CONTENTS

1. Evolution

2. Diversity and Distribution

3. Anatomy and Physiology

4. Diving and Breath-holding

5. Sensory Systems

6. Feeding and Ecology

7. Intelligence and Communication

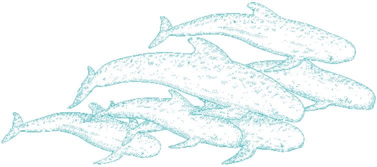
8. Social Structure and Mating Systems

9. Life History

10. Threats and Conservation

11. Myths and Folklore

12. Curious Facts



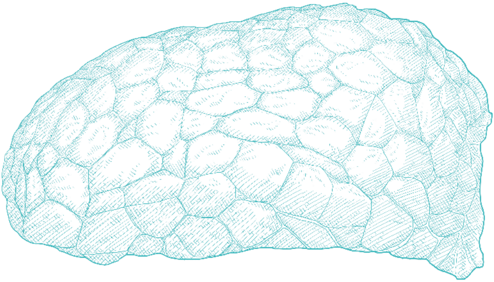
SALT AND WATER BALANCE

Humans are largely unaffected by short-term submersion in salt water, but if a human drinks salt water, dissolved salts will diffuse across the gut into the blood, where they will soon be removed by the kidneys. Unfortunately, the human kidney cannot produce highly concentrated urine, so a greater volume of water than was originally ingested is required to excrete the absorbed salts, causing rapid dehydration.

THE CETACEAN SOLUTION

Whales do two things differently: they get their water primarily from their food and they have kidneys that can make a more concentrated urine. Most bony fish actively regulate their body fluids to contain about one-third the salt concentration of seawater, similar to the body fluids of the whale. Thus, a whale that eats fish gains fluids (water) without excess salts. Whales that eat plankton or squid do not get the same benefit as fish-eaters because invertebrate bodies are isotonic with seawater (they have the same salinity), providing little advantage over drinking seawater.

Even eating fish is not a perfect solution, as an end product of digesting fish protein is urea, a nitrogenous waste that must be excreted in the urine, again leading to water loss. Thus, obtaining water from



food is not a complete solution. Ultimately, cetaceans rely on more efficient kidneys made up of many lobes, or reniculi, structures that are roughly the size and shape of grapes. Each reniculi acts as a mini-kidney, filtering the blood and collecting wastes to direct them toward the bladder. The cumulative efforts of the many reniculi—up to thousands per kidney—are more efficient than a typical kidney and produce urine with a higher salt concentration than seawater. Thus, cetaceans can excrete their accumulated salts without a net loss of water.

The impressive capabilities of marine mammal kidneys, however, do not make them the champions of salt and water balance among mammals. That title goes to desert-dwelling mammals, such as the kangaroo rat, whose kidneys can produce urine that is 17 times more concentrated than their blood, retaining fresh water while excreting unwanted wastes.

~ What about freshwater species? ~

River dolphins live in fresh water and do not have the same issue with salinity. It seems that other cetaceans should also be able to invade fresh waters easily, and although this is true in the short term, even estuarine cetaceans can experience potentially lethal difficulties with prolonged exposure to fresh water. The skin of most cetaceans is adapted to salt water, and skin lesions, infections, and increased vulnerability to unfamiliar freshwater pathogens can develop with extended exposure.

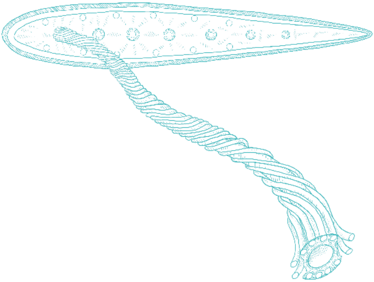
← The cetacean kidney is made up of many functional mini-kidneys called reniculi—up to thousands per kidney, depending on the species.

THERMOREGULATION

Cetaceans maintain an internal body temperature similar to that of humans and most land mammals. This is a challenge since water draws heat away much faster than air. One potential solution is to simply generate more heat with a higher metabolic rate, and in fact, most cetacean species have a slightly elevated metabolism for their size compared to land mammals. There is a limit to this strategy, however, because a higher metabolism requires more fuel, and whales can't simply buy more food at the grocery store. A larger size is also an advantage because in larger animals the ratio of the body's surface area to its volume is small, meaning that a large volume of tissue is metabolizing and generating heat, but there is proportionately less surface area through which the heat can escape. This is an obvious advantage for a large whale, but less so for a small porpoise. Nonetheless, many porpoises live quite successfully in cold waters, so there must be additional strategies.

CIRCULATORY ADAPTATIONS

The circulatory system is also adapted to retain heat through an ingenious system called countercurrent heat exchange. When blood runs near the surface of the body, it releases heat into the water and cools down. As that cold blood returns, the vein is routed alongside a countercurrent artery with warm blood coming from the body's



→ Countercurrent heat exchange vessel emerging from a dorsal fin cross-section consists of a central artery whose warm blood heats the returning cool blood in surrounding veins.

core. Because the blood in the vein and artery are flowing in opposite directions, there is a diffusion gradient for heat along an extended length of the vessels (the artery is always a little warmer than the vein, allowing heat to flow from high to low). Thus, the incoming blood is quickly warmed up to the desired temperature before returning to the body's core. To say that the two vessels run alongside one another is an oversimplification. In fact, the vein surrounds the artery, like a tube within a tube, although the outer "tube" is typically structured as multiple veins surrounding the central artery. This combined structure of countercurrent vessels maximizes the contact surface area and efficiency of heat exchange. Countercurrent vessels are prominently located in the areas most vulnerable to heat loss, including thin appendages such as the dorsal fin, tail fluke, and flippers, as well as the eyes and tongue (a mysticete tongue is enormous and is frequently exposed to cold water).

