Ultimate divers

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An extraordinary variety of mammals, birds, amphibians and reptiles are adapted to life in the oceans. Many of them spend their entire lives there without being able to breathe underwater. But just how do they exploit this hostile environment?

Whales, dolphins, marine turtles, seals and sea lions, penguins and many other species are heavily constrained by the necessity to periodically break the water surface in order to obtain oxygen. Their obligation to surface carries many disadvantages, including limiting time available to explore and forage, and increasing the risk of attack from predators. Yet the existence of all these species shows that they have successfully adapted to exploiting the aquatic environment. Of vital importance has been the evolution of physiological and biochemical adaptations that increase the amount of time these species can remain under water. Many of them have also adapted to exploit resources in particularly deep parts of the ocean. Not only does this require the ability to function without ventilating the lungs for long periods but it also necessitates tolerance to very high hydrostatic pressures.

Inevitably, some air-breathing, diving species are capable of performing dives of much longer duration or to much greater depths than other species, and some achieve astonishing feats of underwater endurance. In a recent article in *Biologist,* Bill Milsom (2000) described many of the physiological and biochemical adaptations of air-breathing divers that enable them to prolong their time beneath the surface. In this article, I debate which species are the world's elite divers, in terms of depth of dive and duration of dive. Present understanding of the adaptations that allow such extreme diving behaviour in these particular animals is also discussed.

Title image: Sperm whale (Physeter catodon) tail (F Nicklin)

Deep divers

So which air-breathing divers are able to travel deepest into ocean waters? Emperor penguins are famous for their deep diving ability since they are able to dive deeper than any other bird species and have been recorded foraging at depths of up to 500 metres. However, marine mammals are generally deeper divers than marine birds and many of the large pinniped species (seals, sea lions and walruses) frequently dive to several hundred metres. Northern elephant seal bulls, the largest and deepest diving of all the pinnipeds, have been recorded at depths of around 1000 m. The cetaceans (dolphins, porpoises and whales) vary considerably in terms of maximum diving depth. However, many of the larger whale species are known to dive very deeply, often up to around 1000 m. The apparent depth barrier of one kilometre for deep diving pinniped and cetacean species may well be related to the depth that sunlight penetrates the ocean. Beyond 1000 m depth, the ocean environment is in complete darkness making foraging impossible for visual predators.

Only one air-breathing species has been recorded diving noticeably deeper than one kilometre, and indeed to depths far in excess of any other air-breathing diver (Figure 1).

