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This is the published version of a paper published in *Human Evolution*.

Citation for the original published paper (version of record):

Schagatay, E., Fahlman, A. (2014)

Man's place among the diving mammals.

Human Evolution, 29(1-3): 47-66

Access to the published version may require subscription.

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Permanent link to this version:

<http://urn.kb.se/resolve?urn=urn:nbn:se:miun:diva-20876>

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KEY WORDS: *breath hold diving,
apnea, semiaquatic, patterns,
maximum, ability, performance,
diving profiles, littoral.*

Man's Place Among the Diving Mammals

A theory was forwarded in 1960 that humans significantly deviate in anatomy, physiology and behavior from their closest relatives, the great apes, and instead resemble diving mammals, as a result of a period of selective pressure to enter the water (Hardy, 1960). Humans can learn how to dive and in many aspects resemble diving mammals, but how similar is man when compared with aquatic species? To evaluate this, we compared diving performances in a number of aquatic, semiaquatic, and terrestrial species. As an index of aquatic diving specialization, we used maximal and average dive depth and duration, and proportion of time spent under water during repeated dives. Our analysis indicates that aquatic "deep divers" form a separate group, to which humans – and most aquatic and semi aquatic mammals – do not compare in diving specialization. Several species perform dives of intermediate duration and to intermediate depths, and form a group of "moderate divers". A great number of species show more modest diving skills, despite being dependent on an aquatic life or food sources, and form a group of "shallow divers". Humans fit well in this latter group and their maximum diving capacity is well within the typical ability performed by shallow near shore foragers. It may be the case that, as most accessible food is present near the shores, a great number of air breathing species have specialized to utilize this niche, while only a smaller group have developed the specialized extreme physiology necessary for extended deep diving. While foraging in shallow water, humans may repeatedly dive to 20 m and spend as much as 60% of the time submerged in shallow diving, and trained individuals have reached depths of 100 m on single maximal dives. From this perspective, human diving capacity is well within that of typical diving mammals.

Background

A great number of species with an evolutionary history on land have evolved aquatic or semiaquatic forms. Typically, co-evolution has enabled these air breathers to forage underwater for extended periods by transiently ceasing to breathe. Several mammalian groups share anatomical and physiological traits that are important for staying under water for extended periods and for reaching considerable depths, including means of effective locomotion under water, and breath-holding ability. In some respects, humans have anatomical, physiological and behavioral features that more resemble marine mammals than our closest relatives, the great apes. It was suggested that these features de-

veloped during a period of time living close to water under the selective force to enter water mainly for foraging (Hardy, 1960). But how well does the aquatic specialization of humans fit among diving mammals of various evolutionary origins, and can humans be categorized as divers? In order to evaluate this hypothesis it is important to review the diverse mammalian divers and their respective abilities, reflecting their different evolutionary pathways and niches. Humans can certainly dive to some extent, but can humans be classified as diving mammals, and if so, what is man's place among diving mammals?

Aquatic and semiaquatic mammals are found in all the world's oceans and many inland waters, and have evolved the capacity to successfully move and forage underwater. There is great variety in their ability to stay submerged, and dive durations range from a few seconds, for the smaller semi-aquatic rodents, to as long as 120 min for the expert divers, such as the elephant seal and beaked whales (Baird et al., 2006; De Long & Stewart, 1991; Hooker & Baird, 1999). There is also a considerable variety in the depths these mammals explore, ranging from a few meters to up to 1600 m (Baird et al., 2006; Hooker & Baird, 1999). While most species perform shallower dives, with durations limited to one or a few minutes, some species, e.g., beaked whales and sperm whale, commonly perform repeated long (> 40min) and deep (> 400m) dives with short periods spent at the surface (Baird et al., 2006; Hooker & Baird, 1999; Miller et al., 2007; Watwood et al., 2006).

When we compare terrestrial and marine mammals, we often tend to exemplify the latter by their extreme but rather atypical representatives. However, here we will survey a number of different diving mammals and categorize their diving patterns, from the most extreme to the most modest divers, aiming to place the human diver in a biological context. The focus will be on depth and duration for regular and occasional diving, in diving species from various groups and, where data is available, we will also include the time spent underwater in "diving bouts" – continuous repeated dives, another factor of great importance for foraging success. While the focus is on the diving patterns of selected species – i.e., species for which such data exists - some other characteristics and the basic taxonomy of the major diving groups will also be included in this survey. Similar species in one group may not be described with the same detail in another, in order to keep the text limited. In a few cases, when "diving ability" is known in terrestrial mammals, examples have been included.

Cetaceans

There are 78 known living species of whales forming the order Cetacea, which is divided into two groups, the toothed whales (Odontoceti, 67 species) and baleen whales (Mysticeti, 11 species), with baleen plates instead of teeth for filtering food from the water. All members of this order are aquatic, in the sense that they do not need land for any portion of their life. Their closest relatives on land are found among the ungulates, and they may, according to some studies, be related to the semiaquatic hippopotamus (Ursing & Arnason, 1998).

Toothed whales

Sperm whale

Sperm whales (*Physeter macrocephalus*) are present in all oceans and prey on a variety of fish and squid species (Clarke, 1996; Martin & Clarke, 1986). They regularly dive to depths > 400 m for at least 40-45 min, and spend an average 9 min at the surface between dives (Miller, Johnson, & Tyack, 2004; Miller et al., 2007; Miller, Aoki, Rendell, & Amano, 2008). The *mean* maximum dive depths do differ between groups and was 985 m in the Atlantic, 644 m in the Gulf of Mexico and 827 m in the Ligurian sea, possibly reflecting variations in the depth of prey (Watwood et al., 2006). The sperm whale is the only living member of its genera (*Physeter*), but similar extreme diving can be found in several species of beaked whales and also in some seals, as discussed below.

Beaked whales

The beaked whales belong to the family Ziphiidae of which there are 21 known species in six genera. Some examples of species are Cuvier's (*Ziphius cavirostris*) and Blainville's (*Mesoplodon densirostris*) beaked whales. These are the least known of all whales as they are seldom seen. Recent tagging studies of their extreme diving behavior explains the reason for this: their diving involves long (50-60 min) and deep (> 400 m) dives and very short surface intervals (2-5 min), and therefore these animals may seldom be spotted at the surface (Baird et al., 2006; Baird et al., 2008; Hooker & Baird, 1999). Given their size and assuming the same diving physiology as the more shallow diving bottlenose dolphin, beaked whales seem to be the "bumble bees of the sea", performing dives that are much too long for the available O₂ stores. This suggests that the diving physiology of these extreme divers is still poorly understood and deserves further study.

Dolphins

The oceanic dolphin family (Delphinidae) is the largest in the cetacean order with approximately 40 species, including six species often considered to be whales, e.g., pilot whales and killer whales. River dolphins, all rare, belong to other families.