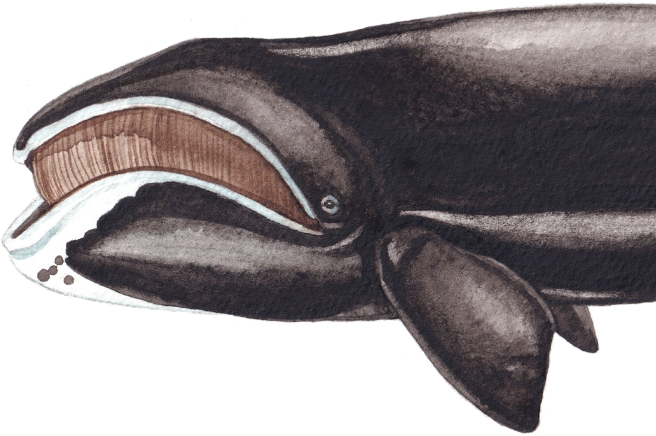
COOLING DOWN

Often forgotten, thermoregulation also requires cooling mechanisms when activity levels increase. In a dolphin dorsal fin, for example, countercurrent vessels run through the center of the fin, away from the cold edges. As activity heats up, the heart rate increases, pumping more blood and dilating the arteries. When the central artery of a countercurrent vessel expands, the surrounding veins are compressed, blocking the returning blood flow. The blood is diverted to peripheral veins near the surface of the fin, where heat can dissipate into cool adjacent waters. This elegant solution automatically switches from a warming to a cooling strategy when heat generation increases.

Another cooling example is the male testes, which require a cooler temperature than the rest of the body for sperm production. Most mammals solve this with external, scrotal testes, but cetacean testes are internal. They are cooled by specialized blood vessels carrying chilled blood from the dorsal fin and tail fluke that have bypassed any countercurrent warming.

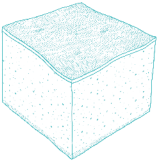
BLUBBER

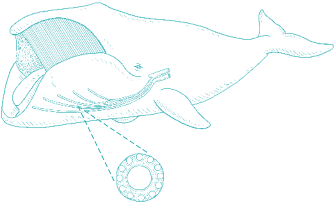
All cetaceans rely on an insulating layer of blubber surrounding their bodies between the skin and muscle. Blubber is a unique tissue not found in land mammals, consisting of a mixture of lipids (fats) and fibrous connective tissue. Oily yet firm and springy in texture, it serves multiple functions, including insulation (low thermal conductivity), energy and water storage for times of fasting or low food intake, buoyancy, and streamlining of the body. Both the thickness and composition of the blubber can vary by species and by position on the body. A higher ratio of lipid to connective tissue provides better insulation, and heat conductivity also varies depending on the type of lipid. Blubber thicknesses can range from less than an inch (2.5 cm) in some dolphins and porpoises to 19 in (48 cm) in bowhead whales. The thickness often changes seasonally in response to both changing environmental temperatures and extended periods of fasting or feeding.



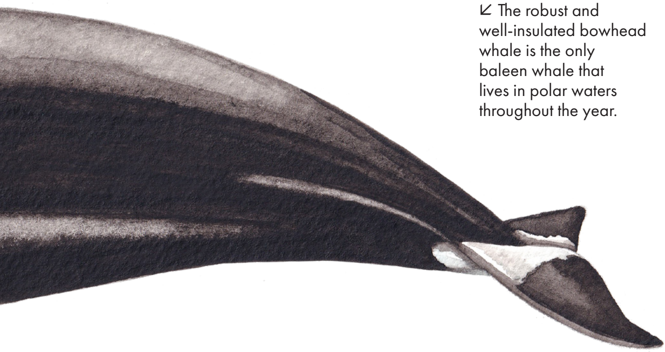
↓ The blubber layer of Arctic bowhead whales is the thickest of any species of whale and can be 19 in (48 cm) thick and greater than 40 percent of the whale's total body mass.

↓ Exposed to frigid polar waters for long periods of time while skim feeding, the enormous tongues of bowhead whales rely on numerous countercurrent vessels to retain heat.





↙ The robust and well-insulated bowhead whale is the only baleen whale that lives in polar waters throughout the year.



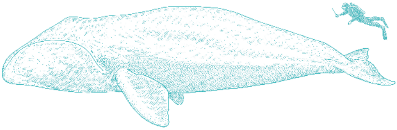
DIVING ABILITIES

With a maximum recorded dive depth of 1.86 miles (2,992 m) and a duration of 3.7 hours, the Cuvier's beaked whale (*Ziphius cavirostris*) holds the record as the deepest diving air-breathing animal. The much shallower-diving loggerhead sea turtle has the longest dive duration, with winter dives lasting 10.2 hours. Unlike the cold-blooded loggerhead, however, whales have a higher mammalian metabolism.