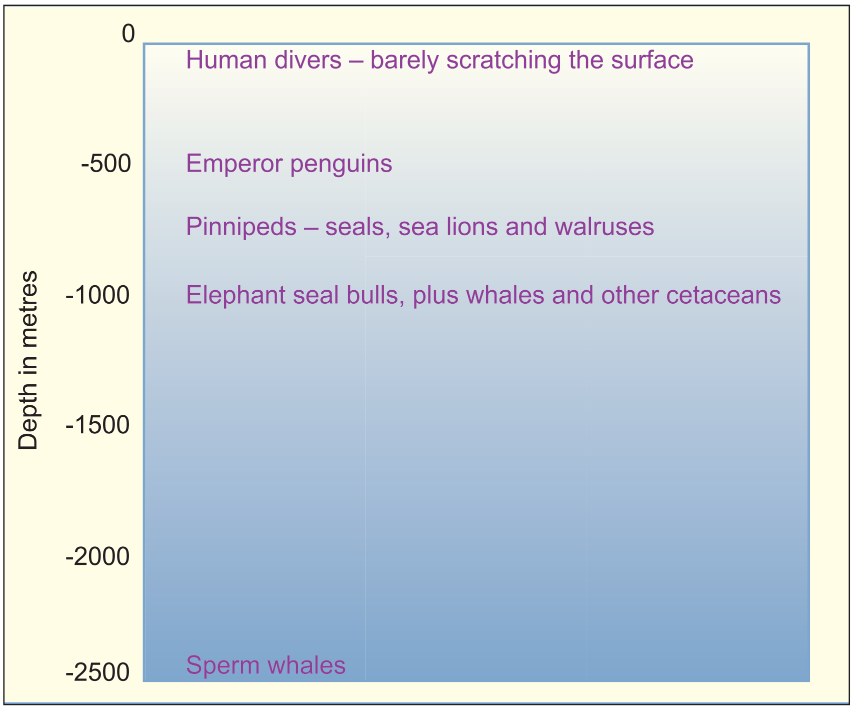

Figure 1. Depths to which mammals and birds dive

The Sperm whale is a huge animal, up to 18.5 m in length and weighing up to 50 tonnes. The deepest recorded dive is 2.25 km (1.4 miles) although the stomach contents of one individual included a species of dogfish found only on the seafloor, suggesting that they may dive to over three kilometres. Their ability to dive to incredible depths is not only reliant upon adaptations to tolerate immense hydrostatic pressures but also upon their ability to maintain a neutral buoyancy in the water at any depth.

Their head accounts for one quarter of their length and one third of their body weight. It contains massive organs filled with waxes, known as spermaceti oils. The density of these oils can be altered, changing the whale's buoyancy, so that it can hang motionless within the water, locating its prey while using up very little oxygen. The wax organs have a second function: they act as an acoustic lens for focusing sound by refraction through the concentric layers of wax. This allows the whale to hunt in partial or complete darkness by using echolocation. Echolocation enables the size, direction and distance of prey to be determined. This sense is highly efficient and blind Sperm whales have been captured in perfect health with food in their stomachs. Their most common prey are giant squid weighing up to 300 kg and bottom-dwelling sharks. Sperm whales also consume cuttlefish and octopuses. They spend 90% of their time in deep water, only resting at the surface intermittently.

Adaptations for deep diving

Although many air-breathing divers exhale before they submerge, they still retain some air in their lungs and often in their respiratory tracts, in order to supply oxygen to their bodies during a dive. The problems that deep divers must overcome develop as the animal propels itself deeper into the water column. This is due to compression of these air-filled cavities.

Mechanical effects

As humans descend through the water column, even short vertical descents cause large volumes of blood to shift into the thoracic cavity. This ensures that pressure in the lungs remains at equilibrium with the increasing external pressure. Compression of the lung is thus seriously depth limiting in humans. However, whales appear not to be restricted in this way. It has been conjectured that their lungs and chests are designed to collapse as pressure increases with depth. The diaphragm is set obliquely and as the abdominal viscera presses on one side, the lungs crumple on the other. The lungs collapse to a fraction of their original size and force the air into the windpipe and the extensive nasal passages.

Increased hydrostatic pressure also causes 'high pressure neurological syndrome', which is exhibited as tremors and eventually a complete seizure in a number of terrestrial vertebrates, including man. It has been presumed that deep divers are not affected since they would otherwise be unsuccessful as predators. Only very recently has an understanding developed concerning some of the adaptations in such species to combat this phenomenon. Studies on toothed whales suggest that they have an increased inhibitory feedback available in their central nervous system, which provides protection against the hyperexcitability of nerves that is induced by high pressure at extreme depths.

Nitrogen tensions

Human divers enter a state of stupor and then a terminal loss of consciousness if they dive too deeply for too long. During descent, nitrogen partial pressures increase in the lungs and nitrogen is absorbed into the arteries and tissues. Nitrogen within the tissues can cause an anaesthetic 'nitrogen narcosis', leading to reduced mental and motor capabilities, euphoria, coma and, ultimately, death. These symptoms are due to the toxic effect of high nitrogen pressure on nerve conduction.