Data from various species of dolphins reveal that while these animals usually dive to shallow depths they have the ability to make deep dives (Ponganis, 2011). The bottlenose dolphin (*Tursiops truncatus*) was observed to typically dive to 20 m with durations of 1 min, but with a maximal depth of 390 m with a duration of 8 min. The harbor porpoise (*Phocoena phocoena*) could make regular dives of 14-40 m with a typical duration of 1 min, with a maximal depth of 226 m and duration of 5 min, and the spotted dolphin (*Stenella attenuata*) had an average depth of 22 m, maximal depth of 203 m, with typical durations of 1-2 m with a maximum of 5 min (Ponganis, 2011).

Pilot whales

Pilot whales (*Globicephala spp*) include two species, the long-finned (*G. melas*) and the short-finned pilot whale (*G. macrorhynchus*). While long-finned pilot whales live mainly in cold water, short-finned pilot whales live in tropical and subtropical seas.

Short-finned pilot whales (*Globicephala macrorhynchus*) in the surrounding waters of the Canary Islands show a bimodal dive depth distribution with dives being either shallow (<100 m) or deep (600-1000 m) (Aguilar Soto et al., 2008). While the dive duration did increase with depth, most dives were short (< 20 min) even when diving to 1000 m. The mean dive duration for deep dives was 15 min, and the maximum dive depth and duration were 1019 m and 21 min respectively (Aguilar Soto et al., 2008). In the US, two previously stranded short-finned pilot whales were released and tracked (Wells et al., 2013). With these animals, most dives were shallow (<50 m) and short (<10 min), but at least one dive to a depth between 1000-1500 m was recorded (Wells et al., 2013). Long finned pilot whales displayed similar depths and durations (Ponganis, 2011).

Baleen whales

Blue whale

Blue whales (*Balaenoptera musculus*) show great diurnal variation in dive depth, ranging from 52-315 m with an average of 190-201 m (Goldbogen et al., 2006; Goldbogen et al., 2008; Goldbogen et al., 2011; Goldbogen et al., 2012). Depths range from 80-200 m at night but are more shallow (20-60 m) during the day, following the diurnal migration of prey (Goldbogen et al., 2006; Goldbogen et al., 2008; Goldbogen et al., 2011; Goldbogen et al., 2012). Dive durations ranged widely from 3.1 to 15.2 min, with an average submergence time of 9.8 min, and a maximum dive duration of 11.6 min (Goldbogen et al., 2012). Surface durations ranged from 16 sec to 6.7 min, with an average of 2.7 min, during which time an average of 10 breaths were taken (Goldbogen et al., 2006; Goldbogen et al., 2008; Goldbogen et al., 2011; Goldbogen et al., 2012). In another study, blue whales dived to 140 m in 7.8 min when foraging, and 68 m in 4.9 min when not foraging, with the longest dives recorded in 14.7 min (Croll et al., 2001).

Fin whale

The average dive duration and depth in 17 tagged fin whales (*Balaenoptera physalus*) was 7 min and 170 m respectively (data in Table 1 in Goldbogen et al., 2012). The maximum dive duration was 9.3 min while the maximum depth recorded was 211 m (Goldbogen et al., 2012). In foraging fin whales, the average dive depth and duration were 98 m and 6.3 min respectively, with the longest recorded dive of 16.9 min (Croll et al., 2001). When not foraging, the same values were 59.3 m and 4.2 min. The diving performances of the much larger blue and fin whales were more modest than the smaller beaked whales (Croll et al., 2001).

Humpback whale

A pair of mother and calf humpback whales (*Megaptera novaeangliae*) were simultaneously followed with a data archiving tag resulting in data from 285 dives (Tyson et al., 2012). The adult female whale dived to a maximum depth of 164 m, but most dives were much shallower with an average of 59 m. The maximum dive depth of the calf was deeper than its mother's (250 m), but the average dive depth was significantly shallower (46 m) (Tyson et al., 2012). The dive duration and proportion of time spent underwater increased with the foraging effort (number of lunges) and depth. For the adult female, the average dive depth was 22 m and the average dive duration was 36 sec, with 63% of the time spent underwater. For an average dive depth of 126 m, the average duration and the proportion of time spent underwater were 354 sec and 80% respectively (Tyson et al., 2012). Summarized data from 4 animals showed an average dive duration of 9.6 min and an average dive depth of 189 m (data in Table 1 in Goldbogen et al., 2012). For those whales, the maximum depth and duration were 214 m and 11.3 min respectively.

Pinnipeds

There are 34 known living species of seals forming the suborder Pinnipedia within the order Carnivora, comprising three families: the true seals (Phocidae, 18 sp), the eared seals (Otariidae 15 sp), including fur seals and sea lions, and the walruses (Odobenidae 1 sp). Pinnipeds are considered semiaquatic as they are dependent on land for breeding, but most species spend the majority of their life at sea. Their closest relatives among the land carnivores may be the bears.

Phocidae

Elephant seals

The two species of elephant seals (Northern elephant seal, *Mirounga angustirostris*; and Southern elephant seal, *Mirounga leonina*) are highly migratory (Hindell et al., 2003) and are capable of extremely deep (> 1500 m) and long (120 min) dives (De Long & Stewart, 1991; Hindell et al., 1991). Southern elephant seals seem to prey primarily on cephalopods, while the northern species prey on a number of fish species (Condit & LeBoeuf, 1984; De Long & Stewart, 1991). While at sea, they spend as much as 80-90% of their time underwater with surface intervals of around 3 min (De Long & Stewart, 1991). The mean dive depth varied from between 250 meters and 700 meters, while the average dive time varied from between 16 minutes to 37 min. Prolonged dive durations, dives exceeding 800 meters, and surface intervals beyond 10 minutes, were rare (Hindell et al., 1991; Hindell et al., 1992; Le Boeuf et al., 1986; Le Boeuf et al., 1988; Le Boeuf et al., 1989). Extended diving bouts are also characteristic of both species; the longest bout measured continued for 40 days in a southern elephant seal and 18 days in a northern elephant seal (Hindell et al., 1991).

Weddell seal

The Weddell seal (*Leptonychotes weddellii*) has been used as a model for deep diving. This species forages under the ice covered sea of the Antarctic, where it relies on the cracks and holes in the ice for breathing between dives. Work on this species was pioneered by Kooyman and involved catching, instrumenting and releasing the animal close to a man-made breathing hole. If no other exit was available, the seal returned to the same site, allowing the dive computer to be recovered. Numerous studies suggest that most dives are < 15 min in duration, with some extreme dives lasting as long as 82 min (Castellini et al., 1992; Kooyman et al., 1980; Kooyman et al., 1971), with average dive depths of around 200 m (Schreer et al., 2001), and a maximal recorded depth of 726 m (Ponganis, 2011).

Harp seal

The harp seal (*Pagophilus groenlandicus*) is a North Atlantic species but it is also observed as far south as Massachusetts, USA. The majority of harp seal dives are shallow (< 80 m) and of short duration (up to 8 min), but they are capable of dives up to >100-300 m (Lydersen & Kovacs, 1993). While foraging, they spend between 22% to 66% of their time underwater (Lydersen & Kovacs, 1993).