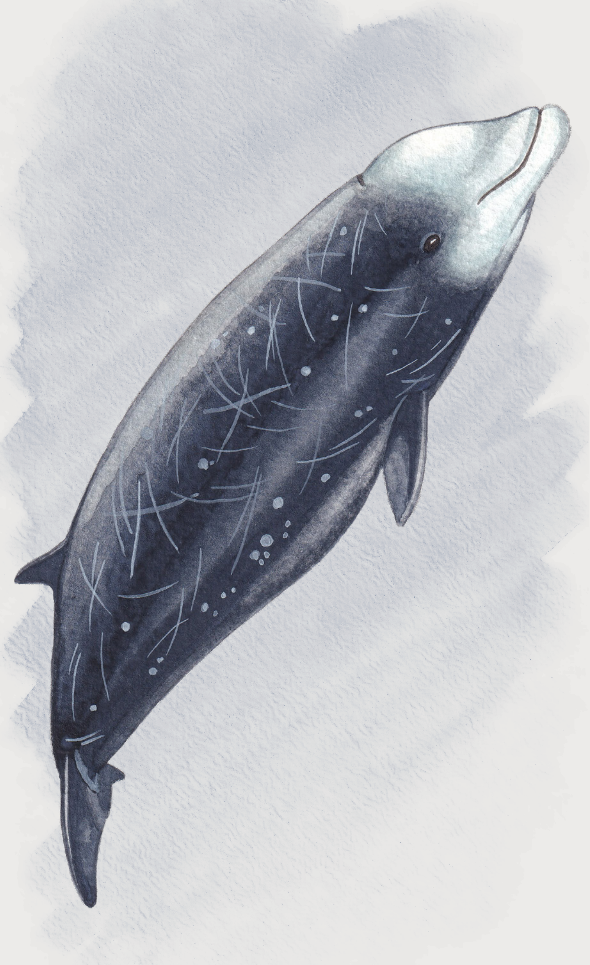
Diving abilities vary greatly among whales. The deepest divers, which also include sperm whales (*Physeter macrocephalus*) and various beaked whales, are all squid specialists. Squid and their relatives are essentially the only deepwater prey worth the trip. Most dives by these diving specialists are shorter and shallower than the record-setters. Numerous species with intermediate abilities exploit more abundant prey resources at depths of around 1,600–3,300 ft (500–1,000 m) or less, typically making dives less than 20–30 minutes long. Meanwhile, many coastal and river dolphins never encounter deep water and only dive for a few minutes, although most can stay down longer if needed.

↓ Time-depth recorder tags, like this suction cup D-tag, attach to whales for anywhere between hours and days. They collect detailed diving data for analysis.

↓ Bowhead whales (*Balaena mysticetus*) are the deepest diving mysticetes (1,909 ft/582 m), feeding on zooplankton overwintering near the seabed.



→ The Cuvier's beaked whale, inhabiting deep ocean waters and reaching lengths of up to 23 ft (7 m), is the deepest diving air-breathing animal. Only three other species are known to dive over 6,562 ft (2,000 m) deep, the sperm whale, the northern bottlenose whale (*Hyperoodon ampullatus*), and the southern elephant seal.



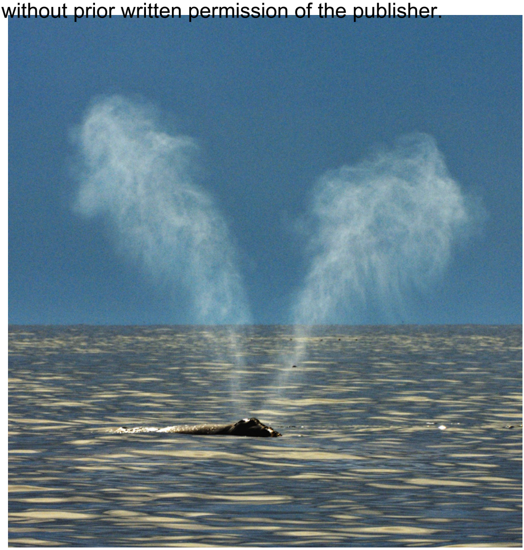
OXYGEN EXCHANGE

Oxygen storage begins with oxygen exchange. Since whales surface less frequently than a typical mammal takes a breath, they must exchange more air per breath. In fact, whales exchange 80–90 percent of the air in their lungs with each breath, as compared to about 10 percent for humans.

Not only do the lungs need to exchange a large volume of air, but they also need to do so quickly. The dorsal position of the blowhole on top of the head greatly improves the swimming efficiency of cetaceans when breathing, but whales need to exhale and inhale quickly in order to remain in an optimum swimming posture, minimize surface turbulence and drag, and maintain momentum. The powerful cetacean diaphragm sits at an oblique angle within the chest, and when it contracts it squeezes the lungs against the solid dorsal wall of the body cavity, virtually crushing the lungs as the air is forced out. The elastic lung tissue is able to withstand this abuse and still spring back when air rushes back in.

LUNGS ARE NOT FOR STORAGE

An understandable assumption is that whales have enormous lungs to store more oxygen, but in reality, that is not the case. In addition to being a buoyancy problem, oxygen stored in the lungs is oxygen not being used, and the better strategy is to redistribute it to where it is needed. Once air fills the lungs, the oxygen is quickly transferred to the blood via dense capillary networks that surround the terminal air sacs, or alveoli.



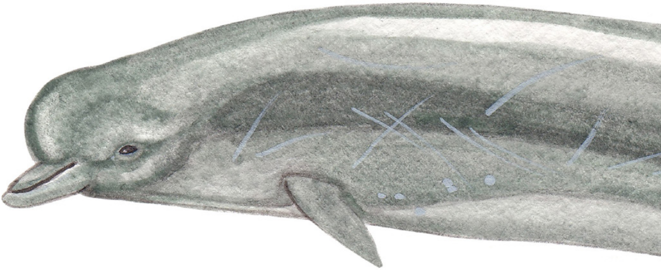
THAR SHE BLOWS!

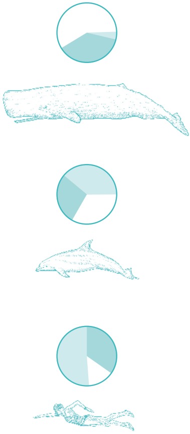
The iconic whale blow (a right whale is shown above, with its spaced nostrils producing a distinctive V-shaped blow) occurs as a muscular plug contracts to open the blowhole and air is rapidly exhaled, an event that is vastly underappreciated. A blue whale (*Balaenoptera musculus*), for example, exhales about 528 gallons (2,000 liters) of air (picture one thousand 68-fl-oz/2-liter drink bottles) in just a couple of seconds through two blowholes about 18 in (46 cm) in diameter. The warm air is further heated under this pressure as it moves through airways toward the blowhole and then instantly expands and cools after it escapes, causing water vapor in the breath to condense. This sudden appearance of water is often mistaken for a waterspout coming out of their head.