After periods of high pressure, decompression causes the gases in the body to expand. Oxygen is quickly absorbed but, if decompression is too rapid, rising nitrogen concentrations in the arteries can cause nitrogen bubbles to form in the bloodstream and death may ensue (in human divers this condition is known as 'The Bends'). Bubbles develop in the capillaries of laboratory animals at nitrogen concentrations around 330 kPa. Nitrogen tensions in the cetaceans seem to remain lower than this. Nitrogen concentrations are probably limited before tensions in the blood and tissues reach this critical level by total lung collapse as the cetacean dives, preventing further nitrogen absorption during the dive. Some of the air from the lungs is forced into the windpipes where it cannot diffuse into the haemoglobin and myoglobin. Similarly, air pushed into the large nasal cavities cannot diffuse further due to the thick membrane lining.

Latent hypoxia

Deep dives by humans expose them to the risk of brain anoxia. This refers to a lack of oxygen within the brain tissues, which can cause unconsciousness. At depth, high partial pressures of oxygen within the lungs can cause rapid diffusion into the bloodstream, raising the pressure of arterial oxygen while lowering the pressure of oxygen in the lungs. During ascent from depth, lung expansion causes a further decrease in lung oxygen tension, which could crucially drop to a level lower than that of the venous blood causing oxygen to diffuse into the lungs. In turn, this can cause arterial oxygen pressure to decline to intolerable levels within the brain. This reversal in oxygen gradient will occur during the diver's ascent through the upper 10 m of the water column. This is where the greatest expansion of the lung occurs as it doubles in volume.

The adaptations of deep divers to cope with this hazard are poorly understood. It is likely that many species counteract this risk through the reduction of lung-blood gas exchange rates at depth. Again, cetaceans would achieve this through lung collapse, nullifying the problem. Furthermore, measurements made in some mammalian divers have shown them to have much lower arterial partial pressures of oxygen in their brains than terrestrial animals, enabling them to cope with low oxygen tensions during ascent.

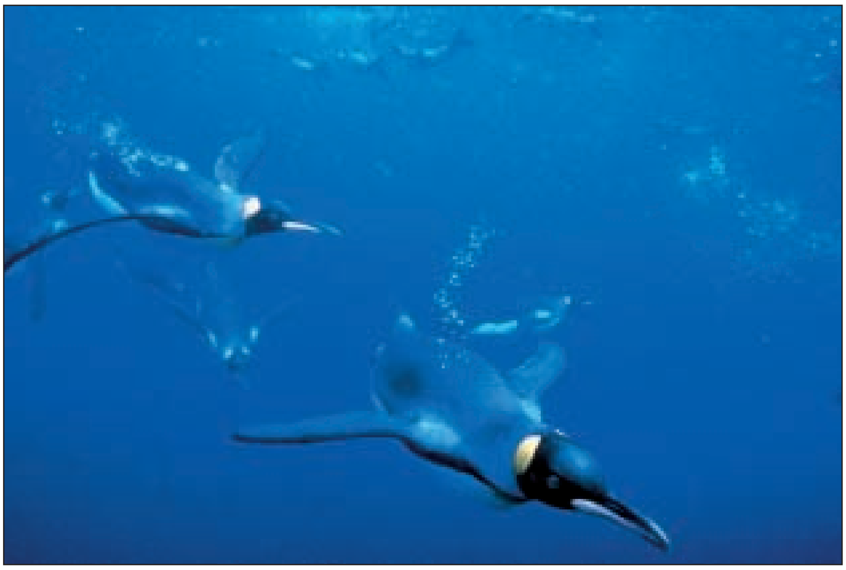

Figure 2. King penguin (Aptenodytes patagonicus) underwater (T DeRoy) © Minden Pictures/FLPA

Long duration dives

For many taxonomic groups of air-breathing divers, positive correlations exist between depth and duration of dives, since dives to greater depths require more travelling time. Nevertheless, certain species may spend considerable amounts of time submerged without descending to particularly great depths. This is because their prey inhabits the upper level of the pelagic zone, or they are only physiologically capable of withstanding relatively low hydrostatic pressures. Therefore, longer dives do not necessarily rely on the ability to dive deeply, but do require the diver to remain active underwater despite not having the opportunity to restock their oxygen stores. (Certain amphibians and reptiles can stay underwater for exceptionally long periods of time; Box 1.)

