in postbreeding periods and after the molt, from March to May. Although long-distance travel by adults occurs, short travel at close range from particular haul outs is more common. Juveniles tend to spend longer periods at sea (Hammond et al., 1993).

C. Sirensians

The best-studied movements by sirensians are of manatees in waters of Florida. Water temperature is a major determinant of seasonal movements of Florida manatees, and dispersal is higher in warmer months. In winter, manatees tend to aggregate in areas of warmer waters, such as natural freshwater springs or the outfalls of power plants (Reynolds and Odell, 1991).

D. Polar Bear

Seasonal movements in polar bears have been reported in all their distribution range. Long-range movements also occur and are mostly related to the ice cover and extent. Predation on seal pups also influences movements, and bears disperse more during pinniped pupping seasons. In summer, when ice melts in many areas, bears move to land, where they remain for a few months, before leaving in November–December. Pregnant females stay longer on land than males.

IV. Study of Marine Mammal Distribution

The study of distribution depends on each species’ habitat and its abundance, so that scale is a significant factor. Distribution changes have to be interpreted in space and time, and different methods are to be used according to species range and density. The distribution of a species occupying an extensive ocean area is best studied by air or shipboard surveys following systematically placed transects. In surveys, visual and/or acoustic data on species are collected according to predetermination protocols. Oceanographic variables and data on position of individuals can be incorporated in spatial modeling (Hedley et al., 1999). Results of this modeling on repeated surveys can be compared to study seasonal patterns and changes over time. In species that live in fragmented habitats and that are not abundant, knowledge of the location of animal aggregations is essential. In these cases, the best possible information is obtained from telemetry studies using high-frequency radio tags, satellite-linked radio tags, and geolocation time-depth recorders, GPS tags, and geolocation tags. The use of telemetry devices is also essential in understanding seasonal movements and patterns. The life of the batteries and permanence of the tags in the animals are critical to the duration of the studies. The study of habitat, an integral part of distribution, changes with the species life time because of the abovementioned factors. It is difficult to monitor a cohort of animals, ideally tagged since birth, because of the long average life span of marine mammals. In practice, the general distribution patterns of a marine mammal population are the sum of the individual specific movements over space and time. Monitoring just a few animals over a restricted time duration (e.g., that of a telemetry device battery) produces partial information on the overall patterns and may show a high variability between individuals. Therefore, inferences at the population level must be made cautiously to avoid biased perceptions of the species distribution.

See Also the Following Articles

Cetacean Ecology • Pinniped Ecology

References


Diving Behavior

BRENT S. STEWART

Except for the polar bear (Ursus maritimus), all marine mammals feed exclusively in aquatic environments, and mostly in the world’s oceans (Reeves and Stewart, 2003). The depths at which they hunt for and capture prey and the time spent submerged vary among pinnipeds, cetaceans, sea otters, and sirenians as a function of physical and physiological adaptations among these taxa, environmental conditions (e.g., coastal or pelagic, tropical or polar, season), and body size, age, and health of individuals. All are ultimately tied to the sea surface to periodically breathe, yet natural selection has operated to minimize the time needed there and to maximize the amount of time that can be spent submerged hunting and capturing prey. What has become known in recent years is that these animals spend substantial parts of their lives moving within
the water column to relatively great depths and some over vast geographic areas in search of food. Among the amphibious pinnipeds, these aquatic foraging bouts can extend, with minor interruptions, for several weeks to several months, punctuated by periods of several days to weeks on land or ice when no feeding occurs when these animals rest, molt, or breed. For the less amphibious sea otters (Enhydra lutris), diving and foraging periods may be separated by periods spent sleeping or resting at the sea surface rather than on land. Among the wholly aquatic cetaceans and sirenians, foraging bouts may last several hours or perhaps days, interrupted by periodic resting periods at the sea surface.

Individuals of some species, particularly sperm whales ( Physeter macrocephalus ) and many mysticete cetaceans, evidently fast during migrations or in particular breeding areas. Although the diving performance and the patterning of individual dives or sequences of dives vary among species, what has become apparent for all marine mammals is that little time is spent at the surface between successive dives to exchange gases (i.e., unload carbon dioxide from tissue and blood and restore tissue oxygen stores). This allows for sustained, repetitive diving and hunting, and is made possible by physiological adaptations for conserving heat and oxygen and by anatomical adaptations that promote effective movement in the aquatic environment (e.g., reducing drag through streamlining and efficient propulsion mechanisms; Reeves and Stewart, 2003).