OXYGEN STORAGE

Oxygen storage strategies vary by whale species and diving ability. While humans store at least half of their oxygen in their lungs, that proportion drops to about a third in shallow-diving coastal bottlenose dolphins (*Tursiops* species) and to only about 5 percent in deep-diving sperm whales. Instead of the lungs, cetaceans store oxygen primarily in their muscles and blood. In muscle, oxygen binds to myoglobin, a protein also present in the muscle of land mammals, but its concentration in whales is 10–30 times higher, especially in the swimming muscles.

In all mammals, oxygen in the blood binds to hemoglobin, a protein found within red blood cells, but cetaceans have a higher concentration of red blood cells per unit of blood, and the volume of blood in their body is two to three times the expected volume for a similar-sized land mammal, especially in deep-diving species. Collectively, these adaptations result in a stored volume of accessible oxygen that can be several times more than what would be expected for land mammals.





← A comparison of oxygen storage sites for a deep-diving sperm whale, a shallow-diving coastal bottlenose dolphin, and a human, showing the proportions stored in the blood (dark), lungs (medium), and muscle (light). Each also stores a small amount of oxygen directly in various organs, especially the brain, which is not shown in this comparison.

↓ The northern bottlenose whale, which is found in the North Atlantic, is among the deepest-diving beaked whales, with dives of over 6,560 ft (2,000 m) deep and durations of more than two hours. The deepest-diving whales store more oxygen in their blood and muscles and less in their lungs.

OXYGEN RATIONING

Additional oxygen storage by itself would enable some whales to dive up to three times longer than a really good human free-diver, but that is a long way from a two-hour sperm whale dive. Oxygen use is behaviorally reduced by the liberal use of passive gliding, especially during the descent and ascent, but the success of long dives relies much more on a series of circulatory system adaptations that ensure the frugal and efficient use of oxygen.

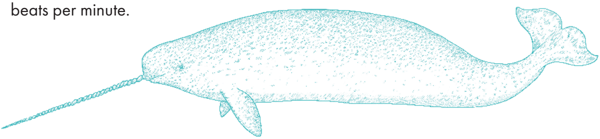
BRADYCARDIA

The first of these adaptations is a dramatic decrease in heart rate, or bradycardia, that occurs during a dive. The heart rate drops to about 10 percent of its normal rate, although there appears to be some degree of conscious control, as longer dives have more extreme bradycardia from the very start. Bradycardia causes oxygen rationing: slower delivery means slower usage.

SELECTIVE RESTRICTION

The second major adaptation is peripheral vasoconstriction, a systemic constriction of blood vessels that cuts off most circulation to the muscles and peripheral areas of the body. The muscles already have their own oxygen stores in their myoglobin, so vasoconstriction prioritizes circulating oxygen for important organs like the heart and brain. Other organ systems, such as the liver, kidneys, and intestines, receive reduced blood flow and decrease their activity during diving.

↘ Bradycardia champions: the heart rate of diving narwhals (*Monodon monoceros*) can drop to only three beats per minute.



CARBON DIOXIDE BUILDUP

Carbon dioxide is the by-product of cellular respiration and, as a dive progresses, it continues to build up in the blood and tissues, increasing acidity. In humans, a high carbon dioxide concentration in the blood triggers the eventually irresistible breathing reflex, but cetaceans are voluntary breathers, so they must think about every breath they take. Whales are resistant to this impulse to breathe and are more tolerant of increased acidity, in part due to greater buffering capacity that limits the change in pH. Nonetheless, when whales finally surface after a dive, they switch to a very rapid heart rate for a short time (tachycardia) in order to rapidly circulate and remove the carbon dioxide (which is exhaled from the lungs), restore blood pH, and recharge the oxygen stores in the blood and muscles.

~ Temporary blood storage ~

Such extreme vasoconstriction means that the volume of blood in the body now has much less plumbing to reside in, and without further adjustments, blood pressure would spike and the heart and vessels would burst. To prevent that from occurring, cetaceans have extensive areas of retia mirabilia (wonderful nets), tangled complexes of normally empty blood vessels that are able to receive blood and act as overflow reservoirs when other vessels have closed down. The most prominent of these networks is ingeniously located adjacent to the lungs along the dorsal body cavity wall, and when increasing pressure during dives compresses the air in the lungs, the increased volume of the blood storage vessels helps to partially counter the collapse of this space.

~ Pumping against pressure ~

Many whales also have an enlarged aortic bulb, which is a wide section of the main artery leaving the heart. The bulb's elastic walls swell with blood when the heart beats, and then the elastic recoil keeps the blood moving during the time between beats, helping to mediate blood pressure fluctuations and relieve strain on the heart.

ANAEROBIC RESPIRATION

Even with their many adaptations for storing and using oxygen, whales will eventually run out of oxygen if they stay submerged long enough. That does not always mean the end of a dive, however, since whales can extend their dive time using anaerobic respiration.

WHAT IS ANAEROBIC RESPIRATION?

The longest dives require anaerobic respiration, or the conversion of carbohydrates into energy in the absence of oxygen. This is a short-term solution to oxygen depletion that is employed by all mammals, but it has a cost. Aerobic (oxygenated) respiration is 19 times more efficient than anaerobic respiration at converting sugars into energy, and the by-product of anaerobic respiration is lactic acid, which must be broken down and removed fairly quickly. That process requires oxygen, so the animal cannot long delay its return to oxygenated conditions. Thus, anaerobic respiration is only used when it is worth it—for example, to remain in a rich prey patch during a dive.

