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MARINE MAMMAL OVERVIEW

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Introduction

The term 'marine mammals' is an ecological grouping that lumps together a phylogenetically diverse set of mammals. The only thing linking them is that marine mammals occupy and rely upon aquatic habitats for all or much of their lives. The cetaceans and the sirenians (see the relevant Encyclopedia articles), or dugongs and manatees, live their entire lives at sea, only coming on land during perilous stranding events. Cetaceans (**Table 1**) evolved from ungulates whose modern members include pigs, while sirenians (**Table 2**) evolved from ungulates related to the modern elephant. One member of the bear family (Ursidae), the polar bear, is categorized as a marine mammal, while two members of the family Mustelidae are considered marine: the sea otter and the marine otter of Chile (**Table 3**). Seals and walruses also evolved from terrestrial carnivores. Most biologists lump the seals and walruses into a suborder called the Pinnepedia, and these are often referred to as pinnipeds, meaning 'finlike feet'. Seals are divided into two families: the Otariidae, or eared seals, and the Phocidae, or true seals (**Table 4**). Walruses are categorized as a separate family, the Odobenidae (**Table 4**). The definition of marine mammals is somewhat arbitrary – river dolphins are considered marine mammals, but river otters are not. Inclusion in this category can have real consequences in the United States, since marine mammals have special protection under the US Marine Mammal Protection Act.

Taxonomy

The basic evolution of marine mammals from carnivores and ungulates is well established, but the details of phylogeny and taxonomy at the species level are in flux, owing in part to recent molecular genetic data. Since there is a relatively well-established nomenclature that has been stable for the past 20 years or so, and which forms the basis for species management, this nomenclature will be used in the following tables, while it is recognized that the developing synthesis of molecular and morphological data will probably change some of the species relations. For example, the US and international agencies responsible for protecting endangered species split right whales of the northern and southern oceans into two species; some taxonomists lump right whales into one species, but the North Pacific and North Atlantic right whales are clearly separated and recent genetic data suggests the division of right whales into three species: Southern, Northern Pacific, and North Atlantic. Where the designation of endangered species focuses on the species level, this lumping of right whales of the North Atlantic and North Pacific, which are highly endangered, with right whales of the South Atlantic, which are doing well, could have profound policy implications.

Adaptations of Marine Mammals

The success of marine mammals is something of a puzzle. How did their terrestrial ancestors, adapted for life on land, compete against all of the life forms that were already so well adapted to the marine environment? Multicellular organisms arose in the oceans of the earth about 700 million years ago (MYa), and for the next 100 million years or so, there was a remarkable burst of evolutionary diversification, as most of the basic body plans of life in the sea evolved. By 350–400 MYa, multicellular animals expanded from the ocean into terrestrial environments, with another evolutionary radiation. Mammals only reentered the sea about 60 MYa, and thus have had less than one-tenth of the time available to the original marine metazoans for adaptation to this challenging environment.

Table 1 Scientific and common names of cetaceans along with conservation status[a]

Scientific name	*Common name*	*ESA*	*MMPA*	*IUCN*
Suborder Mysticeti	Baleen whales			
Family Balaenidae	Right whales			
Balaena mysticetus	Bowhead whale	EN	DEP	
Eubalaena australis	Southern right whale	EN	DEP	
Eubalaena glacialis	Northern right whale	EN	DEP	EN
Family Neobalaenidae				
Caperea marginata	Pygmy right whale			
Family Balaenopteridae	Rorquals			
Balaenoptera acutorostrata	Minke whale			
Balaenoptera borealis	Sei whale	EN	DEP	EN
Balaenoptera edeni	Bryde's whale			
Balaenoptera musculus	Blue whale	EN	DEP	EN
Balaenoptera physalus	Fin whale	EN	DEP	EN
Megaptera novaeangliae	Humpback whale	EN	DEP	VU
Family Eschrichtiidae				
Eschrichtius robustus	Grey whale	EN (NW Pacific)	DEP (NW Pacific)	
Suborder Odontoceti	Toothed whales			
Family Physeteridae	Sperm whales			
Physeter macrocephalus	Sperm whale	EN	DEP	VU
Family Kogiidae				
Kogia breviceps	Pygmy sperm whale			
Kogia simus	Dwarf sperm whale			
Family Ziphiidae	Beaked whales			
Berardius arnuxii	Arnoux's beaked whale			
Berardius bairdii	Baird's beaked whale			
Hyperoodon ampullatus	Northern bottlenose whale			
Hyperoodon planifrons	Southern bottlenose whale			
Mesoplodon bidens	Sowerby's beaked whale			
Mesoplodon bowdoini	Andrew's beaked whale			
Mesoplodon carlhubbsi	Hubb's beaked whale			
Mesoplodon densirostris	Blainville's beaked whale			
Mesoplodon europaeus	Gervais' beaked whale			
Mesoplodon ginkgodens	Ginkgo-toothed beaked whale			
Mesoplodon grayi	Gray's beaked whale			
Mesoplodon hectori	Hector's beaked whale			
Mesoplodon layardii	Strap-toothed beaked whale			
Mesoplodon mirus	True's beaked whale			
Mesoplodon pacificus	Longman's beaked whale			
Mesoplodon peruvianus	Pygmy beaked whale			
Mesoplodon stejnegeri	Stejneger's beaked whale			
Tasmacetus shepardi	Tasman's beaked whale			
Ziphius cavirostris	Cuvier's beaked whale			
Family Monodontidae				
Delphinapterus leucas	Beluga; white whale		DEP (Cook Inlet stock)	VU
Monodon monoceros	Narwhal			
Family Delphinidae	Oceanic dolphins			
Cephalorhynchus commersonii	Commerson's dolphin			
Cephalorhynchus eutropia	Black dolphin			
Cephalorhynchus heavisidii	Heaviside's dolphin			
Cephalorhynchus hectori	Hector's dolphin			EN
Delphinus capensis	Long-beaked common dolphin			
Delphinus delphis	Common dolphin			
Feresa attenuata	Pygmy killer whale			
Globicephala macrorhynchus	Short-finned pilot whale			