I. Methods of Studying Diving Behavior

The simplest method for studying the diving behaviors of marine mammals is direct observation of the timing and location of appearances of individuals at the sea surface, the number of breaths taken there, and the duration of the animal's disappearance under water before reappearing. With some assumptions and strong inference, much can be deduced about what animals are doing while hidden beneath the ocean surface. Indeed, most early knowledge of diving, feeding, traveling, and migratory behaviors was based on such interpretations.

Other techniques for documenting diving behavior have used radio transmitters and telemetry instruments, operating at various radio frequencies. Sonic transmitters, operating at relatively low frequencies or wavelengths, allow the tracking of animals when they are submerged by placing a microphone (hydrophone) beneath the sea surface to listen for and orient to these signals. Higher frequencies or wavelengths, allow the tracking of animals when they are submerged in salt water. When vocalizing underwater, some marine mammals may also be tracked with hydrophones to detect and localize those sounds. All of these techniques require constant tracking and observers must be within a few hundred meters (surface observers) or kilometers (observers in aircraft), as the signals attenuate quickly.

During the past several decades, and in particular since the early 1990s, an enormous amount of information has been added to those simple observations due to technological developments and their application to free-ranging marine mammals. For example, in the late 1960s and the early 1970s, an encapsulated mechanical device was used in the Antarctic to study the diving patterns of Weddell seals ( Leptonychotes weddellii ). That instrument provided a continuous trace on photographic film of the depth of the seal vs time. The spooled film was pulled at a known rate past a small radioactive particle, which rested on a pressure-sensitive arm. Thus a two-dimensional record was made on the film of depth vs time. From these records came the first long-term (about 7 days continuous, based on film capacity) data on the vertical movements of free-ranging marine mammals (Kooyman, 2006). Those instruments, called time-depth recorders (TDRs), were later deployed on a number of species of fur seals and some sea lions to study the effects of variation in body size and environment on the foraging patterns of lactating females. However, because the instruments were rather large and because they were attached with harnesses, they likely had some influence on the recorded durations of dives because of the effects of drag on swimming that they imposed, particularly for fur seals. Other simple instruments used capillary tubes with pressure sensors attached to record the maximum depth of a single dive or the maximum depth achieved during a period of diving.

Mechanical instruments were replaced in the late 1980s with much smaller electronic instruments, armored to keep seawater out under extreme hydrostatic pressures. These instruments could collect and store substantially more data on depth and duration of dives and also had less impact on behavior. Indeed, today most of these instruments weigh less than 50 g and can be glued (Figs 1 and 2) to the hair or fur of pinnipeds for long-term (up to a year) monitoring, attached to the dorsal fin of small cetaceans (Fig. 3), attached to the skin surface of large whales with subdermal anchors or deeply embedded into their blubber, or attached with suction cups to the skin of cetaceans for shorter term (to several days) study. Because these instruments may now also collect data other than just water depth as a function of time (e.g., swim speed, ambient light level, compass bearing, seawater temperature, salinity), they are called time-depth recorders. These instruments are generally controlled by small microprocessors that can be programmed to record measures of various parameters at particular intervals that are then stored in electronic memory for several months or more. Thus, detailed records (e.g., at 1-sec intervals) of a marine mammal's position in the water column, in addition to other environmental and behavioral data, can be collected continuously for months or more.

Even more recently, technological developments and improvements have involved remote sensing of diving patterns and geographic movements of marine mammals using radio transmitters that communicate with earth-orbiting satellites, most notably the

Figure 1  A satellite-linked data recorder (SLDR) glued to the dorsal pelage of an adult male ribbon seal (Histriophoca fasciata). Photo by B. S. Stewart.
two polar-orbiting satellites of the ARGOS Data Collection and Location System (DCLS). These transmitters are known as platform transmitter terminals (PTTs) and packaged instruments that include microprocessor-based data recorders in addition to the PTT are known as satellite relay data recorders (SRDRs). They allow animals to be located several times each day, and also allow small amounts of behavioral and environmental data to be transmitted through the DCLS. Further continuing improvement and miniaturization of film and digital video equipment are allowing the underwater diving, social, and hunting behaviors of marine mammals to be visually documented (Parrish and Littnan, 2008).

