The Biology of Marine Mammals

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INTRODUCTION

Dear students,

Chapter 1

Introduction to Marine Mammals

1.1. Overture

Humans have always been fascinated with marine mammals. These creatures have been the basis of mythical tales since Antiquity. For centuries naturalists classified them as fish. Today they are symbols of the environmental movement as well as the source of heated controversies: whether we are dealing with the clubbing pub seals in the Arctic or whaling by industrialized nations, marine mammals continue to be a hot issue in science, politics, economics, and ethics.

But if we want to better understand these issues, we need to learn more about marine mammal biology. The problem is that, despite increased research efforts, only in the last two decades we have made significant progress in learning about these creatures. And yet, that knowledge is largely limited to a handful of species because they are either relatively easy to observe in nature or because they can be studied in captivity. Still, because of television documentaries, 'coffee-table' books, displays in many aquaria around the world, and a growing whale and dolphin watching industry, people believe that they have a certain familiarity with many species of marine mammals (for more on the relationship between humans and marine mammals such as whales, see Ellis 1991, Forestell 2002).

As late as 2002, a new species of beaked whale was being reported (Delbout *et al.* 2002), in 2003 a new species of baleen whale was described (Wada *et al*. 2003) and in 2005 a new species of dolphin was also described (Beasley *et al*. 2005). Some scientifically recognized species have never been seen alive by humans and are only known because very occasional remains found on beaches. Because of the paucity of obtaining specimens for certain species and variability in morphological characters, we continue to change the scientific names of some of them (e.g., van Helden 2002). With the increased use of molecular techniques and the discovery of new fossils, the systematics of these mammals is also changing almost every year. Given that there are only about 131 living species of marine mammals, such continued modification of our views of their basic classification underscores how little we still know about them.

For example, we still have little understanding of the meaning of the sounds produced by these creatures despite the fact that bioacoustics was one of the first subfields to attract a lot of research. For instance, only relatively recently it was

discovered that among fin whales, only males sing loud songs and that they use such songs in order to attract females (Croll *et al.* 2002). In the evolutionary arena, key discoveries of fossils began to take place in the early 1980's. These discoveries have helped us explain some of the key anatomical transformations leading to the adaption the aquatic environment. Also, some species and/or populations such as the Steller's sea cow and the Caribbean monk seal as well as the North Atlantic population of gray whales have become extinct in the last few centuries. That has left us with many questions about their very basic biology. These are just a few examples of our ignorance.

Yet, the little we know about these animals shows that these creatures are absolutely amazing. Even at the risk of falling into the realm of trivia, the facts presented in Box 1.1, are just some examples of pieces of knowledge that are astonishing.

Box 1.1.

Some Interesting Facts About Marine Mammals

- **The Smallest:** Among dolphins is the vaquita (1.2 m in length); among the pinnipeds is the Guadalupe fur seal with (1.35 m).
- **The Longest:** A 33.5 m female blue whale landed in the Southern Ocean, in 1909.
- **The Heaviest:** A 209-ton female blue whale caught in the Southern Ocean in 1947.
- **The Loudest:** The low-frequency pulses made by the blue whales and fin whales when communicating with members of their own species across the ocean have been measured at up to 188 decibels: the loudest sounds emitted by any living source (See Table 1.1.).
- **The Longest and Most Complex Songs in the Animal Kingdom:** Sung by male humpback whales; each song can last for half an hour or more and consists of several main components.
- **The Longest Migration:** Gray whales migrate between 15,000 and 20,000 km each year.
- **The Fastest:** The pantropical spotted dolphin can reach 40 km per hour in bursts.
- **Deepest Dive:** A sperm whale can dive as deep as 3,000 m or more.
- **The Longest Dive:** 2 hours and 18 minutes by five sperm whales. Their sound clicking was recorded on 11 November 1983, in the Caribbean.
- **The Most Teeth:** Spinner dolphins between 172 and 252 in total.
- **The Fewer Teeth:** Adult baleen whales lack teeth. Many species of toothed whales, such as beaked whales, have only two teeth and in some cases their females do not erupt them.
- **The Longest Tooth**: Narwhals have the longest tooth, up to 267 cm long.
- **Largest Heart:** The blue whale has a heart the size of a small car.

(Based on data in Carwardine *et al.,* 1998, and information in this book)

Yet, that is only the beginning. Once we start to carefully examine the panoply of adaptations that these creatures underwent in 50 million years of evolution in the aquatic environment, is when we really appreciate them for their value to science. Only after we understand their reproductive behavior and ecology, we can really become fully aware of the impact that humans have had, and continue to have, upon them throughout history.

Table 1.1. A sample of levels of noise from human-related sources

Levels of Noise

Sound	**Decibels (dBA)**
Quiet home	20
Normal talking	40
Ringing telephone	60
Air conditioner	75

Sustained exposure to noise over 85 dBAs can cause permanent damage

Shouting	
Subway train	100
Honking horns	
Jack hammers	
Loud music	120
Jet plane	150
Rocket of the Space Shuttle	180

1.2. What is and what is not a Marine Mammal

For the purpose of this book we will include all species of three different orders of mammals: **cetaceans** (whales, dolphins, and porpoises), **pinnipeds** (seals, sea-lions, walrus), and **sirenians** (manatees, dugongs, sea cows). We also include two species of otters (the sea otter and the marine otter) and the polar bear, all of which belong to the order **Carnivora**. Despite the fact that three species of cetaceans are exclusively freshwater (i.e., river dolphins) and one largely estuarine (the tucuxi), we include them in this book because they evolved from marine species and that helps us better understand a number of adaptations that we observe among cetaceans. The same thing can be said of the two species of pinnipeds (the Lake Baikal seal and the Caspian Sea seal) that are found today in enclosed bodies of waters due to the past distribution of their marine ancestors. One species of sirenian (the Amazonian manatee) is also fundamentally a freshwater one, but is derived from a marine ancestor. However, we are taking a different view when it comes to otters. There is a total of 18 species of otters and with the exception of two they all live in freshwaters. We will be studying only the two sea species. We also consider the polar bear a marine mammal because of its adaptations and impact on the marine ecosystem. We do not, however, include here some species of bats that capture marine fish because they do not really present any special adaptation to the

marine environment (they can also fish in freshwaters). All in all, there are 131 species of **extant** (living) or recently extinct mammals that will be examined in this book.