Hooded seal

The hooded seal (*Cystophora cristata*) is another North Atlantic species found in the arctic. It is a deep diver, with regular dives to 400 m and a maximal recorded depth of 1016 m (Ponganis, 2011). It regularly holds its breath for 15 min, with the longest noted time being 52 min.

Harbor and gray seals

Studies indicate that the harbor (*Phoca vitulina*) and gray seal (*Halichoerus grypus*), are typically short (< 3 min) and shallow (< 40 m) divers (Schreer et al., 2001; Thompson & Fedak, 1993). In one study of harbor seals, 45% of all dives were below 4 m in depth (Lesage et al., 1999). However, more recent work has shown that 50% of dives were deeper than 40 m (Gjertz et al., 2001). Similarly, female juvenile gray seals were occasionally found diving over 80 m (Thompson & Fedak, 1993; Vincent et al., 2002). In addition, both species have been found entangled in fishing gear at maximum depths of 122 m (Moore et al., 2009), suggesting that they may not be shallow divers as previously thought.

Otariidae

Sea Lions

Among sea lions, there seems to be great variety in diving behavior both within and between the 6 species, possibly reflecting differences in foraging patterns at different oceanographic locations. For example, the dive patterns in individual Galapagos sea lions (*Zalophus wollebaeki*) were grouped as shallow (mean maximum dive depth around 40 m), deep (mean maximum dive depth > 100m), or benthic, where the mean maximum dive depth ranged from 57 to 149 m (Villegas-Amtmann et al., 2008). In California sea lions (*Zalophus californianus*), the majority of dives were around 80 m, with the deepest dive to 274 m (Feldkamp et al., 1989). Shallower mean depths have been recorded for individuals foraging over the continental shelves where access to food may be closer to the surface (33 ± 37 m) (Weise et al., 2006). In New Zealand sea lions (*Phocarctos hookeri*) a maximal depth of 474 m was recorded, while they regularly dive to a depth of 123 m. The average duration was 4 min and maximum duration was 11 min (Ponganis, 2011). Steller sea lions (*Eumetopias jubatus*) regularly dive to 15 m, with a maximum recorded depth of 250 m. Dive durations are mostly < 2 min, while maximal durations are > 8 (Merrick & Loughlin, 1997; Pitcher et al., 2005; Ponganis, 2011).

Fur seals

When data from different species of fur seals were reviewed by Ponganis (2011), the maximum diving depth of the Northern fur seal (*Callorhinus ursinus*) was found to be 256 m and the average diving depth 65 m, with maximum durations of 8 min and mean durations of 2 min (Ponganis, 2011). The Antarctic fur seal (*Arctocephalus gazella*) was noted to dive to 101m, with an average depth of 30 m, the maximal time noted was 5 min, with an average of 1.5 min (Ponganis, 2011). Galapagos fur seals (*Arctocephalus galapagoensis*) dived to 115 m at most, with a mean depth of 26 m, and the same durations as those of Antarctic fur seals (Ponganis, 2011).

Sea cows

The sea cows or Sirenia include the manatees and dugongs, which, unlike most marine mammals, are herbivorous. They are considered to be entirely aquatic, and present species live in shallow tropical waters.

Manatees

Manatees (*Trichechus spp*) are slow moving, shallow and short duration divers. Voluntary dives in six manatees held in a captive facility indicated that most dives are < 2 min in duration, but they may regularly dive for 5-6 min with maximal dive times of up to at least 10 min (Gallivan & Best, 1980).

Dugong

Data on the diving behavior of 15 free-ranging dugongs (*Dugong dugong*), over an average 10 day period, showed an average dive duration of 2.7 min, with a maximum duration of 12.3 min, and the average and maximum dive depths were 4.8 m and 20.5 m respectively (Chilvers et al., 2004). During their daily diving, these animals spent an average of 47% within 1.5 m of the sea surface, and approximately 50% submerged (Chilvers et al., 2004).

Otters

There may be as many as 13 existing species in the otter subfamily Lutrinae within the family Mustelidae. They are semiaquatic and comprise both marine and fresh water species. The only species where diving ability has been systematically studied is the sea otter (*Enhydra lutris*), with a few observations reported for the other species.

Sea otters

Sea otters (*Enhydra lutris*) live along the Pacific coast in North America, Russia and Asia (Bodkin et al., 2004; Wolt et al., 2012). Sea otters forage almost exclusively on benthic invertebrates, including sea urchins, crabs and molluscs. The average dive depth seems to vary with bathymetry, but is generally between 19 and 27 m, with average durations around 90-110 sec (Bodkin et al., 2004; Wolt et al., 2012). On occasion, deep dives to 100 m are performed, but these are rare events; in 14 animals only five of 12,000 recorded foraging dives were 90-100 m, while 84% were <30 m (Bodkin et al., 2004). Longer dives (2-3 min) to moderate depths of 40-50 m were separated by longer recovery intervals, suggesting that these dives are beyond the aerobic dive limit (Bodkin et al., 2004). There appear to be consistent differences in dive duration between males and females, with males diving longer. In addition, males appear to dive deeper compared to females. Females made 86% and males 37% of their dives < 20 m, while 2% of female and 58% of male dives were between 40-100 m.

River otters

Giant otter

Giant otters (*Pteronura brasiliensis*) live in lakes and slow-moving rivers in South America and, unlike sea otters, generally feed on fish. They use vision and their vibrissae to hunt fish and are dependent on clear water and daylight to successfully forage (Duplaix, 1980). During the day, they spend 40-60% of their time in water. They can dive to 10 m, but generally dive shallower. Little is known about their physiology. Young giant otters are often afraid of water and are taught to dive by their parents. According to various sources, giant otters can dive for several minutes at a time.

Hippopotamus

There are two extant species in the family Hippopotamidae, the hippopotamus (*Hippopotamus amphibious*) and the pygmy hippopotamus (*Choeropsis liberiensis* or *Hexaprotodon liberiensis*), with several subspecies. In the order Artiodactyla, Hippopotami are classified as even-toed ungulates and are distantly related to cattle and pigs, and may be related to cetaceans (Ursing & Arnason, 1998). Unlike the great majority of aquatic mammals, these giant herbivores forage on land and rest in water, probably as a means of thermoregulation. The diving behavior of the hippopotamus is not well studied, but some observations exist. In observations of the breathing patterns of two captive hippos (*Hippopotamus amphibious*), regular breath-holding under water was often in excess of one minute (Mortola & Limoges, 2006). In a study on the communication sounds of hippos it was noted, with regard to time in water, that the time spent underwater was 77% (Barklow, 2004).

