2 Challenges of the breath hold and the environment

The physiological responses and adaptations that underlie the dives of a marine mammal or seabird are just as remarkable as the dive depths and durations described in Chapter 1. To put these into perspective and to prepare for further discussion in later chapters, the physiological challenges of human diving and the physical characteristics of the underwater environment at depth must first be reviewed. In addition, this chapter will conclude with brief comments on the sensory adaptations that allow these animals to navigate, communicate, and forage at depth. Although too complex to have the space to adequately review in this book, these sensory adaptations deserve note as they are just as essential to the success of a dive as the cardiovascular and respiratory responses are to its performance.

2.1 Challenges in human breath-hold diving

Human breath-hold dives are relatively shallow and of short duration in comparison to those of marine mammals and penguins. Most humans probably cannot match the famous diving women of Japan and Korea (the ama), who typically dive to routine depths of 20 m in dives of about 1-min duration during their daily work (Lindholm and Lundgren, 2009). However, even the dives of unassisted, competitive breath-hold divers pale in comparison to the routine deep dives of 25-kg emperor penguins (80 m, 3–4 min duration for humans vs. >500 m, 8–10 min duration for emperor penguins (Ferrigno and Lundgren, 2003), Chapter 1). As of 2009, the depth record for a human diver pulled down by a weight was 214 m during a dive of 4.4-min duration (Lindholm and Lundgren, 2009). The world record for a human breath hold was 10.2 min in 2009; this was accomplished by a swimmer at rest with the head immersed in a pool (Lindholm and Lundgren, 2009). Although these impressive records are far less than the "unassisted" dive performance of many seals, they do provide the framework to consider the physiological challenges and complications facing the human breath-hold diver.

2.1.1 Breath-hold duration "break point"

The duration of a breath hold in a human diver is considered to be determined by a "break point" at which the inspiratory muscles begin to involuntarily contract, and, after

which, the urge to breathe eventually results in inspiration (Ferrigno and Lundgren, 2003). The break point is associated with a threshold level of the partial pressure of carbon dioxide (P_{CO2}), and is reportedly dependent on four factors: (1) tolerance to hypercapnia and hypoxia; (2) O_2 and CO_2 storage capacity; (3) metabolic rate; and (4) willingness to tolerate the experience (Ferrigno and Lundgren, 2003). Alveolar P_{CO2} values typically ranged between 44 and 54 mm Hg (5.8–7.1 kPa) at termination of out-of-water breath holds. A reduced CO_2 sensitivity is one mechanism to prolong breath-hold capacity, and there is some evidence that training can promote greater CO_2 tolerance as well as hypoxemic tolerance (Ferrigno and Lundgren, 2003). Another way to prolong dive duration is to start with a lower P_{CO2} through pre-dive hyperventilation. A lower initial P_{CO2} increases the time to reach the break point P_{CO2} threshold, and can thus prolong the duration of a breath hold.

2.1.2 Shallow water black out

However, pre-dive hyperventilation is a high-risk maneuver in a human breath-hold diver as it increases the risk of shallow water black out during ascent from depth. Shallow water black out is secondary to hypoxia and occurs when the alveolar/arterial partial pressure of oxygen (P_{O2}) reaches a threshold near 30 mm Hg (4.0 kPa) (Ferrigno and Lundgren, 2003, Lindholm and Lundgren, 2009). Pre-dive hyperventilation prolongs time at depth, during which continued oxygen consumption lowers the concentration of oxygen in the lungs. Although the P_{O2} in the lungs at depth may be above the threshold for unconsciousness, the P_{O2} during ascent to the surface may decrease below that threshold due to the decrease in ambient pressure as the diver returns to the surface. This is a consequence of the fact that the partial pressure of a gas is the product of the gas's concentration and the ambient pressure (Henry's Law). While a given O_2 fraction in the lung may result in an adequate P_{O2} at depth, the decrease in ambient pressure during ascent may well result in a P_{O2} below the threshold for unconsciousness. The Korean ama do not hyperventilate prior to dives, and their mean end-of-dive arterial P_{O2} and P_{CO2} values are 60 and 50 mm Hg (8.0 and 6.7 kPa), respectively (Qvist *et al.*, 1993). In competitive breath-hold divers on the verge of unconsciousness, end tidal P_{O2}s have been as low as 19–22 mm Hg (near 3.0 kPa) (Lindholm and Lundgren, 1996, Overgaard *et al.*, 2006). Such episodes in competitive divers have been accompanied by elevations of biochemical markers for brain damage (Andersson *et al.*, 2009b, Liner and Andersson, 2009).