Most of what is now known and summarized below on the diving behaviors of marine mammals is based on two-dimensional (i.e., depth vs time) data from electronic TDRs, which are occasionally supplemented by geographic locations of the animals at the sea surface. Some data have been collected recently on the movements of animals in a three-dimensional ocean space beneath the sea surface for several hours to a couple of days (Harcourt et al., 2000; Simpkins et al., 2001). But the seductiveness of representations of a single spatial vector (depth) vs time as a trace in a two-dimensional, linear spatial format has led some researchers to infer the geographical form of large numbers of dives in three-dimensional space. Moreover, some researchers have extended inferences even further to assign physiological and behavioral function to those guessed three-dimensional spatial forms. Though those inferences and conclusions of function have yet to be substantively validated, they are nonetheless interesting hypotheses for further rigorous inspection (cf. Brillinger and Stewart, 1997; Fedak et al., 2001).

A substantial amount of information has been collected on diving patterns of a number of pinniped species compared to relatively little progress in the study of cetacean diving patterns. The primary reason for the difference in quantity and quality of data between these taxa is principally due to the greater difficulty of keeping instruments attached to cetaceans compared to the long-term attachment of instruments, up to 1 year, to pinnipeds by gluing them to their hair (Fig. 4). Regardless, the dive patterns of virtually all species were limited to particular times of the year and even to particular classes of individuals (e.g., lactating female pinnipeds). Nearly year-round monitoring of northern and southern elephant seals (Mirounga angustirostris and M. leonina, respectively) has been the exception. Consequently, any discussion of diving patterns is conditioned on these important constraints. Moreover, it has not been confirmed for all cases whether hunting or feeding occurs whenever animals are submerged and diving. The incorporation of additional environmental and physiological sensors to TDRs and PTTs will likely help refine studies of diving patterns to more rigorously evaluate spatial form and function of subsurface movements and to enhance the summaries of dive patterns presented here.

II. Pinnipeds

A. Otariids

California sea lion females (Zalophus californianus) dive mostly to depths of around 75 m for about 4 min during summer and then deeper and longer the rest of the year (maximum depth of 536 m and longest dive of 12 min). When at sea for several days at a time and up to 1–2 weeks at some seasons, California sea lions dive virtually continually and rest at the surface for only about 3% of the time. Juvenile Steller sea lions (northern sea lion, Eumetopias jubatus) dive to average depths of 21 m (maximum 200 m). Most dives last less than 2 min. They are generally shallower at night and deeper in spring
and summer and get progressively deeper and longer through autumn and dives are deeper in winter than in autumn (Pitcher et al., 2005).

Southern sea lions (Otaria flavescens) dive mostly at night, apparently to the sea bed, where they hunt at depths down to 250 m. While at sea near the Falkland Islands, these sea lions dive virtually continually. Near Patagonia along the Argentina coast, over half of the time that lactating females are at sea they are diving. Their dives are mostly to depths of 19–62 m (maximum of 97–175 m) and for 2–3 min (maximum of 4.4–7.7 min). Diving is continuous during these bouts, and time spent at the surface between successive dives is brief, around 1 min.

Lactating New Zealand sea lions (Hookers sea lions, Phocarctos hookeri) also dive almost continually when at sea, averaging about 7.5 dives per hour, varying little with time of day. Dive depths average about 123 m (maximum of 474 m) and last between 4 and 6 min (maximum of 11.3 min). Most dives are evidently to the sea bed to forage on demersal and epibenthic fish, invertebrates, and cephalopods.

A few lactating Australian sea lion (Neophoca cinerea) females were reported to repeatedly forage on the sea bottom (~150 m deep) on the continental shelf of South Australia within 30 km of the coast.

Northern fur seals (Callorhinus ursinus) can be at sea continuously for several months or more from autumn through spring, but their diving behavior has not been studied then. Most data come from lactating female fur seals that are foraging near rookeries in the Bering Sea in summer. Then they forage in bouts that mostly occur at night. Seals mostly make shallow dives to depths of 11–13 m, lasting around 1–1.5 min (Baker and Donohue, 1999). These dives tend to be at night when seals are in pelagic habitats.

