two) need not be very great, for the counter-current mechanism of the rete is designed to multiply small effects. A moment’s reflection suggests that the process must rely on some rather special property of the blood, for if the partial pressure of the gas in the venous capillaries of the rete (i.e. after gas has been secreted into the swimbladder) is lower than that in the incoming arterial capillaries, we should expect gas to diffuse across from the arterial to the venous side of the rete, and the whole process of secretion would grind, or rather diffuse, to a halt. As we have seen, the gas secreted in almost all fish is oxygen, so we need to look at some special properties of the blood with respect to its oxygen content.

At this point, we need to be clear about the distinction between the total oxygen content of blood and the oxygen partial pressure ($P_O$). The amount of oxygen held by haemoglobin is dependent upon the partial pressure of oxygen—a relationship expressed by the oxygen dissociation curve. However, the oxygen content of blood (measured as vol%) comprises both oxygen bound to haemoglobin and an amount of oxygen present in simple physical solution,
which varies according to the oxygen partial pressure. **Diffusion of oxygen occurs down a gradient of partial pressure rather than a gradient of oxygen content.** What is needed therefore is some method of raising the \( P_O_2 \) of the oxygen in the blood as it passes through the gas gland and back into the rete, while at the same time lowering the actual oxygen content. In this way, oxygen will diffuse across into the swimbladder and from the venous to the arterial capillaries in the rete.

An important clue as to how the system operates comes from measurements of the effects of lowered pH on the oxygen dissociation curve of fish blood. These show that the acidification of mammalian blood causes a shift in the dissociation curve to the right. This Bohr shift reduces the affinity of haemoglobin for oxygen, but if the \( P_O_2 \) is high, even highly acidified haemoglobin (or haemoglobin exposed to a high \( P_{CO_2} \)) can eventually become fully saturated with oxygen (Figure 4.11a). Haemoglobins displaying a Bohr effect have a reduced affinity for oxygen on acidification, but the amount of oxygen bound when the pigment is fully saturated (i.e. the oxygen-carrying capacity) is unaffected. The blood of most teleost fish responds to acidification in a rather different and more striking way. Not only is the dissociation curve affected, but the total oxygen-carrying capacity of the pigment is greatly changed by acidity. Even at a very high \( P_O_2 \), the acidified pigment fails to attain full saturation. This effect is illustrated in Figure 4.11b and is termed the **Root effect.** The important implication is that if the blood is acidified (e.g. by lactic acid or by an increase in \( P_{CO_2} \)) then, even at the very high oxygen partial pressures near an oxygen-containing swimbladder of a fish at depth, the haemoglobin may be incompletely saturated.

**Figure 4.11** (a) The Bohr effect, where an increased acidity of the blood reduces the affinity of the pigment for oxygen (i.e. the curve shifts to the right). (b) The Root effect, shown in the oxygen dissociation curve of the sea robin (*Prionotus carolinus*). Modest partial pressures of carbon dioxide are sufficient to prevent the full loading of the pigment, even when the partial pressure of \( O_2 \) is high.

Elegant experiments on fish that live in shallow water, in particular studies by Berg, Steen and colleagues on eels, have shown how the Root effect contributes to the secretion of gas into the swimbladder. In most fish with open swimbladders, there is little or no gas secretion, and gas is gained by swallowing at the surface. However, the eel has a rather atypical open swimbladder and secretes gas. Berg and Steen succeeded in the extremely delicate task of
removing small samples of venous and arterial blood by cannulation of the vessels just next to an active rete. They found that blood leaving the gas gland has a lower pH and a higher lactic acid content than has blood entering the gland, suggesting lactic acid is secreted by the glandular epithelium of the gas gland. The gas gland cells are rich in glycogen, and in the enzymes carbonic anhydrase and lactate dehydrogenase, and they release lactic acid into the hairpin end loops of the rete as they pass the gland. The acidification of blood produces a significant Root effect: when fully saturated haemoglobin arrives at the gas gland and its pH is lowered, a significant amount of bound oxygen is released from the haemoglobin, even though the ambient partial pressure of oxygen is high. This extra oxygen in solution increases the partial pressure of oxygen in the blood still further. Blood leaving the gas gland therefore has a higher partial pressure of oxygen than blood entering the gland, and in the rete oxygen therefore diffuses from venous to arterial blood.

