Fisheries: Atlantic; Pacific. Small Pelagic Species Fisheries. Southern Ocean Fisheries.

Further Reading

Baisre JA (2000) Chronicles of Cuban marine fisheries (1935–1995): trend analysis and fisheries potential. *FAO Fisheries Technical Paper*, 394. Rome: FAO.

Garcia SM and De Leiva Moreno I (2000) Trends in world fisheries and their resources: 1974–1999. In: *The State of World Fisheries and Aquaculture 2000*. Rome: FAO.

Garcia SM and Grainger R (1996) Chronicles of marine fishery landings (1950–1994). Trend analysis and fisheries potential. *FAO Fisheries Technical Paper*, 359. Rome: FAO.

MARINE MAMMAL DIVING PHYSIOLOGY

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Introduction

Marine mammals are the last major group of vertebrates to adapt widely to the marine environment. Reptiles and birds preceded them by tens if not hundreds of millions of years. The marine reptiles had their greatest success in the Mesozoic. Like the dinosaurs most had disappeared by the end of the Cretaceous, except for sea turtles and crocodiles. Marine diving birds were also present in the Mesozoic, including possibly some penguins. However, as with marine mammals, their greatest diversification occurred during the Tertiary. The lack of competition from such successful and formidable marine reptiles as the mosasaurs, ichthyosaurs, and pleisiosaurs may have enabled this adaptive radiation. Nevertheless, then as now, all three groups had similar physical obstacles to overcome in adapting to marine life. These problems stimulated the evolution of some of the most extreme and unusual physiological and morphological adaptations ever achieved by vertebrates.

The ancestors of whales were the first to begin the invasion of the sea sometime during the Eocene, more than 60 million years ago (Ma). Sea cows, the only herbivorous marine mammal, originated about 50 Ma during the late Eocene, and pinnipeds followed about 30 Ma in the late Oligocene. Pelagic species wander the vast offshore regions of the world's oceans, and dive in waters with depths up to thousands of meters. Because the greatest challenges of the physical environment are preeminent in this region, the pelagic whales and pinnipeds will be discussed in greatest detail.

There are seven major physical obstacles to overcome that require extreme physiological adaptations to life in the oceans.

1. Anoxia: diving into a world that is without oxygen for an air-breathing mammal.
2. Density: just a short distance from the surface the hydrostatic pressure becomes extreme.
3. Breathing: the less time taken for respiration, the more time at depth to search for prey or to avoid being eaten.
4. Vision: even in the best conditions of water clarity in pelagic tropical waters this is a region of twilight to eternal darkness.
5. Acoustics: the limited field of vision underwater increases the importance of hearing over long distances compared to land mammals.
6. Cold: even the warmest tropical sea is 10–15°C cooler than the internal temperature of a hot-blooded marine mammal.
7. Viscosity: there is a reason animals underwater appear to move in slow motion – their movements are slowed by the viscosity of water.

Selection pressure for adaptations to overcome these physical barriers is great and has resulted in some very consistent morphological and physiological adaptations that, in some cases, make it easy to recognize a marine mammal from only a small part of its anatomy. Some of the more salient anatomical features are discussed in relation to their function. Just as there are variations and gradations on the theme of adapting to the marine environment, so too there are extremes that are exemplified by the most pelagic and the deepest divers. **Table 1** shows statistics from each major group regarding the simple assessment of diving ability by the maximum and routine depths and durations. It should be noted that even though the diving ability of some species is impressive, the exploitative ability of marine mammals is superficial considering that the average depth of the world's oceans is 3.5 km and the

Table 1 Routine and maximum diving characteristics of selected marine mammals from some of the major groups that hunt pelagically

Species	*Family*	*Dive duration (min)*		*Dive depth (m)*	
		Mean	*Max.*	*Mean*	*Max.*
California sea lion (*Zalophus californianus*)	Otariidae	2	10	62	274
Northern elephant seal (*Mirounga angustirostris*)	Phocidae	22	90	520	1581
Sperm whale (*Physeter catodon*)	Physeteridae	35	73	792/466	2035
Bottlenose whale (*Ampullatus hyperoodon*)	Ziphiidae	37	70	1060	1453

maximum depth is 11 km. Emphasis will be placed on five of the seven adaptations mentioned.

