EXTREME ADAPTATIONS IN CETACEANS: DEEP DIVING BEHAVIOR AND PHYSIOLOGY

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Author Note

Literature reviews are a tool used by the scientific community to gather and present current information on a particular topic of interest. The goal of this project was to provide well supported information from professional sources in the field of Cetology. All scientific claims and experimental information contained within this document were derived from outside sources. Various resources, to include the university library and research databases, were used to gather reference material cited within this document. As members of the scientific community, we hope that this information can be used to educate others and further demystify the behavior and physiology of deep diving mammals.

ABSTRACT: The term cetacean refers to a unique group of oxygen breathing aquatic mammals, more commonly these species are known as porpoises, whales and dolphins. Around 88 species are classified within this category. The evolutionary history accepted by the general scientific community suggests that cetaceans may have evolved from quadruped type land animals that lived millions of years in the past. Most modern cetaceans exhibit similar physiological traits between species. Examples of this include: modified nostrils (blowholes), slender bodies, smooth skin and extensive thermal insulation. Of these characteristics, one of the most crucial to aquatic survival is an effective respiratory system. Since cetaceans all intake oxygen directly from the air, they must resurface to expel carbon dioxide and intake oxygen to fuel metabolism. Naturally speaking, the more effectively cetaceans can hold their breath, the better chance they have of evading predators and searching for food. As such, extreme adaptations like deep diving behavior have allowed consecutive generations of these creatures to feed and reproduce exceptionally well. It is important to note that the term "deep diving" does not necessarily represent physical depth but rather time spent below surface. This extreme adaptation is not singular and works through the regulation of many different bodily processes. Some examples of these include: Elastic arteries, respiratory physiology, gas regulation, myoglobin, blood circulation, and metabolism.

Keywords: cetacean, whale, adaptation, deep-diving, ecology, behavior, physiology

Deep diving Cetaceans are found in almost all non-landlocked aquatic regions throughout the world (IWC, 2016). A majority of deep diving species live in waters of the Pacific and Atlantic Oceans. The deepest diving cetacean is known as Cuvier's beaked whale (Ziphius cavirostris). Coastal species such as the killer whale (Orcinus orca) typically prefer shallower regions of the arctic. Some species translocate to many different ecological regions, like the Blue Whale (Balaenoptera musculus) and Humpback whale (Megaptera novaeangliae) which make seasonal migrations to breed. Remaining subsurface, migrating, rearing young, and feeding produce a serious challenge for cetaceans. An exceptional amount of energy is expended to sustain deep diving behavior. Cetaceans are among the largest known mammals on earth, and require a substantial amount of food and space in order to live.

Reproductive Strategies

Deep diving cetaceans are isoporous, meaning they can give birth several times during their lives but often with single calves. In order to better understand how different organisms reproduce, ecologists have developed classifications known as selection strategies. Almost all mammals, including humans and cetaceans, follow K type selection strategy (Cain et. Al, 2014). This strategy is often referred to as "opportunistic" strategy. Under this classification, organisms typically have very few offspring. This allows the majority of nutrients and protection to be applied to a single calf. Opportunistic strategy usually results in a high chance of offspring surviving to maturity. For cetaceans, a gestation or pregnancy period is typically around a year.

Many deep diving cetaceans travel in migratory pods. Which mean that whales contribute and interact with several ecological communities stretching over thousands of miles (Braithwaite et. Al, 2015). One of the most notable examples of this is the Humpback whale. During winter months Humpback whales travel thousands of miles south to the Hawaiian Islands in order to give birth. In the summer months, they travel with their newborns north to the more frigid waters near Alaska. The total trip is over 6000 miles long, the longest of any migratory mammal. There are many theories why whales make the grueling trip year-round. Marine scientists hypothesize that food abundance and climate are the main factors. More recently, evidence suggests that this is a risk assessment by the species to avoid calf predation by killer whales (Corkeron & Connor, 1999).

Ecological Role

Cetaceans are involved in a wide variety of ecological interactions including predator prey relationships, migration behavior, nutrient distribution, and symbiotic facilitation. Whales in particular are often referred to as "ecosystem engineers" due to their significant impact on aquatic communities (Roman, 2014). Sediment upheaval from the ocean floor is incredibly beneficial to underwater communities, especially bottom feeding organisms and foragers.

