Diving Physiology of Marine Vertebrates

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Air-breathing marine vertebrates that dive to find food deal with two fundamental problems, the effects of pressure at depth, and the need to actively forage while breathholding. Adaptations to diving can be divided into two categories, those that are associated with adaptations to pressure, and those associated with breath-hold diving. Adaptations to pressure have to deal with the mechanical effects of pressure and the increased solubility of gas at depth. Adaptations to breath-hold diving centre around modifications in metabolism, blood flow and an increased oxygen storage capacity.

Introduction

Air-breathing marine vertebrates that have secondarily re-turned to the ocean include a diverse group of animals that include sea snakes, sea turtles, the marine iguana, marine crocodiles, pinnipeds (sea lions, fur seals and seals), cetaceans (whales and dolphins), sea otters, manatees and dugongs (sea cows). The majority of diving vertebrates make shallow short dives. For example, sea snakes, croc-odiles and marine iguanas are limited to diving in nearshore waters and rarely make dives deeper than 10 m (33 ft). However, a few of these groups are capable of making quite deep or long dives. For example, emperor penguins regu-larly make dives to 400–500 m. These dives usually last 4–5 min, but commonly include dives of 8–12 min with a maximum dive of 22 min. Elephant seals dive continuously, day and night, for periods at sea lasting 2–8 months (**Figure 1**). They spend 90% of the time at sea submerged, averaging 20 min per dive (with maximum dive duration's of up to 2 hr) and spend less than 3 min at the surface between dives. They routinely feed at depths of between 300 and 600 m, occasionally diving deeper than 1600 m. Re-cently, beaked whales, *Ziphius cavirostris* and *Mesoplodon densirostris* have been found to routinely forage at depths far greater than any other air-breathing vertebrate. They routinely foraged to 1070 and 835 m and stayed submerged for an average of 58 and 47 min with a maximum depth and duration of 1888 m and 85 min. **See also**: Vertebrate Respiration and Circulation in Extreme Conditions

Regardless of their taxonomic origin, all of these animals face the same fundamental constraints, that of increased pressure associated with depth, and the lack of oxygen as-sociated with breath hold diving while submerged. Adap-tations to pressure address the direct or mechanical effects of pressure, and the problems associated with the increased solubility of gas (N_2 and O_2) as the pressure increases, while adaptations to breath-hold diving centre around modifications in metabolism, blood flow and oxygen stor-age capability.
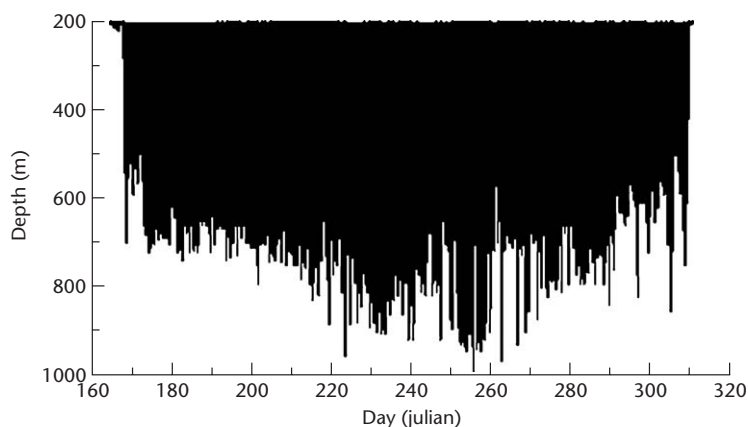

Figure 1 Diving pattern of an adult northern elephant seal female.

Adaptations to Pressure

All air-breathing vertebrates must deal with the direct effect of pressure that is associated with the volume change (collapse) of air-filled spaces as the animal dives. Changes in air volume are most dramatic in the first 10 m of the water column, and are relevant to all diving vertebrates. In contrast, the direct effect of pressure on cellular processes (nervous tissue, organs, membranes etc.) is only an issue at relatively deep depths (500–1000 m), and therefore only a problem for deep-diving marine mammals such as elephant seals, sperm whales and beaked whales. The changes in volume associated with depth follows Boyle's Law:

$$P_1 V_1 = P_2 V_2$$

Boyle's Law states that as the pressure of a closed system increases, then the volume of the system declines in direct proportion. For example, take an animal with a 10-L lung at the surface where the ambient pressure is 1 atm and that animal dives to a depth of 10 m (33 ft). The pressure has increased to 2 atm (1 atm for every 10 m of water depth), and the lung now has a 5 L volume or 1/2 as large as it was on the surface. If the animal dives to 100 m depth, the total pressure is 11 atm (1 atm for every 10 m plus 1 atm at the surface) or a volume 1/11 of its original size. At some point the air volume becomes so small that the lung collapses and ceases to function. A similar problem occurs with the air cavity associated with the middle ear, a condition called middle ear squeeze. **See also**: Vertebrate Respiration and Circulation in Extreme Conditions

Lung collapse

Marine mammals solve the problems associated with lung collapse and middle ear squeeze by specialized adaptations in the thoracic cavity and in the middle ear. Most marine mammals have compliant chest walls that allow for complete lung collapse and possess specialized structures in their lungs that allow the alveoli to collapse first, followed by the terminal airways (**Figure 2**). These structures may also aid in reinflation of the lung. Recent studies show that marine mammals have specialized surfactants in their lungs that aid in postdive reinflation of the lung. With respect to middle ear squeeze, marine mammals have specialized cavernous sinuses in the middle ear that presumably engorge with blood as the animal dives and thus fills the air space.

HPNS

The other direct effect of pressure is on the tissues themselves. The first effect of pressure is exhibited by the nervous system, and shows up in humans as tremors at 150 m, and convulsions at 500 m. This is referred to as high pressure nervous syndrome or HPNS. The great majority of marine mammals and seabirds do not dive deep enough to experience HPNS. However, deep-diving elephant seals, sperm whales and beaked whales that routinely dive to depths between 500 and 1000 m should be susceptible to HPNS. While it is hard to imagine a seal or a whale routinely diving to these depths and experiencing HPNS, there are no data on whether these animals do encounter HPNS, and if so how they tolerate it or avoid it.

Diseases associated with gases at pressure

At high partial pressures both N_2 and O_2 become toxic. Increased concentrations of N_2 causes a narcotic effect, resulting in euphoria and delusions (nitrogen narcosis) in humans. Oxygen is toxic at partial pressures greater than 1 atm and can cause blackout and death. The other problem associated with increased pressure is that body tissues
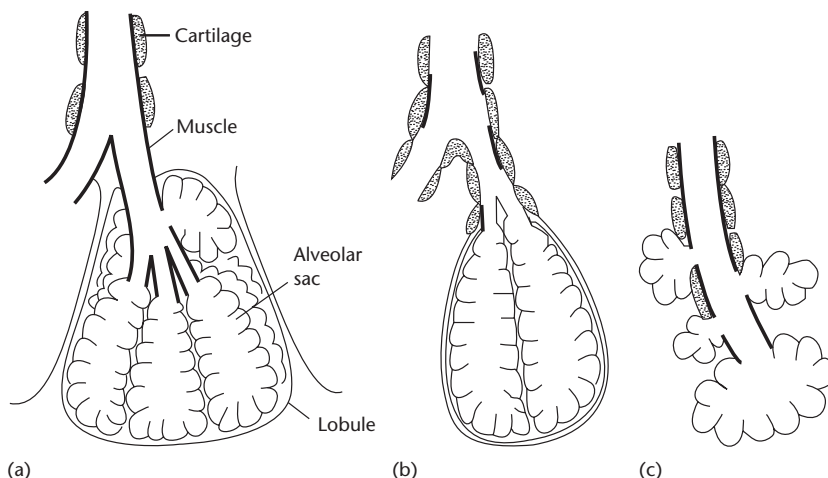
Figure 2 Diagram of the structure of the alveoli and associated structure in (a) a true seal, (b) a sea lion, (c) a walrus. From Kooyman GL (1973) Respiratory adaptations in marine animals. *American Zoologist* **13**: 457–468.