Depths and durations of dives of Galapagos fur seals (Arctocephalus galapagoensis) increase as they get older. Six-month-old seals dive to depths of around 6 m for up to 50 sec and dives occur at all hours. One-year-old seals reach depths of 47 m and durations average 2.5 min. Most of these dives occur at night. When 18 months old, seals are at sea mostly at night, diving continually for periods lasting around 3 min and reaching depths of 61 m (Horning and Trillmich, 1997).

Lactating Juan Fernandez fur seal (Arctocephalus philippii) females dive mostly at night to depths of 50–90 m, although most dives are shallower than 10 m. They last, on average, 1.7–2.0 min (longest 3.46 min).

Lactating female New Zealand fur seals (Arctocephalus forsteri) dive as deep as 274 m, and their longest dives have been measured at around 11 min. Median dive depths are around 5–10 m. They occur in bouts with the longest bouts at night. The deepest dives occur around dawn and dusk. Dives are shallowest (30 m) and shortest (1.4 min) in summer and get progressively deeper and longer through autumn and winter (54 m, 2.4 min) and winter (74 m, 2.9 min; Mattlin et al., 1998).

Most dives of female Australian fur seals (Arctocephalus pusillus doriferus) are to the sea bed on the continental shelf at depths of 65–85 m. The median depth of one foraging male fur seal was 14 m and the median duration of dives was 2.5 min. The deepest dive was to 102 m and the longest was 6.8 min, and the seal spent about one-third of its time at sea diving and foraging, with little variation in activity with time of day.

Lactating female subantarctic fur seals (Arctocephalus tropicalis) at Amsterdam Island dive predominantly at night. These foraging dives get progressively deeper and longer from summer (10–20 m and about 1-min long) through winter (20–50 m and about 1.5-min long). The deepest dive recorded was 208 m and the longest was 6.5 min (Georges et al., 2000).

Lactating female Antarctic fur seals (Arctocephalus gazella) dive mostly at night when they are at sea for periods of 3–8 days at a time in summer. Those dives are shallower at night (to ~30 m) than dives made during the day (40–75 m), closely matching the vertical distribution of krill. Maximum depths and durations of dives have been measured at 82–181 m and 2.8–10 min, respectively, for individual females. Seals apparently adjust their diving behavior to maximize the proportion of time that they spend at depth. Young pups dive mostly to depths of about 14 m, depending on their body size, for mean durations of 20 sec. Their diving abilities continue to develop during their first couple of months of life, and by the time they are weaned at around 4 months of age, they are able to dive to the same depths and for about the same amount of time as adult females.

B. Odobenids

The diving patterns of the walrus (Odobenus rosmarus) are not well studied. It is known, however, that its dives may last 20 min or more, although most may be less than 10 min and not exceed 100 m. The longest dive recorded lasted about 25 min and the deepest was to 133 m. Most dives are likely shallower than about 80 m, as its benthic prey of mollusks are generally found in relatively shallow coastal or continental shelf habitats. Near northeast Greenland, walruses may be submerged about 81% of the time when they are at sea and are presumably diving and foraging most of that time.

C. Phocids

Phocid seals generally are at sea continually for weeks to months and appear to dive, and perhaps forage, virtually constantly (Reeves et al., 1992; Reeves and Stewart, 2003). Elephant seals are perhaps the best studied of marine mammal divers. The dives of weaned southern elephant seal pups are to about 100 m for about 6 min and they dive virtually continuously when at sea for several months. Heavier pups dive deeper (to ~130 m) and longer (7 min) than smaller pups (85 m and 5 min). Dives of juvenile southern elephant seals last around 15.5 min (maximum of 39 min) to depths averaging 416 m (deepest 1270 m) and they spend about 90% of their several months at sea diving. Intervals between dives are brief, rarely lasting more than 2 min. Adult southern elephant seal dives on average 400–600 m and 19–33 min (deepest 1444 m and longest 113 min) and also occur continuously while they are at sea for up to 7–8 months (Campagna et al., 1999).