Pigs

There are several species in the family *Suidae*, with a known fondness for water and the ability to dive to some extent. One example is the south American Peccary group with four species, some with abilities to swim and possibly dive. The pig family also includes the African red river hog (*Potamochoerus porcus*), which lives close to water and is a good swimmer. Domestic pigs (*Sus scrofa*) have been reported to dive and even catch fish in domestic outdoor conditions (Schagatay, unpublished information from farmers). Consequently, we chose pigs as a terrestrial diving model for studies on breath holding ability and diving response (Schagatay & van Kampen, 1995; Schagatay & Holm, 1996). Four young pigs were trained using positive feedback for voluntary head immersion and maximal breath holding. After about 4 weeks of daily training, all pigs could immerse and breath-hold repeatedly for 10 s, and a maximal duration of 53 s was noted in one pig. The longest breath hold duration was 15-40 s in two animals, while the fourth pig never held its breath for longer than 15 s. For stretches of a few minutes, pigs could produce serial short apneas with approximately 40% of the time breath holding (Schagatay, 1996).

Hominidae

Of the five primate species in the family Hominidae, four are not known to dive voluntarily in free-living conditions. However, one species is a remarkably good diver.

Humans

Humans (*H. sapiens*), despite being considered terrestrial, when exposed to water

soon after birth show automated breath holding and under water swimming behavior, and also learn to swim to the surface with little or no assistance (Schagatay, personal observations). When a child is exposed to water after the critical infant period, lasting at least the first 6 months, it has to learn to voluntarily breath hold and swim at the surface. In traditionally diving ethnic groups, children learn to dive at an early age from older siblings, and they may swim and dive before they can walk.

Human breath-hold divers are found at most non-arctic coastal areas of the world. Some examples are the diving populations in Asia, the Ama in Japan, and the Bajau and Suku Laut in South East Asia (Holm et al., 1998; Rahn & Yokoyama, 1965; Schagatay & Lodin-Sundström, 2011). Other similar groups of subsistence divers exist, or have existed until recently, in Tierra del Fuego, Australia, in the Mediterranean sea and in prehistoric Scandinavia. The present day populations are examples of how modern man can live a self-sustained life based on marine resources obtained mainly by apnea diving (Schagatay & Lodin-Sundström, 2011). The divers typically make short serial dives to shallow depths, spaced by short breathing intervals, in order to spend as much time as possible foraging at the seabed. The average dive time in the Ama was 38 s, with a surface interval of equal duration, thus they spent 50% of the time under water, when diving to 5-12 m (Schagatay & Lodin-Sundström, 2011). Due to the current fisheries regulations, the Ama dive for 4 h per day, but previously they continued for as many as 8 h per day (Rahn & Yokoyama, 1965). In the Bajau population in Indonesia, dives to depths of 5-7 m had an average duration of 28 s, followed by surface intervals with a mean duration of 19 s (Schagatay & Lodin-Sundström, 2011). The Bajau can spend up to 9 h diving, but bouts are usually between 3-5 h per day (Schagatay & Lodin-Sundström, 2011). Consequently, during a working day when the Bajau spend 60% of their time underwater, this may amount to between 1.8 and 5.4 h. During deeper dives, more travel time is necessary to reach the seabed, with a greater surface time needed for recovery, resulting in a reduced proportion of time underwater (see Abrahamsson & Schagatay, this issue). The maximum dive depth observed in the Ama was approximately 30 m (Rahn & Yokoyama, 1965) while the Bajau occasionally reached 40 m while searching for black coral. Modern spearfishing practices usually entail maximum depths of about 40 m, with dive durations of up to 3.5 min. Surface intervals for recovery following such dives are generally much longer than dive time.

Competitive breath-hold diving in humans is categorized according to different disciplines, with the aim of maximizing dive duration, underwater swimming distance or depth (Schagatay, 2009, 2010, 2011). The establishment of new world records is rapidly occurring as more people are becoming involved and new contestants are discovering and developing their talents (see e.g., Johansson & Schagatay, this issue). The current maximum breath-hold duration is 11 min 35 s, while the maximum dive depth without fins is 101 m and the longest horizontal distance swam under water without fins is currently 218 m (<http://www.aidainternational.org/>). A number of physiological adaptations in man allow such extreme achievements (Schagatay, 2009, 2010, 2011).

Apes

Data on diving in free-living great apes (*Pan troglodytes*; *Pongo pygmaeus*) do not exist to our knowledge but records on captive animals were recently published.

A maximum dive duration of fifteen seconds was recorded for the “diving” activities of a pet chimpanzee (*Pan troglodytes*) by Renato and Nicole Bender (Bender & Bender, 2013). The chimp could breath-hold with its face covered by its hand, sitting in a pool with the head and body submerged for an average duration of 7 s and at a maximum depth of 2 m. In one period of 22 min in the water, the chimp submerged 40 times, with a mean breathhold time of 8 s (Renato Bender, personal communication, 2013). The chimp was observed to swim on the surface for up to 3 m. Thus, although drowning is often reported in captive chimpanzees, even in shallow water (Cousins, 1978), it seems that given time to explore water under safe conditions they may learn to immerse themselves for at least a few seconds while voluntarily holding their breath, and can even learn to swim a few meters (Bender & Bender, 2013).

An orangutan (*Pongo pygmaeus*) was also observed to submerge and, while swimming in a pool, obtained similar results as those of the chimp (Bender & Bender, 2013). This animal was observed swimming a 4 m distance underwater and up to 12 m on the surface. The ability of these apes to submerge demonstrates that the voluntary breath control required during apnea diving is not an exclusively aquatic mammal trait or a human one among hominoids, as was previously stated (e.g., Morgan, 1982). However, whether these great apes can voluntarily control the urge to breathe arising from increasing P_{CO_2} levels following longer apneas (e.g., Schagatay, 2009) cannot be evaluated from these short apneas.

Rodents

Many species of rodents have developed an ability to forage in water. Some examples are the rice rat and the capybara. The only species for which we found data on diving ability were the semiaquatic beaver and captive rats.

Beavers

To our knowledge, few data exist on freely diving beavers (*Castor fiber*; *Castor canadensis*). While the calculated aerobic dive duration, i.e., the duration until aerobic metabolism has depleted the O_2 stores (Kooyman et al., 1980), is approximately 5 min, most dives rarely exceed 1 min (Clausen & Ersland, 1970-1971). When six captive beavers (*Castor canadensis*) were trained to regularly travel between den and pool by swimming in a submerged channel, the average dive duration was 64 s, with surfacing intervals averaging 61 s. As beavers generally live in shallow areas it may not be relevant

to report their maximal diving depth, but the dive distance has been measured and found to be usually shorter than 200 m (Rieder, 1985), and the duration 3 min (Freye, 1978).

Rats

Rats (*Rattus spp*) have been used in recent studies to investigate the cardiovascular responses associated with diving. Studies have used both forced (Fahlman et al., 2011) and voluntary diving animals: Panneton, W.M., Gan, Q., Le, J., Livergood, R.S., Clerc P., and Juric, R., (2012). Activation of brainstem neurons by underwater diving in the rat. *Frontiers in Physiology* 3, 111. In unrestrained rats, voluntary dives have shown that they commonly perform 40 s long dives with maximum durations of around 100 s.

Water shrew

Water shrews (*Sorex palustris*) were found to sustain forced immersion of up to 48 s before becoming exhausted, while *Mus musculus* could sustain the same treatment for 22 s (Beneski & Stinson, 1987).