2.1.3 Oxygen storage

Total O_2 storage in a 70-kg human has been calculated to be near two liters, with 41% in the lungs, 44% in blood, 12% in muscle, and the remainder dissolved in solution in tissue. As reviewed in Ferrigno and Lundgren (2003), greater O_2 storage and longer dive durations in trained divers may be afforded through larger total lung capacity secondary to increased chest wall compliance. In contrast, the blood O_2 store, as reflected by the concentration of hemoglobin (Hb, the O_2 transport protein in blood)

is not elevated at rest in professional divers such as the Korean ama (Hurford *et al.*, 1990, Qvist *et al.*, 1993). However, during diving activity of the Korean ama, the magnitude of splenic contraction and subsequent elevation in blood Hb concentration appears to be greater in the ama than in non-diver controls (Hurford *et al.*, 1990). A 20% decrease in splenic volume in the ama was associated with a 10% increase in blood Hb content. Larger spleens and greater splenic contraction during breath holds have also been reported in elite competitive divers (Schagatay, 2012). Lastly, anaerobic metabolism as evidenced by blood lactate accumulation may also contribute to the diver's breath hold capacity (Ferretti *et al.*, 1991, Scholander *et al.*, 1962).

2.1.4 Carbon dioxide storage

Carbon dioxide storage in humans can be divided between a static store in bone (123 liters) and a labile component (16.6 liters), which is primarily in the lungs, blood, and muscle (Farhi and Rahn, 1960, Ferrigno and Lundgren, 2003). It is in that labile component in which CO_2 accumulates during a breath hold. It is notable that CO_2 storage capacity can be elevated two-fold in elite human divers (Ferretti *et al.*, 1991). Seventy percent of that CO_2 was estimated to be stored in the lungs and blood. Thus, an increased CO_2 storage capacity in trained or elite divers can also delay onset of the "breaking point" and so can prolong dive duration.

2.1.5 Metabolic rate and the dive response

Metabolic rate controls the rates at which oxygen stores are consumed and carbon dioxide produced during a dive. Consequently, because of the effects of P_{CO2} and P_{O2} on dive duration, metabolic rate is a significant factor in how long a diver can stay underwater on a breath of air. As will be reviewed in later chapters, heart rate is a prime determinant of metabolic rate because the oxygen consumption of many tissues is perfusion dependent. Declines in heart rate during breath holds were first noted in ducks by the French physiologist Paul Bert in the late 1800s (Bert, 1870). In 1935, Irving and colleagues suggested that this dive response (a low heart rate (bradycardia) and peripheral vasoconstriction) served to conserve oxygen for essential tissues (Irving *et al.*, 1935a).

In humans, a diving bradycardia was first reported in 1940 (Irving, 1963, Irving *et al.*, 1940). The subject was a professional underwater alligator wrestler, and his heart rate was as low as 30 beats per minute (bpm). Bradycardias of 40–50 bpm have been recorded in both Korean ama and Australian pearl divers (Hong *et al.*, 1967, Scholander *et al.*, 1962). During simulated dives of three elite divers to 50 m in a pressure chamber, heart rates and cardiac outputs declined to 20–30 bpm and 3 l min^{-1}, respectively (Ferrigno *et al.*, 1997). Evidence for peripheral vasoconstriction in human divers included post-dive elevations in blood lactate concentrations, maintenance and even elevation of blood pressure, decreased limb blood flow, and splenic contraction (Ferrigno *et al.*, 1997, Hurford *et al.*, 1990, Joulia *et al.*, 2009, Scholander *et al.*, 1962). The end result of these cardiovascular responses is conservation of blood oxygen; this has been demonstrated in many studies by decreases in arterial oxygen desaturation rates, and decreased pulmonary gas exchange (Andersson and Evaggelidis, 2009, Andersson *et al.*, 2002, 2008, Ferrigno and Lundgren, 2003, Joulia *et al.*, 2009). Thus, it is advantageous to have a slow heart rate during dives, and many competitive divers train and even use meditation techniques to relax and slow their heart rates during breath holds (Elsner, 2015)

