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## Diving Physiology

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### I. Introduction

Ever since humankind has lived by and gone down to the sea, we have been awestruck by the creatures that make it their home. First we feared them, later we ate them, and now we try to emulate them with humble attempts to set “world” diving records. At present the record for a descent-assisted dive is at 214 m during a breath hold which lasted a little less than 4.5 min. Many marine mammals exceed that depth within the first few months of life. Premier divers such as elephant seals (*Mirounga* spp.) and sperm whales (*Physeter macrocephalus*) will occasionally dive to depths beyond a kilometer (Table I). The spectacular abilities of marine birds and mammals to dive deep and for long periods of time are a source of interest and curiosity for marine scientists and amateurs alike.

When marine mammals descend below the sea’s surface they leave behind the thin skin of the earth’s atmosphere with one of its essential ingredients to all vertebrate life—oxygen. They begin a journey that is incredible in diverse ways. The magnitude of incredulity varies according to the species, but for all, even the most humble of marine mammals such as the sea otter (*Enhydra lutris*), much if not most of the experience is beyond our imagination. Unlike flying, in which our technology now enables us to fly faster, higher, and further than any bird, bat, or pterosaur ever has or did, marine mammals, particular those that dive to great depths, explore and exploit a realm that overwhelms much of our technology and which enables us to gain only fleeting glimpses of what their environment is like. Recently we have enlisted the animals themselves to help us discover more about this cold, dark world without oxygen, where awesome hydrostatic pressures always prevail. However, “crittercams” will only give us fleeting glimpses, under very special conditions, with those few species that lend themselves to the attachment of these cameras. Life in the deep blue remains a mystery. So too do the means that enable diving mammals to exploit this habitat.

This chapter discusses some of what is known about adaptations to breath holding and overcoming the crushing effects of pressure. These adaptations are unique among vertebrates. Even after our primordial fish ancestors overcame great obstacles to adapt to the terrestrial environment, and eventually to spread throughout all land habitats of the world, the sea continued to be a rich habitat that would bring great success to those species that exploited it. Some air-breathing vertebrates are doing just that. In fact, this has occurred

several times in the history of vertebrates as they reinvaded the sea. The marine reptiles of the Mesozoic were diverse, abundant, and no doubt very capable divers. They had at least one major advantage over marine mammals, a small brain. The brains of mammals require a substantial share of the oxygen being supplied to the body, and it is an obligate need with very little reserve for those times when supply is interrupted. Within 3 min after blood flow and oxygen transport to the human brain is interrupted, there is irreversible damage. This sensitivity of large, complex brains to a grave need for oxygen makes it seem a contradiction that animals who routinely breath hold many times every day are all so smart. Proportionately in terms of brain size relative to body size, several cetacean species have some of the largest brains of mammals. Despite this “handicap” marine mammals have been an extremely successful group that are found in all the world’s oceans, in extremely large numbers, and have the biomass of some species matching that of any of the formerly abundant terrestrial mammals of the world.

What is the secret of their success? Some routinely dive to depths of several hundred meters, and a few species may occasionally descend from 1 to 2 km (Table I). Although these depths may seem just a superficial range compared to the ocean limit of 11 km, with an average depth of 3.5 km, the range used by most marine mammals is in the zone of greatest oceanic life. Nevertheless, this region of cold, dark waters requires special adaptations enabling the animal to endure low temperatures and find prey in the “dark.” Marine mammal diving skill provides a dramatic contrast to human capacities. On average we can dive to a few meters for about 30 sec. The super athletes, who make a career of setting records such as the record breath-hold dive of 214 m, require mechanical aids of weights, pulleys, and drop lines. To extend our depth beyond these few meters humans have gone to costly extremes in mechanical devices. Most deep submersibles are usually limited to several hundred meters depth, but ALVIN, the workhorse of the scientific submersibles, can go as deep as 4500 m.

Adaptations of marine mammals to the marine environment are diverse in order for them to become successful marine predators. They involve many systems in and out of the body, ranging from external body shape to overcome the high density and viscosity of water to the sensory systems necessary to find their way and to detect prey and predator. Space will allow for only a few of the numerous

adaptations necessary for a successful marine mammal. The following paragraphs discuss adaptations to hypoxia and pressure. These paragraphs address pelagic, offshore deep divers in which the adaptations are the most extreme.