Adaptations to Anoxia

When marine mammals dive below the surface they enter an anoxic environment even though there is much dissolved oxygen in the surrounding water. Lacking gills or any means of extracting oxygen from the water they are without oxygen, except for that stored within their bodies, until they return to the surface. The brain must not be without oxygen for more than three minutes or irreversible damage occurs, and dysfunction occurs even sooner. With such a short margin of resistance, marine mammals had to develop special adaptations to protect the brain and other organs and tissues sensitive to oxygen deprivation. Some of the broad categories of adaptation are: (1) oxygen stores; (2) redistribution of blood flow by cardiovascular adjustments; (3) reduced metabolism during the dive; (4) behavioral patterns that encourage oxygen conservation; (5) reliance on anaerobic metabolism in organs tolerant to hypoxia.

Oxygen Stores

The oxygen consumed during a breath hold is stored in three compartments, the respiratory system, the blood, and the body musculature (**Figure 1**). The respiratory oxygen store is of marginal value since about 80% of the volume is nitrogen, and because there is little gas exchange between the lung and blood while the animal is at depth. The blood oxygen store is dependent on the blood volume, red cell volume, and the concentration of hemoglobin in the red blood cells. As the cell volume increases, so does viscosity, increasing the resistance to blood flow. Some marine mammals have very high blood oxygen storage capacity, whereas in others the blood oxygen storage capacity is little different from that in terrestrial mammals. In contrast, there is an increased concentration of the oxygen-binding protein myoglobin in muscle in all marine mammals which sets them apart from all other mammals. Myoglobin is 3–15 times more concentrated in the muscle of diving compared to terrestrial mammals, and there may be some relationship between the depth of dives the animal routinely makes and the level of the myoglobin in the muscle (**Tables 1** and **2**).

The deepest divers seem to have the largest oxygen stores. In humans the total store is 20 ml $O_2 kg^{-1}$ body mass, which is about a fifth of that in elephant seals (nearly 100 ml O_2 kg^{-1} body mass). Using the human average as a standard of comparison for the typical terrestrial mammal, the elephant seal has a blood volume three times greater, a hemoglobin concentration 1.5 times more, and a myoglobin concentration approximately 10 times more (**Figure 1**).

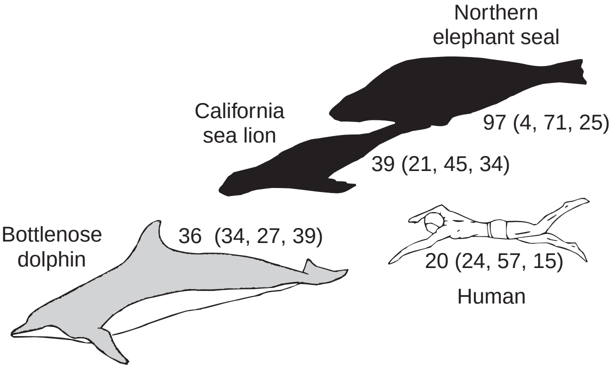

Figure 1 Distribution of oxygen stores within the three major compartments of lung, blood and muscle. Groups represented are the toothed whales (bottlenose dolphin), sea lion and fur seals (California sea lion), and true seals (northern elephant seal). The first number is total body oxygen store; numbers in parentheses are for the lung, blood, and muscle (ml kg^{-1}). (Modified from Kooyman (1989).)

