DIVING PHYSIOLOGY OF MARINE VERTEBRATES

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Air-breathing marine vertebrates that dive to find food deal with two fundamental problems:

1. The effects of pressure at depth
2. The need to actively forage while breath holding

Adaptations to diving can be divided into two categories

1. Associated with adaptations to pressure
2. Associated with breath-hold diving
Air-breathing marine vertebrates that have secondarily returned 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. However, a few of these groups are capable of making quite deep or long dives.

- Emperor penguins regularly make dives to 400–500m. 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. They spend 90% of the time at sea submerged, averaging 20 min per dive.

- Beaked whales, 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.
Regardless of their taxonomic origin, all of these animals face the same fundamental constraints.

- **Adaptations to pressure**
  - Direct or mechanical effects of pressure
  - Problems associated with the increased solubility of gas (N₂ and O₂)

- **Adaptations to breath-hold diving**
  - Modifications in metabolism
  - Blood flow and oxygen storage capability
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.

A similar problem occurs with the air cavity associated with the middle ear, a condition called middle ear squeeze.

The changes in volume associated with depth follows Boyle’s Law:
\[ P_1 V_1 = P_2 V_2 \]

For example, an animal with a 10-L lung at the surface where the ambient pressure is 1atm and that animal dives to a depth of 10m. The pressure has increased to 2atm, and the lung now has a 5L volume or 1/2 as large as it was on the surface. If the animal dives to 100m depth, the total pressure is 11atm 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.
LUNG COLLAPSE

- 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.
- Recent studies show that marine mammals have specialized surfactants in their lungs that aid in post-dive re-inflation 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.
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 150m, and convulsions at 500m. This is referred to as high pressure nervous syndrome or HPNS. Manifestations include headache, tremor, myoclonus, neuropsychiatric disturbances and Electroencephalography (EEG) changes.
Diseases Associated with Gases at Pressure

- At high partial pressures both N2 and O2 become toxic.
  - Increased concentrations of N2 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 absorb greater amounts of gases (N2 and O2) at higher pressures.
  - 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.
- 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 N2 accumulation by allowing their lungs to collapse during the initial period of the dive.
when a captive mammal or bird was forced to dive, there was an overall reduction in metabolism with an increased reliance on anaerobic (without oxygen) metabolism as indicated by a post-dive release of lactic acid.

- Only two ATPs 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 ATPs.
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.
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, 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.
Haematocrit of diving mammals increased during a dive.

- 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.

- 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.
- When problems associated with viscosity are not as important as maximum oxygen storage ability, red cells are released from the spleen into the circulation.
To increase their ability to stay submerged, diving animals have increased the amount of oxygen stored in their internal tissues. This can be thought of as an ‘internal scuba tank’ and is composed of three primary compartments, the O$_2$ contained in the lung, muscle and blood.

- Diving mammals have greater haematocrit and blood volume than terrestrial animals.

![Diagram of oxygen stores in dolphins, sea lions, and humans](image-url)
Maximum time an animal could remain submerged without utilizing anaerobic metabolism as the aerobic dive limit (ADL) and was calculated as:

$$ADL \text{ (min)} = \frac{\text{total oxygen store (mLO2)}}{\text{diving metabolic rate (mLO2 min}^{-1})}$$
OTHER DETERMINANTS OF DIVING BEHAVIOR

- Large body size also confers greater diving ability. The larger the animal the lower its mass-specific metabolism for a given oxygen storage capacity.

- 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.
REFERENCE

- Diving Physiology of Marine Vertebrates; Daniel P Costa, Department of Ecology and Evolutionary Biology, University of California-Santa Cruz, Santa Cruz, California, USA