Diving deep

Coping with pressure

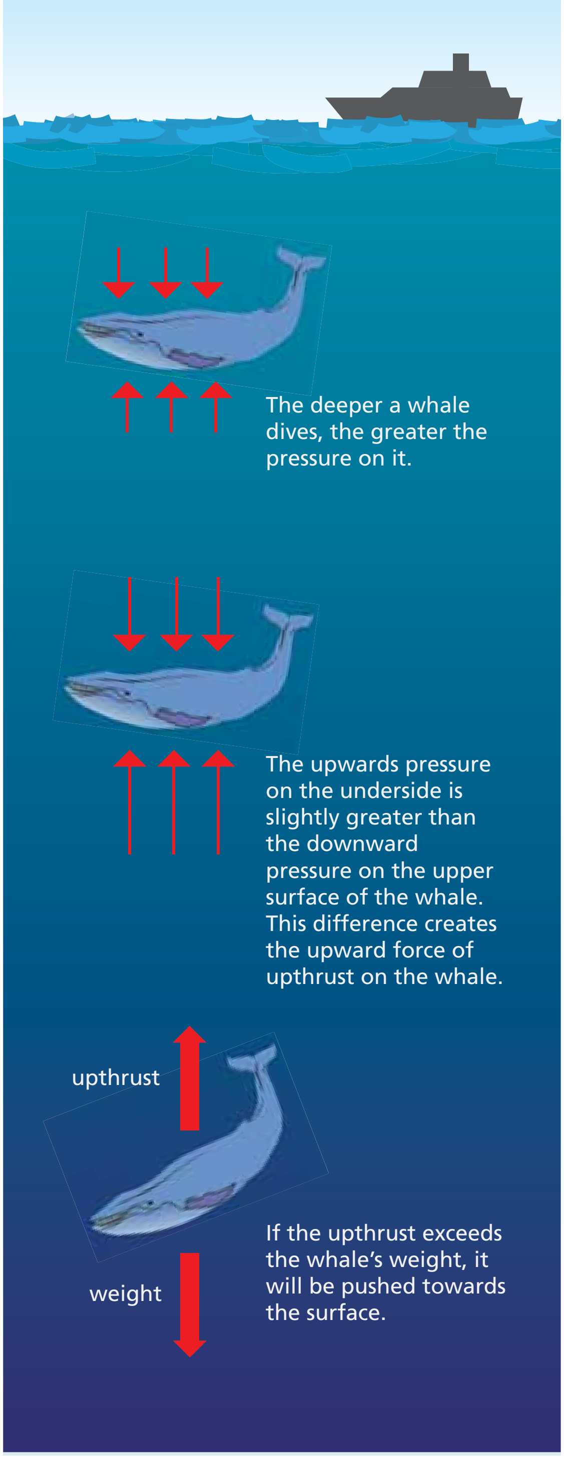
Caroline Wood

It's fascinating how diving mammals such as whales and dolphins can remain submerged for long periods of time, as they dive to depths of 2000 metres or more in search of their prey. As ***Caroline Wood*** *explains, several mechanisms have been discovered but we still don't fully understand how they do it.*

Experiments from the 1870s onwards have sought to determine the adaptations that allow some mammals to remain submerged for extended periods of time and at great depths. Starting with forced submersion experiments on dogs and seals, these investigations have become increasingly more complex as scientific equipment has advanced. Over time, these have given us insights into the physiological, biochemical and even behavioural mechanisms that allow prolonged breath-holding under water.

Humans are poorly adapted to surviving at depth – a submersible such as JAGO is designed to withstand the pressure at depths up to 400 m. Some whales dive to five times this depth.

Physics for whales



Key words

adaptation

aerobic respiration

pressure

mammals

Underwater, the pressure increases by about 1 atmosphere for every 10 m the whale descends. A whale that dives 2000 m experiences must withstand 200 times atmospheric.

Hold your breath

Why is it that whales and seals can hold their breath for so much longer than humans? Crucially, these animals have a physiology that is specifically equipped for lengthy submersion. Shallow divers, such as sea otters, have larger relative lung volumes (compared with non-diving mammals) and this helps provide a store of oxygen during a dive.