HIGH TOLERANCE FOR ANAEROBIC RESPIRATION

Whales and deep-diving seals are experts at managing anaerobic respiration, since their blood and tissues have a high buffering capacity to mediate increases in acidity (see page 53). In addition, peripheral vasoconstriction during the dive ensures that most of the lactic acid produced in the muscles and other isolated tissues does not circulate in large amounts, thus protecting the brain and heart from acidic conditions. Upon surfacing from an anaerobic dive, whales must circulate fresh oxygen to metabolize and eliminate the lactic acid. This is enhanced by the increased heart rate that always occurs upon surfacing, but for anaerobic dives, the heart rate is particularly fast.

→ A sperm whale descends to the depths. On their longest dives, more than half of the dive is anaerobic.

HOW MANY DIVES GO ANAEROBIC?

It is difficult to determine how long a whale's oxygen supplies will last. Sperm whales can dive for two hours, but most dives last less than 45 minutes, and it is assumed that the aerobic dive limit is about that long. Whales often take a longer surface interval between dives following an anaerobic dive, giving more time to eliminate the lactic acid and recharge oxygen stores. However, this is not always the case, and beaked whales in particular are mysterious. Cuvier's beaked whales do not take longer breaks after dives exceeding 75 minutes, suggesting that they either have very long aerobic dive limits or unusual abilities to manage the effects of anaerobic respiration.

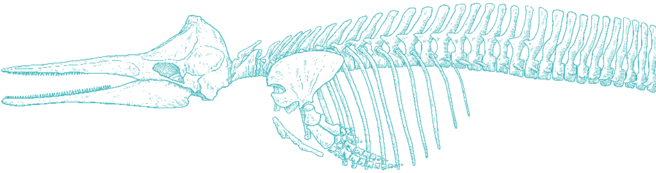
PRESSURE

By simply diving in the deep end of a swimming pool, we are acutely aware of the pressure from the weight of the overlying water. Whales dive much deeper and have developed adaptations to deal with increased pressure.

THE COLLAPSIBLE RIB CAGE

You have likely felt the pain of an ear squeeze when diving just a few meters deep. Whales do not have that problem because they don't have large air spaces in their middle ears or sinuses to be squeezed. Their lungs, however, compress as water pressure increases. If a human free-diver goes too deep, their lungs and chest will collapse beyond recovery. In contrast, the more elastic fibers of cetacean lungs spring back from complete collapse, and interestingly, so can their rib cage. Whales have more floating ribs (ribs that do not connect to the sternum) than terrestrial mammals, and even the sternal ribs are either cartilaginous or connect with flexible ligaments that allow the rib cage to temporarily collapse during deep dives.

↘ Deep dives require partial collapse of the rib cage, made possible by numerous floating ribs and flexible rib joints.



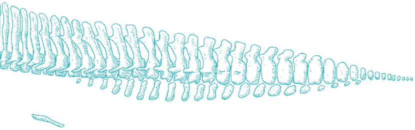
THE DECOMPRESSION PROBLEM

Another potential pressure-related problem is decompression sickness (DCS, also known as “the bends”), a well-known hazard for scuba divers who stay down too long or ascend too quickly (see Chapter 12, page 145). At depth, higher pressures allow more gas to dissolve in the blood than at the surface. If a diver ascends too quickly, the decreasing pressure causes the gas to bubble out of solution within the blood vessels before it can be expelled at the lungs. The bubbles can block circulation, causing injury or death. The main culprit is nitrogen, an inert gas that makes up 78 percent of air and is abundant in the blood.

DCS is a significant risk for scuba divers, who continually breathe compressed air at depth, but even free-diving whales can get DCS under the right conditions. While at depth, nitrogen in the lungs from a whale’s initial breath at the surface can diffuse into the blood in larger amounts than it would at the surface. If the whale surfaces for a short interval and re-submerges for the next dive before it has outgassed all of the previously absorbed nitrogen, it will carry down a slightly elevated blood nitrogen content. If the whale does this over and over, it can gradually build up enough nitrogen in its blood to cause bubble formation.

~ Preventing bubble formation ~

Generally, cetaceans avoid DCS because their lungs collapse at depths of 164–328 ft (50–100 m), depending on the species. As the lung’s alveoli air sacs collapse under pressure, air is pushed into the bronchiole air passages, which are held open with stiff cartilage rings. With no air in the alveoli, no gases are exchanged with the blood at high pressure, so blood nitrogen levels do not rise and DCS is avoided. A whale can still be vulnerable to DCS, however, if it dives repeatedly, with short intervals between dives, to depths slightly above where the lungs collapse.



SOUND AND HEARING IN WATER

Hearing is the most important sense for whales, effective across long distances and unhindered by dark or murky water. Sound travels farther and faster in water than in air. Low frequency (low pitch) sounds in particular can travel across whole ocean basins, and under the right conditions, whale calls can potentially travel thousands of miles. Whales are known to react to calls on the scale of tens of miles, but whether they actually share information over hundreds of miles or more is a fascinating and unanswered question.

FREQUENCY RANGES FOR HEARING

Most of what we know about hearing in whales comes from captive studies of smaller odontocetes. Humans can hear frequencies ranging from low-pitch sounds at 20 Hertz (Hz, wavelengths per second) to high sounds around 20,000 Hz (20 kHz). Mysticetes can generate and hear infrasonic sounds as low as 10 Hz, too low for humans to hear, despite being quite powerful. Their upper frequency range is unknown but unlikely to be much over 20 kHz. Odontocetes can hear across a much wider range of frequencies, from about 70 Hz to over 150 kHz, depending on the species. The emphasis on ultrasonic (greater than 20 kHz) sounds among odontocetes is important for echolocation (see page 64). Echolocation is an active sense in which sound is directed toward a target and the returning echo provides information about size, shape, and distance. Echolocation occurs in a handful of animal groups (sight-impaired humans have shown modest abilities), but truly advanced abilities are only found in toothed whales and bats.