Lactic acid has another important effect. An increased concentration of any solute decreases the solubility of any gas in solution. (The absorption coefficients of oxygen decrease with increasing salinity, which explains why saltwater has a lower oxygen content than freshwater at the same partial pressure.) The addition of lactic acid to the blood passing through the gas gland therefore decreases the solubility of oxygen, which causes the $P_{O_2}$ to increase. This salting-out effect influences the solubility of all dissolved gases, which may account for the high partial pressure of nitrogen in the swimbladders of some deep-sea fish. Theoretical grounds seemed to suggest that salting-out would deposit gas only at a very low rate, and also could not raise the partial pressure of swimbladder gases to more than about $10^3$ kPa, well below the measured values of about $10^4$ kPa. However, more recent calculations indicate that salting-out effects may be more significant than originally supposed.

We now know that the major factor that elevates the $P_{O_2}$ in the blood near the gas gland depends upon the unique loop-like arrangement of the capillaries of the rete and gas gland. Figure 4.12a shows diagrammatically how a single capillary forms a ‘hairpin loop’ near the gas gland epithelium. We already know that lactic acid raises the partial pressure of oxygen in the blood passing through the gas gland both by the Root effect and by salting-out. This increased $P_{O_2}$ can be termed for convenience the ‘primary effect’. Consequently, there is diffusion of oxygen from venous to arterial blood of the rete. Thus, the blood now entering the gas gland via the arterial capillaries will have a $P_{O_2}$ greater than 20 kPa (see Figure 4.12b) and, when this blood in turn is acidified, the $P_{O_2}$ in the blood adjacent to the gas gland increases still further. Because the $P_{O_2}$ of the blood in the venous capillary is always greater than the $P_{O_2}$ of the blood in the arterial capillary, free oxygen is constantly returned to the arterial capillary and the hairpin loop accumulates oxygen in the end of the rete nearest the gas-gland epithelium (Figure 4.12c). Thus the primary effect is multiplied in the presence of counter-current flow to produce a modest $P_{O_2}$ gradient across the rete, from the venous to the arterial side, and a very substantial gradient along the length of the capillary vessels (Figure 4.12d). This process of counter-current multiplication means that the rete has the potential to accumulate oxygen in the blood entering the gas gland to very high levels (Figure 4.12e).

But there is one potential snag in the system. The capillary walls of the rete are permeable to lactic acid, which (along with the oxygen and ions) tends to diffuse across from the venous to the arterial side of the rete. The loss of lactic acid by
diffusion means that as the blood flows away from the gas gland and through the rete, it becomes progressively more alkaline, so haemoglobin begins to pick up oxygen again and become fully saturated. Why does this process not have the disastrous effect of increasing the oxygen content of the blood leaving the rete, thus reducing the amount of oxygen available for secretion in the swimbladder? The important point is that the half-time of the loading of the haemoglobin with oxygen following increased alkalinity (the Root-on effect) is slow (10–20 s) compared with unloading in response to increased acidity (the Root-off effect), which takes only 50 ms. The free oxygen molecules can therefore recombine with haemoglobin to only a small extent before the outgoing blood has left the rete, provided that the flow rate of blood through the rete is sufficiently high. This process ensures that the outgoing blood of the rete contains less oxygen in chemical combination than does the incoming blood, although the partial pressures of the incoming and outgoing bloods (and their acidity) may be almost identical. The difference in oxyhaemoglobin content of the two bloods represents the oxygen available for secretion into the swimbladder. Counter-current multiplication in the rete permits the build-up of free oxygen at the gas gland until a diffusion of the gas can occur from the gland into the lumen of the swimbladder.

There is general agreement amongst physiologists who have studied swimbladder gas secretion, that the scheme briefly summarized above, worked out by experiments on shallow-water fish, must in essence, be applicable also to deep-sea fish. But the relative importance of the Root shift and the salting-out effect is still uncertain for deep-sea fish, and some puzzles remain. First, at oxygen tensions above 40 × 10^2 kPa (i.e. a depth of around 400 m) not all deep-sea fish show a Root shift when their blood is acidified, so the salting-out effect seems the more important. Second, the multiple retia (Figure 4.9) of many deeper-living fish seem to be devices for ensuring slow blood flow through the retia and hence, even if there is a Root shift, it would seem that the Root-on shift would occur within the retia, just what is not wanted. Perhaps flow within the venous capillaries of the rete is more rapid than in the arterial capillaries as they are often much larger than the arterial capillaries and offer less resistance to flow.