Dogs

Four mongrel dogs (*Canis lupus*) were trained to voluntarily immerse the snout in water (Gooden et al., 1974). After 6 weeks of training the dogs could immerse the snout and hold their breath for 20 to 30 s. When immersed, they displayed a diving bradycardia similar to that of more aquatic species (Gooden et al., 1974).

Platypus

The platypus (*Ornithorhynchus anatinus*) is a small semiaquatic monotreme mammal and was recently studied for diving patterns. Diving activity was measured in 11 free-living Platypuses using data loggers. The mean dive duration was 31 s with 72% of all dives lasting between 18 and 40 s. The mean surface duration was 10 s. The mean dive depth was 1.3 m with a maximum of 8.8 m. The Platypuses performed a mean of 75 dives per hour and spent approximately 75% of the time submerged (Bethge et al., 2003).

Discussion

The objective of this paper was to summarize the various metrics of diving capacity in a range of mammals to determine man's place among them. There appears to be great variety in the diving abilities of different species. One group of diving species can clearly be classified as "deep divers" (DD), and this group contains both species of cetaceans and pinnipeds. The extreme deep divers include the sperm whale and a number of beaked whale species, and the Weddell and elephant seals. They regularly dive to more than 200 m of depth, with maximum depths beyond 400 m. These species also have the ability to dive for extended periods, with regular dive durations of >20 min and maximal dives being > 60 min.

Another group can be identified as the "moderate divers" (MD), consisting of those species that regularly dive to 100 m at most, but have the ability to reach 200 m at least occasionally. This group contains most of the pinnipeds and cetaceans. Available data suggest that no other mammalian groups visit these depths, except human breath hold divers when using aids for both ascent and descent, where the current record is 2014 m. These intermediate divers often perform dives of less than 10 min duration but during deeper dives can reach dive durations of 20 min.

The remaining species can be placed in the category of "shallow divers" (SD), where the typical range is within the first 50 m of depth, with maximum regular depths of around 100 m. This group contains several species of pinnipeds and cetaceans, but also most semi aquatic species, including otters, beavers, hippos, and sirenians and humans. Typical dives for this group are 2 min in duration and maximum durations may be up to 10 min. With maximum dive durations of approximately 10 min and depths of 100 m, human divers fit well into this category. Also based on mean dive durations and depths in regular diving, and proportion of time spent under water during diving, our species appears to be representative of this group. Figure 1 shows the different groups of divers based on their recorded maximal depth. In the 25 species for which values were available, there was a positive correlation between maximum dive depth and dive duration ($r^2 = 0.8$; $P < 0.001$).

There appears to be great variety also within some species in their foraging patterns. For example, in the dive patterns of individual Galapagos sea lions, the depths could either be shallow, with a mean maximum dive depth of 40 m – or deep, with a mean maximum depth of beyond 100 m (Villegas-Amtmann et al., 2008). In sea otters, males were found to dive deeper than females (Bodkin et al., 2004), while in elephant seals, the average depth of females, 456 m, was greater than males, 312 m (Le Boeuf et al., 2000). In humans, among some groups like the Ama of Japan, women are the specialist divers, while in competition diving male records are deeper and longer.

A bimodal diving pattern was seen in individual otters – they were engaged either in shallow or deep diving, with much fewer dives per day during deep diving (Bodkin et al., 2004). Similarly, diving in humans can be either directed toward long foraging

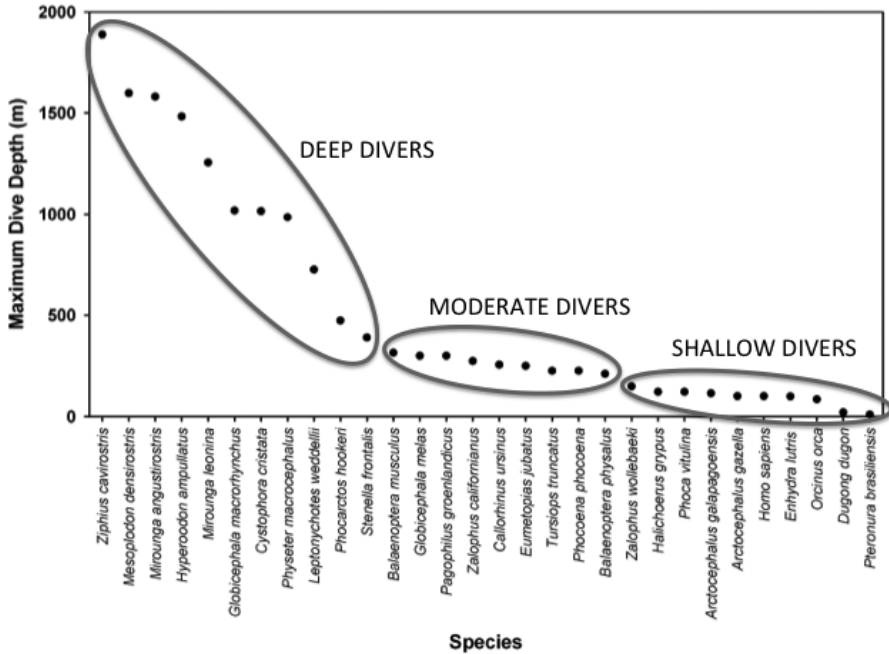


Figure 1. Data showing reported maximum dive depths for several species of mammals. Categorization of species was made to divide divers into 3 groups based on maximal diving depth: deep divers, moderate divers, and shallow divers. Humans fall into the category shallow divers.

time accumulated by repeated diving at shallow depth – or a few deep dives. The human diving patterns, when combining diving for harvesting and competitions, closely mimic the bimodal diving activity of sea otters, with serial short dives to <20 m, longer deeper dives to 40-50 m, separated by longer recovery intervals, and in extreme cases, dives to 100 m (Bodkin et al., 2004). Some other species, however, dive with great regularity, e.g., large mysticetes (Goldbogen et al., 2012).

Diving physiology

Numerous studies have shown that the maximum dive duration is linked to the O₂ store and the utilization rate of this resource, the metabolic rate, which during diving can be reduced to varying degrees by the diving response. The relative size of the storage compartments for O₂, the lung, blood and muscle, vary greatly between species reflecting their diving specializations (Kooyman & Ponganis, 1998; Ponganis, 2011). Deep divers, e.g., the sperm and beaked whales and elephant seal, have elevated blood and

muscle O₂ storage capacity and generally do not rely on the lungs for O₂ storage. This is in sharp contrast to shallow diving species, like the sea otter and human, where the lung is or can be trained to be unusually large and a major O₂ storage compartment. As the mass-specific metabolic rate decreases with body size, there is also a clear relationship with body size and dive duration. While it is clear that the diving capacity of each species is closely linked to the types of physiological specialization for deep, moderate and shallow divers, it is beyond the scope of this review to include such a comparison here. It should be noted that with increased diving specialization, other features e.g., related to life on land, may have to be sacrificed.