Table 2 Myoglobin concentrations in the major groups of marine mammals

Species	*Myoglobin ($g\,100g^{-1}$ wet weight)*
Manatee (*Trichechus manatus*)	0.4
Sea otter (*Enhydra lutris*)	3.1
Walrus (*Odobenus rosmarus*)	3.0
California sea lion (*Zalophus californianus*)	2.8
Weddell seal (*Leptonychotes weddellii*)	5.4
Northern elephant seal (*Mirounga angustirostris*)	5.7 (8 months old)
Fraser's dolphin (*Lagenodelphis hosei*)	7.1
Sperm whale (*Physeter catodon*)	5.0

Cardiovascular Adjustments

Specializations of the cardiovascular system varies among the different families of marine mammals. The least cardiovascular modification appears to be in the sea lion, sea otter and manatee. At the other extreme are the cetaceans with numerous variations or entirely new structures, most of which have unknown function. For example, most toothed whales have an extreme development of the thoracic retia mirabilia. This complex network of arteries is invested in the dorsal aspect of the thorax as well as embedded between the ribs. One of its main functions appears to be to provide the primary blood supply to the brain. This role has been usurped from the internal carotid, which does not reach the brain before it ends as a tapered down and occluded vessel. The reason for this complexity, and other possible functions of the thoracic retia are unknown.

A more universal structure is the aortic bulb, an enlargement of the aortic arch, that functions as a capacious, elastic chamber. This bulb absorbs much of the flow energy developed during systole by the left ventricle. This absorbed pulse is then more evenly spread through the rest of the cardiac cycle. The maintenance of blood flow pressure is especially effective during the bradycardia that occurs during a dive.

There is considerable modification of the venous circulation in seals. The intravertebral extradural vein that lies within the vertebral canal above the spinal cord is responsible for most of the brain return flow. It also drains portions of the back musculature and the pelvic area. Much of the blood volume returns via the intercostals to the azygous vein and then to the anterior vena cava to the heart. The major blood return of the body is from the inferior vena cava, which drains into a large hepatic sinus. This vessel passes through a narrow restriction, the vena cava sphincter, at the diaphragm before entering the thoracic cavity. The sphincter is a circular muscle capable of reducing flow return to the heart.

Finally, at least in pinnipeds, there is an enlarged spleen that acts as a reservoir for about 50% of the total red blood cell volume while the seal is resting or sleeping. The splenic mass in terrestrial mammals is about 0.5–2% of body mass, whereas it is 4–10% in seals. Once the seal begins to dive these cells are injected into the circulation and raise the hematocrit about 50% above the resting value. Once a diving bout is concluded much of the red blood cells are again stored in the spleen.

The most complete information on cardiovascular function is from seals in which information has been obtained while the animals are making routine foraging dives. Most data from other diving mammals have been collected during trained dives, or during resting submersions. In general, as the dive begins, a rapid onset of bradycardia ensues that may range from 20–90% of the resting heart rate. This is dependent on the duration of the dive, probably the swim speed, and whether the dive is routine or an evasive response that incurs some level of stress. The latter dives are when the most extreme declines in heart rate occur. Concurrent with the reduced heart rate there is the necessary decline in cardiac output, which is greater than would be predicted from the change in heart rate alone. This happens because there is also a reduction of 50% in stroke volume. During the longest dives, there is a reduction in splanchnic blood flow to hypoxic-tolerant organs such as the liver and kidneys, and in somatic blood flow to many of the muscles. The brain, which is not hypoxic tolerant, does not have a reduced blood flow and it becomes a major consumer of the stored oxygen of the circulatory system. What the rate of oxygen consumption is during the dive remains one of the most important unanswered questions in diving physiology.