→ This common dolphin (*Delphinus delphis*), which stranded alive with other pod members, is given a painless hearing test to assess its health prior to being cleared for release.

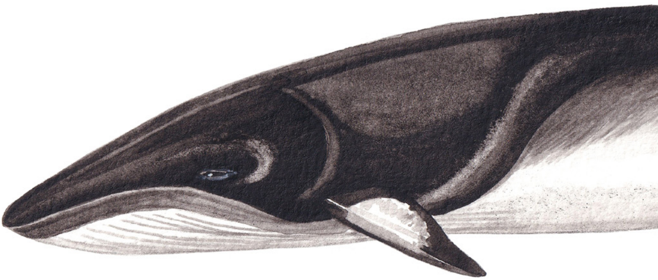
HEARING BY BONE CONDUCTION

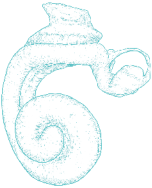
Underwater hearing in cetaceans relies on sound conduction via bones and acoustic fats. The densities of water and the soft tissues of the body are similar, so sound waves in water pass right through soft tissues and reflect off the dense bones, causing the bones to vibrate. This is how humans hear under water as well, but our ears are not built for bone conduction, so many sounds are muffled and dull. Furthermore, the sound waves vibrate the entire skull, disguising whether the sound reaches the right or left ear first and eliminating our directional hearing. Cetaceans, especially odontocetes, have perfected hearing via bone conduction.

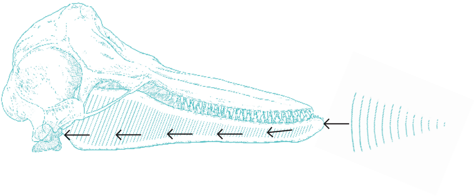
HEARING

Cetaceans receive sounds primarily via vibrations of the mandible, or jawbone. In odontocetes, the partially hollow jawbone is filled with specialized acoustic fats that provide exceptional conduction of sound directly to the left and right auditory bullae (ear bones), abutting the base of the jaw.

A defining character of cetaceans in evolutionary studies, the auditory bulla is comprised of two dense bones, the tympanic and periotic, which house the middle and inner ears. Suspended from the skull by ligaments and encased in foamy, oily tissue, the bulla is isolated from the disruption of additional acoustic vibrations from the skull. The ear drum has morphed into a calcified ligament that helps to transfer tympanic bone vibrations to the three tiny, middle ear bones within and, as in terrestrial mammals, these “ossicles” transfer vibrations to the cochlea, a fluid-filled, spiraling organ whose hair cells vibrate and fire, sending information about sound frequency and power to the brain.



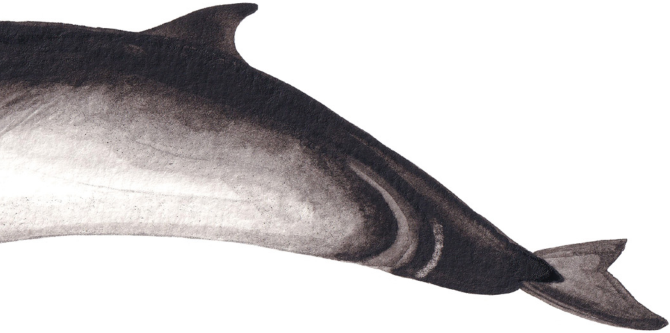




↑ Found within the periotic bone, the cochlea is the inner ear organ that interprets the frequency and power of sounds. Sensitive hair cells fire as they sense vibrations, sending information to the brain.

↑ Sounds are transmitted to the ear via specialized acoustic lipids in and around the jaw that help to conduct sound vibrations along the mandible, delivering them directly to the adjacent auditory bulla.

↙ The first hearing test of a baleen whale was recently conducted on a northern minke whale (*Balaenoptera acutorostrata*), revealing a wide frequency range, extending slightly into the ultrasonic range.



ECHOLOCATION STRUCTURES

Echolocation is an active sense—cetaceans must intentionally make sounds in order to generate echoes for interpretation. Although mysticetes may use a primitive version to interpret navigational echoes from the seafloor and major underwater features, only the odontocetes have evolved a precise underwater echolocation sense routinely used for fine-scale investigations and orientation.

ECHOLOCATION ABILITIES

Echolocation is often described as "seeing with sound." In controlled studies, captive dolphins can observe a complex shape under water using only echolocation and then distinguish it from a similarly complex shape using only vision, demonstrating both the fine-scale resolution of echolocation and the translation of information between echolocation and vision. Unlike vision, echolocation can provide precise measurements of distance, size, and even body composition, as the characteristics of echoes vary with the density and internal components of objects. Objects with large density differences, such as fish with air-filled swim bladders, are particularly good reflectors, while a large, colorful jellyfish with a density similar to water is much harder to detect.

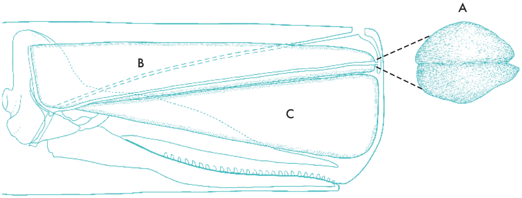
SOUND GENERATION AND FOCUSING

Both observations and anatomy suggest that baleen whales generate sounds in their larynx like other mammals, but odontocetes produce both their echolocation clicks and communication (whistle) sounds from a pair of muscular "phonic lips" located between the skull and blowhole and associated with a system of nasal air sacs. Air moving into and between the sacs is forced through the phonic lips, causing them to vibrate and generate sound. Much of the sound passes forward into the adjacent melon, which is the large, fatty forehead of odontocetes. The melon fats are specialized, low-density lipids with excellent sound conduction properties, similar to those of the jaw. Like a hand lens with light, the melon serves as an acoustic lens, creating a focused beam of sound that proceeds from the front of the

THE UNIQUE SPERM WHALE DESIGN

Sperm Whales (*Physeter macrocephalus*) represent an intriguing exception to the general odontocete design. Their enormous head is dominated by two large features: the tapered, barrel-shaped spermaceti organ, encased within cable-like, fibrous strands and filled with over 500 gallons (about 2,000 liters) of liquid spermaceti oil, and the underlying "junk," a layer of oily tissue of lesser value to early whalers in comparison to the more accessible liquid spermaceti oil (see Chapter 11, page 140).