Northern elephant seals also dive continually when at sea for several months or more, with only brief periods at the surface (1–3 min) between dives. Dives of adults are to modal depths of 350–400 m and 700–500 m (maximum of 1567 m), and average 20–30 min (maximum of 77 min). Depths and durations of dives differ between adult males and females depending on season and geographic location (Stewart and DeLong, 1995). Generally, these seals feed on pelagic fish and squid, although some seals may also dive to and feed near the sea floor near the coastlines of continents and islands.

Dives of Hawaiian monk seals (Monachus schauinslandi) are between 3- and 6-min long and mostly shallow, between 10- and 40-m deep, where the seals forage near the sea bed on epibenthic fish, cephalopods, and other invertebrates. Adults may occasionally dive to greater depths of up to 550 m when foraging outside of the shallow atoll lagoons of the northwestern Hawaiian Islands (Stewart et al., 2006).

Weddell seals forage for much, if not most, of the year beneath the unbroken fast ice and the more open pelagic pack ice zones of the Antarctic. Diving and foraging occur in bouts of about 40–50
consecutive dives over a several hour period, usually to depths of 50–500 m. Dives of young pups are relatively shallow and brief but get progressively deeper and longer as pups age. They plateau when the pups are weaned when about 6–8 weeks old. The dives of 1 year olds are somewhat shallower, to around 118 m, compared to adult females (163 m). The deepest dive recorded is about 750 m and the longest over 73 min. Dives are shallower (350–450 m) in spring (October–December) than in summer (January; 50–200 m) evidently reflecting a shift in preferred hunting depths.

Among the Antarctic pack ice seals, Ross seals (Ommatophoca rossii) are also relatively deep divers. One female that was monitored near the Antarctic Peninsula in summer dove exclusively at night, mostly to depths of 110 m (maximum of 212 m) and for about 6.4 min (longest 9.5 min). Diving was continual while the seal was in the water with about 1 min between dives. The deepest dives (175–200 m) occurred near twilight and the shallower (∼75–100 m) at midnight (Bengtson and Stewart, 1997).

In summer, crabeater seals (Lobodon carcinophaga) dive primarily at night and haul out on pack ice during the day, although some diving bouts may last up to 44 h without interruption. Most dives are 4–5 min long to depths of 20–30 m, with maximum depths of 430 m and 11 min, respectively. Dives near twilight are deepest and those near midnight shallowest (Bengtson and Stewart, 1992). Diving patterns in other areas of the Antarctic are similar (cf. Nordoy et al., 1995; Wall et al., 2007).

Baikal seals (Pusa sibirica) apparently dive continually from September through May, when the freshwater Lake Baikal is frozen over, and haul out only infrequently then (Stewart et al., 1996). Most dives are 10–50 m deep in the middle of Lake Baikal where the water depth is around 1000–1600 m. Occasionally, seals descend to more than 300 m. Dives last between 2 and 6 min but some have been measured at more than 40 min.

Dives of another closely related freshwater seal, the Saimaa seal (Pusa hispida saimaaensis) of Lake Saimaa in eastern Finland, last about 6 min in spring and increase to about 10–11 min by autumn. In summer and autumn, long series of sequential dives lasting more than 10 min each may occur over 3 h or more. The longest dive recorded is about 23 min, when the seal may actually have been resting on the bottom rather than feeding.

Modal dive depths for breeding age, male ringed seals (P. hispida hispida) are 10–45 m and for subadult males and postpartum females 100–145 m. Durations of dives for adult males are around 4 min and around 7.5 min for adult females.

Harbor seal (Phoca vitulina) diving behaviors have been studied in several areas throughout their range in the North Pacific and North Atlantic Oceans. Dives in the Wadden Sea (northeast Atlantic) average from 1–3 min (maximum of 31 min) with little variation between night and daytime behavior. When in the water, about 85% of their time is spent diving. In the western Atlantic, foraging dives of adult males are mostly deeper than 20 m but are shallower during the mating period, when they are defending aquatic territories or searching for females to mate with instead of foraging (Bowen et al., 1999). Dives of lactating females are 12–40 m and occur in bouts lasting several hours, mostly during the day. In southern California, dives are as deep as 446 m. Most, however, are to modal depths of 10, 70, or 100 m with an occasional mode at around 280. Harbor seals near Monterey dive to and forage at depths between 5 and 100 m for up to 35 min (Eguchi and Harvey, 2005).