The number of species of extinct marine mammals that have been found in the fossil record is in the hundreds and continues to increase rapidly. As for any other major animal taxon, there is a larger number of species in the fossil record than those that are alive today. There are also examples in the fossil record of species of marine mammals unrelated to the above-mentioned groups such as hippopotamus-like desmostylians, bizarre bear-like carnivores like *Kolponomos*, and the aquatic sloth *Thalassocnus*.

1.3. A Question of Names

In the English-speaking world common names for marine mammals are confusing to say the least. That is particularly true when dealing with whales and dolphins. For example, in general, 'whales' are large in size, 'dolphins' are medium size, and 'porpoises' are the small ones. But this is confusing because some whale species are smaller than the largest species of dolphins and some species of porpoises are larger than the smallest dolphin species. Further, the term 'great whales' is applied to large baleen whales as well as to the largest species of toothed whales: the sperm whale. Also, there are six species of 'whales' (the killer whale or orca, the false killer whale, the pygmy killer whale, the short-finned pilot whale, the long-finned pilot whale, and the melon-headed whale) that should be called dolphins because they all belong to the family Delphinidae (the family of dolphins). The short-finned pilot whale is also called 'blackfish' in the Caribbean while there is a fish called 'dolphin' (*Coryphaena hippurus*). There are two right whale dolphins named after the northern and southern right whales since all four species have finless backs. Also, not all 'white beak dolphins' have white beaks. The Irrawaddy dolphin lives not only in the Irrawaddy River but also in Brahmaputra, Ganges, Mekong, and Makakam rivers, and in the coastal waters of Southeast Asia.

Sometimes the same species of cetaceans have many common names in English. For example, *Stenella longirostris* is called long-snouted spinner dolphin, spinner dolphin, long-beaked dolphin, rollover, and longsnout while *Balaenoptera physalus* is called fin whale, herring whale, finback, finner, common rorqual, and razorback, and all that without counting non-English names. For example, *Balaenoptera musculus* is known as blue whale (English), ballena azul (Spanish), baleine bleue (French), Blauwall (German), balenottera azzurra (Italian), Baleia azul (Portuguese), blyuval (Russian), Blauwe Vinvis (Dutch)**,** blåhval (Norwegian and Danish), blåval; dvärgblåval (Swedish)**,** shironagassu kujira (Japanese), lan de hweil (Chinese), and cá voi xanh (Vietnamese). In English we also find different spellings for the same common name: bottlenose, bottlenosed, and bottle-nose dolphin.

You may think that because of this confusing situation, scientists came out with a system of scientific names aimed to establish some order. Although that was the intention, sometimes the results are confusing. For example, the first fossil of a whale was described in 1834 using the generic name of *Basilosaurus*, which means 'the king of lizards' because it was believed that such a fossil was that of a dinosaur. Since other biologists usually criticize taxonomists because they keep changing scientific names, they have to come up with a set of elaborate rules (called the Rules of Zoological Nomenclature), and some of them have to do with precedents, in other words, the first

name is the one that counts even if that name, like in the case of *Basilosaurus*, is totally misleading about the nature of the animal being named.

Also, some of the scientific names are based on native vernacular names such as *Inia* (Guarayu of Bolivia) for the boto or Amazonian freshwater dolphin, *Sousa* (Hindi) for the Indo-Pacific, Indian, or the Atlantic humpback dolphin, *Grampus* (English) for the Risso's dolphin, *Feresa* (French) for the pygmy killer whale, *Dugong* (Malay) for the manatee-like animal of the same name, *Pusa* (Inuit of Greenland) for either the Caspian or the Baikal seal, *Mirounga* (Australian aboriginal) for either the southern or the northern the elephant seal. Further, many of both common and scientific names are given after a person's name. For example, the Bryde's whale, *Balaenoptera brydei*, is named after Johan Bryde, a Norwegian who, in 1912, financed the first scientific investigation of whales in South Africa. *Mesoplodon bowdoini* was named after George Sullivan Bowdoin (1833-1913), a trustee of the American Museum of Natural History of New York who financially supported the study of cetaceans at that institution.

Sometimes scientific names are given to honor a famous scientist or even two people at the same time: that is the case of Baird's beaked whale whose scientific name is *Berardius bairdii* honoring two people: Auguste Bérard who was the French commander of the ship that carried the type specimen of the genus from New Zealand to France in 1846, and Spencer Fullerton Baird (1823-1887), a famous American naturalist. As generous these gestures could be, they tell us nothing about the nature of the creature. Actually, marine mammalogists are prone to give people's names to animals, a practice that has been largely abandoned by specialists of other groups such as ichthyologists and ornithologists (see policies by the American Fisheries Society's Committee on Names of Fishes [Robins *et al.,* 1991] and the American Ornithologists' Union's Committee on Classification and Nomenclature [AOU, 1998]).

Taking subjectivity to an extreme, *Sotalia*, which is the generic name of the tucuxi or estuarine South American dolphin, was coined as arbitrarily as a brand name for a detergent. Also, because many species are very rare, not all of them have been given a 'common name' by the 'common' people. For example, when the species in question has never been seen alive, scientists have to invent the 'common' name. That is the case of *Mesoplodon perrini* that has been named Perrin's beaked whale and *Mesoplodon traversii* that has been called the spade-toothed whale.

Box 1.2.

To Be Somebody's Dolphin

In European and Latin American political jargon, the term 'dolphin' refers to a person who is or has been a 'political prince' of a senior politician, a person to inherit public offices from his mentor and to follow his policies. Where does this term come from?

The use of the surname involving the root 'dolphin' dates back to the fourth century when we find the second bishop of Bordeaux (ca. 380 CE) using the name Delphin. By the thirteenth century this name had become common in the Basses Alpes (southeastern France) and in northern Italy in different forms (dolfin, dolfino, delfino, delphin, delfina, delfine, delphine) (Fraser 1977).