Table 1 *Continued*

Scientific name	*Common name*	*ESA*	*MMPA*	*IUCN*
Globicephala melas	Long-finned pilot whale			
Grampus griseus	Risso's dolphin			
Lagenodelphis hosei	Fraser's dolphin			
Lagenorhynchus acutus	Atlantic white-side dolphin			
Lagenorhynchus albirostris	White-beaked dolphin			
Lagenorhynchus australis	Peale's dolphin			
Lagenorhynchus cruciger	Hourglass dolphin			
Lagenorhynchus obliquidens	Pacific white-sided dolphin			
Lagenorhynchus obscurus	Dusky dolphin			
Lissodelphis borealis	Northern right whale dolphin			
Lissodelphis peronii	Southern right whale dolphin			
Orcaella brevirostris	Irrawaddy dolphin			
Orcinus orca	Killer whale			
Peponocephala electra	Melon-headed whale			
Pseudorca crassidens	False killer whale			
Sotalia fluviatilis	Tucuxi			
Sousa chinensis	Indo-Pacific hump-backed dolphin			
Sousa teuszii	Atlantic hump-backed dolphin			
Stenella attenuata	Pantropical spotted dolphin		DEP (ETP)	
Stenella clymene	Clymene dolphin			
Stenella coeruleoalba	Striped dolphin			
Stenella frontalis	Atlantic spotted dolphin			
Stenella longirostris	Spinner dolphin		DEP (ETP)	
Steno bredanensis	Rough-toothed dolphin			
Tursiops truncatus	Bottlenose dolphin		DEP (mid-Atlantic coastal)	
Family Phocoenidae	Porpoises			
Phocoena dioptrica	Spectacled porpoise			
Neophocaena phocaenoides	Finless porpoise			
Phocoena phocoena	Harbor porpoise			VU
Phocoena sinus	Cochito; Vaquita	EN	DEP	CR
Phocoena spinnipinis	Burmeister's porpoise			
Phocoenoides dalli	Dall's porpoise			
Family Platanistidae	River dolphins			
Platanista gangetica	Ganges river dolphin			
Platanista minor	Indus susu	EN	DEP	
Family Iniidae	River dolphins			
Inia geoffrensis	Boutu; boto			
Lipotes vexillifer	Baiji	EN	DEP	
Pontoporia blainvillei	Franciscana			

[a]CR = Critically endangered; DEP = Depleted; EN = Endangered; ESA = US Endangered Species Act; IUCN = International Union for the Conservation of Nature; MMPA = US Marine Mammal Protection Act; TH = Threatened; VU = Vulnerable. (Sources: Reynolds and Rommel, 1999; IUCN red book.)

The ocean poses a hostile environment to mammals, yet a remarkable diversity of mammalian groups from carnivores such as bears and otters to ungulates have adapted to the marine environment. Most marine animals maintain their bodies at the temperature of the surrounding sea water and obtain any oxygen required for respiration directly from oxygen dissolved in sea water. Marine mammals need to breathe air and maintain their bodies at temperatures well above the typical temperature of sea water. Many marine animals release thousands to millions of eggs into the hostile marine environment, where the odds are that only a handful will survive. Mammals produce only a handful of offspring at a time, and must rely upon parental care to enhance the survival of their offspring.

Some of the mammalian adaptations that are well-suited for terrestrial life appear to create risks and drawbacks of life in the sea, yet these adaptations opened new niches for marine mammals in four of the five trophic levels of marine ecosystems.

Table 2 Scientific and common names of sirenians along with conservation status[a]

Scientific name	*Common name*	*ESA*	*MMPA*	*IUCN*
Family Trichechidae				
Trichechus inunguis	Amazonian manatee	EN	DEP	
Trichechus manatus	West Indian manatee	EN	DEP	VU
Trichechus senegalensis	West African manatee	TH	DEP	VU
Family Dugongidae				
Dugong dugon	Dugong	EN	DEP	VU

[a]DEP = Depleted; EN = Endangered; ESA = US Endangered Species Act; IUCN = International Union for the Conservation of Nature; MMPA = US Marine Mammal Protection Act; TH = Threatened; VU = Vulnerable. (Sources: Reynolds and Rommel, 1999; IUCN red book.)