For obvious reasons, we know little about the rates of gas secretion in deep-sea fish. However, it is easy to measure how fast secretion takes place in fish living in shallower water. Simple experiments in which fish were subjected to pressure increases which decreased the volume of the swimbladder, and were then left to secrete gas until neutral buoyancy was achieved again, showed that fish with closed swimbladders such as cod (Gadus morhua) and saithe (Pollachius virens), could secrete around 1.5 cm^3 kg^-1 body weight h^-1, whilst eels (Anguilla) and goldfish (Carassius auratus) with open swimbladders secreted gas at around one-quarter of this rate. So gas secretion is relatively slow, much slower than gas resorption.

### 4.3.4 Swimbladders and habitats

Quite a large number of teleost fish have reduced swimbladders or none at all, and are always negatively buoyant. This situation seems very curious, considering the advantages of neutral buoyancy conferred by gas-filled swimbladders. Because the problems of gas secretion and retention become more severe the deeper a fish lives, we might not unreasonably guess that fish with
gas-filled swimbladders would be rare in the deep sea. However, Marshall, who has greatly increased our knowledge of the structure and function of swimbladders in marine fish, has shown that swimbladders are found in fish living near the bottom of oceans, even at great depths. However, generally they are reduced or absent in fish that live near the surface, (though some fish near the surface have them) and they are absent from many fish living at moderate depths (Figure 4.13).

![Copyright material removed]

**Figure 4.13** The distribution of fish with and without swimbladders in the oceans. Arrows indicate groups that show vertical migrations.

If fish normally rest on the sea bottom, as do flatfish such as plaice (*Pleuronectes platessa*), it is unnecessary for them to be neutrally buoyant, and such fish have no swimbladders. Increased density is probably advantageous in preventing them being swept along by currents. Similarly, in fast-flowing freshwater streams, many fish reduce the volume of their swimbladders in order to be negatively buoyant, and so avoid being swept downstream. For example, the darter (*Percina*) in rapid streams, has no gas in its swimbladder. On the other hand, fish that seek their food by slowly cruising or hovering just off the bottom need to be neutrally buoyant, as is the darter in slow streams (where its swimbladder is full of gas). Even at great depths, where the problems of gas secretion and retention are very severe, there are fish with swimbladders (such as macrourids) living near the bottom. We know from photographs and videos taken from deep sea vehicles, that macrourids do in fact cruise slowly around just off the sea bottom.
Near the surface, where gas secretion and retention pose fewer problems than in the deep sea, we might expect that all bony fish would have swimbladders to provide neutral buoyancy. Of course, some do (Figure 4.13). It turns out, when we look at these, that they are all fish which live close to the surface, such as flying fish or garfish, and these have swimbladders comprising the usual 5% of the fish’s volume. However, fast-swimming fish, such as mackerels or tunas living mainly near the surface, have either reduced the swimbladder to only 2% of the fish’s volume, or they have lost it altogether.

Why do these fish forego the advantages of neutral buoyancy?

Unlike flying fish, they move up and down in the upper layers of the sea, and part of the answer lies in what happens as they change depth.

Remembering that for every 10 m depth increase in the oceans, ambient pressure increases by 101.3 kPa, you can see that a change in depth from the surface to 10 m doubles ambient pressure from atmospheric pressure of 101.3 kPa to 202.6 kPa and, if such fish had a swimbladder, its volume would be halved. So, near the surface, fairly small changes in depth have large effects on the volume of the swimbladder and on the buoyancy of the fish. The deeper the fish normally lives, the less significant will be the effect of such small changes in depth. For example, a fish living at 400 m that moved down to 410 m would experience a change in ambient pressure of 101.3 kPa. This increase is only 2.5% of the ambient pressure at 400 m (4052 kPa), and would cause a decrease in swimbladder volume of 2.5%, which would have only a marginal effect on the fish’s buoyancy. The inevitable large changes in volume as fish change depth near the surface, suggest that a swimbladder is not well suited to be a buoyancy device there, but this is not the whole answer to why fish such as mackerels and tunas have lost it. We saw earlier that most pelagic sharks are not neutrally buoyant, and that the extra drag associated with lift generation becomes less significant the faster the fish swims. It is because tunas and mackerels are designed for fast swimming that they can ‘afford’ to be negatively buoyant.