Although some popular beliefs claim that the meaning of dolphin as a follower comes from the bow-riding behavior of these marine mammals when close to a vessel, the fact of the matter is that such a title was given for the first time in twelfth century France. Dauphin (French for dolphin) is a French title, borne first by the counts of Vienne (also called Viennois). A prince of that house, Guigues IV (1133-1142), had been surnamed 'le Dauphin' and this became the family name of his successors becoming, thus, the family name of the counts of Vienne, who adopted the dolphin as their heraldic device in the twelve century. Their territory came to be called the dauphiné, or dauphinate, of Vienne and that term was extended to any seigneuries, and a province subject to them was also called *Dauphiné*. The title dauphin passed, with the Dauphiné, to the direct heirs of the French kings when in 1349 Dauphin Humbert II of Vienne (who was childless) sold the region to King Philip VI of France and attached the condition that the eldest son of the French king had to use it so it could be perpetuated. When Philip died (1350) his grandson, later King Charles V, became the first heir to the throne to bear the title. After Louis XI the title was merely honorific. Louis Antoine, duc d'Angoulême (1775–1844), son of King Charles X, was the last dauphin, so the title was used only until 1830.

1.4. Myths and Legends

Some of the earliest representations of marine mammals date back to the Upper Paleolithic (about 25,000 years ago). That is the case of paintings originally thought to be of dolphins but later interpreted as those of the Mediterranean monk seal (*Monachus monachus*) which have been found in the Cave of Nerja, Málaga, southern Spain (Dams, 1989). The earliest known portrayal of a cetacean in art is an ancient drawing of an orca carved into coastal rocks in northern Norway estimated to be 9,000 years old. Ancient rock cravings of the finless porpoise (*Neophocaena phocaenoides*) have been found in caves in Thailand. The first illustration of a dolphin on paper can be found in the manuscript *Babur-Nama* written ca. 1500 in India.

Ancient Greeks and Romans referred to real whales and fantastic sea monsters in both mythology and natural history writings that was unique in words and language for its richness and diversity. Homer, for example, depicted dolphins as 'kings of the sea and Lord of fishes.' Others anonymous authors started a number of myths that have been perpetuated until our days. One example is that of dolphins saving castaways by returning them to land. Others depict as dolphins gladly allowing being ridden by men. Today's claims of dolphins been enchanted by music is based on the legend of Arion, the first famous mythological Greek singer and the player of zither. According to the legend after embarking in a vessel, the crew decided, once at sea, to murder the musician to seize his fortune. However, Arion was granted the favor to sing for a last time before being thrown into the waters. Once in the water, Arion was saved by dolphins that had been enchanted by the melodious accents of the singer, taking him to land.

It was also a dolphin that arranged the marriage of Amphitrite and Poseidon who, to mark his gratitude, installed in heavens, the constellation of the Dauphin, close to the Eagle. And there was another dolphin that carried Apollo and his son Icadius up to Mount Parnassus, where the temple of Delphis was built. Because of this, the killing of

dolphins was considered offensive and Greek fishers left them alone. The by-products of stranded dolphins were, however, possibly used for medicinal purposes. For example, fat was used for the treatment of the edemas; their ashes for certain skin diseases; the liver to reduce fevers.

Ancient representation of dolphins was common, being founded on numerous currencies of Abydos, Egine, Argos, Métaponte, Posidonie, Tarente and Rome. We can find coins from Syracuse (ca. 500 BCE) with inscriptions of dolphins. Also, a medal of Vespasian (9-79 CE) shows a dolphin entwining an anchor and was used to indicate the Emperor's naval superiority. Dolphin representations were also used in coins in Byzantium. In Rome the animal was depicted, most of the time, accompanied with an anchor symbolizing the Roman ascendancy on nostrum puddle. The former Italian 5-lira coin displayed a dolphin. Heraldic dolphin is particularly spread in England, where it appears in the weapons of numerous families of very ancient nobility. In France, dolphins can be commonly seen in coins of provinces so remote from the sea as Auvergne and Dauphiné.

The same can be said about a long and rich tradition of iconographic representations in ancient art, particularly of fabulous sea monsters, one that extends from Aegean prehistory into the Classical era and well beyond (Papadopoulos and Ruscillo 2002). Dolphins are commonly represented in the Ancient Greek society through artistic portraits and in myths and legends. Dolphin motifs are common in ancient Greek and Roman art such as paintings, mosaics, sculptures, vases, and coins (Matthews 1968, Sweeney 1972, Fraser 1977). Dolphin representations dating back from 3500 to 2200 BC are found in the form of frescoes in the Minoan Palace of Knossos, Crete (Fig. 1.1). Paintings of dolphins dating from 1600 BCE have been found in the ancient Peloponesian city of Tirynis (Montagu 1963). We can find coins from Syracuse (ca. 500 BCE) with inscriptions of dolphins. Dolphin representations were also used in coins in Byzantium.

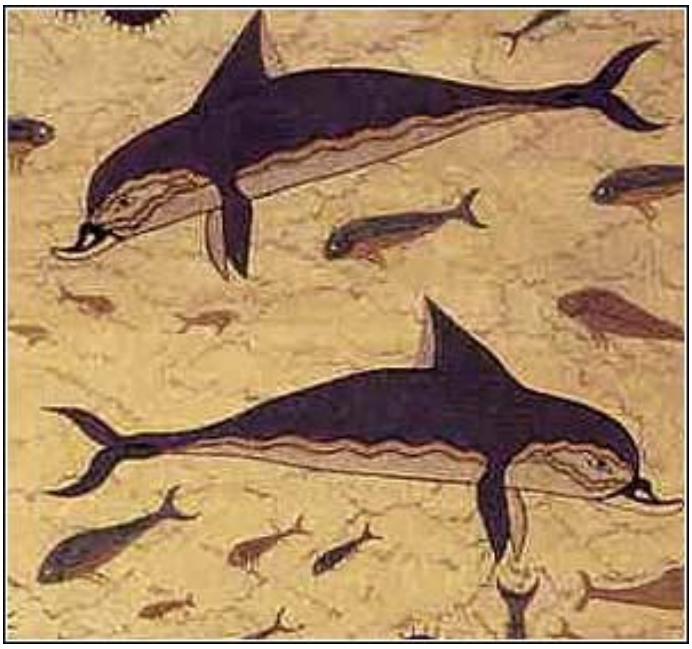
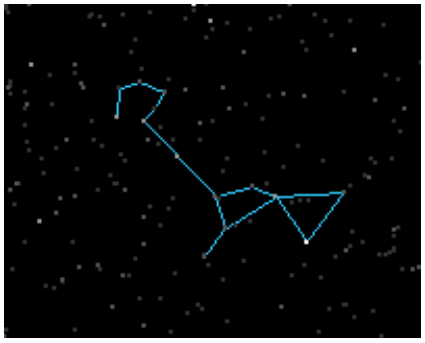


Fig. 1.1 Dolphins in a fresco from the Queen's Megaron in the east wing of the Palace of Knossos, Crete. The coloration and morphological details indicate that it is a stripped dolphin, *Stenella coeruleoalba*, which is a common species in the Mediterranean.