These adaptations may be particularly important for predators. For example, the mammalian adaptation of homeothermy, or maintaining a constant body temperature, requires a metabolic rate 10–100 times that of an animal whose body stays at ambient temperature. Biochemical reactions occur at different rates at different temperatures, so animals that do not regulate their temperature as precisely as mammals may not have sensory or motor systems operating as rapidly. All a predator needs is a small marginal advantage in ability to detect or locate prey or in locomotor ability and maneuverability in order to succeed. The high metabolic cost of homeothermy in marine mammals may thus be offset by their potential predatory advantage. This high-cost/high-gain strategy is unique in the oceans to marine mammals and marine birds, although some predatory marine fish also warm muscles or the central nervous system for similar advantage. Marine mammals provide parental care to their young, and can better afford to put more reproductive effort into fewer offspring than is typical of marine organisms. Marine mammals often feed in areas that are separated from the places where they give birth. This has led to an adaptation unknown among terrestrial mammals (except for bears) – the ability to lactate while fasting.

Table 3 Scientific and common names of marine mustelids and ursids along with conservation status[a]

Scientific name	*Common name*	*ESA*	*MMPA*	*IUCN*
Enhydra lutris	Sea otter	TH	DEP	EN
Lutra marina	Marine otter	EN	DEP	EN
Ursus maritimus	Polar bear			

[a]DEP = Depleted; EN = Endangered; ESA = US Endangered Species Act; IUCN = International Union for the Conservation of Nature; MMPA = US Marine Mammal Protection Act; TH = Threatened; VU = Vulnerable. (Sources: Reynolds and Rommel, 1999; IUCN red book.)

Mammals evolved an ear specialized to analyze the frequency content of sound. Air-breathing mammals also have a vocal tract well-adapted to producing loud and complex sounds. When mammals took to the sea, these acoustic adaptations took on a special importance. Light does not penetrate more than a few hundred meters in clear open ocean and only a few meters in some coastal areas, so vision, which is a primary distance sense in air, has a limited range under water. Sound, by contrast, propagates extremely well under water. Many marine mammals have evolved specialized abilities of hearing and sound production that are used for communication and exploring the environment. Many of the toothed whales feed on elusive and patchy prey in the dark of the deep sea or at night. Many species have evolved a high-frequency biosonar that allows them to detect and chase prey. Many baleen whales migrate thousands of kilometers annually, yet are quite social, and they produce low-frequency sounds that can be detected at ranges of hundreds if not thousands of kilometers.

Locomotion

Terrestrial animals have evolved special adaptations to support their bodies and for moving along a solid substrate. Efficient swimming puts very different selection pressures on marine compared to terrestrial locomotion. Water is close to the same density as most animal tissues. This freed aquatic mammals such as the sirenians and cetaceans completely from the need to support their bodies. However, water is also much more viscous than air. This resistance to motion allows marine animals to move by pushing against the medium, but also creates a strong selective pressure for mechanisms to reduce drag. Two different kinds of drag forces act on marine mammals. Viscous drag selects for a smooth skin and a low ratio of surface area to volume. Pressure drag relates to how fluid flows around the body given pressure differences, and this selects for a streamlined hydrodynamic shape. Most marine mammals that swim long distances in the water thus have a slick skin and a low-drag shape that makes them look quite different from their terrestrial ancestors (see **Figure 1**).

Table 4 Scientific and common names of pinnipeds along with conservation status[a]

Scientific name	*Common name*	*ESA*	*MMPA*	*IUCN*
Family Odobenidae	Walrus			
Odobenus rosmarus	Walrus			
Family Otariidae	Eared Seals			
Subfamily Otariinae	Sea lions			
Eumetopias jubatus	Stellar or Northern sea lion	TH	DEP	EN
Neophoca cinarea	Australian sea lion			
Otaria byronia	Southern sea lion			
Phocarctos hookeri	New Zealand sea lion			VU
Zalophus californianus	California sea lion			
Subfamily Arctocephalinae	Fur seals			
Arctocephalus australis	Falkland or South American fur seal			
Arctocephalus forsteri	New Zealand fur seal			
Arctocephalus galapagoensis	Galapagos fur seal			VU
Arctocephalus gazella	Antarctic fur seal			
Arctocephalus philipii	Juan Fernandez fur seal			VU
Arctocephalus pusillus	Australian or S. African fur seal			
Arctocephalus townsendi	Guadelupe fur seal	TH	DEP	VU
Arctocephalus tropicalis	Subantarctic fur seal			
Callorhinus ursinus	Northern fur seal		DEP	VU
Family Phocidae	Earless or True seals			
Subfamily Phocinae	Northern phocids			
Cystophora cristata	Hooded seal			
Erignathus barbatus	Bearded seal			
Halichoerus grypus	Gray seal			EN (NE Atl)
Phoca caspica	Caspian seal			VU
Phoca fasciata	Ribbon seal			
Phoca groenlandica	Harp seal			
Phoca hispida	Ringed seal	EN (Saimaa)	DEP	VU EN (Saimaa)
Phoca larga	Larga seal			
Phoca sibirica	Baikal seal			
Phoca vitulina	Harbor (US) or common (UK) seal			
Subfamily Monachinae	Southern phocids			
Hydrurga leptonyx	Leopard seal			
Leptonychotes weddellii	Weddell seal			
Lobodon carcinophagus	Crabeater seal			
Mirounga angustirostris	Northern elephant seal			
Mirounga leonina	Southern elephant seal			
Monachus monachus	Mediterranean monk seal	EN	DEP	CR
Monachus schauinslandi	Hawaiian monk seal	EN	DEP	EN
Monachus tropicalis	Caribbean monk seal	EN	DEP	EX
Ommatophoca rossii	Ross seal			