## II. Adaptations to Hypoxia

### A. Oxygen Stores and their Distribution

An increased total body O<sub>2</sub> store is considered an essential factor in the breath-hold capacity of diving mammals. The oxygen consumed by body metabolism during a breath hold is stored in three compartments, the respiratory system, the blood, and the body musculature. The theoretical maximum amount of oxygen available in each compartment is a function of several criteria. The respiratory oxygen store is dependent on lung volume and the concentration of oxygen in the lung at the start of a breath hold. The blood and muscle oxygen stores are dependent on blood volume and muscle mass, and the concentration of the oxygen-binding proteins of hemoglobin in blood, and myoglobin in muscle. From the measurements of myoglobin concentration in the muscles of many species of divers it is clear that one of the most consistent hallmarks of oxygen storage in all marine mammals that dive to depth is an elevated myoglobin concentration (Kooyman and Ponganis, 1997; Kooyman *et al.*, 1999). This trait is more characteristic of deep divers than any changes in blood volume, hemoglobin concentration, or respiratory volumes. However, increased blood volume and hemoglobin concentration often contribute to elevated oxygen storage.

As the distribution of oxygen stores vary among species, so do the ranges of the total oxygen store (Table I). In humans the total store is 20 ml O<sub>2</sub>/kg body mass, which is about a fifth of the nearly 100 ml O<sub>2</sub>/kg body mass in elephant seals (*Mirounga* spp.). Using the seal as our basic model it is noted that most of its oxygen is in blood and muscle. The large amount relative to terrestrial animals, using the human average as a standard, is a result of a blood volume 3 times, a hemoglobin concentration 1.5 times, and a myoglobin concentration approximately 10 times the human value. In seals the lung is a minor source of oxygen, as it is in most other marine mammals. It is less than 5% of the total in part because seals exhale to 50% of their total lung capacity just before diving. Furthermore, at depth the lung is collapsed and does not exchange gas.

TABLE I  
Distribution and Quantity of Oxygen Stores, Maximum and Routine Diving Depths, and Durations for Some Marine Mammals

Species	Body mass (kg)	Total store (ml/kg)	Lung	Blood (%)	Muscle	Routine depth (m)	Maximum depth (m)	Routine duration (min)	Maximum duration (min)
Human	70	20	24	57	15	5	214	0.25	6
Weddell seal	400	87	5	66	29	200	741	15	93
Elephant seal	400	97	4	71	25	500	1,653	25	120
California sea lion	100	40	21	45	34	40	275	2.5	10
Bottlenose dolphin	200	36	34	27	39		535		
Cuvier's beaked whale	3,000					1,070	1,888	58	85
Sperm whale	10,000	77	10	58	34	500	2,035	40	73

Note: There is an extensive list of diving capabilities of many species of diving animals at: <http://polaris.nipr.ac.jp/~penguin/penguiness/index.html>

## B. Cardiovascular Responses

The cardiovascular response to breath holding falls into at least two categories of whether the dive is extended or of routine duration for that species. Measurements of cardiovascular and metabolic responses under these circumstances are very limited for any species and most measurements are from seals. Diving mammals are arrhythmic breathers with pauses between each series of breaths. The resting maintenance heart rate is probably most closely reflected in the rate during the respiratory pause or apnea. Using the heart rate during apnea as a basis of comparison for heart rates during a routine dive, the heart rates during the dive are lower than the rate of a resting apneusis, and this occurs despite the fact that the mammal is swimming. When an extended dive is performed, the heart rate is even lower than that during routine diving. Because no measurements of blood flow distribution have been directly measured during dives of marine mammals, it is by extrapolation from indirect measures of other organ functions that allude to what may be occurring. During routine dives it is likely that gastric, renal, and hepatic functions are reduced to a small amount, but no more than what can be compensated for by higher than normal performance during the short, breathing intervals at the surface. Muscle may utilize a small part of the circulating blood oxygen, but it probably relies on its internal store of oxygen bound to myoglobin for much of aerobic metabolic needs.