Limitations

For natural reasons, most free-living aquatic species have not been studied. The species included here only represent examples of the diving activities of selected species from which we found available data. Also, the true diving ability within a species appears to be difficult to assess as they seldom seem to dive to their limit. In modern humans, only a few people ever explore their diving capacity – while other mammalian divers may – or may not – reach their true limits in voluntary dives. Furthermore, for obvious reasons, most terrestrial mammals cannot be studied in voluntary diving situations, and forced diving cannot be compared with data from free ranging, voluntarily diving animals. Therefore, a comparison between species, where such data exist, can only give an indication of the range and behavior typical of aquatic activity in mammals.

Conclusions

Mammalian divers, dependent on water for essential parts of – or their whole life, show great variations in diving abilities. As a result of different evolutionary histories and different proportions of time spent on land, they have evolved different specializations for entering water and establishing in their respective niches. Some features, however, are shared by nearly all mammalian divers. These include: swimming ability, an effective diving response, enlarged oxygen stores, and other means of prolonging the breath-hold duration. Humans share these features with the semiaquatic mammals (reviewed in Schagatay, this issue). With regard to diving ability, we can identify three different categories: deep divers, moderate divers, and shallow divers, all represented by a number of species with different phylogenetic origins. The maximum human diving capacity is within the range typically demonstrated by shallow near shore foragers. It may be the case that since most accessible food is present near the shore, a great number of air breathing species have specialized in order to utilize this niche, while only a smaller group have developed the extreme specialized physiology necessary for extended, deep

diving. We conclude that humans, when compared to a range of aquatic and semiaquatic mammals, fit well among the diving mammals in the category of shallow divers, most of whom are semiaquatic, having also kept the ability to stay on land.

ACKNOWLEDGEMENTS — We would like to thank our fellow researchers for all of the various studies and the many participants for their cooperation during these experiments.

References

- Aguilar Soto, N., Johnson, M.P., Madsen, P.T., Díaz, F., Domínguez, I., Brito, A., & Tyack, P. (2008). Cheetahs of the Deep Sea: Deep Foraging Sprints in Short-Finned Pilot Whales off Tenerife (Canary Islands). *Journal of Animal Ecology*, 77(5): 1-12. doi: 10.1111/j.1365-2656.2008.01393.x
- Allers, D., & Culik, B.M. (1997). Energy Requirements of Beavers (*Castor canadensis*) Swimming Underwater. *Physiological Zoology*, 70(4): 456-463.
- Baird, R.W., Webster, D.L., McSweeney, D.J., Ligon, A.D., Schorr, G.S., & Barlow, J. (2006). Diving Behaviour of Cuvier's (*Ziphius cavirostris*) and Blainville's (*Mesoplodon densirostris*) Beaked Whales in Hawai'i. *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, 84(8): 1120-1128. doi: 10.1139/z06-095
- Baird, R.W., Webster, D.L., Schorr, G.S., McSweeney, D.J., & Barlow, J. (2008). Diel Variation in Beaked Whale Diving Behavior. *Marine Mammal Science*, 24(3): 630-642. doi: 10.1111/j.1748-7692.2008.00211.x
- Barklow, W.E. (2004). Amphibious Communication with Sound in Hippos, *Hippopotamus amphibius*. *Animal Behaviour*, 68: 1125-1132.
- Bender, R., & Bender, N. (2013). *Brief Communication: Swimming and Diving Behavior in Apes (Pan troglodytes and Pongo pygmaeus)*: DOI: 10.1002/ajpa.22338. Published Online in Wiley Online Library - wileyonlinelibrary.com.
- Beneski, J.T., & Stinson, D.W. (1987). Sorlex palustris Mammalian Species. *The American Society of Mammalogists*, 296: 1-6.
- Bethge, P., Munks, S., Otley, H., & Nicol, S. (2003). Diving Behaviour, Dive Cycles and Aerobic Dive Limit in the Platypus *Ornithorhynchus anatinus*. *Comparative Biochemistry and Physiology Part A*, 136: 799-809.
- Bodkin, J.L., Esslinger, G.G., & Monson, D.H. (2004). Foraging Depth of Sea Otters and Implications to Coastal Marine Communities. *Marine Mammal Science*, 20(2): 305-321.
- Castellini, M.A., Kooyman, G.L., & Ponganis, P.J. (1992). Metabolic Rates of Freely Diving Weddell Seals: Correlations with Oxygen Stores, Swim Velocity and Diving Duration. *Journal of Experimental Biology*, 165(1): 181-194.
- Chilvers, B.L., Delean, S., Gales, N.J., Holley, D.K., Lawler, I.R., Marsh, H., & Preen, A. R. (2004). Diving Behaviour of Dugongs, Dugong Dugon. *Marine Biology and Ecology*, 304(2): 203-224.
- Clarke, M.R. (1996). Cephalopods as Prey. III. Cetaceans. *Philosophical Transaction of the Royal Society London B*, 351: 1053-1065.
- Clausen, G., & Erslund, A.-R. P.(1970-1971). Blood O₂ and Acid-Base Changes in the Beaver During Submersion. *Respiration Physiology*, 11: 104-112.
- Condit, R., & LeBoeuf, B.J. (1984). Feeding Habits and Feeding Grounds of the Northern Elephant Seal. *Journal of Mammalogy*, 65(2): 281-290.