[a]CR = Critically endangered; DEP = Depleted; EN = Endangered; ESA = US Endangered Species Act; EX = Extinct; IUCN = International Union for the Conservation of Nature; MMPA = US Marine Mammal Protection Act; TH = Threatened; VU = Vulnerable. (Sources: Reynolds and Rommel, 1999; IUCN red book.)

How Different Marine Mammals Fall on a Continuum from Aquatic to Terrestrial

While all marine mammals use the marine environment, some species are amphibious and need to function in air and in water. The polar bear, for example, is a strong swimmer but retains a body form quite similar to that of terrestrial bears (see **Figure 1**). Polar bears live on sea ice when they can, and their primary diet is seals, but they often live ashore during four months in the later summer and fall when sea ice has receded. Otariid seals can walk on land, but have a body shape transformed for swimming compared to their terrestrial ancestors (see **Figure 1**). The finlike limbs of seals are designed to push against the water with a large cross-sectional area. Marine mammals with limbs designed for swimming have large muscles attached to shorter bones, giving more power and a greater mechanical advantage to the swimming motion. The sirenians and cetaceans never come onto land except during a stranding, and their bodies are the most transformed for swimming – neither group has legs or separate hind flippers, but rather a broad tail (see **Figure 1**). Cetaceans and sirenians use their axial musculature running along the entire vertebral column as they swim. Their tail flukes do not need to function for walking, only for swimming, and they are more efficient at generating thrust than are the seal flippers.

Sensory Systems

Just as these groups differ in their adaptation for locomotion in air and under water, so their sensory systems fall in different places on the continuum from adaptation to terrestrial versus aquatic life. The cetaceans are so fully adapted for marine life that they have lost most olfaction, which senses airborne odors. As mentioned above, sound is a particularly useful modality in the sea, but even for acoustic communication there is variation in the importance of airborne versus underwater sound. The otariid pinnipeds, sea otter, and polar bear communicate primarily in air; some phocid seals communicate both in air and under water; while sirenians, cetaceans, some phocid seals, and the walrus use sound to communicate primarily underwater. There are differences in the relative importance of hearing in air versus water for three different pinniped species whose hearing has been tested in both environments. The Otariid California sea lion is adapted to hear best in air; the phocid harbor seal can hear equally well in air and under water; and the auditory system of the phocid northern elephant seal is adapted for underwater sensitivity at the expense of aerial hearing.

Feeding

Marine mammals feed at a variety of trophic levels from herbivore to top predator. The sirenians are herbivores and eat sea grass that grows in coastal

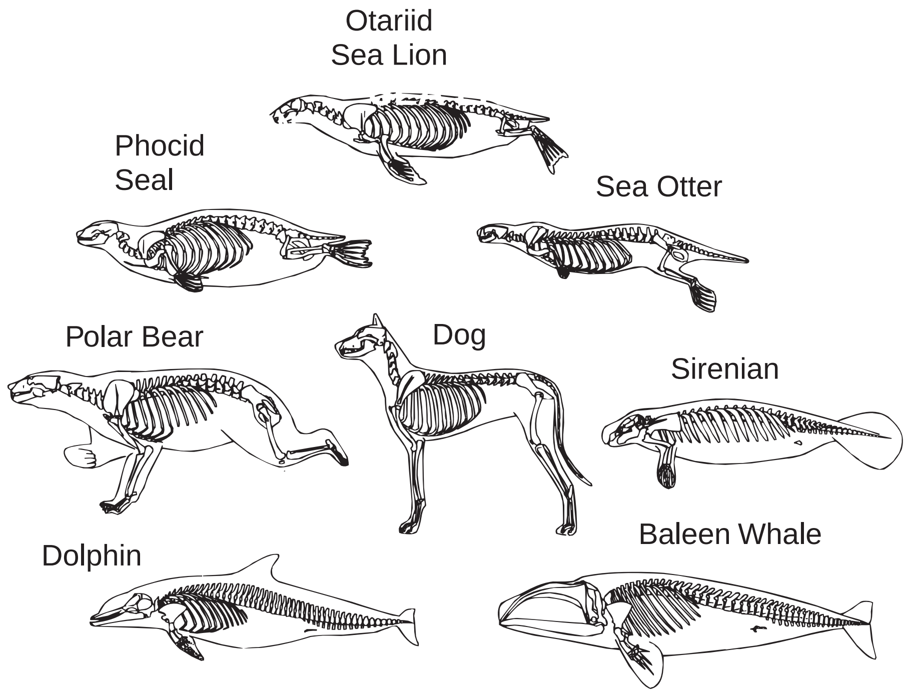

Figure 1 Body outlines and skeletons of selected marine mammal species. (From Reynolds and Rommel (1999), Figures 2–8.)