Size advantage

The two overriding factors influencing how long an animal can dive for are considered to be their oxygen storage capacity and their efficiency at consuming oxygen. Allometric studies have demonstrated positive trends between body size and dive duration across many taxa of air breathing divers. Larger diving species have a body mass advantage because, as body size increases, blood volume increases more rapidly than resting metabolic rate. Therefore, larger divers store a greater supply of oxygen, and metabolise that oxygen more slowly, in relation to their body mass. Sperm whales are not only the deepest divers but also one of the longest divers, taking advantage of their great mass. They spend long periods travelling to and from their deep feeding sites as well as considerable time locating prey. Sperm whales have additional adaptations that enable them to dive for longer than similarly sized cetaceans; for instance, they have significantly higher myoglobin stores than baleen whales, allowing them to store more oxygen in their muscles.

However, the majority of larger species, including cetaceans, do not tend to remain submerged for very long relative to their body mass. The pantropical spotted dolphin, weighing about the same as a man, averages only half a minute underwater. This may be due to the relatively low myoglobin concentrations in their skeletal muscles. Furthermore, some smaller species regularly endure submergence for incredibly long periods of time when considering their low oxygen storage capacities and high metabolic rates relative to their body mass. This suggests that they possess particularly specialised behavioural and/or physiological adaptations.

Box 1. Inactive submergence

Certain reptiles and amphibians can stay submerged for weeks at a time at low temperatures if they remain inactive, such as the snapping turtle and the green turtle. During cooler seasons, these animals can reduce their metabolic rates to well below their normal resting levels. The oxygen concentration of the water also affects their submergence times since they are capable of limited gaseous exchange across their skin. Reptiles other than turtles do not tend to voluntarily dive for longer than an hour in the laboratory; for example, the Nile monitor lizard submerges for around 15 minutes at 25ºC. The elephant-trunk snake dives for up to 30 minutes during night time foraging bouts. However, field observations have recorded startled Iguana remaining submerged and inactive for over four hours at 25ºC. Perhaps the most impressive recordings are from observations of the Lake Titicaca frog, which lives on the bottom of the lake at an altitude of 3800 m and at an average temperature of 10ºC. They have never been observed surfacing in their natural environment but do so in laboratory conditions if the partial pressure of oxygen is sufficiently reduced.

Endurance divers

While many aquatic birds are considered relatively poor divers (such as tufted ducks, which weigh 0.8 kg and only average dives of 12 seconds) penguin species demonstrate more impressive breath-holding capabilities. The Emperor penguin (Figure 2), at only 30 kg, can dive for well over 10 minutes. However, when comparing body size against dive duration, the family of divers that remain submerged the longest are the Alcidae, a taxon of small Atlantic seabirds including guillemots and razorbills.

The champion endurance diver, according to current data, is the Black guillemot (Figure 3). They weigh less than 0.5 kg and can travel through the water column for over two minutes. The Black guillemot is ubiquitous species across the North Atlantic, breeding in all marine waters north of the cool subtropical zone, including the British Isles. There they breed in small groups or pairs

Figure 3. Black guillemot (Cepphus grylle) calling. © S Jonasson/FLPA – images of nature.

along rocky coasts, mainly in Scotland and Ireland. They have a wider prey spectrum than the other alcid species that includes fish, jellyfish, sponges and crustaceans. Their diet during the breeding season reflects their coastal habitat: they feed on animals found on the sea bottom in shallow water. However, during the rest of the year they feed further out to sea in deeper waters, often around icebergs or pack ice.