The ancient Greeks held dolphins in great esteem and their killing was tantamount to killing a person, both crimes were punishable by death. One of the earliest literary references to dolphins is Aesop's fable 'The Monkey and the Dolphin' which dates back to about 600 BCE. It tells that during a violent storm a ship was capsized, and among those thrown into the water was a monkey. Observing its distress, a dolphin came to its rescue, and took the monkey upon its back the dolphin to shore. Near Piraeus, the harbor of Athens, the dolphin inquired of the monkey whether he was an Athenian. 'Oh, yes,' replied the monkey, 'and from one of the best families.' 'Then you know Piraeus,' said the dolphin. 'Very well, indeed,' said the monkey, 'he is one of my most intimate friends.' Outraged by such a deceit, the dolphin took a deep dive and left the monkey to its fate.

Another account tells that Apollo Delphinus and his son Icadius were carried by a dolphin to the coast near Mt. Parnassus, where he built the Temple of Delphi -the navel of the earth. Delphis, the son of Poseidon and Melantho is credited with the foundation of Delphi, and Poseidon, Neptune of the Romans, was the god of the sea. This is the origin of the word 'Delphis' which will be translated among most western countries as 'dolphin' and that still is used in the scientific naming of these animals.

In the fifth century BCE an Athenian astronomer compiled a weather calendar in which the constellation of *Delphinus* was mentioned. In the fourth century BCE the astronomer Eudoxus (ca. 366 BCE) added the constellation of *Cetus* (whale, sea monster). Aratus (ca. 270 BCE) enumerated 44 constellations, among them the northern *Delphinus* and the southern *Cetus*. In 1603 John Bayer's *Uranometria* was published which also included, again, the constellations *Cetus* and *Delphinus*.



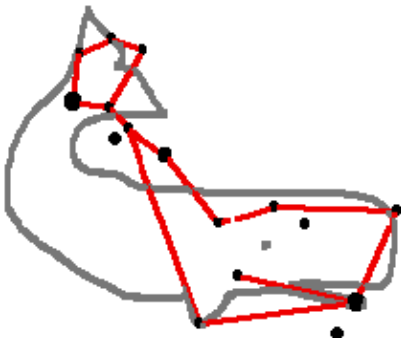


Fig. 1.2 The Cetus constellation

We are familiar with the story of Jonah and how he was cast into the sea by sailors to calm the raging tempest, how he was swallowed by a whale and after three days vomited up onto dry land. The Bible, however, says nothing of a whale. 'The Lord had prepared a great fish to swallow up Jonah.' The episode, which is an allegory, has been a favorite one for illustration by artists for many centuries, and in the days when whales were thought to be fish, what could be more natural than to depict the great fish as a whale? Another biblical beast that is often thought to be a whale is leviathan, a gigantic animal 'apparently the sea or water equivalent of Behemoth the king of animals on dry land.' In Job XLI 14, 15 and 16, it seems to be a crocodile for, 'His teeth are terrible round about. His scales are his pride, shut up together as with a close seal. One is so near to another, that no air can come between them,' but in verse 31 he is more whalelike: 'he maketh the deep to boil like a pot: he maketh the sea like a pot of ointment.' In Isaiah XXVII, 1: 'the Lord was his sure and great strong sword shall punish leviathan the piercing serpent, even leviathan that crooked serpent; and he shall slay the dragon that is in the sea.' And in Psalms civ. 25 and 26, 'So is this great and wide sea, wherein are things creeping innumerable, both small and great beasts. There go the ships: there is the leviathan, whom thou hast made to play therein.' As leviathan was so big the name has been applied poetically to the great whales, and indeed to anything else for large size, particularly ships.

In the Ninth Century, the Norwegians prided themselves in knowing 23 species of whales and dolphins and in the thirteenth century a book titled *Speculum Regale* or Mirror of Royalty, said that the only interesting thing to see in Iceland were whales. Also, in the thirteenth century Icelandic *Mariu saga* we learn how a man sits on a freshly flayed oxhide (the hide of an ox) with squares drawn round it until 'the devil reveals the future'. Other sources tell of those Icelanders who 'sit out' wrapped in the hide of a sheep, walrus or bull to gain knowledge from the dead (for other early references to dolphins and whales see Montagu 1963, Fraser 1977).

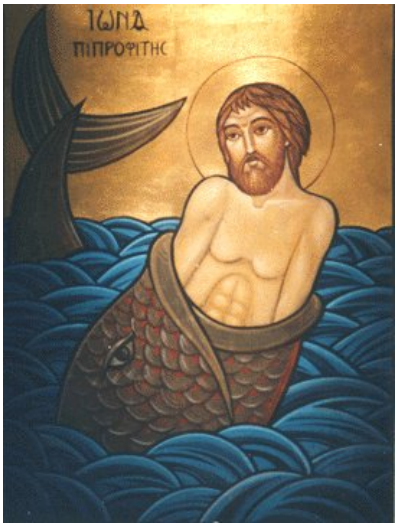


Fig. 1.2. Ancient representation of Jonah

Fig. 1.3 An illustration from *Theatrum Orbis Terrarum (1570) by* A. Ortelius. It represents a number of marine mammals off the coasts of Iceland, seen as monsters in the sixteenth century.

Non-western civilizations have also produced an incredibly rich tradition of myths and legends about marine mammals. Ancient Chinese believed that the ruler of the sea was a strange mythical figure, with the body of a huge whale but the hands and feet of a human being. In Japanese mythology the hare and the tortoise in Aesop's fable are replaced with a whale and a slug. Islamic texts tell of a whale that was believed to support the world. Whales appear in Inuit myths about the beginning of the world. Australian aborigines, Polynesians, and many Native Americans traditionally regard them as spirits or messengers of the gods.