Bearded seal (Erignathus barbatus) adult females near the coast of Spitsbergen, Norway, dive mostly at night to depths of around 20 m (deepest at 288 m) and for 2–4 min (longest 19 min). Nursing pups may dive to around 10 m (maximum of 84 m) for about 1 min (maximum of 5.5 min). Pups spend about 40% of their time in the water diving. Depths and durations of dives increase as the pups age (Kraft et al., 2000).

Most dives of lactating female gray seals (Halichoerus grypus) are to the sea floor and last about 1.5–3 min (maximum of 9 min). Most foraging dives of juvenile gray seals in the Baltic Sea are to depths of 20–40 m (Sjøberg and Ball, 2000).

Lactating female harp seals (Pagophilus groenlandicus) dive about 40–50% of the time that they are at sea. Dives average about 3 min (maximum of 13 min) to depths of up to 90 m.

Hooded seals (Cystophora cristata) repeatedly dive to depths of 1000 m or more and for 52 min or longer. Most feeding dives appear to be to depths of 100–600 m.

### III. Cetaceans

#### A. Odontocetes

Limited data for odontocete cetaceans so far indicate that short-beaked common dolphins (Delphinus delphis) may forage at depths of up to 260 m for 5 min or more, although most dives are around 90 m deep, last about 3 min, and are mostly at night. Pantropical spotted dolphins (Stenella attenuata) dive to at least 170 m; most of their dives are to 50–100 m for 2–4 min and most feeding appears to occur at night. Atlantic common bottlenose dolphins (Tursiops truncatus) near Grand Bahama Island off southeastern Florida often dive to the ocean bottom (7–13 m depth) and burrow into the sediment (“crater-feeding”) to catch fish dwelling or hiding there. Long-finned pilot whales (Globicephala melas) dive to over 500–600 m for up to 16 min. Northern bottlenose whales (Hyperoodon ampullatus) regularly dive to the sea bed at depths of 800–1500 m for more than 30 min per dive and occasionally for 2 h (Hooker and Baird, 1999).

Harbor porpoise (Phocoena phocoena) near Japan have dived almost continuously when observed for short periods. Maximum dive depths are around 70–100 m, although about 70% of dives may be less than 20 m. These porpoises descend to and ascend from depth at greater rates when diving deeply than when the dives are shallow.

In waters near Denmark, porpoises dive as deeply as 84 m and for up to 7 min from spring through late autumn.

Female beluga (white) whales (Delphinapterus leucas) dive more often between 2300 h and 0500 h than during the day, although males may dive at the same rate at all hours. Dive rates and time spent at the surface decline whereas dives deepen and lengthen from early through late autumn. Most dives are deep (400–700 m), with the deepest recorded at 872 m, and last about 13 min on average (maximum of 23 min). Dive duration increases with body size (Martin and Smith, 1999).

Narwhals (Monodon monoceros) regularly dive to more than 500 m and occasionally deeper than 1000 m, but most dives are to depths of 5–52 m and last less than 5 min, although as long as 20 min on occasion. The rate of diving varies between adult males and females. When diving shallowly, narwhals descend and ascend relatively slowly (<0.05 m/sec) compared with deeper, longer dives (1–2 m/sec) where substantially more time is spent at maximum depth.

Killer whales (Orcinus orca) along the northern coast of North Island, New Zealand, dive to the ocean bottom (∼12 m depth or less) after stingers and perhaps probe into the sediment to catch them.

Sperm whales are deep and long-duration divers. Near Kaikoura, New Zealand, the average duration of dives is about 41 min with
about 9 min spent at the surface between dives. Both durations and surface intervals are longer in summer than in winter. Males spend little time at the surface compared to females (Jaquet et al., 2000). Average dive durations have been measured at 36 min near Sri Lanka and about 55 min near the Azores. Sperm whales in the Caribbean were reported to make dives averaging 22–32 min during the day (longest 79 min) and 32–39 min at night (longest 63 min). Off Japan, sperm whales dive to around 550–650 m along the Kumano coast with no differences between day and night patterns, whereas dive patterns are strongly diurnal to around 470 m at night and to around 850 m at night near the Ogasawara Islands, evidently related to differences in behaviors of their prey (Aoki et al., 2007).

B. Mysticetes

As yet there is no evidence for a taxonomic relationship between body size and maximum dive depths for mysticete cetaceans, although preliminary correlations have been reported between maximum dive durations and body size.