2.1.6 Pressure: gas laws

The other major challenge faced by human breath-hold divers is depth (hydrostatic pressure). The primary physiological effects of pressure are two: gas compression and elevated blood nitrogen levels (P_{N2}). Both of these effects are due to the effects of pressure on gases, and are explained by well-known gas laws. Compression effects are due to Boyle's Law, which states that the product of pressure times volume is constant. Elevated P_{N2} is secondary to Henry's Law, which, as discussed above, states that the partial pressure of a gas is the product of its concentration and ambient pressure. Ambient pressure, of course, increases as the diver descends to depth.

2.1.7 Pressure: barotrauma

Increased ambient pressure can lead to tissue damage (barotrauma) when air volume within a relatively rigid body cavity is compressed to a lesser volume than that of the cavity (Ferrigno and Lundgren, 2003). Most divers are familiar with the need to equilibrate pressure within the chambers of the bony nasal sinuses and middle ear in order to avoid barotrauma to those structures (mucosal bleeding and ear drum rupture). The same constraint is also true of the thoracic cavity. Theoretically, the chest is at its lowest volume when the lung is at residual volume (RV), the lung volume after a maximal exhalation. In humans, this value is about 1 L or approximately 20–25% of total lung capacity (TLC). On the basis of the TLC/RV ratio, humans should not be able to breath-hold dive beyond a four- to fivefold compression of the lungs, i.e. about 40 m depth. Otherwise, the lung would be at less than RV, and the diver would suffer from "chest squeeze."

Clearly, human breath-hold divers are not limited to 40 m depth. There are several explanations. First, as described above, trained divers may have a more compliant chest wall, and lower effective RV. Second, exceptional divers may have larger than normal TLCs due to body habitus (Schagatay, 2012). Third, due to compression of the body, blood is redistributed from the extremities into the thoracic cavity. This can be as much as 1–2 L of blood (Craig, 1968, Ferrigno and Lundgren, 2003). This increased intrathoracic blood volume thus occupies space as the lung is compressed below residual volume. However, intrathoracic pooling of blood may also distend the pulmonary vasculature and heart, predisposing deep divers to pulmonary edema (Liner and Andersson, 2008), pulmonary hemorrhage (Lindholm *et al.*, 2008), and cardiac arrhythmias (Hansel *et al.*, 2009, Scholander *et al.*, 1962). Fourth, there are various pre-dive maneuvers which may increase the start-of-dive air volume in the chest (Ferrigno and

Lundgren, 2003). Both the ama and Tuamotuan pearl divers whistle as they exhale; this is thought to transiently increase intrathoracic pressure, decrease intrathoracic blood volume, and thereby allow for a larger final inspiration of air prior to a dive. And, then, there is "lung packing" (Lindholm and Lundgren, 2009). Here, the diver inhales to total lung capacity, and then gulps in air forcing it through an open glottis with a swallowing-like maneuver. This has been reported to increase TLC as much as 39%, thus creating a much larger TLC/RV ratio. This technique, however, elevates airway pressures, which may lead to lung rupture, and which may also decrease venous return to the heart, lowering blood pressure and predisposing the diver to loss of consciousness (Andersson *et al.*, 2009a).