Whale excrement, otherwise known as fecal plumes, help to redistribute nutrients over huge areas and several oceanic communities. Many different organisms, including phytoplankton and oceanic bacteria, utilize these delivery systems to gather much needed nutrients (Roman, 2014) .

Another ecological role whales serve occurs after death is when a carcass falls to the seafloor, referred to as a "whale fall". Whale falls provide massive inputs of organic matter into the seafloor biome, providing enough food energy for detritivores to last for decades (Smith, & Baco, 2003). According to Smith and Baco, whale falls are relatively common on the seafloor, potentially acting as food stepping stones for isolated deep sea communities that occur in areas such as hydrothermal vents.

Behavioral Ecology and Adaptive Evolution

Deep diving itself is a behavioral adaptation to find food in areas of the water column that are otherwise inaccessible to other oxygen breathing mammals (Cain et al., 2014). Accessing new depths allowed for a new niche to be utilized by marine mammals. Cetacean communities are made up of "pods" that can include many individual whales and offspring. Aside from local migrations from the surface to the deeper feeding columns, many species of whale utilize long distance migration from feeding grounds to calving grounds (Braithwaite et al., 2015). Migration is a very interesting adaptation because of how dangerous long distance travel through the open ocean is for any organism. There is a very distinct cost and benefit that affects cetaceans ability to feed, reproduce, and survive. Whales migrate to find food-rich areas of ocean in the lower latitudes during summer months, and to rear calves in tropical waters that are safer during the winter months when food is scarcer. (Kennedy et al., 2013). Whales need to build up substantial fat to last through the winter calving period. Natural selection is causing adaptive evolution in whales by favoring individuals that are successful at feeding and rearing calves.

Symbiotic Influence

Deep diving whales such as the Humpback Whale (Megaptera novaeangliae) are subject to commensalism type interactions in the form of barnacles (Coronulidae) on their outer skin. The whales essentially provide a mobile buffet for barnacle species to feed. This also greatly increases the breeding range of the hitchhiking marine life. Whale carcasses, or "whale falls" also provide a food source for an abundance of marine life (Fujiwara et al., 2010). Observations have shown that this food source has a huge impact on the organisms that scour the ocean floor. Once settled to the bottom and colonized, the whale carcass can support communities for years at a time.

Predator/Prey Relationships

Cetacean whales can be separated into two distinct categories: toothed whales and baleen whales. Baleen whales eat small krill sized prey by the thousands by gulping large amounts of water then slowly filtering the water out through the baleen plates. Toothed whales are usually faster hunters as their prey is much larger and quicker than that of baleen whales. Toothed whale prey includes; squid, fish, sharks, seals and even other whales. Diets range by species distribution and seasonal abundance. Cetaceans greatly vary in size, with the largest being the Blue whale (Balaenoptera musculus) known for reaching over 200+ tons (WWF, n.d.). These species require a huge amount of nutrition to dive, travel, and raise young. Some estimates include over one ton of food (2000lbs) is ingested per day. Deep diving species like the sperm whales feed exclusively at specific depths and are considered a top predator and one of the few species able to effectively consume large squid.

Adaptation Summary

Cetaceans have lived exclusively in the water for over 53 million years. After the transition from terrestrial to aquatic life, whales went through a series of adaptations that distinguish themselves among deep-sea diversity: (1) Distal airways that are reinforced by cartilage allows for the movement of oxygen from the alveoli to the bronchi during lung compression. (2) The ability to completely collapse the lung prevents the uptake of nitrogen into their bloodstream, preventing decompression sickness. (3) Adaptive changes in the cardiovascular systems in response to hypoxic conditions known as dramatic bradycardia, which is the lowering of the heart rate. To achieve normal function at great depths, blood flow is reduced by selectively constricting blood flow to non-essential areas such as the skin, muscle and gastrointestinal system. Blood flow is instead redirected to the central nervous system and the heart by a process called selective peripheral vasoconstriction. (4) High concentrations of hemoglobin and hematocrit in cetaceans' circulatory system allow for increased oxygen storage for extended dive duration. (5) Elastic arteries regulate circulatory pressure at extreme depths. (6) The ability to withstand high concentrations of myoglobin allows cetaceans to dive to extreme depths. (7) Unique muscle characteristics provide additional ATP production for optimum locomotion. (8) Behavioral tendencies drive adaptive evolution in whales for food foraging and reproductive success.