Metabolic Responses

Even a modest reduction in metabolic rate of the liver, kidney, and gastrointestinal tract will help to conserve the body's oxygen store since they account for about 50% of the total resting oxygen consumption. A small reduction can be easily made up while the animal is ventilating at the surface. The other major consumer is the locomotor muscles. Even under conditions of foraging when the animal may be anxious to swim to the prey patch, the axiom of 'make haste slowly' is applicable. It must conserve the muscle oxygen as much as possible, and one option for doing this is to take advantage of its natural buoyancy. Gliding, the behavior that achieves this result, has now been measured. In four species, two seals, a bottlenose dolphin, and a blue whale, it is now known that during the descent below a depth of 20–40 m the animals glide to greater depths. One elephant seal was observed to glide down to 400 m. In this condition only the brain remains uncompromising in its need of a large oxygen requirement. It has been estimated that gliding to depth can result in an energy saving of over 50% compared to a dive in which there is swimming at all times. These are conservative estimates because the drag caused by the attached camera must have been substantial for all species except the blue whale, and this would incur a cost that in the unfettered animal would be much less. Even at depth there is an additional reduction of metabolic rate for swimming as the streamlined animal strokes intermittently and glides as much as possible. Away from surface effects, the resistance to forward propulsion is at a minimum.

The economy in swim effort results in important savings in oxygen consumption as propulsive muscle does less work. In addition, it is likely that there is a reduced blood flow to muscle as it relies more on the internal store of oxygen rather than that from the circulating blood, which is the main oxygen source for the hypoxic-intolerant brain. The high concentration of myoglobin in all marine mammals indicates that it is a key adaptation for diving. As the muscle oxygen depletes, the need for supplemental energy from anaerobic catalysis of creatine phosphate and glycogen rises. Both of these compounds produce adenosine triphosphate (ATP) that is essential for electron transfer, and the conversion of chemical energy into mechanical work. However, anaerobic glycolysis results in an inefficient use of the glycogen store because of incomplete combustion of glucose to lactate which results in a metabolic acidosis that has a limit of tolerance. Diving mammals have a broad tolerance of acidosis because of their exceptional capacity to buffer the acidity of lactate. Most divers avoid this condition, and reliance on anaerobic metabolism occurs only in exceptional cases when the dive has to be extended beyond the routine foraging durations. This threshold is when a net production of lactate results in a rise in arterial blood lactate after the dive. This has been called the aerobic diving limit (ADL).

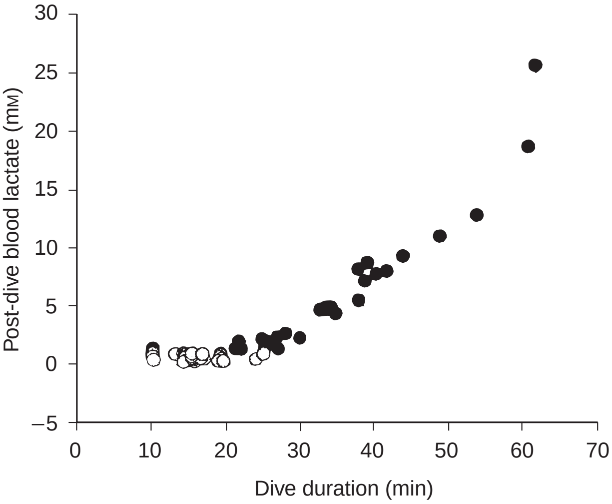

Figure 2 Peak concentration of lactate in arterial blood after dives of different duration in adult Weddell seals. The inflection represents the transitions from completely aerobic dives and is considered the aerobic diving limit (ADL). Open circles reflect blood values of dives in which there is no net production of lactate, and black circles are those in which there was a net production. (Reproduced with permission from Kooyman (2000).)