A good many different kinds of fish with swimbladders make regular vertical migrations. The champion migrators are probably the little myctophid lantern fish, some of which rise to the surface at night, and return at dawn to their daytime depths of 200–300 m. Larger fish, such as saithe, move to the surface at night from a daytime depth of 100 m or so. Cod and herring move less spectacular distances, but enough to experience significant changes in ambient pressure. Gas secretion and resorption are much too slow to cope with the speed of the depth changes of fish like myctophids, and they are too slow for cod and saithe as well. After an increase in ambient pressure equivalent to a move from the surface to a 10 m depth, saithe take 24 hours to compensate by restoring the original swimbladder volume. When the pressure change is reversed, it takes only 5 hours for the resorption of gas to occur. So fish which make these vertical migrations cannot be neutrally buoyant throughout their depth range. Curiously, the small Myctophum punctatum is almost always slightly negatively buoyant at the surface during the night, and is almost certainly negatively buoyant at depth during the day. Presumably, the access to a reliable source of food (copepod crustaceans) outweighs the extra energy cost of swimming (and perhaps escape from predators at the surface is important too).
Myctophids are small oceanic fish, and so not easy to study. We know much more about buoyancy changes with depth in cod, thanks to interesting work recently published by the Lowestoft Fisheries Laboratory. 300 kHz ultrasound tags were fitted to cod, which could then be tracked continuously by sector-scanning sonar for up to 2 days, as they swam freely up and down in the North Sea. The fish were either released at the surface or from a cage on the bottom where they had been kept for some time to adapt to ambient pressure. Figure 4.14a and b shows two of the results obtained. In the first (Figure 4.14a), the cod released at the surface made a rapid dive and then returned near the surface, and thereafter steadily descended (apart from a short rest on the bottom in the early hours of the second morning). Presumably it was secreting gas throughout its gradual descent. The second fish adapted to the ambient pressure on the bottom (Figure 4.14b) and stayed there, making ascents well within the depth range with which it could cope (as shown by laboratory experiments). Most likely, cod are negatively buoyant and rest on the sea bottom, rising off it to feed, becoming near neutrally buoyant, but not exceeding its upper limit of swimbladder expansion (25%).

Why do you think that a herring chased by a cod could escape being eaten by swimming upwards?

Herring have open swimbladders and release gas via the anus as they ascend. This allows them to keep the swimbladder volume and hence their density constant so that they are able rise directly from any depth to the surface without having to pause to equilibrate. The cod on the other hand, can only cope with changes in swimbladder volume of some 25%, which means that a cod adjusted for neutral buoyancy at 50 m could only rise to 37 m and still remain neutrally buoyant.

Figure 4.14  (a) The vertical track of a tagged cod released at the surface in the North Sea, and followed by sector-scanning sonar. After an initial dive and ascent, the cod slowly descended remaining within the dashed lines (which indicate the upper and lower limits of the range within which it could remain neutrally buoyant). The cod rested on the bottom (shown by the shaded area) near the end of the trace. (b) The vertical track of a second cod released from a cage on the bottom (at 24 m, indicated by the black arrow) where it had partially adapted to ambient pressure. The dashed line represents the upper limit at which it could have remained neutrally buoyant. This fish was probably negatively buoyant in water deeper than that at which it was released.
What are the advantages and disadvantages of different buoyancy mechanisms?

McNeill Alexander has sought to explain why fish adopt different kinds of buoyancy aids by calculating the metabolic costs of achieving buoyancy by swimbladders, by low-density fats and by fins. He began with the reasonable assumption that the mechanism favoured by evolution would be the one most economical of energy. For fish that swim at high speeds, dynamic lift from hydrofoil-like fins may involve the smallest metabolic cost. (Because the drag incurred in dynamic lift generation decreases as speed increases, it is in fact proportional to $1/v^2$.) Many of the teleost fish that swim all the time at high speeds lack swimbladders, e.g. mackerel and tunas. Likewise, for fast-swimming sharks, which lack swimbladders, we have already seen that hydrofoils are probably more economical than low-density lipids. Slow-moving sharks like the basking shark, however, need to have static lift from lipids.