Reinforced Airways

Diving to extreme depths can distort distal airways and cause tissue compression. The lungs of some cetaceans are capable of completely collapsing to avoid compression damage, However, the distal airways are reinforced by cartilage to allow for the movement of oxygen from the alveoli to the bronchi during lung compression (Bostrom et al., 2008). Without this reinforcement, compression would constrict blood flow within the alveoli and also prevent airflow from leaving the alveoli during dives.

Alveolar Collapse

The role of the lungs are to take the oxygen from the air and transfer it to the red blood cells. Once the oxygen is carried through the bloodstream oxygen is exchanged for CO2 And the lungs aid in removing the CO2 waste by exhalation. Different cetaceans use different strategies to manage gas exchange. For example, bottlenose dolphins can take a quick single breath of air and dive to depths of 100m without collapsing their lungs. On the other hand, larger cetaceans such as sperm whales, remain on the surface for longer periods of time and ventilate several times to replenish oxygen storage (Piscitelli, 2010). Once the sperm whale's oxygen levels are replenished, they completely collapse their lungs before submerging. The ability to completely collapse the lung prevents the uptake of nitrogen into their bloodstream. This adaptation prevents decompression sickness when the sperm whale resurfaces from extreme depths. Since deep divers do not rely on their lungs for oxygen storage, oxygen is stored in the muscle and blood.

Cardiovascular System

The ability to keep supplying oxygen to muscles is crucial for subsurface traveling. Cetaceans are unique in the fact that they can store large amounts of oxygen in their circulatory system, upwards of ~75%. In comparison humans are limited to only about ~35% oxygen storage (Bostrom et al., 2008). Cetaceans have uniquely adapted to hypoxic conditions by balancing cardiac responses during underwater exercise.(Williams et al. 2015) found that bradycardia and tachycardia were inversely correlated with depth and exercise. The study found that the heart rate of deep-drivers decreased with increased depth and locomotion switches from actively swimming to a slower glide-like movement. Oppositely, heart rate and locomotion increased as depth decreased. The behavioral response in not completely understood, however, blood flow is reduced by selectively constricting blood flow to non-essential areas such as the skin, muscle, and gastrointestinal systems. Blood flow is instead redirected to the central nervous system and the heart by a process called selective peripheral vasoconstriction (Williams et al., 2015). This adaption allows for extended dive times at minimal metabolic cost.

Elastic Arteries

Deep diving cetaceans such as seals and pinnipeds have developed what's known as elastic arteries or aortic ballooning. In Mammalia, the aorta acts by supplying oxygen to the rest of the circulatory system. The seal aortas are unique in the fact that they are extremely flexible but also more rigid to contend with pressure fluctuations (Joyce, 2016). This means the circulatory pressure can be regulated at extreme depths and continue to fuel the muscles and organs with oxygen.

Metabolism

Cetaceans have large energetic requirements that are essential for success in their ecosystem. However, when they are deep diving their energy expenditures must decrease. One adaptation that aids in this process is by having a lower metabolic rate, which will then lower the rate of using the stored oxygen (Roos, 2016). To survive during deep dives and for long periods of time, metabolism is decreased so that oxygen consumption needs are also decreased. This adaptation allows for deep divers to be more efficient with their oxygen-rich blood which is then shunted to vital organs by way of selective peripheral vasoconstriction (iron and oxygen binding protein in the muscle tissues of vertebrates.)

Myoglobin

The single evolution of the protein myoglobin (Mb) has given cetaceans a major adaptation for the ability to swim at such deep depths. Because of this the large sperm whales can dive for about an hour at one kilometer deep. Increasing in the length of dive requires 10-20 times higher Mb concentration, which is mostly found in their skeletal muscles. About half of the whale's oxygen levels are also found in their skeletal muscles. Holm et al. (2015) found a direct relationship between Mb concentrations and oxygen storage. High concentrations of myoglobin found in humans result in the clumping of the myoglobin, which leads to illnesses such as Alzheimer's and diabetes. Whales on the other hand adapted to surviving with exceedingly high concentrations of myoglobin and use it to maximize their oxygen carrying capacity. Researchers (Mirceta et. Al, 2013) found that the myoglobin in whales are positively charged. The positively charged myoglobin molecules repel each other and do not stick and clump together. Thus, creating an environment within the cells of muscle tissue that are adaptable tolerant to support high concentrations of myoglobin, which allows for extended dive duration under hypoxic conditions.