Extended dives, those that are 3–5 times the routine dives, are uncommon. They are most likely to occur because of some urgent need such as a Weddell seal (*Leptonychotes weddellii*) searching for a new hole under sea ice, or an elephant seal hiding at depth to escape notice from a passing pod of killer whales (*Orcinus orca*) near the surface. The cardiovascular response in these extreme cases may be a limitation of blood flow to obligate aerobic tissues, the most conspicuous of which is the brain. Having no internal store of oxygen, and a need to be at full functional capacity, a constant supply of oxygen and other metabolites provided by the blood, as well as transport of waste products of metabolism from the brain, means that constant blood flow is essential. There is a lesser need for transport of oxygen to the heart because of a reduced work load (the slower heart rate) and small store of internal oxygen. Blood flow to muscle is reduced to a trickle as it draws from the large oxygen store within the muscle and the internal store of glycogen for the production of the high energy compounds of adenosine triphosphate (ATP). The high concentration of myoglobin in *all* mammals that dive to depths greater than about 100m indicates that myoglobin is a key adaptation for diving. Blood flow would be a liability since the affinity of myoglobin for oxygen is much higher than is the affinity of hemoglobin for oxygen. Consequently, any flow to muscle that had utilized much of its oxygen store would strip oxygen from the circulating blood and deprive more vital organs such as the brain from oxygen. A reduced blood flow to muscle also decreases cardiac output needs and, hence, the work of the heart and its oxygen consumption. Thus, the degree of muscle blood flow reduction during long and short dives is key to understanding the management of oxygen stores. Unfortunately, little is known about this crucial topic. Unlike other organs, muscle is widely distributed in the body, and the vascularity is diffuse. Consequently, it is an intractable problem which has not lent itself to study.

Muscle also has a great capacity for anaerobic metabolism and tolerance for high concentrations of the metabolic end product of lactic acid which is stored in the form of lactate. Nevertheless muscle must continue to function for locomotion either continuously as a Weddell seal swims below the sea ice, or intermittently as in an

elephant seal as it drifts in the depths, but in the end must call upon muscle to provide the locomotion to return to the surface. In contrast, the splanchnic organs may shut down or greatly reduce function until the diving mammal returns to the surface.

## C. Metabolic Responses

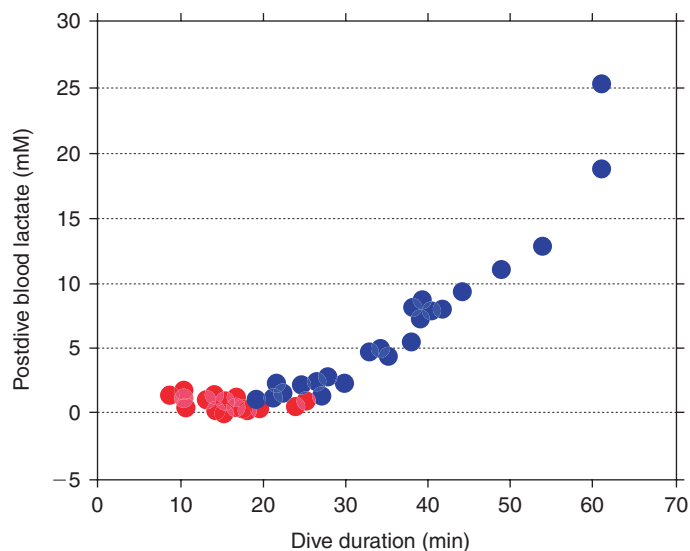
The cessation of metabolic function in the splanchnic organs will reduce metabolic rate substantially since these organs functioning at normal rates account for nearly 50% of the total resting metabolism of the animal. In addition the heart is beating more slowly and performing less work, which may also be the case for striated muscle. In the cold environment at depth some tissues may also be cooling which would result in an additional savings in energy consumption. The final result is to lower the overall metabolic rate to below the resting level during these short and metastable conditions.