absorb greater amounts of gases (N_2 and O_2) at higher pressures. As the absolute pressure of the gas mixture increases, the relative pressure of the various gases also increases. In turn, the solubility of gas in the tissues increases as pressure increases, resulting in more gas being absorbed by the tissues. At the surface, 1 atm of air is composed of N_2 and O_2, with relative partial pressures of 0.79 atm for N_2 (79% of 1 atm) and 0.21 atm for O_2. At 100 m, where the absolute pressure is 11 atm, the partial pressure of N_2 would be 8.69 atm and 2.31 atm of O_2. **See also**: Neural Development: bHLH Genes

Higher gas solubility at depth means that the animal will absorb more gas until the tissue becomes saturated at that pressure. When the animal returns to the surface, the solubility of the gas in the tissue is lower and it now flows out of the tissue into the blood. This is especially problematic for human divers who breathe air from a scuba tank. As they descend, the pressure increases and they inhale air at greater pressure. Their tissues absorb gas that is now more soluble and dissolved gas accumulates in the tissue. If the diver returns to the surface without taking sufficient time to allow the gas to slowly come out of the tissues (decompress), the gas will come out of solution and form bubbles. This is called decompression sickness, the bends or caisson disease.

Marine mammals have an advantage in that, unlike human divers, they exclusively breath-hold dive. That is they carry only a limited amount of air in their lungs during a given dive. Some deep-diving marine mammals appear to avoid problems associated with tissue N_2 accumulation by allowing their lungs to collapse during the initial period of the dive. As the lung collapses, air is expressed into the large bronchioles and trachea where gas uptake cannot occur. Given that N_2 and O_2 tensions in the blood remain relatively low during the dive, nitrogen narcosis, decompression sickness and oxygen toxicity are thought to be avoided. While this appears to prevent decompression sickness in animals that undergo lung collapse, there are many species of diving vertebrates such as penguins, sea lions and fur seals that make many repetitive dives on a full lung. It is unclear how these animals avoid the bends as they make repeated dives to significant depths over a period of many hours or even days. If, during these dives, the animals spend more time under water than at the surface, it is possible they accumulate sufficient N_2 in their tissues to cause decompression sickness. Symptoms consistent with decompression sickness have been reported in human pearl divers undergoing prolonged repetitive breath-hold dives. To date, only one study has examined tissue nitrogen levels in a repetitively diving animal, the bottlenose dolphin *Tursiops truncatus*. While this study found relatively high levels of N_2 in muscle tissue, it was unclear whether the levels of muscle N_2 were sufficiently high as to cause bubble formation. Further, the researchers were not able to determine whether there was a mechanism that kept the N_2 in the tissue, or whether there was some capacity to tolerate N_2 bubbles if they formed.

Interestingly, recent histological observations of bone necrosis in sperm whales are consistent with symptoms associated with decompression sickness. This suggests that sperm whales, and possibly other toothed whales, suffer from periodic decompression sickness in the wild. Similar observations of fossil mosasaurs and plesiosaurs also suggest that these ancient diving reptiles had difficulty avoiding decompression sickness. This is of more than academic interest, as there has been considerable concern whether diving mammals are more susceptible to the bends when they are exposed to military sonars. The issue is whether sonar stimulates bubble formation and/or elicits aberrant diving behaviour that results in acute and severe decompression sickness.

Diving metabolism

Early work showed that when a captive mammal or bird was forced to dive, there was an overall reduction in metabolism. This reduced metabolism or hypometabolism was associated with an increased reliance on anaerobic (without oxygen) metabolism as indicated by a postdive release of lactic acid (**Figure 3**). The advantage of anaerobic metabolism is that adenosine triphosphate (ATP) (energy) can be produced in the absence of oxygen. However, this comes at a cost, as only two ATP are produced per molecule of glucose when lactic acid is the end product of glycolysis. In contrast, aerobic (with oxygen) metabolism allows the production of 38 ATP. This is because aerobic metabolism allows glucose to be fully oxidized to CO_2 and H_2O. The advantage of anaerobic metabolism is that ATP can be produced in the absence of oxygen, but the disadvantage is that only 1/19 as much energy is produced. Furthermore, lactic acid is toxic, and the body can only tolerate a limited amount of it before tissue damage occurs. Some diving animals have greater buffering capacity in their muscles that provides a higher tolerance to lactate acid. These animals also have higher concentrations of key glycolytic enzymes such as lactate dehydrogenase (LDH) that enhance the ability to process lactic acid. A greater glycolytic capacity may also be associated with greater tolerance to hypoxia. For example, harbour seals hearts are capable of withstanding reductions in the coronary blood flow that would cause a heart attack and damage to the heart of a dog or human. **See also**: Adenosine Triphosphate; Energy Cycle in Vertebrates; Vertebrate Respiration and Circulation in Extreme Conditions