Muscle Characteristics/ Muscle Type Trade-offs

There is a vast amount of different muscle adaptations for deep diving whales, due to the sheer complexity and number of muscle systems a single organism may possess. This number is then multiplied by the number of different species possessing muscle adaptations based on factors such as depth of dive and dive time. One of the ways scientists are comparing the various adaptations is by comparing the fiber-type composition of muscles. (Sierra, 2015.) Type I fibers are slow type fibers that have high potential for ATP production in aerobic (high oxygen) environments. Type II fibers are fast twitch and have high potential for ATP production in anaerobic (low oxygen) environments. Skeletal muscles of whales are composed of both types, yet the ratio of fiber type present fluctuates based on whether the species is a deep-diving or shallow-diving whale. Deep-divers have higher ratios of type II fibers to be able to effectively produce energy in low oxygen environments.

The ratio of muscle fibers serves as a good example of a trade-off in locomotor performance. Orcas are quick hunters and have more Type I fibers for sustained endurance (high oxygen) locomotion in chasing prey. They have less ability to conserve their blood oxygen for long duration deep dives because of the ratio of muscle type fibers favors Type I, which have high ATP yield in aerobic environments. (Sierra, 2015)

Species Conservation and Human Impact

The history of humans hunting marine mammals can be traced all the way back to ~2,000 BCE (Society, N. G. 2012). Whale meat, seals, and other pinnipeds have been a staple diet of worldwide indigenous tribes for thousands of years. In the past few centuries, the demand for oil derived from harvested whales has pushed many species toward endangerment. Sperm whales were exclusively hunted for the waxy substance, spermaceti, for which the species is named. Spermaceti is found in the upper part of the mammal's head above the nasal cavity. Prior to electricity, spermaceti oil was commonly burned for heat and light. In the mid part of the 20th century whale populations had been reduced to near unsustainable levels by the fishing industry.

Overfishing and climate change have been a long-standing threat to the deep diving community. Whales are often targeted for human consumption and harvested for food and blubber. Although, this is not as common in the 21st century due to federal protection.

The Marine Mammal Protection Act (MMPA) of 1972 banned the hunting of marine mammals in U.S. waters, closely followed by the U.S. Endangered Species Act of 1973 (ESA). Since the passing of legislation over 45 years ago, population rates have slowly increased. Modern impacts on whale populations can be attributed to increased oceanic traffic. International shipping and commercial whale watching continue to threat migration patterns and breeding behaviors of deep diving species (Blair et al., 2016). The application of audio tracking buoys and Unmanned Aerial Systems (UAS) technology has been a critical asset to cetacean preservation (Nowacek et al., 2016). The UAS provides less costly research approaches and allows for larger conservation coverage. These techniques allow scientists to observe whales without endangering themselves in often hazardous ocean conditions, while simultaneously reducing the invasiveness of research by reducing boat motor sound and boat/whale collision risk. As new research techniques continue to emerge, the future of cetacean preservation looks promising.

Although, deep diving populations seem to be on the rise. according to statistics by the International Whaling Commission (IWC) published as recently as 2016. Whaling is still practiced in many parts of the world, to include many coastal areas in Japan and the remote communities of the arctic.

Conclusion

Due to increasing demands on species fitness, cetaceans adapted behaviorally and morphologically to survive. Many millennia have passed in order for mammals to develop deep diving behaviors and morphology. The ocean's severe environment has forced ancestral species of cetaceans to exhibit many of the aforementioned adaptations in order to successfully feed and reproduce. These adaptations are expansive and continually subject to challenging environmental pressures. The ability to effectively breathe underwater requires the synchrony of several physical and behavioral adaptations. Abnormally reinforced airways help cetacean lungs to collapse while efficiently directing blood and oxygen into the alveoli. Alveolar collapse prevents uptake of nitrogen in the circulatory system, assisting in the ability to use stored oxygen while diving. Additionally, an improved cardiovascular system supports hypoxic conditions and improved muscle characteristics make for a more capable anatomy. These are but a few of the many ways cetaceans have evolved into successful aquatic organisms. Cetaceans play a key role in many ecological processes and help contribute to a diverse underwater community. Many preventable external factors are causing harm to these incredible mammals. It is the responsibility of the scientific community and citizen alike to assist in the preservation of these masters of the deep for generations to come.

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