However, deep divers such as sperm whales tend to have small lung volumes. This is partly to avoid decompression sickness, known as 'the bends', a potentially lethal condition caused by the high pressures encountered during deeper dives. High pressure forces gases (especially nitrogen) to dissolve into the blood. If ascent occurs too quickly, bubbles can then form as the gases come out of solution, causing the bends. To reduce the risk of this, the lungs of a sperm whale collapse as it dives. This also helps in diving by reducing buoyancy. Re-enforcing cartilage bands on the bronchi help the lungs to withstand these shape changes, whilst **surfactant proteins** coating the alveoli air sacs stop them from sticking together during collapse.

Surfactants are compounds made of proteins and lipids that prevent the wet surfaces of the alveoli (air sacs in the lungs) from sticking together.

Sea otters are shallow divers and so do not show the same adaptations to deep diving as whales and dolphins.

Oxygen stores

Small lung volumes, however, mean that deep-diving mammals cannot use these as a store of oxygen during submersion. Instead, more oxygen is stored in the blood; this is achieved through both large blood volumes and increased blood haemoglobin (see Table 1). The muscles also have enriched oxygen stores due to a high **myoglobin** content; this gives the tissue a dark red colour.

Myoglobin is a protein related to haemoglobin which acts as a long-term store of oxygen in the heart and muscles.

Mammal (*=diver)	Haemoglobin (grams per 100 ml blood)	Blood volume (ml per kg of body weight)	Oxygen (ml per kg of body weight)
Human	16.0	80.0	16.0
Dog	14.8	86.0	18.7
Horse	11.1	62.0	13.3
Harbour Seal*	20.0	159.0	42.0
Elephant Seal*	20.7	207.0	56.9

Table 1 *Comparison of haemoglobin content, blood volume and oxygen reserves for non-diving and diving mammals.*

Larger diving mammals also benefit from having a higher proportion of inert, non-metabolic tissues such as bone and fat which do not need to be supplied with oxygen.

These fundamental adaptations help diving mammals to stay underwater for extended periods but they do not tell the full story. An estimate of the maximum submersion period, called the 'Aerobic Dive Limit' (ADL) can be calculated using the resting metabolic rate and the approximate mass of oxygen stored in the blood and muscle. This gives the length of time an animal can hold its breath before oxygen reserves run out and anaerobic respiration (and subsequent lactic acid build up) commence.

resting metabolic rate = volume of oxygen used per hour

Aerobic Dive Limit = volume of oxygen stored/metabolic rate

The surprising thing is that deep diving mammals can typically stay submerged for much longer than the ADL predicts. For instance, the ADL for the Bottlenose Dolphin is 36 minutes yet dives lasting over two hours have been recorded in nature. This shows that other changes must be occurring during the dive itself.

Bottlenose Dolphin

Controlling blood flow

In the 1930s and 40s, the distinguished comparative physiologists Laurence Irving and Per Scholander developed a model to explain how such extended dives could be achieved. Certain tissues, particularly the heart and brain, cannot tolerate hypoxia (an insufficient supply of oxygen); therefore, oxygen delivery to these tissues must continue until the animal surfaces. This means that other tissues, such as the muscles, must go without oxygen and use anaerobic metabolism during this time. Data showing heavy lactic acid accumulation following submersion in deep-divers supports this theory.

Oxygen delivery to the heart and brain is prioritised by selective narrowing of the arteries leading to other organs. This reduces blood flow (and hence oxygen delivery) to the muscles, kidneys, intestines, etc (see the box Angiograms below). These tissues have greater tolerance to hypoxia, with the muscles additionally having copious reserves of oxygen bound to myoglobin.

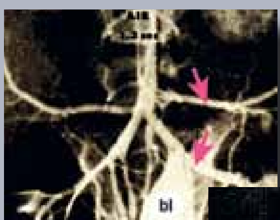
Reducing blood flow to certain areas, however, could cause a catastrophic reduction in blood pressure, preventing blood flow from being maintained. Therefore, other compensatory mechanisms are activated from the onset of the dive. These include a significant reduction in heart rate and hence cardiac output. This can occur to a dramatic extent – in seals the cardiac output may only be 10-20% of the pre-dive level. A reduced heart rate also decreases the workload of the heart itself, lowering the metabolic demand and prolonging oxygen delivery. This effect is not just restricted to diving specialists; the same response can be observed in humans if they submerge their face in cold water.