2.1.8 Pressure: ambient pressure and heart rate

The potential contribution of hydrostatic pressure to regulation of heart rate during breath-hold dives has not been fully evaluated. In breath-hold dives of elite human divers to depths as deep as 50 m, the degree of bradycardia was similar to that during breath-holds of the same subjects at the surface (Ferrigno *et al.*, 1997). It was concluded that depth, per se, did not have an effect on heart rate. However, exposure of human subjects to 3–5 ATA ambient pressure (20–40 m depth) during saturation dives of several days' duration in hyperbaric chambers was associated with a 14–23% reduction in heart rate (Eckenhoff and Knight, 1984). In 2.5% of ECG records in this study, there were isolated supraventricular arrhythmias (atrioventricular nodal escape rhythms and wandering atrial pacemakers); these were associated with the slowest heart rates, and always resolved during exercise. Rare premature ventricular beats also occurred. In experimental studies, extreme increases in ambient pressure (150 ATA, 1490 m depth) did cause a 5–30% decrease in the spontaneous discharge rate of sinoatrial node pacemaker cells and 40% decrease in conduction velocity in the atria and ventricles (Daniels and Grossman, 2003).

2.1.9 Pressure: nitrogen, decompression sickness and nitrogen narcosis

The second major challenge due to pressure in human breath-hold divers is excess nitrogen absorption. Elevated blood nitrogen levels can lead to decompression sickness (DCS) as well as nitrogen narcosis. As the partial pressure of N_2 (P_{N2}) in the lung increases due to the increase in ambient pressure at depth, there will be greater uptake of nitrogen into the blood and tissues of divers. As will be discussed further in Chapter 12, DCS develops after return to the surface secondary to bubble formation due to an increased ratio of blood or tissue P_{N2} to ambient pressure. DCS most commonly occurs in SCUBA (self-contained underwater breathing apparatus) divers because there is a continuous air supply at high ambient pressure (and high P_{N2}) from the SCUBA tank. For a breath-hold human diver, the risk of excess nitrogen uptake from the lungs is probably mitigated by (1) a limited amount of nitrogen (one lung volume); (2) the relatively short duration of time at depth; (3) compression of the lungs and decreased alveolar gas exchange secondary to the development of ventilation–perfusion mismatch; and (4) decreased uptake of nitrogen due to a slower heart rate and lower cardiac output at depth (Ferrigno and Lundgren, 2003).

Nonetheless, DCS-like symptoms have been reported in breath-hold divers. Pearl divers from the Tuamotu Archipelago reported vertigo, syncope, partial paralysis, and even death after diving (Cross, 1965). The syndrome was called "taravana." Such episodes were associated with six-hour work periods of 1.5-min dives to 30-m depth with short surface intervals. Paulev also reported his own DCS experience after 60 1-min submarine escape dives from depths of 15–20 m over a five-hour period (Paulev, 1965). Most breath-hold divers, however, do not make such frequent, repetitive dives. DCS symptoms have not been reported in the Korean ama, presumably due to their relatively shallow, short-duration dives. In a study of Korean women diving 3–6 m deep, venous P_{N2} increased mildly from a baseline of 584 torr to 635 torr (77.9 kPa to 84.7 kPa); at the end of a three-hour work period, P_{N2} declined with a half-time of 36 min and reached baseline in 3–4 hours (Radermacher *et al.*, 1992).

The other potential complication of elevated nitrogen pressure is nitrogen narcosis. This depressant effect of nitrogen on the central nervous system occurs at P_{N2}s equivalent to 30-m depth (corresponding to a P_{N2} of 2400 mm Hg (320 kPa)) (Halsey, 1982). Although common in SCUBA divers, given the constraints described above for breath-hold divers and DCS, it is unlikely that nitrogen narcosis will occur in most human breath-hold divers.

2.1.10 Pressure: high pressure nervous syndrome

Another potential physiological complication due to pressure is high pressure nervous syndrome (HPNS, see Chapter 12 for discussion). Its onset in humans is at a depth of about 190 m (Halsey, 1982). HPNS has been observed during SCUBA diving and pressure chamber dives. Its occurrence in most breath-hold divers is unlikely given its depth threshold. However, competitive divers, as described above, have now reached this depth threshold. As depth limits are further pushed, HPNS may become a serious threat to the safety of such activities.

2.2 Challenges of the environment

The primary environmental physiological challenges to an animal descending into the ocean depths are pressure, the thermal conductivity and specific heat of water, and the absorption of light.