For fish that do not cruise at high speeds, a swimbladder is probably the most economical means of avoiding sinking. But, for fish such as the many myctophids that make large daily vertical migrations, swimbladders filled with gas seem less economical than those filled with lipids. In fact, there is quite a good correlation between the amount of lipid in the swimbladders of different myctophids and the extent of their vertical migrations. However, swimbladders have important secondary functions that may outweigh some of the energetic disadvantages in vertically migrating fish. The swimbladder plays an important role in hearing in several fish groups, including the herring-like fish, and in the production of sound, in which the swimbladder may act as an important resonator. Some of these other functions may be impaired when the swimbladder volume changes as the fish undergoes extensive vertical migrations and more attention should be paid to its additional roles, particularly in deep-sea fish and the many species that undergo vertical migrations. Fish with swimbladders are about twice as sensitive to external pressure changes than have fish without them, and they can detect changes of around 0.5%. Stretch receptors in the swimbladder wall are thought to be involved, firing at different rates according to the changes in swimbladder volume resulting from pressure changes.

There is still much that we do not know about swimbladders, and if the reader is still pondering why it is that the swimbladders of fish undertaking vertical migrations are not designed like that of the eel or herring, i.e. with the possibility of rapid loss of gas on ascent as a safety measure against being swept to the surface, you may feel encouraged to know that so too are all fish physiologists who have considered the matter!

**Summary of Section 4.3**

Because of its very low density, gas offers a greater amount of upthrust per unit of volume, so modest amounts of gas can provide fish with sufficient lift. But if a fish with a gas-filled swimbladder is to retain neutral buoyancy at a range of depths, some mechanism must enable the mass of gas in the swimbladder to be altered so that the total volume is kept constant. Reducing the mass of gas is relatively easy because gas is lost into the general circulation via the oval (in closed swimbladders) or the pneumatic duct (in open swimbladders). Gas is retained in the closed swimbladder and in that of the eel by an enveloping layer
of guanine, and by a rete mirabile, composed of closely juxtaposed venous and arterial capillaries. The rete also enables gases, including oxygen, to be secreted into the lumen of the swimbladder via the gas gland. Because of the Root effect, acidification of the blood at the gas gland readily results in unloading of oxyhaemoglobin, even when the ambient $P_O_2$ is very high. (The reverse process of loading when the pH rises is relatively slow.) The ‘hairpin’ counter-current arrangement of capillaries tends to accumulate oxygen within the capillaries until a substantial gradient of oxygen partial pressure is established along the length of the rete. The addition of lactic acid also increases the partial pressure of gases by salting-out. These processes are sufficient to add gas to the swimbladder against substantial gradients of partial pressure. Note, however, that although gas secretion is understood in general terms, some puzzles concerning gas secretion in deep-sea fish still remain.

## 4.4 Conclusion

Most fish are more dense than the water in which they swim, and they have to generate dynamic lift by using outspread pectorals as lifting foils. This process generates drag, and hence increases the energy of such fish. One way in which fish can reduce the muscular energy expenditure required to maintain their station in water is to store sufficient low-density material which makes them the same density as water. Fish use quite different materials to provide static lift. Gas is efficient in providing lift, since its density is low, and many teleosts possess gas-filled swimbladders. However, some fish, including some deep-sea species, have replaced gas with lipid. Although lipid is a lot bulkier than gas, it has the advantage that the lift provided varies little with depth because changes in ambient pressure have relatively little effect on the volume of lipid. The fact that many mid-water fish species that undergo substantial vertical migrations use lipid as a source of static lift probably reflects the difficulties of regulating buoyancy with a gas-filled bladder over a wide range of depths.

## Objectives for Chapter 4

After completing Chapter 4 you should be able to:

4.1 Define and use, or recognize definitions and applications of, each of the **bold** terms.

4.2 Explain the advantages of neutral buoyancy, and outline the advantages and drawbacks of using lipid or using gas in a flexible bag as a source of static lift.