waters of the tropics. Several marine mammals specialize on benthic prey. The walrus feeds primarily on benthic mollusks; sea otters feed on benthic mollusks, echinoderms and decapod crustaceans. Sea otters are a keystone predator; their feeding on echinoderms is thought to structure kelp forest ecosystems. Grey whales feeds on benthic amphipods in the Bering Sea; their feeding turns over 9–27% of the seafloor there each feeding season, which probably enhances the abundance of colonizing benthic species. Baleen whales do not have teeth, and baleen whales other than the grey whale use their baleen to strain prey from sea water. They have been compared to grazers, because they feed on whole patches of prey, but their prey is typically large zooplankton or even schooling fish, which often require a predator-like ability to find and pursue prey. Most seals and toothed whales chase individual prey items, often fish or squid. Very little is known about the feeding behavior of deep diving toothed whales such as sperm whales. Our ignorance of the behavior of sperm whales and their deep squid prey may cause us to underestimate their ecological importance, for it has been calculated that they must take out of the ocean about the same biomass as all human fisheries.

Annual Feeding and Reproductive Cycles of Marine Mammals

Polar Bear and Pinnipeds

Polar bears and seals have a strong annual breeding cycle, with a short birthing and mating season, and delayed implantation that allows them to mate in spring well before they settle into a winter den for a short gestation period. Polar bears feed primarily on seals in the Arctic sea ice. Feeding is particularly intense during the spring birthing season for ringed seals, when up to a quarter of ringed seal breathing holes show predation attempts by polar bears. Up to 44% of the seal pups may be taken by polar bears at this time. Spring is not only the prime feeding season but also the breeding season for polar bears. Pregnant females delay implantation of the fetus until the feeding season is over. By summer, the sea ice habitat breaks up, forcing the polar bears either to summer on pack ice or to come ashore. A female who has come to ashore cannot hunt efficiently, and she may fast. By late September or early October, she will enter a winter den. Once she enters the den, the fetus implants and the pregnancy progresses, with a gestation period of only 3–4 months. The young are small and poorly developed when born. The eyes do not open for 40 days and the infant must nurse several times an hour and rely upon the mother to keep warm.

Cetaceans, sea otters, and sirenians never need to come to shore and do not have any lairs or dens that act as refuges. Seals are like the polar bear in that they must give birth on land or ice. Most seals also have a strong annual breeding cycle, with a short birthing and mating season and delayed implantation. A primary difference between otariid and phocid seals is that otariid mothers will leave their pups on shore as they forage. By contrast, many phocid mothers stay with their pups and fast throughout lactation. Many phocids give birth on the ice. Selection appears to favor a short, intense period of lactation in this setting. For example, the hooded seal suckles her young for an average of 4 days. The milk is $>60\%$ fat and the female suckles more than twice an hour. The pup gains more than $7\,\mathrm{kg\,d^{-1}}$ during this period.

Annual Cycle of Baleen Whales

Researchers debate whether cetacean swimming is more or less energetically costly than terrestrial locomotion, but living in a buoyant medium has certainly freed cetaceans to grow to larger sizes. The blue whale is the largest animal ever to live on Earth, many times more massive than the largest dinosaurs. Aquatic animals are freed from some of the constraints on size imposed on terrestrial animals, but baleen whales are also larger than any other aquatic animals. This large size is part of a suite of adaptations driven by an annual migratory cycle of most baleen whales, feeding in the summer and mating and giving birth in the winter (see **Figure 2**). Most species of baleen whales have adapted to take advantage of a seasonal burst of productivity in the summer in polar waters. Summer is the feeding season for most migratory baleen whales, and they feed intensively during the summer, building up fat reserves. The primary prey are invertebrate zooplankton such as krill and copepods; some balaenopterid whales also feed on schooling fish. Once the polar pulse of summer productivity is over, there is little reason to stay in these waters. Most baleen whales migrate away from the feeding grounds to separate winter breeding and calving grounds. They seldom feed during these seasons, and live off of their fat reserves from summer feeding.