When dive durations are plotted against lactate concentration in arterial blood (**Figure 2**) there is a distinct inflection where lactate concentration increases sharply. Beyond this dive duration anaerobic metabolism contributes a greater amount to the energy needs of the animal, mostly in the muscle. There is a cost in addition to the inefficient use of glycogen stores. An imbalance occurs in metabolic endproducts, and there is acidification in the cells and the circulatory system which must be restored to normal acid–base balance. To do this there may be an extended surface period for recovery, or if the recovery is continued during the next dive, it is likely to be shorter because of the reduced oxygen and glycogen stores which cannot return to full capacity until the acid–base balance of the body returns to normal levels. In order to avoid the problem inherent in relying on extensive anaerobic metabolism during a dive, most dives of marine mammals are within the ADL. Circumstances during which the ADL might be exceeded occur during foraging when a rich source of prey might be at such a depth that the dive has to be longer than the ADL, or during avoidance of a predator when diving unusually deep might aid in a successful escape. For the Weddell seal it might be to travel an exceptionally long distance under ice to a new breathing hole.

Adaptations to Pressure

Once marine mammals developed the capacity to breath hold for a few minutes they were exposed to the second most dominating physical effect of the marine environment – the density of water. Just a short distance from the surface, the hydrostatic pressure becomes overwhelming for any terrestrial animal which lacks the adaptations found in marine mammals. In order to tolerate the effects of pressure, marine mammals have adapted to live with it rather than to resist it as human made submersibles do. Instead of an outer shell that protects the internal organs from the crushing pressure of depth, marine mammals give and absorb the pressure. The chest is almost infinitely compliant allowing the lungs to be compressed to a solid organ. There are no air sinuses in the skull such as the facial sinuses of humans, and the vascular lining of the middle ear can expand and reduce in volume to match the ambient pressure. There are no disparities of pressure between the inside and outside of the body. This has many ramifications, but the most important relates to how diving mammals avoid absorbing the lung gases that comprise 80% nitrogen while diving to great depths. Such a volume is adequate, depending on the distribution of blood, to cause blood and tissue nitrogen tensions to reach a level where gas bubbles could form during the animal's rapid ascent. The result is decompression sickness or the 'bends'.

By yielding to the compressive effects of pressure marine mammals avoid the problem. The lungs of marine mammals are similar in all groups, but distinctive from terrestrial mammals (**Figure 3**). As a result of robust cartilaginous support that is absent from terrestrial mammals the most peripheral airways are less compliant. As the chest wall compresses, it allows the lungs to collapse; this takes place in a graded fashion with the gas from the alveoli being forced into the upper airways where gas exchange does not occur (**Figure 4**). Consequently, the gas is sequestered while the animal is at depth. For some seals this collapse may occur at depths of only 20 m. No matter how much deeper the dive is, the arterial blood nitrogen tension does not rise above 2300 mmHg, within the range where gas bubbles will not form even if the decompression rate is extremely rapid. Curiously, the most robust peripheral airways are not always in the deepest divers. Furthermore, in some of these species the airways seem to be armored to a far greater degree than is necessary to ensure a graded collapse as they descend to depth.

Adaptations for Ventilation

Because of the compliant chest wall and the robust peripheral airways the lungs of most marine mammals empty to an unusually low volume, about 5–10% of total lung capacity (TLC), compared to