Among native North Americans from the West Coast, myths of marine mammals abound. For the Nootka culture in the creation myth, the sea lion's services are enlisted by the Raven to help him land in exchange for a fur coat so he can swim in the coldest of waters and keep warm. The Legend of the Killer Whale is a tale of Natcitlaneh who was abandoned on an island by his brothers-in-law who were jealous of his prowess as a hunter. He was rescued by the sea lions and taken to their village in a cave where he healed their Chief. In gratitude, the sea lions gave him supernatural powers, which enabled him to carve eight wooden killer whales. These whales came to life when they were placed in the sea and avenged him by killing his brothers-in-law.

Legends about marine mammals also occur among many peoples that traditionally inhabit the Orinoco delta area in South America. Human characteristics are attributed to whales and dolphins and most other wildlife. Tales about some animals portray them to be good while others clearly consider them to be bad; while some indigenous people kill some species others species are respected and beloved (de Barral 1961, García 1971, Wilbert 1970).

Yet of all these myths, none was so spread and persistent as the one of the mermaids. The Babylonians were known to worship a mermaid-like, sea-god called *Oannes* or *Ea*. The Syrians and the Philistines were also known to have worshipped a Semitic mermaid moon-goddess: the Syrians called her *Atargatis* while the Philistines knew her as *Derceto*. The Hindus, among their many gods, worshipped one group of water-gods known as the *Asparas*. In Japanese and Chinese legends there were not only mermaids but also sea-dragons and the dragon-wives. The Japanese mermaid was known as *Ningyo* and was depicted as a fish with a human head. The Polynesians believed that one of their creators was *Vatea* who was depicted as half-human and half-porpoise.

Greek and Roman mythology generated the first literary description of mermaids. Homer mentions the Sirens during the voyage of Odysseus but without giving a physical description. Ovid on the other hand writes that the mermaids were born from the burning galleys of the Trojans where the timbers turned into flesh and blood and the 'green daughters of the sea'.

With the arrival of Christianity, we start seeing a transformation in the image of mermaids. Like with other Pagan ideas, Christians transformed the myth of the sirens for their own purposes. Thus, by the Middle Ages, the imagery of mermaids with their comb and mirror in hand came to represent vanity and female beauty which could lure males into their own destruction. Mermaids are depicted sometimes sitting on the rocks and singing, which was supposed to lure sailors to their doom. This is why they are sometimes confused with sirens. The 'mermaids' seen by Christopher Columbus in the American continent were manatees; no wonder he felt disappointed for their lack of human-like beauty.

Fig. 1.4. 'Sirenes', a 16 X 18 in oil canvas by Luberisse Arol, a Haitian artist, shows a current representation of mermaids.

The mermaid as a myth starts to disappear in the fifteenth and sixteenth centuries with the increased world exploration. Yet, mermaids became familiar figures in the literature. Shakespeare makes allusion of mermaids and/or sirens in his *Comedy of Errors* and in *A Midsummer Night's Dream*. Hans Christian Andersen's *The Little Mermaid* and Charles Kingsley's *The Water Babies* are additional examples of mermaids becoming popular figures in literature, particularly within the Romantic Movement.

In the twentieth century mermaids continued to be a source of fascination and commercialism: from P.T. Barnum's *Feegee Mermaid* (a fish and a monkey sewn together and put on display in a tank of something like formaldehyde), to the main subject in the movie *Splash* with Daryl Hannah and Tom Hanks, to one of the episodes of the X-Files (see Further Readings for a list of some sources on marine mammal mythology).

Box 1.3.

About Moby Dick

'Call me Ishmael. Some years ago — never mind how long ago precisely— having little or no money in my purse and nothing particular to interest me on shore, I thought I would sail about a little and see the watery part of the world.' This is the opening of one of the most celebrated pieces of American literature: *Moby Dick* by Herman Melville.

Few literary productions have yielded more speculation and discussion than Melville's opera magna. *Moby Dick*, the white whale (actually an albino sperm whale), has been interpreted as the personification of evil or the victim of human irrationality; in any case, it is one of the most mysterious characters in American literature. Part of the beauty of the book resides on the fact that on one hand the story is relatively simple, yet the book itself is full of metaphors that many have interpreted as representative of the struggle between good and evil, reason and madness, capitalism and environmentalism. The references to ambiguous sexuality, race representation, and religious imagery make the book as contemporary today as it was when written. It continues to yield different interpretations since first published, which is, perhaps, the best proof of its timelessness (e.g., Slochower 1950, Dahl 1959, Pachmuss 1979, Sachs 1980).

The book chronicles the heyday of American whaling, when hundreds of thousands of whales (particularly sperm whales at that time) were killed for their oil. The main human character is Captain Ahab, a bitter man because he lost a leg in a battle with *Moby Dick*, the biggest and most majestic sperm whale of them all. He now wears an ivory leg. Ahab is obsessed with killing the whale and hunts it all over the world. Eventually, Moby Dick sinks the ship, the *Pequod*, and Ahab goes down with it. A young sailor called Ishmael (Biblical name that means outcast or wanderer) narrates the story. He is the sole survivor of the deadly confrontation. He not only tells us about what he witnesses but also describes whale species, whaling ships, harpooning techniques, and other aspects of the industry in great detail (Chapter 32 of the book is titled 'Cetology' and is a pretty good summary of what was known to that date in terms of whales and dolphins).

This novel is based on the real experiences of Herman Melville (*b*. 1 August 1819, New York City, NY; *d*. 28 September 1891, New York City) in the Pacific. He was an American writer who published numerous books (some of them posthumously). He left an uninteresting career as a bank clerk to sail, in 1841, as a 23-year-old adventurer aboard the New Bedford sperm whaler *Acushnet*. As it was the case in all whaling ships of the times, life was horrible and after few months when they anchored in Nukahiva, in the Marquesas, Melville jumped ship (a common occurrence among whaleship crews). Within a few weeks he was heading for Tahiti, aboard the Australian whaler *Lucy Ann*. But that trip was not better than the previous one, and after a rather disorganized mutiny, he had to spend a few days in a Tahitian jail. He was released and signed aboard his third ship in less than a year, the Nantucket whaler *Charles & Henry*, which took him to Lahaina in Hawaii. He jumped ship again and returned to the U.S. as an ordinary seaman on the frigate *United States*. The idea of a sperm whale striking and sinking a ship is not

fictional but based on a real story, the sinking of the whaleship *Essex* in 1821 (Philbrick 2000).