## D. Anaerobic Metabolism

Dominating the many factors that affect how long an animal may breath hold is the amount of oxygen available and its rate of utilization. Through oxygen supported metabolic pathways 18 times more high energy ATP is produced from glucose than through anaerobic processes. Furthermore, carbon dioxide and water, the end products of oxygen supported catabolism are less polluting to the cells and circulation than those of anaerobic catabolism. Finally, nerve cells, especially within the brain, are completely dependent on aerobic metabolism. Therefore, the duration of time an animal may breath hold is most strongly affected by the availability of oxygen, with subsidiary support from anaerobic glycolysis and creatine phosphate catabolism. Although an animal may extend its dive considerably by relying on anaerobic glycolysis, the subsequent recovery is in turn extensive because of the time required to process lactic acid and restore the acid base balance of the cells and circulatory system. For routine dives that occur in sequence over many hours aerobic metabolism is the only practical option. Oxygen supported metabolic pathways are also the only means of producing ATP that is derived from catabolism of fat and protein.

## E. Aerobic Diving Limit

The only diving mammal in which there has been a detailed correlation of the diving duration and the postdive blood lactate concentration is the Weddell seal (Fig. 1) (Kooyman *et al.*, 1980; Ponganis *et al.*, 1993). The source of the lactate has been shown to be from muscle, in which it accumulates rapidly as muscle oxygen is depleted. After the seal surfaces, there is increased blood flow to muscle and much of the lactate is flushed into the circulation and gradually disappears over several minutes. If the seal should dive again before all of the blood lactate is processed, it will continue to decline over the course of the dive unless that dive exceeds what has been termed the aerobic diving limit (ADL). The ADL is defined as the diving duration beyond which there is a net increase in lactate production (Kooyman, 1985). This rise in lactate concentration first occurs primarily in muscle, and eventually diffuses from the organ into the circulation where it can be measured easily. It has been proposed that this threshold be called the diving lactate threshold (DLT) to avoid confusion about the numerous ways that the ADL has been derived since the first measurements were made on Weddell seals (Butler and Jones, 1997). From those measurements it was also shown that with some reasonable accuracy the ADL could be obtained from the quotient of the O<sub>2</sub> store divided by metabolic rate, the calculated ADL (cADL). Because this limit predicts basic information



**Figure 1** 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) or diving lactate threshold (DLT). Red circles reflect blood values of dives in which there is no net production of lactate, and blue circles are those in which there was a net production.

about the foraging behavior of diving animals as well as clarifying physiological responses and models to breath holding, it has been calculated for many diving species. Some of the most intriguing calculations have been made for the elephant seal, a continuous diver who appears to allow no surface time for recovery from dives exceeding the cADL. There are several possibilities that could resolve this puzzle. A recent computer simulation of oxygen store depletion provides a physiological model of aerobic diving that may clarify this problem, and provide direction for further studies.

This comprehensive, numerical model uses as its data source the Weddell seal because there is extensive information on this species. The calculations in the model are based on or derived from available data on cardiac output,  $O_2$  depletion rates of blood and muscle, blood flow patterns in various organs, and the diving metabolic rates that may occur in the Weddell seal. The model demonstrates how the matching or mismatching of oxygen transport and regional oxygen consumption can affect the ADL. This theoretical treatment of the ADL goes a long way in understanding how oxygen must be managed during a dive, and in particular, explains how 31% of the body  $O_2$  store remains unconsumed under the most optimal cardiac output conditions. The model also shows that only 49% of the muscle oxygen provision comes from the internal store during the longest possible aerobic dive. In regard to recovery from an extended dive, the oxygen replenishment rate is much more rapid than the reconversion of lactate to glycogen (Davis and Kanatous, 1999).

Assuming that the model can be applied to other aquatic species, it may help to explain the enigma of the serial dives in the elephant seal which exceed previous cADLs. However, the model does not take into account the influence of creatine phosphate to support the few dives that may appear to exceed the ADL, and for which some have invoked some unusual hypometabolic responses. Because creatine phosphate concentration is 15–20 mmol/kg in mammals, this is enough to have a significant effect on the magnitude of the ADL

and the production of energy without oxygen, but before measurable amounts of lactate are produced (Butler and Jones, 1997).