Winding between and around these features, one of the nasal passages leads to a blowhole at the front tip of the head and another leads to the phonic lips (A) and associated air sacs that generate sound at the anterior tip of the spermaceti organ (B). The sound is projected back through the spermaceti organ toward air sacs along the nearly vertical wall of the skull, where it is reflected forward again through the junk (C), which serves as the focusing melon for sperm whales. At peak power, the resulting beam of sound is possibly the loudest sound generated by any animal.



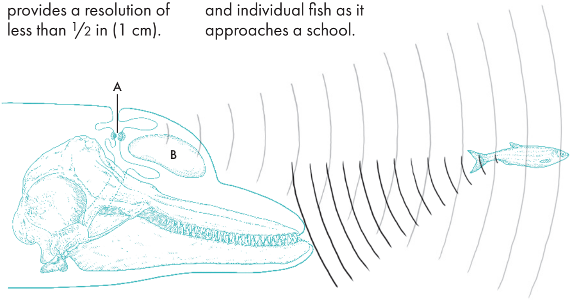
melon. Any generated sounds that are directed backward will be reflected forward again through the melon by the odontocete skull, whose parabolic shape was evolutionarily crafted for this purpose. Thus, the majority of the sound energy is directed forward into a highly directional beam in search of a target. When the echoes return, the sounds are received via the lower jaw, as previously described.

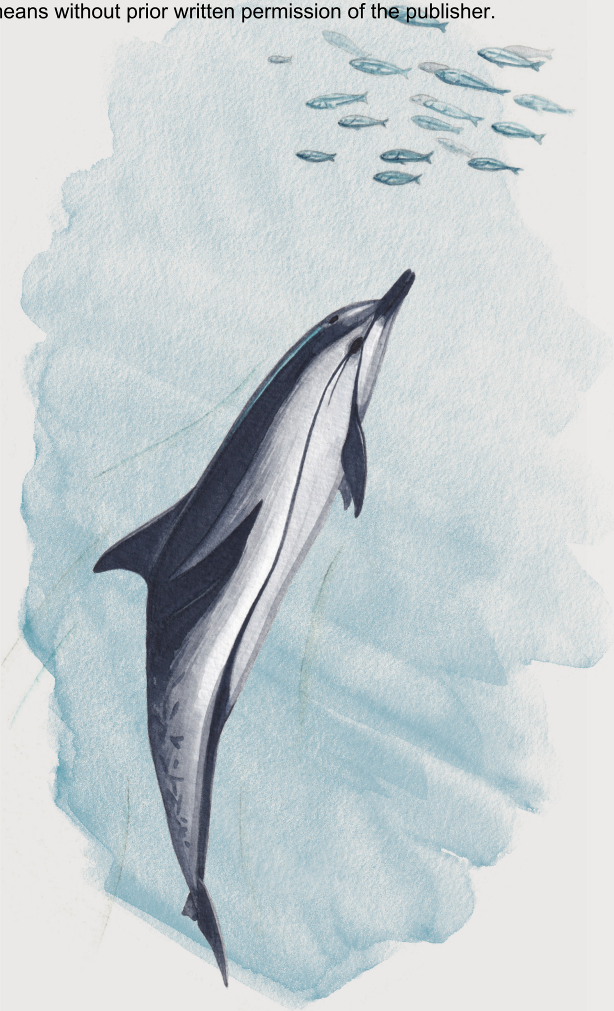
ECHOLOCATION IN ACTION

Since the determination of distance to a target requires a distinct start time and return time for sound, echolocation sounds are very short-duration "clicks." Odontocetes send out another click only after the first echo returns, with a series of clicks forming a rapidly repeating click train or "buzz." The clicks span a broad range of frequencies. Lower frequencies travel long distances, but their long wavelengths will not reflect off objects smaller than the wavelength. Higher frequencies, with shorter wavelengths, reflect off smaller objects and provide higher resolution, but they dissipate quickly, so have a limited range. Thus, a dolphin may initially search using clicks with a peak frequency (greatest power) around 7 kHz, capable of detecting an 8-in (20-cm) fish hundreds of yards away, but as the dolphin gets closer, peak frequencies will increase to provide greater detail, while the click repetition rate gets faster since each echo returns more quickly. At close range, hundreds of echolocation clicks (up to 150 kHz) are generated each second.

↓ Echoes return from sounds generated in the phonic lips (A) and focused by the melon (B). A 150 kHz frequency provides a resolution of less than ½ in (1 cm).

→ A striped dolphin (*Stenella coeruleoalba*) relies on echolocation to identify school size, movement patterns, and individual fish as it approaches a school.





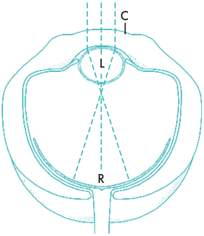
VISION

The eye lens commonly gets all the credit for focusing, but two-thirds of the focusing in human vision occurs when light bends (refracts) as it passes from air into the denser cornea and fluid-filled eyeball. The elliptical shape of our convex lens is designed to complete only the final third of focusing, delivering a crisp image to the photoreceptors lining the retina.