Redistribution of blood flow

The dive response is also associated with a reduction in heart rate or bradycardia. As the heart rate declines so does cardiac output, and overall blood flow to the body is reduced. To keep blood pressure constant, peripheral resistance increases and blood is shunted primarily to the heart,
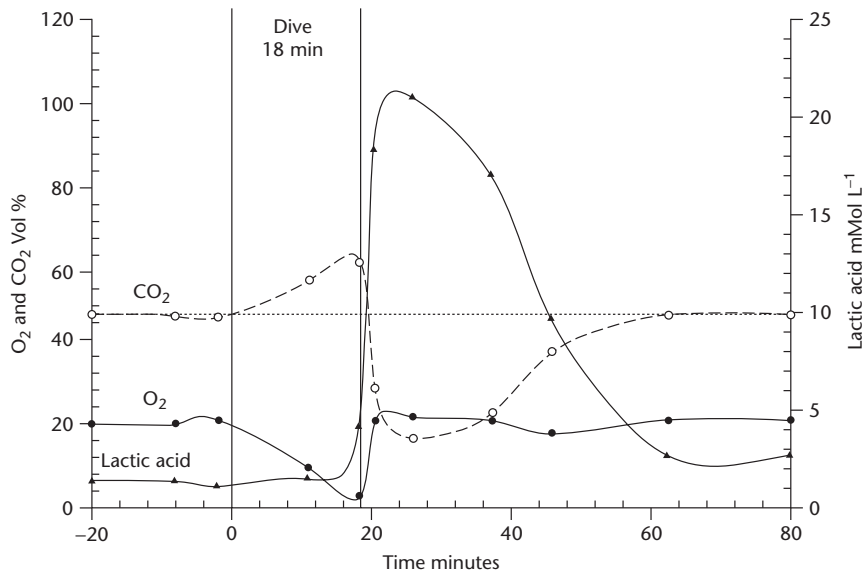
Figure 3 The concentration of O_2, CO_2 (left hand side) and lactate (right hand side) in the arterial blood of a grey seal, before, during and after an 18 min forced laboratory dive. From Scholander PF (1940) Experimental investigation on the respiratory function in diving mammals and birds. *Hvalradets Skrifter* **22**: 1–131.

lung and brain, with little or no blood flowing to the peripheral tissues. This in turn results in an overall reduction in metabolism, as the work of many organs is reduced (particularly the kidney and liver). A novel adaptation to keep blood pressure while the heart rate is reduced is the highly elastic nature of the aorta in some diving mammals. The aorta of true seals is highly compliant (elastic) and stores some of the energy with each heartbeat and releases it over the intervening period, thus keeping the blood pressure constant smoothing out an highly otherwise pulsatile blood. The almost complete redistribution of blood flow to the heart, lung and brain was confirmed in a study that used microspheres. In this study, small radio-labelled microspheres were injected into the blood of a seal breathing at the surface and compared to a seal which had microspheres injected while it was in a forced dive. The tiny microspheres accumulate in those tissues that have the greatest blood flow. Differences in the rate of accumulation are indicative of changes in blood flow to specific tissues where the microspheres concentration is measured. **See also**: Circulation in Vertebrates; Respiration and Circulation in Vertebrates: Overview

An initially confusing observation was that haematocrit of diving mammals increased during a dive. The ratio or percentage of red blood cells for a given volume of blood is called the haematocrit. A higher haematocrit means more red blood cells and thus more oxygen, however, it was not clear where the red blood cells were coming from. One suggestion was that they were released by the spleen, the other was that they came from the hepatic sinus. It is important to note that, compared to terrestrial animals, diving mammals have larger spleens and that the hepatic sinus of seals has a large diverticulation of the vena cava that can also hold significant amounts of blood. This problem was resolved when elephant seals were trained to dive while in a magnetic resonance imaging system. It was observed that during a dive the seal's haematocrit increased from 57 to 63, while the spleen volume decreased from 3141 to 513 mL. Further, the decrease in spleen volume was associated with an increased volume in the hepatic sinus. This study indicates that while breathing at the surface, a seal sequesters red blood cells in the spleen, however, when the seal dives the spleen contracts, pushing the red cells into the circulation. These circulated red cells also appear in the hepatic sinus, where they are more readily available to circulate. This is advantageous because when the haematocrit is high (generally above 55%) blood is more viscous and is energetically more expensive to pump. Therefore, when the seal is breathing at the surface, it can maintain a haematocrit that is optimum for moving blood rapidly through the body, but when problems associated with viscosity are not as important as maximum oxygen storage ability, red cells are released from the spleen into the circulation.