Angiograms

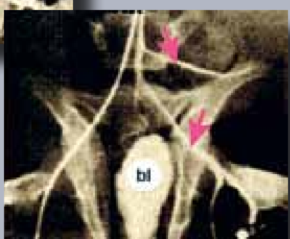
Angiograms of abdominal arteries of a harbour seal (*Phoca vitulina*) with the bladder marked (bl). At the surface (1), the arteries to the flanks (upper arrow) and hind flippers (lower arrow) are well supplied with blood. During the dive (2), these arteries become narrower, restricting blood supply to these areas.

An angiogram is an X-ray image which shows the diameter of blood vessels. It is produced by inserting a small tube (catheter) into an artery. A dye which absorbs X-rays is injected through the catheter and enters athe main circulation system, travelling in the blood vessels whilst X-ray images are taken. In the image, the blood vessels appear white because no X-rays have passed through them.

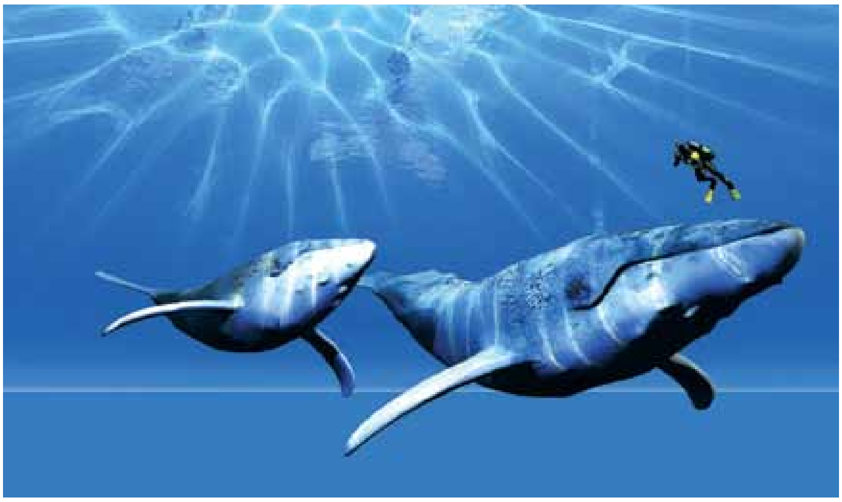
You can't make a seal dive with an X-ray machine strapped to it so, to perform angiograms in seals, the animal is restrained to a board and anaesthetised while the dye is injected. Diving is then simulated by wrapping the seal's head in a towel sufficiently to stop breathing and pouring water over the towel. Although this may seem highly unlike a natural diving scenario, the diving-related responses of bradycardia and artery vasoconstriction can be induced in this way. The seal recovers quickly afterwards.



1 at surface



2 at depth



Humpback whales make shallow dives so that they can approach their prey (krill and fish) from below.

Staying under

A high build up of lactic acid, caused by anaerobic respiration, would necessitate a long period at the surface for recovery following each dive. Extended surface intervals, however, are not typically observed in nature. Studies on female Northern Elephant Seals (*Mirounga angustirostris*), for instance, found that almost continuous deep diving was maintained over a 2 ½ month period. The mean dive rate was 2.5-3.3 dives per hour with the mean surface interval less than a minute long. Recent insights have provided some clues as to how the basic Irving-Scholander Model can be extended to explain this. Attaching video cameras to whales and seals has revealed that many species show a characteristic 'swim and glide' pattern of behaviour. Bursts of propulsion from the flukes or tail are followed by gliding, further reducing the metabolic cost of the dive.

A head for depths

Some species show unique specialisations, such as the Sperm Whale (*Physeter macrocephalus*). Much of the head cavity is filled with a spongy tissue containing a white waxy substance called spermaceti oil. The low melting point of the spermaceti oil allows the whale to manipulate the density through temperature regulation.

At the start of the dive, cold water is passed into the cavity, causing the wax to solidify. Wax contracts as it solidifies and so its density increases. This helps the whale to overcome buoyancy and so reduces the effort needed to dive.

On ascent, the arteries in the skin surrounding the cavity dilate (vasodilation), increasing blood flow. This raises the temperature and melts the wax, reducing its density.

Whether further advances in the methods and equipment used by comparative physiologists will reveal more species-specific adaptations, or mechanisms used by diving mammals in general, only time will tell.

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