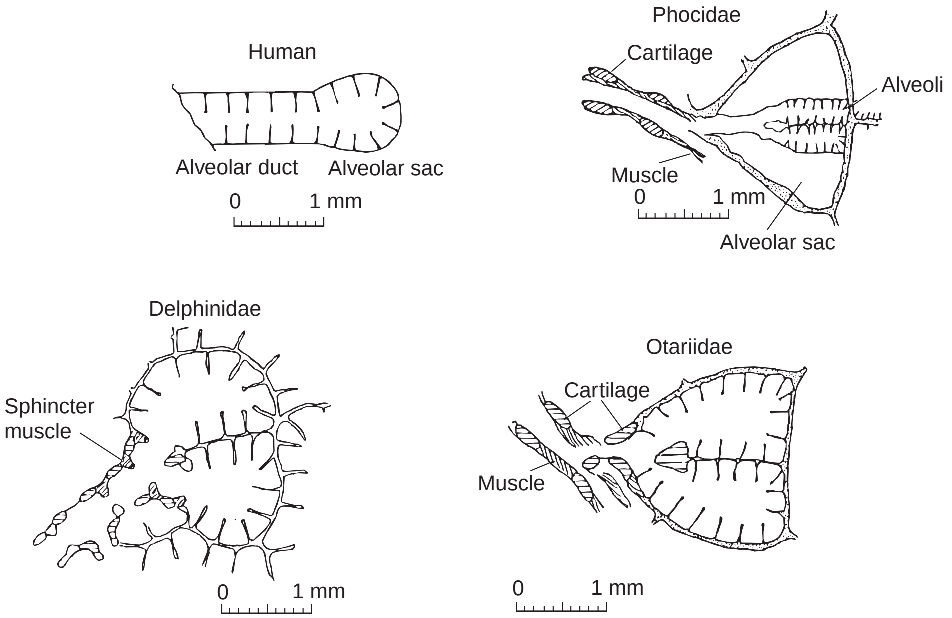

Figure 3 Diagrams of the terminal airways and alveoli of a human and three major groups of marine mammals. The human alveolar duct is thin-walled and exchanges gas with the capillaries. The seal (Phocidae) has a short alveolar duct if present at all and the terminal bronchiole is reinforced with cartilage and muscle. The sea lion (Otariidae) has no gas exchanging surfaces except within the alveolar sac, and the cartilage is robust throughout the terminal bronchiole. The dolphin (Delphinidae) has similar robust cartilage reinforcement within the terminal bronchiole, but in addition there is a series of sphincter muscles. This muscle configuration is unique to the toothed whales. (Modified from Denison DM and Kooyman GL (1973) The structure and function of the small airways in pinniped and sea otter lungs. *Respir. Physiol.* 17: 1–10.)

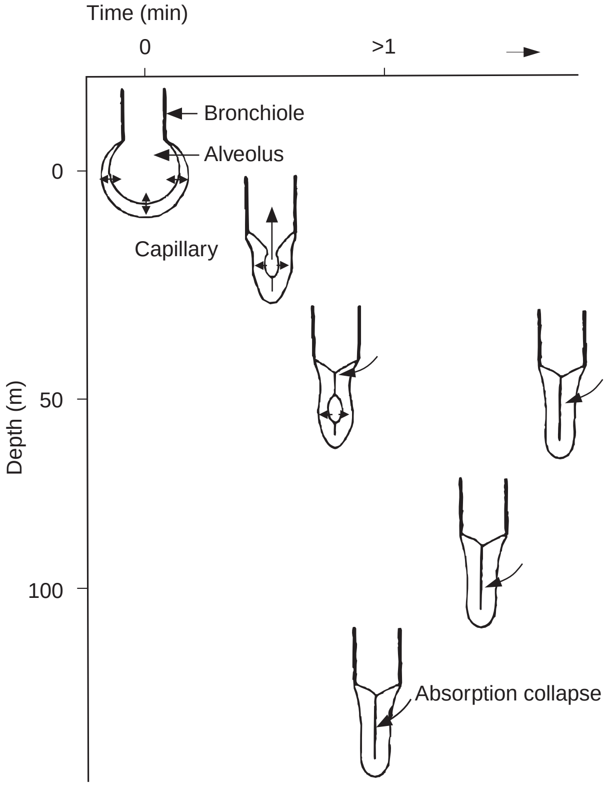

Figure 4 Diagram of the graded collapse of the alveolar gas into the upper airways of a seal as it descends to depth. It is presumed that the same type of collapse occurs in other kinds of marine mammals. The time axis is relative, but emphasizes the short period over which this collapse occurs as the seal descends to depth. The arrows within the alveolus and across the alveolar membrane indicate the direction of gas flow. The curved arrow indicates the further closure of the alveolar space as absorption collapse occurs. The thickness of the arrow's stem indicates the rate. The deeper the seal descends the faster the uptake of gas into the capillaries. Thus, the staircase configuration of the collapsed alveoli showing that the collapse will occur sooner the deeper the animal descends. (Modified from Kooyman GL, Schroeder JP, Denison DM *et al.* (1972) Blood N_2 tensions of seals during simulated deep dives. *American Journal of Physiology* 223: 1016–1020.)