4.3 Draw diagrams to show the structure of open and closed swimbladders.

4.4 Explain the mechanism by which gas is secreted into the swimbladder.

4.5 Explain the role of the swimbladder in species that migrate vertically and describe any additional functions the swimbladder may have.
Questions for Chapter 4

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

Question 4.1 (Objectives 4.1–4.5)

For each of the following statements, decide whether the statement is true or false and explain why.

(a) The amount of lift generated by a swimbladder full of oxygen is not influenced by the depth at which the fish is swimming.

(b) If a fish is more dense than seawater, a considerable part of its propulsive power may go towards maintaining its level in the water.

(c) No known fish has the ability to contain gas within a rigid chamber, where the volume does not change as ambient pressure alters.

(d) Unless the total volume of its swimbladder is kept constant, the overall density of a fish will increase as it moves down deeper in the sea.

(e) Because oxygen has to be moved into the swimbladder against substantial gradients of partial pressure, oxygen is transported by active processes that require ATP.

(f) In all fish with open swimbladders, the sphincter muscle at the oval may regulate the extent to which oxygen is added to the bladder.

(g) Those fish that demonstrate daily vertical migrations in the sea are likely to move up or down slowly, and this allows compensatory resorption or secretion of oxygen to maintain neutral buoyancy.

(h) Some of the non-buoyancy functions of a swimbladder might be impaired if its volume were to change during vertical migration.

Question 4.2 (Objectives 4.2 and 4.4)

Provide an explanation in physiological terms for the following observations (a–g).

(a) The amount of guanine present in the wall of the swimbladder is greatest in fish that live at substantial depths and least in those that live near the surface.

(b) The rete associated with the gas gland in deep-sea fish is unusually long compared to that of fish from shallower waters.

(c) Gas-gland tissue shows a very high activity of glycolytic enzymes, especially lactate dehydrogenase.

(d) Some freshwater fish have closed swimbladders that are filled almost entirely with nitrogen.

(e) The concentration of carbon dioxide within the swimbladder is usually close to zero.

(f) There is a gradient of lactate along the rete of Anguilla in both the arterial capillaries conveying blood to the gas gland and in the venous capillaries conveying blood away. For both types of capillary, there is a higher lactic acid content at the end of the vessel nearer the gas gland.

(g) As a general rule, lipid stores are used as a source of static lift much more by marine fish than by freshwater species.
Question 4.3 (Objective 4.4)

From the following statements (a–i), referring to the operation of counter-current multiplication in the swimbladder, identify the four that are true, and then place them in the appropriate chronological order in which they occur, starting with (a), (b) or (c).

(a) Blood from the heart eventually arrives at the far end of the rete with a $P_{O_2}$ of 200 kPa, and with most of the oxygen contained in the blood present in simple physical solution.

(b) The haemoglobin begins to unload oxygen at the oval, and the relaxation of the sphincter muscle ensures that the unloaded oxygen passes into the swimbladder.

(c) The blood arriving at the rete has a partial pressure of about 20 kPa, most of the oxygen in it is bound as oxyhaemoglobin and its concentration of lactic acid is only slightly higher than in the systemic circulation.

(d) Oxygen that at an earlier stage was unloaded from haemoglobin now starts to recombine with it as the pH increases, although this happens relatively slowly.

(e) Lactic acid passes into the blood from the gas gland, but, because of the Root effect, the partial pressure of oxygen in the blood remains unchanged until counter-current multiplication begins.

(f) The pH of the blood passing towards the gas gland decreases because of inward diffusion of lactic acid, and the $P_{O_2}$ therefore begins to increase.

(g) The addition of lactic acid to the blood at this point has the effect of increasing the solubility of the gases in the plasma, although this has no effect on the partial pressure of the gas.

(h) The oxygen partial pressure in the arterial capillaries of the rete now begins to increase because of diffusion of oxygen from the venous capillaries.

(i) As the venous blood is leaving the rete capillaries, it has a $P_{O_2}$ that is approximately the same as that of the blood entering the rete (20 kPa), but its oxygen content is much higher.

Question 4.4 (Objective 4.2)

Explain, in physiological terms, the following generalizations:

(a) Many of the teleosts that inhabit the upper layers of the sea tend not to have a swimbladder, unless they live exclusively just at the surface.

(b) Many (but not all) of the deep-sea teleosts lack a swimbladder or have a swimbladder filled with lipid rather than gas.