Oxygen stores

To increase their ability to stay submerged, diving animals have increased the amount of oxygen stored in their internal tissues (**Figure 4**). This can be thought of as an 'internal scuba tank' and is composed of three primary
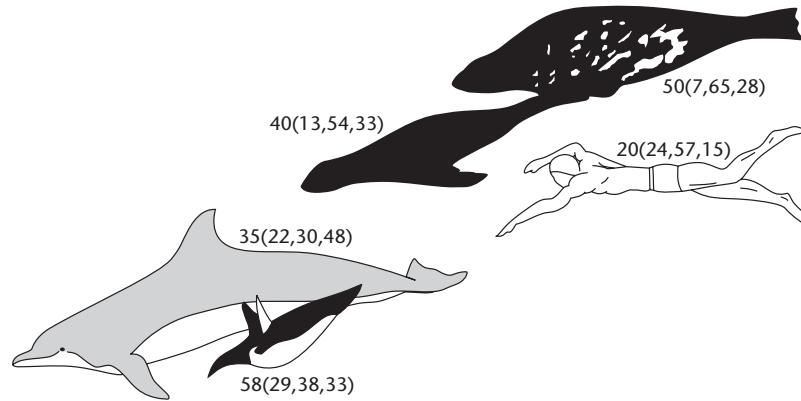
Figure 4 The oxygen stores of dolphins, sea lions and fur seals, true seals, humans and penguins are provided in mL O_2 per kg body mass. The numbers in parenthesis are the relative contribution of O_2 stored in the lung, blood and muscle. From Kooyman GL (1989) *Diverse Divers: Physiology and Behaviour.* Berlin: Springer.

compartments, the O_2 contained in the lung, muscle and blood. The muscle and blood of diving vertebrates have greater concentrations of the oxygen-carrying pigments, haemoglobin and myoglobin. Myoglobin is an oxygen-binding pigment that facilitates oxygen transport into and storage of oxygen in the muscle. The concentration of myoglobin in the locomotor muscles of diving vertebrates is 10–30 times greater than in their terrestrial relatives. Haemoglobin is the oxygen-carrying pigment in red blood cells and is increased by having both a larger amount of blood and a greater proportion of red blood cells in the blood. The haematocrit in humans varies between 41–50% in males and 36–44% for females. In contrast, the haematocrit of diving mammals varies across species, but ranges between 50 and 68%. Similarly, the blood volume of diving mammals is also greater than terrestrial animals. For example, in humans 7% of the body mass is blood, while the blood volume of diving mammals ranges from 10 to 20% depending on the species. The highest values belong to the longer, deeper diving mammals like elephant seals and sperm whales. **See also**: Respiration and Circulation in Vertebrates: Overview

ADL and the physiology of freely diving animals

Early studies of force-dived animals showed a profound bradycardia, with heart rates dropping from 140 to less than 10 beats per minute. However, when the same seal was asked to voluntarily dive, the heart rate dropped from 140 to only 40 beats per minute. This showed that the dive response was graded and could be managed as appropriate to the circumstances in which the animal found itself. Although this pioneering work provided insight into the maximum physiological response of a diving mammal, its relevance to the natural setting was unclear. A major breakthrough in the study of diving physiology came with

studies carried out with freely diving Weddell seals, *Leptonychotes weddelli*, where animals could be studied freely diving from an isolated hole in the ice. One of the first experiments examined heart rate and dive response in freely ranging dives. This work confirmed earlier laboratory studies that animals had considerable control over their heart rate and could modify it as appropriate to the needs of a specific dive. Further, changes in heart rate occurred at the beginning of the dive indicating that the seal knew ahead of time what type of dive it was about to make.