While in shallow coastal lagoons during the spring breeding season, gray whales (Eschrichtius robustus) dive for about 1–5 min (maximum of 28 min) to average depths of 4–10 m (maximum recorded of 20.7 m). It is not clear what the function of these dives may be other than perhaps subsurface resting, as breeding whales are presumed to fast. In the Bering Sea in summer, when whales are feeding on the bottom, dives average 3–4 min at depths ranging from less than 10 to 79 m (Würsig et al., 1986).

Fin whales (Balaenoptera physalus) in the Ligurian Sea dive repeatedly to depths around 180 m (maximum 474 m) for around 10 min (longest 20 min) while they prey on deep-dwelling krill. Elsewhere, fin whale dives have been reported to last about 5 min near Iceland and about 3 min in the North Atlantic and near Long Island, New York, in summer. Elsewhere, fin whales dive to around 95 m for 6 min when foraging and to around 59 m for 4 min when not foraging (Croll et al., 2001).

When chased by commercial whalers, dives of blue whales (Balaenoptera musculus) lasted up to 50 min. Blue whales off central and southern California otherwise spend about 94% of their time submerged. Dives lasting longer than 1 min are 4.2–7.2 min, on average (longest 18 min), and to around 105 m (deepest 150–200 m). When foraging, blue whales dive to around 140 m for 8 min and to 68 m for 5 min when not foraging (Croll et al., 2001). Dives of pygmy blue whales (B. musculus brevicauda) have been measured to average 9.9 min (longest 26.9 min).

Humpback whales (Megaptera novaeangliae) in Frederick Sound, Alaska, make rather brief (most less than 3 min) and shallow (60 m or less) dives, although some may exceed 120 m on occasion.

When on summer feeding grounds in the Beaufort Sea, dives of bowhead whales (Balaena mysticetus) last 3.4–12.1 min and some are to the relatively shallow sea bed. Dives of calves are very short compared to adults and they also spend more time at the surface between dives. Most dives of juveniles last about 1 min (longest 52 min) to depths of around 20 min. Longer dives, up to 80 min, have been observed for bowhead whales that were harpooned and being chased by whalers. Dives lasting longer than 1 min (“sounding dives”) average between 7 and 14 min. Dives made while whales are migrating through heavy pack ice are deeper and longer than those made while in open water. Lactating females dive less often and for shorter periods than other adult whales.

Dives of North Atlantic right whales (Eubalaena glacialis) near Cape Cod, Massachusetts, last around 2.1 min.

IV. Other Marine Mammals

Manatees (Trichechus manatus, T. inunguis, and T. senegalensis) feed on floating and submerged vegetation in shallow nearshore habitats, so it is unlikely that their dives often exceed 25–30 m. Direct observations of free-ranging animals have shown that most dives are less than 5 min, although a few have been timed at more than 20 min. These longer dives may have periods of rest at the bottom rather than feeding activity. Dugongs (Dugong dugon) also feed on submerged vegetation, most often in coastal and offshore seagrass beds either on the sea bottom to depths of 20 m or in surface canopies. The longest foraging dives observed are around 6 min, but most have been reported to last only between 2 and 4 min.

Sea otters dive and forage mostly on the seafloor in shallow nearshore waters. Dives may be in bouts lasting several hours during the day and night, interrupted by periods at the surface to groom, process food, or rest. Juvenile males often dive in deeper water, for longer periods, and further from shore than juvenile and adult females (Balls et al., 1995). In southeast Alaska, sea otters spend about 11–12 h each day diving, about 9 h of that actively foraging. Adult males in recently occupied habitats spend less time foraging than do adult females and also less time foraging than do sea otters in less recently colonized habitats (Bodkin et al., 2007).

Polar bears are powerful swimmers and probably make some dives while moving among ice floes, the fast-ice edge, or coastlines, but nothing is known of the details of such diving performance. They prey mostly on ringed seals and whale carcasses on the surface of the ice or along shorelines and also on white whales and narwhals that they may attack and kill at the sea surface and then drag out of the water to consume.

See Also the Following Articles

Feeding Strategies and Tactics ▪ Swimming ▪ Telemetry

References


Diving Physiology

GERALD L. KOOYMAN

I. Introduction

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

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

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