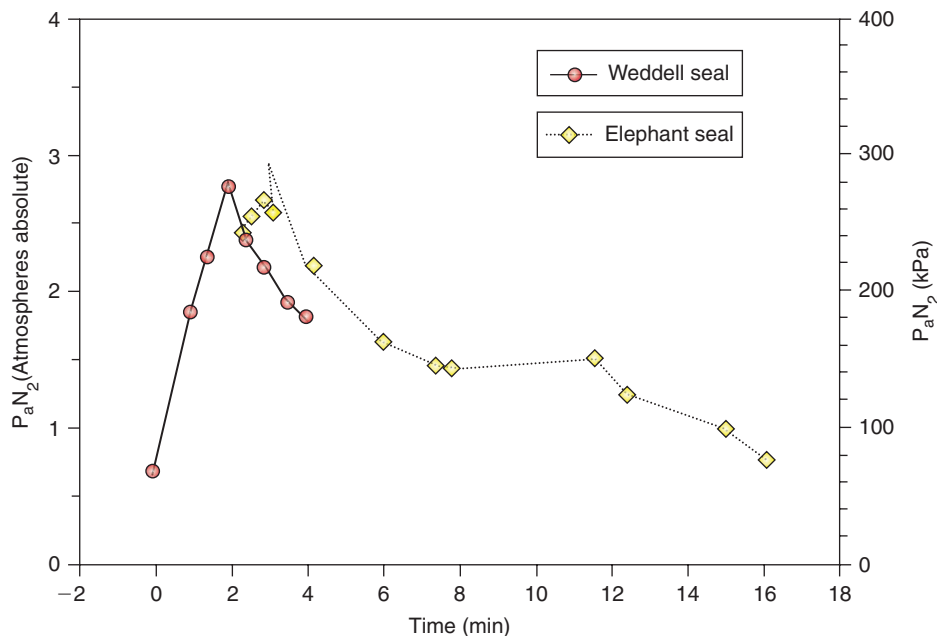
### III. Adaptations to Pressure

Once a marine mammal descends below the surface it not only must deal with the lack of oxygen but also with the effects of pressure. This is one of the most imposing physical variables to which vertebrates must adjust (Kooyman, 1989). We become especially sensitive to pressure during the most modest dive to depth because our airspaces such as the middle ear and facial sinuses make us acutely aware of any difference between the ambient pressure and our internal pressure. More subtle is the effect of pressure on the lung. For humans the lung is an important oxygen store, but in deep-diving mammals the lung is not an important oxygen store. Over a long period of evolution the main function of the vertebrate lung became the exchange of gases between blood and air. During the descent to depth, this function is diminished in deep-diving marine mammals. As the transfer of gases between the lung and blood slackens or ceases, the rise in nitrogen partial pressure within the lung is not matched in the blood. The lack of gas exchange also results in the avoidance of nitrogen narcosis and oxygen toxicity. Even with this adaptation there is still the pure physical effect of hydrostatic pressure on the nervous system. In terrestrial mammals pressure causes over stimulation or uncoordinated nerve conduction and dysfunction called high pressure nervous syndrome (HPNS). How do marine mammals manage to avoid these problems that are manifested in their terrestrial relatives?

The pressure within all airspaces must closely match that of the ambient pressure or suffer damage to the membranes and blood vessels lining the space and a breakdown in normal function. There are at least three major airspaces within most mammals that are liabilities for diving. First are the facial sinuses. Any experienced diver or airline passenger is aware that flying or diving during or soon after having a head cold is a bad idea. The blockage that may ensue during rapid pressure changes can cause extreme pain and serious damage to tissues and blood vessels lining the walls of these cavities. Marine mammals do not have this problem because they have no facial sinuses. Thus, one problem is dealt with by the absence of the airspace.

Similar to all other mammals there is a cavity that forms the middle ear. This is a rigid structure that has little or no compressibility. A pressure differential is prevented, at least for seals and sea lions, because of a complex vascular sinus lining the wall of the middle ear cavity. As the pressure within the middle ear cavity begins to fall below that of the vascular tree, the blood sinuses volume increases. This is a result of the close match between ambient pressure and blood pressure transferred from one fluid (sea water) to another (blood). Another problem is resolved by the reduction of an airspace by hydraulic compression through the vascular system.