Most baleen whales migrate to tropical waters for the winter breeding season. It is tempting to assume that they migrate to the tropics to avoid the winter cold and storms in polar seas, but many smaller marine mammals can thermoregulate well in polar

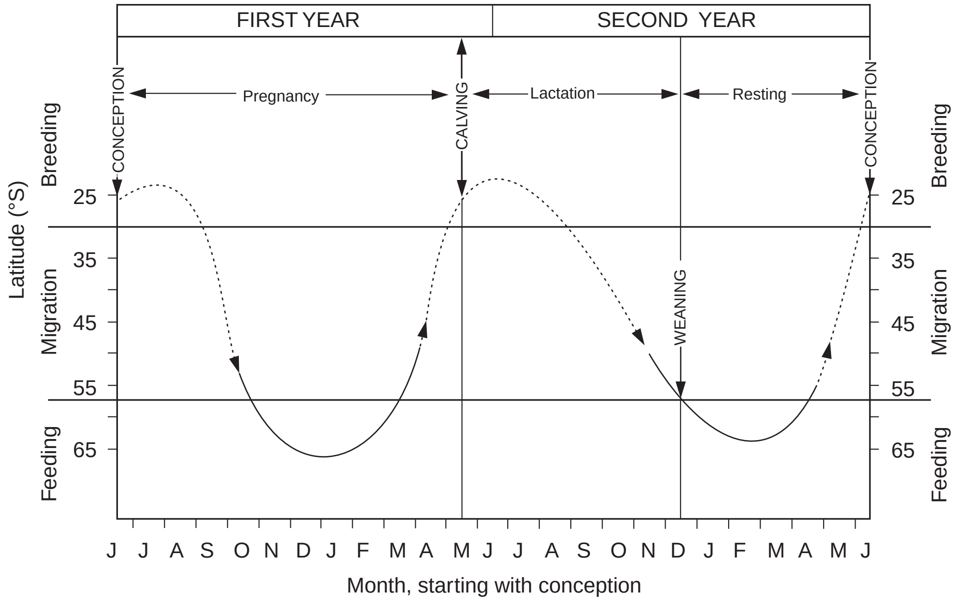

Figure 2 Annual migratory feeding and reproductive cycle of baleen whales. (Adapted from Reynolds and Rommel (1999), Figures 6–19.)

areas in winter, so this raises questions about the reasons for migrations to tropical waters in winter. Grey whales migrate roughly 8000 km from feeding grounds in the Bering Sea to breeding grounds in the coastal lagoons of Baja California, but bowhead whales remain in the Bering Sea during winter. There is a need for better modeling of the energetic costs and benefits of migrating thousands of kilometers to warmer water. Many whale species select calm, protected waters with relatively low predation risk for calving, and this may also influence the choice of breeding area.

The annual cycle of baleen whales and the way in which they forage have selected for large size. Baleen whales engulf many prey items within a dense patch of prey, straining prey from sea water using the baleen for which they are named. The habit of feeding on as many prey within a patch as possible selects for large size in the whales. If whales feed in the summer months, and must live off of their energy stores for the rest of the year, then they must be large enough to store enough energy for the whole year. If whales feed in high latitudes and winter in low latitudes, then they must swim thousands of kilometers, and larger animals can swim more efficiently. All of these factors have acted in concert to select for large size in these largest of animals. The growth of a baleen whale calf is truly extraordinary. During the first half-year of life, a blue whale calf will grow on average $3.5\,\mathrm{cm\,d^{-1}}$ and 80 kg/day (**Figure 3**). This is supported entirely by the mother's milk, which comes from fat reserves since the mother is still migrating up to the feeding area. The annual cycle may select for such rapid growth so that the calf is ready to wean during the summer feeding season.

Prolonged Growth and Maturation in Odontocetes

Odontocetes do not have as pronounced an annual feeding cycle as baleen whales. Many odontocetes do have a breeding season, but few reproduce on an annual basis. Most odontocetes have a gestation period of about one year, but the larger odontocetes have longer gestation, up to 14–16 months in the sperm and killer whales. Most dolphins and larger toothed whales have a prolonged period of dependency that contrasts particularly strikingly with the record short periods of lactation in some phocid seals. For example, the short-finned pilot whale and sperm whale may suckle young for over 10 years in some cases. The prolonged maturation of toothed whales makes particularly stark contrast with the large baleen whales. **Figure 3** shows the growth and maturation of the blue whale versus the sperm whale. The blue whale has weaned by 6 months and is sexually mature by 10 years. By contrast, a male sperm whale suckles for many years and may not reach sexual maturity until 20–25 years of age. Even though baleen whales mature more rapidly than sperm whales, they may live longer. Recent evidence suggests that bowhead whales may live more than a century.