the 25% residual volume of terrestrial mammals. This makes possible a vital capacity of about 90% of TLC, which is often equivalent to tidal volume in species that rapidly ventilate such as dolphins. For a fast-swimming dolphin or sea lion to make effective use of such a large tidal volume it needs to be turned over rapidly during the brief time the blow hole or nostrils are near the surface (**Figure 5**). The bottlenose dolphin can turnover about 90% of its TLC within 0.7 s. Indeed, these dolphins and some whales aid this process by exhaling most of the tidal volume just before breaking the surface, so that most of the time at the surface can be used for inhaling. Inhalation is slower because although the chest wall is actively expanded, lung expansion is a passive process that relies on the elastic properties of the lung for inflation.

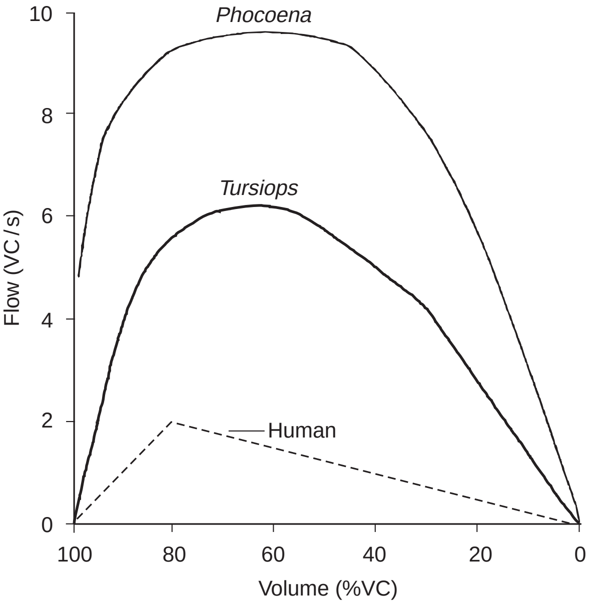

Figure 5 The rapid expiration of gas from the excised lungs of a porpoise (*Phocoena phocoena*) during a forced expiration. The forced expiration curve from a trained bottlenose dolphin (*Tursiops truncatus*). The maximum rate of expiration of a human is shown for comparative purposes. (Modified from Kooyman and Sinnett (1979) Mechanical properties of the harbor porpoise lung. *Respiratory Physiology* 36: 287–300; Kooyman and Cornell (1981) Flow properties of expiration and inspiration in a trained bottlenose porpoise. *Physiological Zoology* 54: 55–61.)

Adaptations for Locomotion

The similarity in shape of different marine mammals, from seals to whales, can be seen in **Figure 1**. There are strict rules for this, which are related to density and viscosity of water (*see* **Fish Locomotion**). The density of water is about 1000 times greater than air, and at 0°C the kinematic viscosity is about seven times that of air. In order to minimize resistance to movement, marine mammals like many fish had to evolve a special shape of the body. The ideal shape has a fineness ratio, i.e., body length divided by the maximum body diameter, of about 4.5. This shape greatly reduces form drag, which at the speeds marine mammals swim, is over 90% of the total drag. Also the routine swim speed of all marine mammals is about 2–3 m s^{-1}. At these speeds and through such a dense medium the rates of progress are slower than that of many land mammals, but the burst and glide swimming that are used and the support to the body mass makes their progress seem almost effortless, and accounts for the low metabolic rates discussed earlier.