2.2.1 Challenges of the environment: pressure

Pressure increases by one atmosphere (ATM) every 10 m of depth. One atmosphere is equivalent to 760 mm Hg or 101.3 kPa. Some of the physiological consequences of pressure have already been alluded to above, and will be further discussed in Chapter 12. One other frequently used measure of pressure is the term "atmospheres absolute"

(ATA). At the surface, pressure is considered one ATM, and is equivalent to one ATA. At 10 m depth, the pressure has increased by one ATM and is at two ATA. In diving physiology, the use of the term ATA is thus an index of the ambient pressure at depth relative to that at the surface.

2.2.2 Challenges of the environment: temperature and heat loss

Heat loss of a human is greater in water than in air due to both the specific heat and thermal conductivity of water (Mekjavic *et al.*, 2003). Specific heat is the energy required to raise the temperature of 1 kg of a substance by 1 K (degree kelvin). The specific heat of water at 30 °C is 4180 joule kg^{-1} $°K^{-1}$; this value is more than four times greater than that of air. And, on a volume basis, the specific heat of water is even greater, at 3500 times that of air. Thermal conductivity is the quantity of heat that passes in a unit of time through a unit area of a substance with thickness equal to unity when its opposite face differs in temperature by one degree. The thermal conductivity of water at 27 °C is 6096 W cm^{-1} $°K^{-1}$, about 23 times that in air. In addition, heat loss due to convection is maximized in air with air speeds greater than 4.2 m s^{-1}, whereas in water it is maximized at 0.5 m s^{-1}. As a result, core temperature in humans decreases 2–5 times faster during immersion in water than during exposure to air at the same temperature.

As will be reviewed in Chapter 8, immersion in cold water elicits a range of physiological responses to prevent hypothermia. In humans, peripheral vasoconstriction and increased heat generation through muscular exercise or shivering serve to preserve core temperatures. However, additional insulation is needed in cold water, and has been achieved with the use of wet suits and dry suits. In animals, insulation is provided by fur, feather, and fat insulation (see Chapter 8). One additional physiological consequence of peripheral vasoconstriction and body compression at depth is the intrathoracic pooling of blood and distention of cardiopulmonary baroreceptors. Baroreceptor stimulation results in increased diuresis, which may predispose divers working in cold water over long periods to dehydration.

2.2.3 Challenges of the environment: light

The third environmental challenge faced by divers is the absorption of light by water (Duntley, 1963, Wozniak and Dera, 2007). Although less than 5% of sunlight is reflected by water, the penetration of light to depth is limited by scattering and by its absorption by water molecules, pigments, and various particulates. Red, yellow, and orange wavelengths are absorbed most quickly. By 1-m depth, 60% of incoming light has been absorbed, and by 10 m, 85% of light – and this is in clear water. The upper 100–200 m of the ocean are considered the photic zone, and by 150-m depth, 99% of light has been absorbed. Amazingly, blue-green light, the least absorbed, has been detected photoelectrically as deep as 600 m. Given the absorption of light by water and the dive depths of many of the species reviewed in Chapter 1, sensory adaptations are required in these animals for successful detection and capture of prey.

2.3 Sensory adaptations

Investigations of sensory adaptions have been primarily conducted in marine mammals. This research has focused on vision, tactile vibrissae, and sound production/hearing.

2.3.1 Sensory adaptations: olfaction

Olfactory adaptations have not been extensively studied, but it should be noted that olfactory structures in the central nervous system including cranial nerve I, the olfactory bulb, and olfactory tract are absent in all toothed whales examined to date (Oelschlager and Oeschlager, 2008). In mysticetes, a few observations suggested the presence of such structures, and, recently, anatomical examinations in bowhead whales (*Balaena mysticetus*) have confirmed their presence (Thewissen *et al.*, 2011). The authors suggested that olfaction may play a role in the detection of krill, on which these whales feed. Olfactory brain structures are present in pinnipeds, but whether olfaction participates in prey detection is unknown (Thewissen *et al.*, 2011, Watkins and Wartzok, 1985). Olfaction may play a significant role in location of prey by procellariiform seabirds. Dimethyl sulfide, a compound associated with phytoplankton, has been shown to attract petrels and prions at sea (Nevitt *et al.*, 1995). Behavioral investigations have also demonstrated that Humboldt penguins (*Spheniscus humboldti*) and South African penguins (*S. demersis*) are able to detect dimethyl sulfide (Culik, 2001, Wright *et al.*, 2011).