- Cousins, D. (1978). The Reaction of Apes to Water. *Int. Zoo. News*, 25: 8-13.
- Croll, D.A., Acevedo-Gutierrez, A., Tershy, B.R., & Urban-Ramirez, J. (2001). The Diving Behavior of Blue and Fin Whales: Is Dive Duration Shorter Than Expected Based on Oxygen Stores? *Comparative Biochemistry and Physiology Part A*, 129: 797-809.
- De Long, R.L., & Stewart, B.S. (1991). Diving Patterns of Northern Elephant Seal Bulls. *Marine Mammal Science*, 7(4): 385-394.
- Duplaix, N. (1980). Observations on the Ecology and Behaviour of the Giant River Otter *Pteronura brasiliensis* in Suriname. *Revue d'Ecologie: La Terre et la Vie*, 34: 496-620.
- Fahlman, A., Bostrom, B.L., Dillon, K.H., & Jones, D.R. (2011). The Genetic Component of the Forced Diving Bradycardia Response in Mammals. [Original Research]. *Frontiers in Physiology*, 2(63): 1-7. doi: 10.3389/fphys.2011.00063
- Feldkamp, S.D., DeLong, R.L., & Antonelis, G.A. (1989). Diving Patterns of California Sea Lions, *Zalophus californianus*. *Canadian Journal of Zoology*, 67: 872-883.
- Freye, A.H. (1978). Castoridae-Biber. In J. Niethammer & F. Krapp (Eds.), *Handbuch der Säugetiere Europas* (Vol. 1, pp. 182-200). Wiesbaden: Naegeli I. Akad. Verlagsgesellschaft.
- Gallivan, G.J., & Best, R.C. (1980). Metabolism and Respiration of the Amazonian Manatee (*Trichechus inunguis*). *Physiological Zoology*, 53: 245-253.
- Gjertz, I., Lydersen, C., & Wiig, O. (2001). Distribution and Diving of Harbour Seals (*Phoca vitulina*) in Svalbard. *Polar Biology*, 24: 209-214.
- Goldbogen, J.A., Calambokidis, J., Shadwick, R.E., Oleson, E.M., McDonald, M.A., & Hildebrand, J.A. (2006). Kinematics of Foraging Dives and Lunge-Feeding in Fin Whales. [Research Support, Non-U.S. Government. Research Support, U.S. Government, Non-P.H.S.]. *J. Exp. Biol.*, 209(Pt 7): 1231-1244. doi: 10.1242/jeb.02135
- Goldbogen, J.A., Calambokidis, J., Croll, D.A., Harvey, J.T., Newton, K.M., Oleson, E. M.,... Shadwick, R.E. (2008). Foraging Behavior of Humpback Whales: Kinematic and Respiratory Patterns Suggest a High Cost for a Lunge. [Research Support, Non-U.S. Government. Research Support, U.S. Government, Non-P.H.S.]. *Journal of Experimental Biology*, 211(Pt 23): 3712-3719. doi: 10.1242/jeb.023366
- Goldbogen, J.A., Calambokidis, J., Oleson, E., Potvin, J., Pyenson, N.D., Schorr, G., & Shadwick, R.E. (2011). Mechanics, Hydrodynamics and Energetics of Blue Whale Lunge Feeding: Efficiency Dependence on Krill Density. *Journal of Experimental Biology*, 214: 131-146.
- Goldbogen, J.A., Calambokidis, J., Croll, D.A., McKenna, M.F., Oleson, E., Potvin, J., ... Tershy, B. R. (2012). Scaling of Lunge-Feeding Performance in Rorqual Whales: Mass-Specific Energy Expenditure Increases with Body Size and Progressively Limits Diving Capacity. *Functional Ecology*, 26: 216-226.
- Gooden, B.A., Stone, H.L., & Young, S. (1974). Cardiac Responses to Snout Immersion in Trained Dogs. *Journal of Physiology*, 242: 405-414.
- Hardy, A. (1960). Was Man More Aquatic in the Past? *The New Scientist*, 7: 642-645.
- Hindell, M.A., Slip, S.J., & Burton, H.R. (1991). The Diving Behaviour of Adult Male and Female Southern Elephant Seals, *Mirounga leonina* (Pinnipedia : Phocidae) *Australian Journal of Zoology*, 39: 595-619.
- Hindell, M.A., Slip, S.J., Burton, H.R., & Bryden, M.M. (1992). Physiological Implications of Continuous, Prolonged, and Deep Dives of the Southern Elephant Seal (*Mirounga leonina*) *Canadian Journal of Zoology*, 70: 370-379.
- Hindell, M.A., Bradshaw, C.J., Sumner, M.D., Michael, K.J., & Burton, H.R. (2003). Dispersal of Female Southern Elephant Seals and their Prey Consumption During the Austral. Summer: Relevance to Management and Oceanographic Zones. *Journal of Applied Ecology*, 40: 703-715.

- Holm, B., Schagatay, E., Kobayashi, T., Masuda, A., Ohdaira, T., & Honda, Y. (1998). Cardiovascular Change in Elderly Male Breath-Hold Divers (Ama) and their Socio-Economical Background at Chikura in Japan. *Journal of Physiological Anthropology*, 17(5): 181-187.
- Hooker, S.K., & Baird, R.W. (1999). Deep-Diving Behaviour of the Northern Bottlenose Whale, *Hyperoodon ampullatus* (Cetacea: Ziphiidae). *Proceedings of the Royal Society of London B Biological Sciences*, 266: 671-676.
- Kooyman, G.L., Kerem, D.H., Campbell, W.B., & Wright, J.J. (1971). Pulmonary Function in Freely Diving Weddell Seals, *Leptonychotes weddelli*. *Respiration Physiology*, 12(3): 271-282.
- Kooyman, G.L., Wahrenbrock, E., Castellini, M., Davis, R., & Sinnett, E. (1980). Aerobic and Anaerobic Metabolism During Voluntary Diving in Weddell Seals: Evidence of Preferred Pathways from Blood Chemistry and Behavior. *Journal of Comparative Physiology B*, 138(4): 335-346.
- Kooyman, G.L., & Ponganis, P.J. (1998). The Physiological Basis of Diving to Depth: Birds and Mammals. [Research Support, U.S. Government, Non-P.H.S. Review]. *Annual Review of Physiology*, 60: 19-32. doi: 10.1146/annurev.physiol.60.1.19
- Le Boeuf, B.J., Costa, D.P., & Huntley, A.C. (1986). Pattern and Depth of Dives in Northern Elephant Seals, *Mirounga angustirostris*. *Journal of Zoology, London A*, 208: 1-7.
- Le Boeuf, B.J., Costa, D.P., Huntley, A.C., & Feldkamp, S.D. (1988). Continuous, Deep Diving in Female Northern Elephant Seals, *Mirounga angustirostris*. *Canadian Journal of Zoology*, 66: 446-458.
- Le Boeuf, B.J., Naito, Y., Huntley, A.C., & Asaga, T. (1989). Prolonged, Continuous, Deep Diving by Northern Elephant Seals. *Canadian Journal of Zoology*, 67: 2514-2519.
- Le Boeuf, B.J., Crocker, D.E., Costa, D.P., Blackwell, S.B., Webb, P.M., & Houser, D.S. (2000). Foraging Ecology of Northern Elephant Seals. *Ecological Monographs*, 70(3): 353-382.
- Lesage, V., Hammil, M.O., & Kovacs, K.M. (1999). Functional Classification of Harbor Seal (*Phoca vitulina*) Dives Using Depth Profiles, Swimming Velocity, and an Index of Foraging Success. *Canadian Journal of Zoology*, 77: 74-87.
- Lydersen, C., & Kovacs, K.M. (1993). Diving Behaviour of Lactating Harp Seals (*Phoca groenlandica*) Females from the Gulf of St Lawrence, Canada. *Animal Behaviour*, 46(6): 1213-1221.
- Martin, A.R., & Clarke, M.R. (1986). The Diet of Sperm Whales (*Physeter Macrocephalus*) Captured between Iceland and Greenland. *Journal of the Marine Biological Association of the United Kingdom*, 66(04): 779-790. doi: doi:10.1017/S0025315400048426
- Merrick, R.L., & Loughlin, T.R. (1997). Foraging Behavior of Adult Female and Young-Of-The-Year Steller Sea Lions in Alaskan Waters. *Canadian Journal of Zoology*, 75: 776-786.
- Miller, P.J., Johnson, M.P., & Tyack, P.L. (2004). Sperm Whale Behaviour Indicates the use of Echo-location Click Buzzes "Creaks" in Prey Capture. [Comparative Study Research Support, Non-U.S. Government Research Support, U.S. Government, Non-P.H.S.]. *Proceedings of the Royal Society B*, 271(1554): 2239-2247. doi: 10.1098/rspb.2004.2863
- Miller, P.J., Jochens, A., Belabbassi, L., & Biggs, D. (2007). *Diving Behavior of Sperm Whales in Relation to Oceanographic Characteristics*. Paper presented at the Information Transfer Meeting (ITM), Jan 19, 2007, New Orleans.
- Miller, P.J., Aoki, K., Rendell, L.E., & Amano, M. (2008). Stereotypical Resting Behavior of the Sperm Whale. [Letter]. *Current Biology*, 18(1): R21-23. doi: 10.1016/j.cub.2007.11.003
- Moore, M.J., Bogomolni, A.L., Dennison, S.E., Early, G., Garner, M.M., Hayward, B. A., ... Rotstein, D. S. (2009). Gas Bubbles in Seals, Dolphins, and Porpoises Entangled and Drowned at Depth in Gillnets. *Veterinary Pathology*, 46.
- Morgan, E. (1982). *The Aquatic Ape*. London: Souvenir Press.
- Mortola, J.P., & Limoges, M.-J. (2006). Resting Breathing Frequency in Aquatic Mammals: A Comparative Analysis with Terrestrial Species. *Respiratory Physiology & Neurobiology*, 154: 500-514.