Melville's first two books were very popular: *Typee* (1846) and *Omoo* (1847), but *Mardi* (1847) was a financial disaster. Then he published *Redburn* (1849) and *White Jacket* (1850), which were financially successful. *Moby Dick* was written in 1850 and published in 1851. Reviews were very bad and two years after publication all unsold copies were destroyed in a fire. Melville went through very bad financial times for the rest of his life. To support his family, Melville was forced to become a customs inspector in New York. When he died not only his greatest book but also his name had been almost forgotten.

Not until at least 40 years after the death of the author, *Moby Dick* was recognized as a masterpiece. Actually it was a Hollywood production of the story that revived the book. The first movie version, in 1926, was titled *The Sea Beast* with John Barrymore as Captain Ahab. This was a silent movie. However, it was so popular, that publishers released the actual novel with the famous actor on the cover of the book. Although the Hollywood version of the story was very different from the book, people started to read Melville again. In 1930 there was a new version (this time a 'talkie') of *Moby Dick*. Again John Barrymore plays Ahab but now the script gets even cheesier by including a happy ending. In 1956 a new version was released. This is a great movie directed by John Houston. Ray Bradbury (author of '*The Martian Chronicle*s') wrote the script, Gregory Peck played Ahab, and Richard Basehart was in the role of Ishmael. In 1998 HBO produced a miniseries with Patrick Stewart as Ahab and with a cameo appearance by Gregory Peck. This is also an excellent production.

Curiously enough, the book and movie *Jaws* have some elements of *Moby Dick* when portraying the shark chaser as a sort of Ahab. Even Jaws' famous musical theme, seems to allude the rhythm of Ahab's limp on his ivory leg.

Other famous films where marine mammals play a major role are *The Day of the Dolphin* (1973), *The Big Blue* (1988), *Free Willy* (1993), *Flipper* (1996), *Whale Rider* (2002), and *Luna: Spirit of the Whale* (2007). But of all the mythical marine mammals, *Moby Dick* is, without a question, the most famous of all (for more on Melville and *Moby Dick* see ssection of suggested readings).

Fig.1.5. Herman Melville

1.5. Why and How to Study Marine Mammals

1.5.1. Why

Human fascination and simple curiosity aside, we have very good practical reasons why to investigate these animals. They can be grouped as follows:

A. Scientific Reasons: Marine mammals have evolved from terrestrial ancestors through a number of unique adaptations to the aquatic environment. Both, fossil and living marine mammals have given us insights on a number of biological phenomena, from convergent evolution to deconstructive evolution (the loss of morphological features such as legs and hair), from hydrodynamics to communication. These scientific advances have benefited basic and applied research such as in the fields of biomedicine and engineering.

B. Ecological Reasons: Marine mammals have become major subjects of research in ecology (broadly defined) for a number of reasons. On one hand these creatures are usually at the top of their aquatic food chain, so their ecological health is also a reflection of their ecosystem's health. Many marine mammal die-offs have been attributed to pollution. Given the low reproductive rates for most of them, they face special challenges when it comes to ecological recovery after prolonged and/or intense exploitation. Further, there is some evidence that climatic changes may change their distribution and also affect their population structure.

C. Economic Reasons: Some practical research on their abundance is aimed to either propose their exploitation or their conservation, as well as to understand their interaction

with fisheries of other marine species. Marine mammals displayed in aquaria and zoos also attract a large number of visitors, which is an incentive for many to keep them in captivity. Whale watching is increasingly an important economic activity in many areas. For that activity to be both profitable and non-damaging, appropriate studies must be conducted in order to make sure that there are enough animals for a long enough period of time throughout the year to create an actual market. On the other hand, the behavior of the whale watching vessels and crews must be as little intrusive as possible and to that end the behavior of the animals involved must be understood and closely monitored.

D. Ethical Reasons: More and more people are interested in protecting marine mammals not only for their ecosystem value but also for ethical reasons. Thus, a great deal of effort has been made to advance our knowledge in areas such as strandings, captive care, and releases into the wild.

1.5.2. How

A. From individuals washed ashore:

1. If an animal is washed shore, we take all measurements, observe general condition, sex, and reproductive status.

2. Lab studies to determine age (by counting the number of growth layers deposited on teeth, like the rings of a tree), checking body tissues for pollutants, identifying stomach contents, and collecting genetic material.

3. Then results are analyzed and put into a larger context.

B. From captured individuals in fisheries: A great deal of information has been obtained through the study of animals that have been captured either on purpose or accidentally. Actually, a number of researchers have been able to generate abundant information by studying animals captured by the whaling and sealing industry or in by-catch in fisheries. Even logbooks of whaling ships are used today to determine past distribution and abundance of certain species of marine mammals as well as certain aspects of human culture related to these animals.

C. From captive individuals: This type of research has generated a large number of ethical and scientific questions. For example, do captive animals behave like wild ones? How much of extrapolation can we make? Still, to study cetaceans in the wild is so difficult that study of captive individuals have generated useful information, particularly about behavior.

D. Field Studies: First ingredient: Patience. You are dealing with wild animals whose behavior (and even presence) is not always predictable. Yet, this is an area in which new technologies are making a great impact. They include:

Visual Observations: Most species identifications are based on visual observations that may be aided with photo and/or video cameras. For **species identification** among the things to watch for are the body shape and size, shape and position of fins, the mouth, the blow (very useful to differentiate among different species of 'great whales'), and dive sequence (also useful to differentiate large species of whales and a few small toothed whales). Additionally, other features can be used for identification such as color(s), group size, behavior, or any other unusual features. For individual identification natural markings, scarring and bandings, and attachment tags can be used.