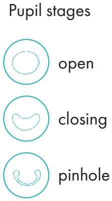
Ciliary muscles within the eye slightly deform the shape of the lens for fine-scale focusing of close or distant objects. Under water, however, the tissues and fluids of the eye are similar in density to the water, so the bending of light at the cornea is largely eliminated. Our elliptical lens is simply not strong enough to do all of the focusing by itself, so the focusing point under water ends up well beyond the back of the eye, resulting in a blurry image.

CETACEAN FOCUSING UNDER WATER

Physics works the same for whales—refraction by the cornea is negligible under water. However, whales (and fish) have solved the underwater focusing problem by having a spherical lens. The spherical shape bends light more strongly, focusing the image on the retina all by itself. Cetaceans lack ciliary muscles (a spherical lens is not easily deformed), so any fine-scale focusing that may occur is thought to be caused by muscles shifting the position of the eyeball within the orbit, altering the intra-occular pressure and moving the lens slightly forward or back.



← Cross-section of a cetacean eye, showing: (C) the slightly flattened cornea, (L) the round lens, and (R) light projecting on to the retina. The closing of the pupil results in pinhole openings that assist with in-air focusing.



LOW LIGHT AND COLOR VISION

Nearly all photoreceptors in the whale retina are rods, specialized for low light levels in deep or murky waters. When fully dilated under water, the extra-large pupil collects as much light as possible and a reflective layer behind the retina called the tapetum lucidum reflects light back through the photoreceptors a second time, acting as an efficient light multiplier. In addition to rods, 1–2 percent of cetacean photoreceptors are cone cells, required for color vision. However, the types of cones present are calibrated for blue or green wavelengths, the most abundant wavelengths in water, and this limited variety does not span enough wavelengths to allow a comparative perception of colors. Behavioral studies in aquaria also indicate that dolphins do not distinguish colors.

CETACEAN FOCUSING IN AIR

Amazingly, cetaceans also have good vision in air, even though their strong spherical lens should combine with corneal refraction in air to over-bend incoming light. The mechanism by which they avoid this problem is not fully understood and likely has multiple components. Many cetaceans have a partially flattened cornea, minimizing the corneal refraction in air for perpendicular, incoming light. The cetacean pupil also constricts unconventionally, forming a U-shaped slit that closes almost completely in bright, aerial conditions, leaving two pinhole openings at either end of the U. Light passing through a tiny opening has a focusing effect, so a pinhole pupil or a narrow slit can potentially deliver focused light over a range of distances. The pinhole openings line up with regions of high nerve cell density in the retina, suggesting alternative specialized focal regions for underwater and aerial vision. Light passing through these pinhole areas may also be directed along peripheral regions of the lens, potentially refracting differently than when passing through the core.

OTHER SENSES

Though hearing, echolocation, and vision have dominated researchers' attention, whales also rely on other senses, including chemoreception (taste and smell), touch, and, at least in some species, an electromagnetic sense.

SMELL AND TASTE

The sense of smell is understudied in whales. It has been completely lost in odontocetes, but mysticetes still have olfactory receptors, along with an olfactory nerve and bulb (brain region). Given their lack of echolocation abilities, a sense of smell may help mysticetes identify productive feeding waters, which often have a rich, organic, fishy odor.

The sense of taste is present in both toothed and baleen whales, with taste buds in localized areas on their tongues. Cetaceans have evolutionarily lost the primary genes for nearly all major taste categories (except "salty"), but in behavioral studies, trained dolphins have responded to each category—although their sensitivity is often very low. Despite these results, dolphins routinely press their rostrums to genital areas and swim through excretions of other dolphins, leading to speculation that they may identify excreted hormones and other signaling molecules based on taste.

TOUCH

The tactile sense is most developed in two regions of the cetacean body: the area surrounding the blowhole, which facilitates the timing of breathing as the animal clears the surface, and the sensory hairs (vibrissae) and empty hair follicles of the rostrum and chin. Humpback whales (*Megaptera novaeangliae*) have an array of fist-sized bumps (tubercules) on their rostrum and chin, each with a single, stiff vibrissa hypothesized to identify vibrations from prey aggregations in the water. Most dolphins have vibrissae along their rostrum that fall out before or soon after birth, although Amazon river dolphins (*Inia geoffrensis*) retain them as adults. The empty follicles remain well enervated for life, and dolphins will sometimes investigate objects by rubbing their rostrums against them.

Interestingly, the empty rostral hair follicles of bottlenose dolphins (*Tursiops* species) and Guiana dolphins (*Sotalia guianensis*) have recently been shown to develop into electroreception organs in adults, capable of detecting weak electric fields like those produced by the muscular ventilation of fish gills. Although not quite as sensitive as sharks to electric fields, this ability is another tool for locating hidden bottom-dwelling prey at close range. It also suggests a potential mechanism for a biomagnetic navigational sense, long hinted at by studies correlating live whale stranding patterns with the orientation of magnetic field lines and other geomagnetic anomalies.

↓ Small hairs on the rostrum and chin of this southern right whale (*Eubalaena australis*) provide a tactile sense that has been hypothesized to aid in sensing feeding currents.

SKIMMERS AND GULPERS

Depending on the species, mysticetes have 200–400 baleen plates on each side of their upper jaw. The size and structure of the baleen, and the entire body plan, is closely linked to the feeding technique they use.

SKIMMERS

The balaenids—right whales and bowhead whales (*Balaena mysticetus*)—are skimmers. These whales, which reach lengths of around 45–60 ft (14–18 m), hold their mouths wide open as they swim through dense zooplankton patches of mainly copepods (crustaceans less than half the size of a grain of rice), or somewhat larger, shrimp-like krill. Water enters at the front and filters out the sides through their 8–10-ft (2.5–3-m) long baleen. Emerging from the gums and made of keratin, baleen is akin to an enormous fingernail hanging

(continued...)

INDEX