- Panneton, W.M., Gan, Q., Le, J., Livergood, R.S., Clerc, P., & Juric R. (2012). Activation of Brainstem Neurons by Underwater Diving in the Rat. *Frontiers in Physiology*, 3(111): 1-13.
- Pitcher, K.W., Rehberg, M.J., Pendleton, G.W., Raum-Suryan, K.L., Gelatt, T.S., Swain, U.G., & Sigler, M.F. (2005). Ontogeny of Dive Performance in Pup and Juvenile Steller Sea Lions in Alaska. *Canadian Journal of Zoology*, 83: 1214-1231.
- Ponganis, P.J. (2011). Diving Mammals. *Comprehensive Physiology*, 1: 517-535. doi: DOI: 10.1002/cphy.c091003
- Rahn, H., & Yokoyama, T. (1965). *Physiology of Breath-Hold Diving and the Ama of Japan*. Paper presented at the The Physiology of Breath-hold Diving and the Ama of Japan, Washington.
- Rieder, N. (1985). Erste Versuche zur Wiedereinbürgerung des Bibers Castor Fiber in Südwestdeutschland. *Angew. Zool.*, 72: 181-189.
- Schagatay E, & van Kampen, M. (1995). Apneic Snout Immersion in Trained Pigs Elicits a “Diving Response”. In J. G. Semple, L. Adams and B. J. Whipp (Eds.), *Advances in Experimental Medicine and Biology*. New York: Plenum Press.
- Schagatay, E., & Holm, B. (1996). Effects of Water and Ambient Air Temperatures on Human Diving Bradycardia. *European Journal of Applied Physiology*, 73: 1-6.
- Schagatay, E. (1996). *The Human Diving Response – Effects of Temperature and Training*. (PhD), Lund University, Lurf.
- Schagatay, E. (2009). Review: Predicting Performance in Competitive Apnoea Diving, Part I: Static Apnoea. *Diving and Hyperbaric Medicine*, 39(2): 88-99.
- Schagatay, E. (2010). Review: Predicting Performance in Competitive Apnea Diving. Part II: Dynamic Apnea. *Diving and Hyperbaric Medicine*, 40(1): 11-22.
- Schagatay, E. (2011). Predicting Performance in Competitive Apnea Diving. Part III: Depth. *Diving and Hyperbaric Medicine*, 41(4): 216-228.
- Schagatay, E., & Lodin-Sundström, A. (2011). Underwater Working Times in Two Groups of Traditional Apnea Divers in Asia: The Ama and the Bajau. *Diving and Hyperbaric Medicine*, 41(1): 27-30.
- Schreer, J.F., Kovacs, K.M., & O'Hara Hines, R.J. (2001). Comparative Diving Patterns of Pinnipeds and Seabirds. *Ecological Monographs*, 71(1): 137-162.
- Thompson, D., & Fedak, M.A. (1993). Cardiac Responses of Grey Seals During Diving at Sea. [Research Support, Non-U.S. Government]. *J. Exp. Biol.*, 174: 139-154.
- Tyson, R.B., Friedlander, A.S., Ware, C., Stimpert, A.K., & Nowacek, D.P. (2012). Synchronous Mother and Calf Foraging Behaviour in Humpback Whales *Megaptera novaeangliae*: Insights from Multi-Sensor Suction Cup Tags. *Marine Ecology Progress Series*, 457: 209-220. doi: doi: 10.3354/meps09708
- Ursing, B.M., & Arnason, U. (1998). Analyses of Mitochondrial Genomes Strongly Support a Hippopotamus-Whale Clade. *Proceedings Royal Society London B*, 265(1412): 2251-2255.
- Villegas-Amtmann, S., Costa, D.P., Tremblay, Y., Salazar, S., & Auriolles-Gamboa, D. (2008). Multiple Foraging Strategies in a Marine Apex Predator, the Galapagos Eea Lion *Zalophus wollebaeki*. *Marine Ecology Progress Series*, 363: 299-309.
- Vincent, C., Ridoux, V., Fedak, M.A., & Hassani, S. (2002). Mark-Recapture and Satellite Tracking of Rehabilitated Juvenile Grey Seals (*Halichoerus grypus*): Dispersal and Potential Effects on Wild Populations. *Aquatic Mammals*, 28(2): 121-130.
- Watwood, S.L., Miller, P.J., Johnson, M., Madsen, P.T., & Tyack, P.L. (2006). Deep-Diving Foraging Behaviour of Sperm Whales (*Physeter macrocephalus*). [Research Support, Non-U.S. Government Research Support, U.S. Government, Non-P.H.S.]. *Journal of Animal Ecology*, 75(3): 814-825. doi: 10.1111/j.1365-2656.2006.01101.x

- Weise, M.J., Costa, D.P., & Kudela, R.M. (2006). Movement and Diving Behavior of Male California Sea Lion (*Zalophus californianus*) During Anomalous Oceanographic Conditions of 2005 Compared to Those of 2004. *Geophysical Research Letters*, 33: 1-6. doi: doi:10.1029/2006GL027113
- Wells, R.S., Fougères, E.M., Cooper, A.G., Stevens, R.O., Brodsky, M., Lingenfelter, R., ...Douglas, D.C. (2013). Movements and Dive Patterns of Short-Finned Pilot Whales (*Globicephala macro-rhynchus*) Released from a Mass Stranding in the Florida Keys. *Aquatic Mammals*, 39(1): 61-72.
- Wolt, R.C., Gelwick, F.P., Weltz, F., & Davis, R.W. (2012). Foraging Behavior and Prey of Sea Otters in a Soft- and Mixed-Sediment Benthos in Alaska. *Mammalian Biology*, 77: 271-280.