Although this work suggested that our understanding of the physiology of diving mammals was incomplete, it was not until investigators were able to monitor blood lactic acid levels before and after a dive that they were able to show that Weddell seals dove aerobically during the majority of their dives. This work showed that lactic acid levels remained constant for dives up to 20 min and thereafter rapidly increased with increasing dive durations (**Figure 5**). They concluded that Weddell seals can dive aerobically for up to 20 min. This work defined the maximum time an animal could remain submerged without utilizing anaerobic metabolism as the aerobic dive limit (ADL) and was calculated as ADL (min) = total oxygen store (mL O_2)/ diving metabolic rate (mL $O_2 \, min^{-1}$). An important observation was that when Weddell seals exceeded the aerobic threshold, the postdive surface interval increased disproportionately relative to dive duration. A disproportionately greater surface interval was needed to clear the lactic acid after dives that exceeded the ADL. Whereas there was no difference in postdive surface in dives less than the 20 min ADL. One of the disadvantages of using anaerobic metabolism is that while a diver may increase the duration of a single dive, the total accumulated time spent under water is less. This is because the animal spends proportionately more time at the surface clearing lactic acid. While Weddell seals offer a truly exceptional system to study diving physiology, it only represents a single species in a very unusual situation. The only other diving animal
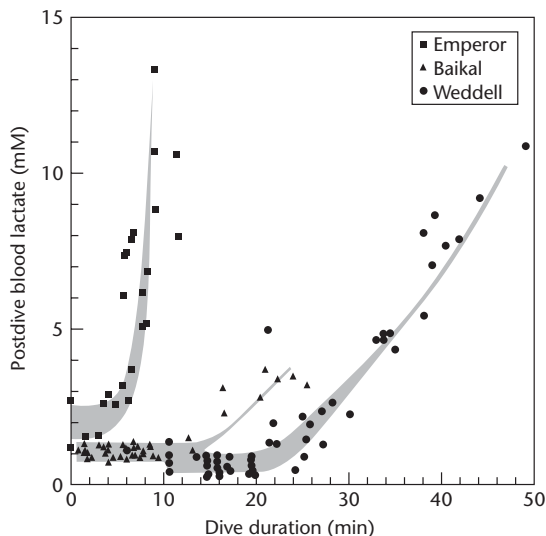
Figure 5 Blood lactate levels for an Emperor Penguin, a Baikal seal and a Weddell seal as a function of dives of different duration. The point where the lactate level starts to increase is the aerobic dive limit. From Kooyman GL and Ponganis PJ (1998) The physiological basis of diving to depth: birds and mammals. *Annual Review of Physiology* **60**: 19–32.

that has been studied in this way was the emperor penguin. However, comparable results have been obtained in a few studies where aerobic dive limits have been measured using freely diving trained bottlenose dolphins, *Tursiops truncatus*, California sea lions, *Zalophus californianus*, Beluga whales, *Delphinapteras leucas* and captive Baikal seals, *Phoca sibirica*. All of these studies support the ADL model as originally proposed.

With the exception of the work done on Weddell seals and emperor penguins, we do not have direct measurements of when or how often diving vertebrates produce lactic acid under normal conditions in the wild. Therefore, recent studies have compared actual diving behaviour with calculations of how long the animal's total oxygen stores would last, given estimates of their diving oxygen consumption. For example, these calculations suggest that Antarctic fur seals, *Arctocephalus gazella*, utilize a smaller proportion of their oxygen stores as they make short shallow dives feeding near the surface. In contrast, such calculations suggest that Australian *Neophoca cinerea* and New Zealand *Phocarctos hookeri* sea lions routinely use a greater proportion of their oxygen reserves. These animals make long and/or deep dives feeding at or near the sea bottom and consume large prey that may require long dives to capture. Such measurements are not just of interest to physiologists, but have relevance to wildlife managers as well. It is important to know, for example, whether a species in decline is operating at, or close to, its maximum physiological capacity. This is because if it is, it will be less capable of compensating to normal environmental or human-caused changes in its environment. In contrast, an animal that is operating well within its physiological capacity will have more 'reserve capacity' and should have a greater capacity to respond to environmental fluctuations. Such animals would be able to draw on a greater physiological reserve to pursue prey deeper, dive longer or forage for greater periods. Over the past decade many fur seal populations (South American fur seal, *Arctocephalus australis*, New Zealand fur seal, *A. forsteri* and California sea lion respectively) have experienced spectacular population growth that is in marked contrast to an apparent stability or even decline in all of the sea lions that feed on or near the bottom (Steller, *Eumatopias jubatus*, Australian, southern, *Otaria flavescens*, and New Zealand sea lion). Many of these declining sea lions are sympatric with near surface feeding fur seals whose populations are increasing.