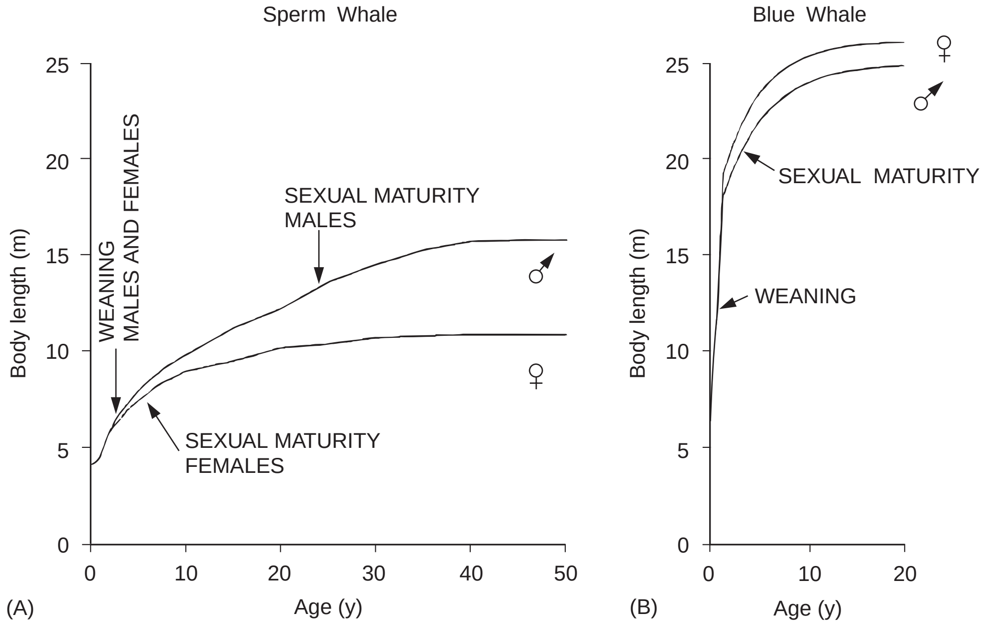

Figure 3 Growth and maturation of (A) sperm whale and (B) blue whale (data from Best, 1979; Lockyer, 1981). Baleen whales live well beyond the 20 years indicated in the figure, which is designed to show ages at which these animals reach full growth. In fact, there is some evidence that bowhead whales may survive for more than a century.

Even where lactation may not be this prolonged, there is still often a prolonged period of dependency in odontocetes. For example, bottlenose dolphins in Sarasota, Florida, are sighted with their mothers for 3–4 years, typically until the mother has another calf. There is a paradox in this prolonged dependency. On the one hand, odontocete young are extremely precocial in their senses and motor abilities for vocalizing and swimming. On the other, they appear to need many years of parental care for success. Many biologists believe that this parental care does not just involve the nutritional care of suckling, but may also involve a long period in which the young learn from the mother and other conspecifics. Among the odontocetes, porpoises and river dolphins live life in the fast lane, weaning within a year of age. These species grow and mature more rapidly than most other odontocetes, and do not rely upon as long a period of dependency.

Navigation and Migration

Many marine mammals are highly mobile, and may swim over $100\,\mathrm{km\,d^{-1}}$. Some coastal animals such as sea otters, dugongs, or coastal bottlenose dolphins may have home ranges only kilometers to tens of kilometers in scope. All species are mobile enough to require abilities to navigate. Some ice-loving seals range over kilometers, but must find holes in the ice to breathe through. Failure to find these holes could easily be fatal. When Weddell seals are caught at a breathing hole and transported several kilometers by scientists to a new man-made one, they can swim under thick ice to find the original hole. These seals must be very skilled at timing their dives to be sure they can return to this original hole when they need to breathe. When sunlight is available, antarctic Weddell seals and arctic ringed seals appear to use downwelling light to navigate. It seems that holes and cracks in the ice, and under-ice features, may provide the same kind of cues for landmarks and routes as used by terrestrial animals. If vision is not available seals restrict their diving but appear to be able to use acoustic cues to locate holes. Seals use some sounds to orient, but ringed seals may avoid sounds of stepping or scraping at an airhole. This makes sense, since these sounds may come from a polar bear or Inuit waiting to kill a seal as it surfaces. At close range, even a blindfolded seal can use its vibrissae to center in an airhole. These animals thus rely upon local knowledge and a combination of sensory cues for navigation.

Many marine mammals, such as the baleen whales, migrate thousands of kilometers annually. Scientists have suggested that marine mammals may use visual, acoustic, chemical, and even geomagnetic cues to orient for migration, but little is known about the sensory basis of orientation or migration. Most whale calves will stay with their mother on their initial migration from calving ground to feeding ground, so they may have an opportunity to learn about migration routes. When bowhead whales migrate, they make low-frequency calls, apparently to coordinate movements and to detect ice obstacles in their path. Most pelagic odontocetes live for several years in the group in which they were born, providing opportunities for learning about navigation. Elephant seals also have migrations of thousands of kilometers, but a young seal is left on the beach by its mother. When a weaned seal leaves the beach, it is thought to leave alone and to have to learn diving, foraging, and orientation on its own. The tracks of satellite-tagged migrating seals and whales are often remarkably well-oriented. Coupling such tags with experimental manipulations may illuminate the sensory basis of migration in marine mammals.

Conservation of Marine Mammals

Many populations of marine mammals have been endangered by humans. They have traditionally been tempting targets for commercial hunting because they carry quantities of valuable meat and fat or oil, and because humans can catch them when they surface to breathe. Species that hauled out on land were particularly vulnerable. Human hunters drove the Steller's sea cow (*Hydrodamalis gigas*) to extinction in about 25 years in the mid-eighteenth century. In the twentieth century most of these commercial hunts were regulated to protect populations. The US Marine Mammal Protection Act was passed in large measure to reduce the unintentional killing of dolphins in a tuna fishery in the eastern tropical Pacific. Marine mammals are still killed during fishing activities or by ghos t gear. Many of the great whales remain so endangered from commercial hunting that no human take is allowed. In spite of the prohibition on taking severely endangered whales such as the northern right whale, of which fewer than 300 individuals survive, right whales are regularly killed by entanglement in fishing gear or by collision with large ships.