Third, the largest airspace of all, and potentially the most problematic is the lung. Volume pressure curves of the chest wall and lung of the ribbon seal, *Histriophoca fasciata*, show that both the chest and the lung are nearly limitless in the degree of compression collapse that they can tolerate. This must be so for other diving mammals as well, and in less detailed studies it has been shown that there is exceptional compressibility in other seals, sea lions, and dolphins. Dolphins and other toothed whales show the most extreme modifications within the lung among marine mammals, or any other mammal. Most notable is the reinforcement of peripheral airways, the loss of respiratory bronchioles, and the presence of a series of bronchial sphincters. Sea lions also have robust cartilaginous airway reinforcement extending to the



**Figure 2** Arterial  $N_2$  tensions in elephant seals and a Weddell seal. The elephant seal submersion (yellow diamonds) were simulated in a water filled hydraulic compression chamber to pressures equivalent to a sea water depth of 136m. Compression began at zero; at 11 min pressure was released and at 14 min the submersion ended. The Weddell seal (red circles) made a free dive to 89m under Antarctic ice. Maximum depth was reached at 5 min, and the dive ended after 8 min.

alveolar sac, but there are no bronchial sphincters. In seals there is no cartilage in the terminal airway, but the walls are thickened by connective tissue and smooth muscle, which reduces their compliance to less than that of the alveoli. Hence, during compression the more compliant alveoli collapse first and the gases within these alveoli are squeezed into the upper airway spaces.

These airways enable a graded collapse of the lung to occur during a dive to depth. The result is that most of the lung air is forced into the upper airways where gas exchange with the blood ceases. It has been shown that blood  $P_{aN_2}$  in seals only rises slightly, no matter how deep the dive. During simulated and actual dives to depth, the  $P_{aN_2}$  of the elephant seal, *Mirounga angustirostris*, peaked at 300 kPa and equilibrated to 200 kPa where it was approximately the same as venous  $P_{N_2}$  (Kooyman *et al.*, 1972). This was independent of the ambient pressure from 30 to 136 m (1460 kPa). Similar values were obtained for Weddell seals diving voluntarily to depths as great as 230 m (2400 kPa) (Fig. 2) (Falke *et al.*, 1985). These small increases in  $P_{aN_2}$  indicate that lung collapse in both species occurred between 20–50 m. The early occurrence of lung collapse in seals makes the lung almost useless as an  $O_2$  store, but it limits  $N_2$  absorption during the dive. These  $N_2$  values are below the minimum  $P_{N_2}$  of 330 kPa found to be necessary for bubble formation in cats, and it is assumed that a similar threshold for bubble formation prevails in marine mammals. An additional benefit of early lung collapse is that it eliminates the likelihood of nitrogen narcosis. This condition is often experienced by SCUBA divers descending to depths greater than 30 m. At these depths tissue nitrogen level is at least 399 kPa; greater than the  $P_{aN_2}$  measured in seals. A final thought is the intriguing condition of elephant seals at sea when they spend 90% of their time underwater and at depths greater than 100 m. At these times the lung does not do what it was originally evolved to do, i.e., to exchange gas with the blood and with the atmosphere. Instead it is collapsed to

a solid organ, and the alveoli become unavailable for gas exchange. Nevertheless, there are recent incidences of Cuvier's (*Ziphius cavirostris*) and Blainville (*Mesoplodon densirostris*) beaked whale strandings that are shrouded in mystery. Fatal strandings of these species were associated with US Navy sonar experiments. Postmortem dissections of some of the beaked whales showed the presence of gas bubbles that appeared to have occurred *in vivo* (Jepson *et al.*, 2003). We know that these species make extreme dives while hunting for prey (Tyack *et al.*, 2006). Is it possible that gas bubbles could have formed during abnormal diving behavior related to the sonar tests, which resulted in decompression sickness?

Finally, in humans and other nonaquatic animals descending to depths of more than 100 m and at rates of 100 m/min the mechanical compression on nervous tissue can cause HPNS. The symptoms are modest to severe tremors throughout the body that can become so severe as to be incapacitating. The range of depths and rate of descent are modest compared to that of some deep-diving marine mammals. Surely a well-adapted mammal does not experience HPNS, which leads to the compelling question of what the difference is between the neural makeup of a marine mammal that protects it from experiencing HPNS and that of a terrestrial mammal that is susceptible to HPNS. We must conclude that the structure of the nervous system is modified in a unique way for a life at high pressure.