Other determinants of diving behaviour

Large body size also confers greater diving ability. Metabolic rate scales to body mass$^{0.75}$ whereas oxygen storage capacity scales to body mass$^{1.0}$. Therefore, the larger the animal the lower its mass-specific metabolism for a given oxygen storage capacity. All things being equal, large mammals should be able to dive longer and deeper than small ones based simply on body size. While diving animals can reduce their metabolic rate through bradycardia, they still need to move through the water to capture their food. The most accomplished divers are also very efficient swimmers and have a very hydrodynamic body that facilitates efficient underwater locomotion. They also use burst and glide locomotion. Burst and glide locomotion occurs when the animals become negatively buoyant after lung collapse and they glide during the descent phase, thus saving effort and oxygen. Some species such as right whales are naturally buoyant. These positively buoyant species actively swim during descent and glide up during ascent. **See also**: Ecological Implications of Body Size

Given a larger oxygen store and a lower relative metabolic rate, large animals should be able to dive longer and/or deeper. This in part explains why the largest members of the various taxonomic groups have the greatest diving ability (i.e. emperor penguins, elephant seals, beaked and sperm whales). However, this is at odds with the rather unimpressive diving behaviour of the largest marine mammal, the blue whale, which has been observed to dive on average for 6.6 min to depths of 113 m. There are a variety of reasons why animals do not always dive to their maximum capability. The first is simply that there may be no reason to dive for so long or so deep. Most dives are associated with finding food and thus there may be no reason to go any deeper than where the prey are. The greatest abundance of marine organisms occurs in the epipelagic and mesopelagic regions well above 1000-m depth. Furthermore, benthic foragers are limited by the depth of the ocean floor where they find their prey. The most productive

benthic habitats are associated with the continental shelf and most continental shelves are relatively shallow (<200 m). Therefore most benthic foragers will be diving less than 200 m. Deep dives require more time in transit and are therefore longer than shallow dives. While deep dives are longer, the longest dives are usually not the deepest. This is because deep dives require active swimming to get to depth, which utilizes oxygen stores more rapidly. In contrast, the longest dives are relatively shallow as the animal swims as little as possible often passively sinking. The longest recorded dive for an elephant seal (2 h) was not particularly deep for an elephant seal. It is suspected that the animal was hiding at depth, not swimming and was slowly sinking. It probably reduced its metabolism to the greatest extent possible to get the longest dive possible out of a finite store of oxygen.

Returning to the blue whale example, unlike most other diving animals, whales of the family Balaenopteridae, which includes blue, fin, sei, bryde's and minke whales, are gulpers, that is, they feed by engulfing entire schools of prey. The blue whale finds a school of krill, and opens its mouth engulfing the entire school of krill. The whale then expels the water through its baleen plates, retaining the krill in its mouth. Consider how much drag, and thus increased effort, it takes to swim with an open mouth the size of a blue whale through the water! Given their feeding behaviour it makes sense that blue whales and their kin have a very costly method of feeding that uses oxygen rapidly.

Such studies of diving behaviour would not have been possible without significant developments in digital electronics that have provided field biologists with a new form of 'biotechnology'. This biotechnology has enabled the study of complex behaviour and physiology in freely ranging animals over entire ocean basins. Electronic tags have been used to obtain information on the acoustic and physical environment, heart rate, ventilation rate, swim speed and acceleration while they freely go about their activities. Data are obtained from the tags when they are recovered (archival tags) or the data are transmitted via satellite. These tags have been deployed on a wide array of marine organisms including squid, fish, turtles, mammals and birds, and are providing remarkable insights into the physiology and ecology of many marine species.

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