As direct mortality has been increasingly controlled, newer threats to marine mammals have also surfaced. Humans have treated waterways as dumping grounds for toxic wastes, and most contaminants in water ultimately enter the sea. Some marine mammals carry heavy loads of organochlorine compounds such as polychlorinated biphenyls (PCBs) or DDT and toxic elements such as mercury or cadmium. We know little about what pathologies may be linked to these exposures, but some evidence suggests associations between impaired reproduction and exposure to some organochlorine compounds. Whales have died after eating fish contaminated with saxitoxin from a harmful dinoflagellate bloom. Many human seafaring activities also create noise pollution. Humans use sound to explore the oceans with sonar and use intense sounds to explore geological strata below the seafloor. The motorized propulsion of ships has increased ocean noise globally, and underwater explosions have killed endangered whales and river dolphins. All of these threats can be considered forms of habitat degradation.

There has also been growing concern about the effects of climate change upon some marine mammals. Many marine mammals depend upon sea ice. In years with little sea ice, harp seals may have decreased reproduction and increased mortality, and polar bears may not be able to feed as well, leading to lower reproductive rates. If global warming reduces the amount or quality of ice used by marine mammals, this may degrade or eliminate critical habitats. Most current laws to protect marine mammals were designed to prevent humans from killing animals directly. Since marine mammals sample most trophic levels of marine ecosystems and can be counted and observed at the surface by humans, many biologists consider marine mammals to be indicator species, helping us to monitor the health of marine ecosystems. New ways of thinking will be required to protect marine mammal populations from habitat degradation.

See also

Acoustic Noise. Acoustics in Marine Sediments. Anthropogenic Trace Elements in the Ocean. Baleen Whales. Bioacoustics. Chlorinated Hydrocarbons. Copepods. Inherent Optical Properties and Irradiance. Krill. Marine Mammal Diving Physiology. Marine Mammal Evolution and Taxonomy. Marine Mammal Trophic Levels and Interactions. Metal Pollution. Phytoplankton Blooms. Primary Production Distribution. Primary Production Processes. Seals. Sea Ice: Overview; Variations in Extent and Thickness. Sea Otters. Sirenians. Sonar Systems. Sperm Whales and Beaked Whales.

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MARINE MAMMAL SOCIAL ORGANIZATION AND COMMUNICATION

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Introduction

All animals face the same basic behavioral problems – obtaining food, avoiding predators and parasites, orienting in the environment, finding and selecting a mate, maintaining contact with relatives and group members. When the ungulates and carnivores that ultimately evolved into today's marine mammals entered the sea, the basic problems did not change, but the context in which the animals had to solve them changed radically. Different marine mammal groups have a different balance in the extent to which they use the underwater versus the in-air environments. All sirenians and cetaceans live their entire lives in the sea, and cetaceans show the most elaborate and extreme specializations for life in the sea. All marine mammals other than sirenians, the sea otter, and cetaceans spend critical parts of their lives on land or ice. These other species, including the pinnipeds and polar bear (*Ursus maritimus*), rely upon land refuges for giving birth, and for taking care of the young.

The ocean is a hostile environment for air-breathing mammals. There is little room for error – if an animal misjudges a dive or becomes incapacitated, it may have only minutes to correct the error or there is a risk of drowning. In the days of sail, humans responded to the notion that 'the sea is a harsh mistress' with an apprenticeship system, whereby a young cabin boy spent years learning the ropes before being entrusted to make the decisions required of a captain. Some cetaceans have similarly long periods of dependency when the young can learn how to feed, avoid predators, dive, and orient within their natal group. Pilot whales and sperm whales may even continue to suckle up to 13–15 years of age, and pilot whale females have a post-reproductive period when they switch their reproductive effort fully to parental care. By contrast, some seals that suckle on land have drastically curtailed the period of lactation, so that their young can leave the land-based refuge early. The hooded seal suckles her young twice an hour for an average of just four days before the pup is weaned. Even seals that lactate longer may still leave the young to an early independence. Elephant seals are deep divers on a par with the sperm whale, yet they must learn to navigate the sea alone. When an elephant seal pup is weaned, the mother leaves the pup on the beach. Pups spend about 2.5 months on the rookery, learning to swim and dive. They must fend for themselves as they make their first pelagic trip, lasting about four months. This solo entry into the sea exerts a heavy cost; fewer than half of the pups survive this trip.

Feeding Behavior

Behavioral ecologists divide feeding behavior into a sequence of steps: searching for prey, pursuit, capture, and handling prey. Marine mammals use many different senses to detect their prey. Walruses, sea otters, and gray whales feed on benthic prey. The walrus uses vibrissae in its mustache to sense shells in the mud; experiments with captive walrus show that they can use vibrissae to determine the shape of objects. Most seals are thought to use vision to find their prey – seals that feed at depth have eyes adapted to low light levels. Most toothed