Population Estimation: One of the most important pieces of information about any marine mammal species is its population size. That can be done through different techniques: A) **distance sampling** (counting animals in a particular area by either surveying them through a straight line, also known as **line transect sampling,** or by counting all cues detected within a sector within an area from the observation platform, also known as **cue counting**). B) **Mark-recapture** (commonly used in ecology with other organisms). C) **Migration counts** (by counting how many migrating animals go through a point during their migration, which is good for assessing populations of gray whales). D) **Colony counts** (by counting the number of animals on a rockery; good for pinnipeds). A by-product of these kinds of studies is **stock identification and assessment**, i.e., a group of individuals that are managed (from the fisheries viewpoint) independently. A number of genetic and mathematical techniques are used to assess the size and potential growth of that specific biological unit.

Individual Photo-Identification: In some whales, dolphins, and porpoises, the differences among individuals can be quite subtle, and some animals are difficult to approach closely, or are so small and fast that it is hard to see details of any markings. Since the risk of human error is so high, most researchers do not rely merely on sight and memory. They prefer to take photographs of each animal instead. These help to confirm the identity of the individual and even share that information with other researchers in other latitudes, which is useful in trying to ascertain migratory patterns. The type or markings can range from patterns of callosities in right whales, to shapes and/or markings on fins, scars in the bodies of dolphins and pinnipeds, and the black and white markings on the underside of their tails.

Radio Transmitters and Satellite Tracking: Tracking requires firing with a specially designed gun or a crossbow, a small, battery-powered transmitter. That transmitter is anchored into the thick blubber of the whale's back. Either handheld antennae or satellites can track the signals from the transmitters. Both generate information about the position of the animal being studied. Technological advances in microelectronics have made possible the application of satellite telemetry and time-depth recorders which have led to the discovery that elephant seals regularly dive to depths of 1000 m with consistently long dive durations typically lasting 15 to 45 min. It is an invasive technique causing at least a temporary discomfort to the animal. With advances in microelectronics the transmitters are getting smaller.

Animal-Borne Video System: This system consists of placing a video camera to record an animal's behavior as if we were riding it. It is invasive because, obviously, the animal senses that an apparatus has been attached to it. Yet, it can provide us with some insights on their behavior.

Hydrophones: Great deal of information can be obtained by using hydrophones. Sometimes we can listen to certain species without interfering with their behavior whatsoever. As a mater of fact, sound recording can be used to identify species that tend to be shy or difficult to recognize visually, as well as to identify different pods of animals based on heir 'dialects.' Currently, new equipments are opening new horizons in the application of acoustic technologies for the study of marine mammals. In 1992 the US Navy decided to give some researchers access to its **SOund SUrveillance System (SOSUS)**. It comprises a series of hydrophone sensors placed on the ocean floor and connected to shore facilities where the acoustic data are received, processed, and reviewed by an acoustic analyst. SOSUS reports surface ship activity and supports anti-submarine warfare command and tactical forces by detecting, classifying, tracking, and reporting submarine activity. SOSUS enjoyed tremendous success during the Cold War tracking submarines by their faint acoustic signals. Now it continues to provide a critical element of the **Integrated Undersea Surveillance System** (IUSS). Additionally, SOSUS provides support, on a not-to-interfere basis, on dual-use areas such as global warming, seismic activity, marine mammal research, and fisheries law enforcement. Thanks to that system, whale movements are being tracked and the number of whales can be counted. Other interesting developments include arrays of hydrophones that, together with synthetic filters and appropriate software, can automatically identify and recognize the low-frequency sounds of baleen whales (Mellinger and Clark 1997).

DNA fingerprinting: DNA fingerprinting is being used to identify species (for either taxonomic purposes or to verify species identification when monitoring commercial products from marine mammals), to determine paternity among calves of the same mother, the role played by fathers in the upbringing of calves, and the genetic relationship among members of the same pod. DNA samples can be taken by either firing a small dart from a crossbow to take a small sample of the animal's skin or by collecting pieces of skin that flake off naturally, like whale dandruff, as the animal dives. One of the most spectacular results of the application of molecular techniques has to do with providing forensic evidence. For example, it has been shown that some countries that have what are called 'scientific permits' by the International Whaling Commission (IWC) to kill certain number of whales of a particular stock of a particular species only, are in fact killing individuals of species and/or of whales whose hunting is completely prohibited by the IWC (Baker *et al.* 2000). For that purpose, researchers just buy whale products in Japanese and South Korean supermarkets and perform the genetic analysis.

Unmanned Aerial Vehicle (UAV): Probably the least intrusive way of conducting behavioral observations of animals is by aerial observations (Jones IV *et al.* 2006). That is particularly true in the case of marine mammals since the animal does not feel intruded by a surface, noisy boat. Yet, this procedure can be challenging for a number of reasons such as the fact that many species spend considerable periods beneath the surface of the

water of that device used for this type of observations has limited range and/or activity time. Some of the devices that have been developed to that end include a 'blimp-cam': a video camera mounted on a small ovoid-shape, helium-filled aerostat (blimp) (Fig. 1.6) Hodgon (2007). They are small, cheap and easy to operate and can be flown at a height of 50 m providing visual information at distances up to 200 m.

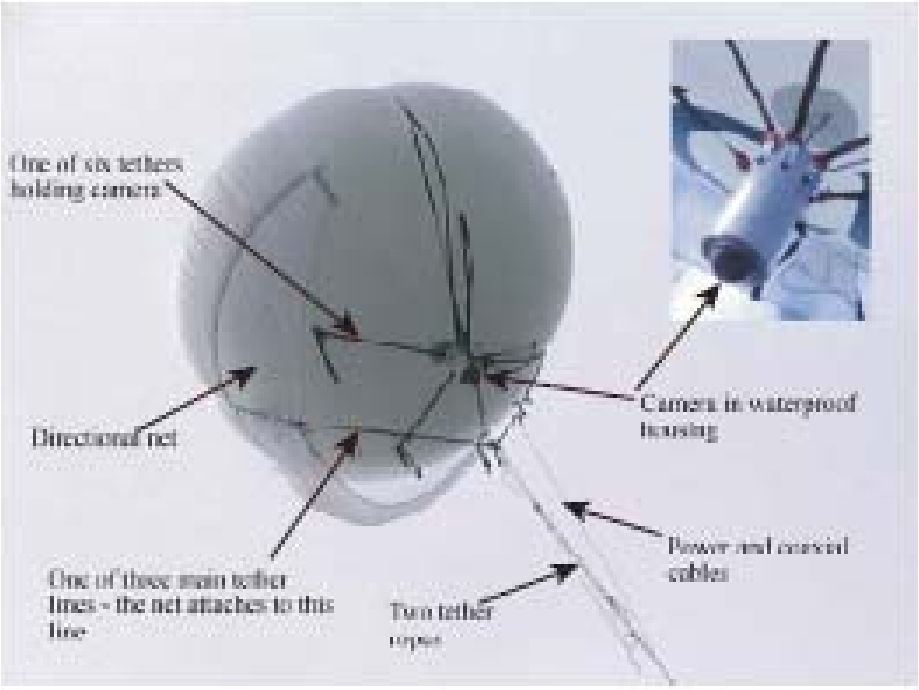


Fig. 1.6. The 'BLIMP-CAM' (from Hodgon 2007)