2.3.2 Sensory adaptations: vision

Successful detection of underwater prey is dependent on vision in many diving species. Visual adaptations have occurred at both the anatomical and biochemical levels. Because of the similarity of the refractive indices of water (1.34) and corneal tissue (1.35), the cornea does not participate in light refraction, and, as a consequence, is flattened in cetaceans, pinnipeds, penguins, and other seabirds (Martin, 1998, 1999, Martin and Brooke, 1991, Mass and Supin, 2009). In contrast, because of the refractive index of air (1.0), corneas in terrestrial mammals are convex, and the anterior chambers of eyes are larger than in marine mammals. In both marine mammals and diving birds, the lens tends to be spherical as it is primarily responsible for light refraction (Mass and Supin, 2009, Suburo and Scolaro, 1990).

Because of the absorption of light by water and decreased illumination at depth, the size of the eye and that of the fully dilated pupil are large, especially in deep divers (Levenson and Schusterman, 1997, 1999, Martin, 1999). It has also been noted that the range of maximum pupillary dilatation in the elephant seal (*Mirounga angustirostris*) and king penguin (*Aptenodytes patagonicus*), is extreme (469- and 300-fold, respectively) (Levenson and Schusterman, 1999, Martin, 1999). Those authors suggest that a pinpoint, constricted pupil at the surface limits incoming light sufficiently that the retina is pre-adapted for darkness (the retinal rod cells are not "bleached out"). Such dark pre-adaptation, as well as rapid pupillary dilation, during descent would allow optimal

retinal function even during the relatively short descent times of these animals. Evidence for this has been found in the elephant seal's dark adaptation curve; adaptation from daylight to maximum sensitivity requires only 6 min, similar to its descent times to routine foraging depths (Levenson and Schusterman, 1999).

In addition to a large eye, adaptations for low-light vision include a predominance of rod photoreceptors (98–99% of photoreceptors in pinnipeds and cetaceans) and a well-developed tapetum lucidum, the reflective layer which reflects light back through the retina and increases light sensitivity (Mass and Supin, 2009, Walls, 1942). There are no short-wave (S) cone cells in all cetacean and pinniped species examined to date (Levenson and Dizon, 2003, Peichl *et al.*, 2001). Peak sensitivity of the rod pigments of bottlenose dolphins is 488 nm, and is considered blue-shifted in relation to the 500–550 nm peak sensitivities of rods from terrestrial mammals and most pinnipeds (Levenson *et al.*, 2006, Mass and Supin, 2009). Only the rod pigments of the deep-diving elephant seals are as blue-shifted as in the dolphin (Levenson *et al.*, 2006, Lythgoe and Dartnall, 1970). The middle- and long-wavelength (M/L) cone pigments of pinnipeds have maximum sensitivities near 550 nm, again similar to terrestrial mammals but greater than that in the dolphin (525 nm) (Levenson *et al.*, 2006, Lythgoe and Dartnall, 1970). Overall, therefore, it appears that both the rods and cones of the completely aquatic cetaceans as well as the rods of the deep-diving elephant seals are blue-shifted in relation to terrestrial mammals. And, in both cetaceans and pinnipeds, there is an absence of S cones.

2.3.3 Sensory adaptations: touch

Tactile sensation may contribute significantly to successful underwater foraging. In manatees, modified vibrissae, perioral bristles, have a functional role in prey manipulation and ingestion (Marshall, 2009, Marshall *et al.*, 1998). The dense innervation of the elaborate vibrissae of ring seals and bearded seals is about ten-fold greater than in terrestrial mammals (Hyvärinen, 1989, Marshall *et al.*, 2006). It has been suggested that such vibrissae are adaptations for benthic foraging. In addition to a role in prey detection and ingestion, the vibrissae of some pinnipeds, may contribute to the long-range detection and tracking of prey. The whiskers of harbor seals (*Phoca vitulina*) are capable of detection of movement in water (Dehnhardt *et al.*, 1998). Blindfolded seals and sea lions can both successfully follow hydrodynamic trails (Dehnhardt *et al.*, 1998, 2001, Gläser *et al.*, 2011, Hanke *et al.*, 2010, Schulte-Pelkum *et al.*, 2007, Wieskotten *et al.*, 2011a, 2011b).