So, what makes alcids such effective divers? Unfortunately, answers to this question are unclear because, in contrast to the Sperm whale, their diving prowess is rather paradoxical. Since alcids are adapted for flying, they are not particularly specialised divers. They have not been able to increase their body density, and so reduce their buoyancy to the extent of flightless diving birds, such as penguins. Their energy demands in shallow waters are therefore higher.

Furthermore, alcids do not seem to possess unique physiological or biochemical adaptations to enable them to stay underwater for longer. For their size, they have similar oxygen storing capacities to other marine birds and their metabolic rates are also comparable. Nevertheless, alcids have been recorded regularly diving for longer periods than expected according to their oxygen storage capacity and the rate at which they utilise that oxygen while diving.

Behavioural adaptations in alcids

Alcids may be able to use their oxygen stores more efficiently by getting deep into the water column quickly. Unlike the majority of diving species, alcids have a distinct advantage when propelling themselves downwards through the water. Rather than commencing the dive from a 'standing start' on the water surface, they take advantage of their flying capability and plummet towards the water, which provides them with considerable momentum as they hit the surface. Their streamlined shape means that they efficiently use this momentum to descend a considerable distance through the water. By the time they start to utilise their oxygen stores to continue descending by wing propulsion, they have already reached depths where the hydrostatic pressure has compressed their internal air cavities and reduced their buoyancy. This results in negligible energy, and oxygen, being used to maintain their level in the water column; the same trick employed by the Sperm whale but by very different means. A further adaptation is that alcids regularly consume all of their oxygen supplies underwater and continue to remain submerged by employing anaerobic metabolic pathways (Box 2). For such species, predictions of dive duration based on oxygen stores and metabolic rate will never fully account for their diving endurance.

Concluding remarks

The record for the deepest human dive is 73 m, where descent and ascent was aided by a rope. The longest breath-hold is seven minutes and 38 seconds, although this record only requires that the face is immersed in water and is by no means comparable to an active dive. While these feats are impressive, they serve to underline the incredible degree of specialism that many aquatic air-breathing divers have to their water environments. Just as extraordinary is the vast array of these air-breathing divers, representing the evolution of such an enormous diversity of adaptive solutions for exploiting the oceans. Consequently, the history of investigation of diving animals is extensive but, even today, our understanding of these expert divers is limited and their appeal is unabated. Furthermore, recent misuse of the ocean's resources has made preservation of these species a major stimulus for future research. Ongoing investigation will help to explain the poorly understood physiological adaptations to depth for diving. Most importantly, in light of current environmental concerns, it will develop our appreciation of how diving species interact with their environments, both aquatic and terrestrial, so that we can ensure their continued and enchanting presence in the world's oceans.

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Box 2. Optimal foraging

Dives that are long enough to incorporate significant periods of anaerobic metabolism are energetically less efficient than aerobic dives. For this reason, many species always surface before their oxygen stores have run out. However, for some underwater foragers, longer duration dives involving a significant element of anaerobic metabolism are likely to be optimal under certain circumstances. When they do surface, they minimise this phase of the dive cycle by tolerating lactic acid build up in their muscles rather than metabolising it. This allows them to concentrate simply on resaturating their lungs and blood with oxygen. Alcids feed on shoaling fish that are mobile and camouflaged and so difficult to locate initially. When they find a school, it is important that they maintain contact because resurfacing would allow their prey to escape. Alcids often feed on fish that inhabit deep waters, so maintaining pursuit will sometimes require particularly lengthy and deep dives. Such dives are likely to involve anaerobic metabolism, along with the ability to tolerate the presence of considerable lactic acid, while remaining highly active. Bouts of anaerobic dives cannot continue indefinitely because this form of respiration causes lactate fermentation in the muscle cells, which produces fatigue if it is allowed to accumulate. As such, this diving strategy is usually terminated by an extended surface period enabling removal of the lactate.

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Website

www.acsonline.org/links.htm

The American Cetacean Society website allows access to a broad array of information on marine mammals in general, cetaceans specifically, and also an interesting number of sites on cetacean evolution, including Sperm whales in detail.

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