#### IV. Epilogue: Mysteries of the Deep

Our understanding of the physiology of diving in marine mammals is still elementary. These animals have adapted to some of the most extreme conditions on the planet. What we can learn from them about hypoxia and pressure is of much intellectual interest as well as of clinical significance. In addition to the brief summary presented, there is a host of other adaptations not mentioned and

in some cases not studied. Some of these are, blood and muscle interactions under extreme hypoxia, acoustical and visual sensing under the extreme conditions of depth where pressure is intense, the cold is penetrating, and light from the surface is at times nil. Many organisms have adapted to a life under these various conditions, but marine mammals commute to the depths, and where they excel is in their adaptability to rapid changes in these extremes as they move from the conditions at the interface of air and water to those of several hundred meters to even a few kilometers beneath the surface.

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# Dugong *Dugong dugon*

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The dugong (*Dugong dugon*) looks rather like a cross between a rotund dolphin and a walrus. Its body, flippers, and fluke resemble those of a dolphin without a dorsal fin. Dugongs can be difficult to distinguish from dolphins in the wild, especially as they often occur in muddy water. They surface very discreetly, often with only their

nostrils showing above the water. Dugongs tend to move more slowly than dolphins and lack a dorsal fin. The Dugong's head looks somewhat like that of a walrus without the long tusks. Growing to a length of up to about 3m, the dugong is the only extant plant-eating mammal that spends all its life in the sea. The other sea cows (or sirenians), the three species of manatee, all use fresh water to varying degrees (Reynolds and Odell, 1991).

## I. Characteristics and Taxonomy

Adults are gray in color but often appear brown from the air or from a boat. Older “scarback” individuals may have a large area of unpigmented skin on the back above the pectoral fins. The dugong's head is distinctive with the mouth opening ventrally beneath a broad, flat muzzle. The tusks of mature males and some old females erupt on either side of the head. The eyes are small and not prominent. Externally the ears consist of only small openings, one on either side of the head. The flippers are short and, unlike those of the West Indian and West African manatees, lack nails. There are two mammary glands, each opening via a single teat situated in the “armpit” or axilla. The mammarys are somewhat reminiscent of the breasts of human females, a similarity which probably explains the legendary links between mermaids and sirenians. Hindlimbs are absent. Unlike manatees, which have a paddle-shaped tail, the tail of the dugong is triangular like that of a whale (Fig. 1).

There is one species of Dugong, *Dugong dugon*, in the family Dugongidae. The only other recent (but extinct) dugongid is *Hydrodamalis*, Steller's sea cow. Dugongidae and Trichechidae (manatees) are the two modern families of Sirenia.

## II. Distribution and Abundance

The dugong has a large range. Its extent of occurrence is some 140,000km of coastline across more than 40 countries and includes tropical and subtropical coastal and island waters from East Africa to Vanuatu, between about 26° and 27° north and south of the equator (Marsh, 2006). Timed depth recorders show that dugongs spend most of their time feeding in shallow water less than 10m deep (Chilvers *et al.*, 2004), suggesting a potential area of occupancy of more than 125,000km<sup>2</sup>. The dugong's historic distribution was broadly coincident with the tropical Indo-Pacific distribution of its seagrass food plants. It is believed that throughout most of its range outside Australia and the Arabian region, the dugong is currently represented by relict populations separated by large areas where it is close to extinction or extinct. The degree to which dugong numbers have dwindled, and their range fragmented, is not known. It is encouraging that dugongs still seem to be present at the high latitude limits to their range, Okinawa Japan, Mozambique, Shark Bay, and Moreton Bay Australia, New Caledonia, and Vanuatu.

Over most of its range, the dugong is known only from incidental sightings, accidental drownings, and the anecdotal reports of fishermen. However, within Australia, extensive aerial surveys have resulted in a more comprehensive knowledge of dugong distribution. A significant proportion of the world's dugongs is found in northern Australian waters from Moreton Bay in the east to Shark Bay in the west. Dedicated aerial surveys of dugong populations in Australian waters indicate that dugongs are the most abundant marine mammal in the inshore waters of northern Australia. Some areas of suitable habitat have not been surveyed. Nonetheless, the available population estimates sum to about 85,000 dugongs (Marsh *et al.*, 2002, 2003). This accuracy of these estimates is unknown as there is still uncertainty about the correction factor used for the number of animals that are not available to observers due to water turbidity.