2.3.4 Sensory adaptations: sound production

The sounds created by prey, predators, and the environment undoubtedly contribute to the underwater behavior of both marine mammals and seabirds (Van Opzeeland *et al.*, 2010). Although relatively little is known about the role of sound in the activities of diving birds, sound production and hearing have been extensively studied in marine mammals, especially odontocetes, which use echolocation to find prey. Underwater sound production in pinnipeds and sirenians is thought to involve shunting of air between

the trachea and pharyngeal/nasal structures, and may involve vibration of tracheal membranes (Frankel, 2009). In mysticetes, sound production is probably accomplished through the vibration of a laryngeal U-shaped tissue fold, which, in contrast to the vocal cords of terrestrial mammals, is parallel to the flow of air (Reidenberg and Laitman, 2007). Sound frequencies range from as low as 7 Hz in the long-distance calls of blue whales (*Balaenoptera musculus*) to 24 kHz in singing humpback whales (*Megaptera novaeangliae*) (Frankel, 2009). Sound production in odontocetes, however, involves unique structures in the nasal region of the head. The "monkey lips"/dorsal bursae complex, located beneath the blowhole, is the source of clicks and whistles in odontocetes (Cranford *et al.*, 1996, 1997, Madsen *et al.*, 2013). Sound frequencies produced by dolphins and porpoises can be as high as 120 kHz or greater (Frankel, 2009). Readers are referred to detailed descriptions of the anatomy and pathway of sound transmission in these animals (Cranford *et al.*, 1996, 2008, Madsen *et al.*, 2013). In regard to physiology and compression due to pressure, the important point here is that the nasal passages, especially in deep divers, must have air available from the respiratory system for sound production at depth. For example, beaked whales do not begin to echolocate until they reach depths of 400–500 m (Johnson *et al.*, 2006, Tyack *et al.*, 2006).

2.3.5 Sensory adaptations: hearing

Adaptations for the underwater detection of sound by the ear are most extreme among the cetaceans. In pinnipeds, hearing in air is accomplished by sound transmission from the tympanic membrane (ear drum) to the middle ear ossicles and then to the cochlea. Underwater sound transmission in pinnipeds is thought to be accomplished through bone conduction (Nummela, 2009).

In sirenians, it is unclear how sound reaches the cochlea. The external auditory meatus ends in a blind sac. The middle ear bones are large and have the highest bone density of any mammal. It has been proposed that underwater sounds are transmitted via the zygomatic process of the squamous bone via bone conduction (Chapla *et al.*, 2007, Nummela, 2009).

In cetaceans, the external auditory meatus is narrow, and the tympanic membrane does not function in sound reception (Nummela *et al.*, 2007). Sound transmission to the inner ear of odontocetes occurs via fat pads extending from the mandibular canal (Cranford *et al.*, 2008, 2010, Norris, 1968). In mysticetes, the primary sound path to the inner ear probably involves the transmission of skull vibrations (Cranford and Krysl, 2015). Another mechanism may involve pressure transmissions through soft tissues. Fats pads adjacent to the inner ear have been recently documented (Nummela, 2009, Yamato *et al.*, 2012). Relevant to diving physiology and gas compression are the presence of air sinuses around the tympanic bulla, which isolate the inner ear and prevent bone conduction. Maintenance of this air layer even at depth is essential in odontocetes to allow for directional hearing (Nummela, 2009). As that air volume is compressed, "ear squeeze" is avoided by engorgement of large venous plexuses within the sinuses (Cranford *et al.*, 2010). Similar venous plexuses are also found in the middle ear of pinnipeds (Odend'hal and Poulter, 1966, Welsch and Riedel-Sheimer, 1997).