Adaptations to Light Extremes

Marine mammals are creatures of the night. Even those that may be active during the day search for most of their food at depths where the light level is similar to twilight or less. Hence, they might be thought of as marine bats. Some echolocate to find their prey, whereas others hunt visually. Seals and sea lions are visual hunters and like many nocturnal mammals they have large eyes. The eye of the southern elephant seal has an internal anterior and horizontal diameter of 52 by 61 mm, compared to the human eye of 24 by 24 mm. These eyes have a high concentration of rods, the light-sensitive element within the retina, that is 10–50 times more dense than the human eye. At least some have visual pigments adjusted to the blue light that is the dominant ambient light source at depth. All have a tapetum lucidum layer behind the retinal layer and a large pupillary area. In comparison to humans, a diurnal primate whose pupil area ranges from 3.2 to 50 mm^2, or the domestic cat, whose pupil ranges from 0.9 to 123 mm^2, the northern elephant seal pupil area ranges from 0.9 to 422 mm^2. Less extreme is the California sea lion, which dives to much shallower depths, and whose pupillary dimensions are only 8.4–220 mm^2. At light levels where the sea lion pupil is expanded maximally, which is roughly equivalent to a clear, full-moon night, that of the elephant seal is only at 22% of its maximum diameter. Indeed the maximum pupillary expansion of the elephant seal does not occur until there is total darkness. At this level the eyes are still functional because although no light is produced by the physical environment, biological light is produced by most marine organisms. Hence, when elephant seals descend to depths beyond the limit of surface light there is still much light in the environment. As marine mammals commute with great rapidity to and from the depths it is essential that there is rapid adaptation to the dark. Whereas land mammals may take tens of minutes to adapt to darkness, elephant seals may do so within 4–6 min. The shallower-diving harbor seal takes 18 min and humans about 22 min. Elephant seals may be helped in this adaptation because the contracted pupil is so small that even at the surface the amount of light reaching the retina is not great enough to saturate the rod receptors.

Conclusions

The management of oxygen stores has been a long standing topic of study in the history of marine mammal physiology since the first key works were published in the 1930s and 1940s. Progress in understanding the adaptations of marine mammals to conserve and utilize those stores efficiently has been fitful, depending on the techniques available. The research emphasis has shifted from restrained and forced submersions in the laboratory to experiments on free-ranging animals. New and powerful tools are becoming available that will enhance progress in this field. In other areas such as determining the function of some of the vascular retia of whales, or the function of some of the peculiar lung structure in these animals, progress has ceased despite the fact that some of this poorly understood anatomy appears to play a major role in the adaptation of these animals to the marine environment. The lack of investigations relates to unavailability of the animals, and the intrusive measures that would be required to determine function.

See also

Bioacoustics. Fish Locomotion. Fish Vision.

Further Reading

Butler PJ and Jones DR (1997) Physiology of diving of birds and mammals. *Physiological Review* 77(3): 837–899.

Kooyman GL (1989) *Diverse Divers: Physiology and Behavior. Zoophysiology Series*, vol. 23. New York: Springer-Verlag.

Kooyman GL (2000) Diving physiology. In: Perrin WF, Wursig B and Thewissen JGM (eds) *Encyclopedia of Marine Mammals*. San Diego: Academic Press.

Kooyman GL and Ponganis PJ (1997) The challenges of diving to depth. *American Scientist* 85: 530–539.

LeBoeuf BJ and Laws RM (1994) *Elephant Seals: Population Ecology, Behavior and Physiology*. Berkeley and Los Angeles: University of California Press.

Levenson DH and Schusterman RJ (1999) Dark adaptation and visual sensitivity in shallow and deep-diving pinnipeds. *Marine Mammal Science* 15: 1303–1313.

Shadwick RE (1998) Elasticity in arteries. *American Scientist* 86: 535–541.

Watkins WA, Daher MA, Fristrup KM and Howald TJ (1993) Sperm whales tagged with transponders and tracked underwater by sonar. *Marine Mammal Science* 9: 55–67.

Williams TM, Davis RW, Fuiman LA *et al.* (2000) Sink or swim: strategies for cost-efficient diving by marine mammals. *Science* 288: 133–136.