S*ubmersibles:* Although potentially important since they would allow us to actually see these creatures, they are extremely expensive to build and operate. We do not know how we are modifying marine mammal behavior just by being there. Besides, nobody envisions how these vehicles can ever be built to match marine mammals' speed and diving abilities. Yet, some results are promising. A group of Japanese scientists used an automated underwater vehicle that also recorded acoustical signals (Iwakami 2002).

Chapter Summary

Marine mammals have been the source of human fascination for millennia as evidenced by their presence and imagery in literature, fine arts, and history. Yet, only the last few decades, has marine mammal research been increasing in both depth and breadth. There are a number of good reasons why marine mammals should be studied methodically and they can be grouped into purely scientific, ecologic, economic, and ethic in nature. Because where they live, marine mammals are difficult to study, especially if intrusion into their habits is to be avoided. To that end, marine mammalogists take advantage of animals washed ashore and captured (intentionally and unintentionally). Observational techniques include direct observation for both species and individual identification,

population estimations utilizing a number of different counting techniques, telemetry data gathering by using radio transmitters and radio tracking, acoustic surveillance, and genetic analysis.

Critical Thinking Questions

1. Human fascination with marine mammals has generated a great deal of myths and legends throughout history. Today they are an essential component of the environmental movement. Do you think that marine mammalogists should or can disassociate themselves from the cultural context while doing research on these animals?
2. What does mystification of marine mammals tells you about human nature.
3. What kind of technological innovations would you envision that might propel marine mammal research into new areas?

Key Terms

Acoustic telescope
Animal-Borne Video System
Carnivora
Cetaceans
Colony counts
Cue counting
Distance sampling
DNA fingerprinting
Extant
Individual Photo-Identification
Integrated Underwater Surveillance System
Line transect sampling
Mark-recapture
Migration counts
Pinnipeds
Population estimation
Radio Transmitters
Satellite Tracking
Sirenians
Species identification
Stock identification and assessment

Recommended Videos

Moby Dick. 1996. The Learning Channel. Distributed by Discovery Channel Video, VHS 50 min.

Moby Dick: The True Story.2001. CineNova Productions, Inc. Discovery Channel. DVD 52 min.

Further Readings

For more on the mythology of marine mammals, see:

Ellis, R. 1996. *Monsters of the sea*. New York: Doubleday.
Ferguson, D. 2001. *Native American myths*. London: Collins & Brown.
Hodgkins, G.A. 1977. *The sea spirit of the central Eskimo: mistress of sea animals and supreme deity*. Chicago, IL: University of Chicago, Ph. D. Dissertation.
Institut Océanographique (Paris). 1996. *Les mythes de l'eau et de l'océan en Orient: Cycle de conférences de l'Université Inter-Ages: Méditerranée, Egypte ancienne, Arabie, Inde, Birmanie, Indonésie, Chine, Japon*. Paris: Océanographique.
Ke, Y. 1993. *Dragons and dynasties: an introduction to Chinese mythology*. New York : Penguin Books.
Landrin, A. 1870. *Les monstres marins*. Paris: Hachette et Cie.

For more on Herman Melville and Moby Dick, see:

Bloom, H. (Ed.). 1999. *Herman Melville*. Broomall, PA: Chelsea House Publishers.
Delbanco, A. 2005. *Melville: his world and work*. NY: Alfred A. Knopf.
Hardwick, E. 2000. *Herman Melville*. New York: Viking.
Mathewson, S.L. 1989. *The canonical whale: Moby-Dick and American literary history*. Ph.D. Dissertation, University of New Mexico.
Parker, H. 2002. *Herman Melville: A biography* (2 vols.). Baltimore, MD: Johns Hopkins University Press.
Robertson-Lorant, L. 1998. *Melville: a biography*. Amherst: University of Massachusetts Press.
Rollyson, C. & L. Paddock. 2001. *Herman Melville A to Z: The essential reference to his life and work*. New York: Facts on File.
Severin, T. 2000. *In search of Moby Dick: quest for the white whale*. New York: Da Capo Press, 2000.
Stein, S. 2000. *The pusher and the sufferer: an unsentimental reading of Moby-Dick*. New York: Garland.

Literature Cited

AOU. The Committee on Classification and Nomenclature of the American Ornithologists' Union. 1998. Check-List of North American birds. The species of birds of North America from the Arctic through Panama, including the West Indies and Hawaiian Islands. Lawrence, Kansas: Allen Press, American Ornithologists' Union.
Baker, C.S.; G.M. Lento, F. Cipriano & S.R Palumbi. 2000. Predicted decline of

protected whales based on molecular genetic monitoring of Japanese and Korean markets. *Proceedings of the Royal Society of London*, *Series B, Biological Sciences* **267**:1191-1199.

Beasly, I., K.M. Robertson & P. Arnold. 2005. Description of a new dolphin, the Australian snubfin *Orcaella heinsohni* sp. n. (Cetacea, Delphinidae). *Marine Mammal Science*. **21**:365-400.

Carwardine, M.; E. Hoyt, R.E. Fordyce & P. Gill. 1998. *Whales, dolphins & porpoises*. NY: Time-Life.

Croll, D.A., C.W. Clark, A. Acevedo, B. Tershy, S. Flores, J. Gedamke & J. Urban. 2002. Only male fin whales sing loud songs - These mammals need to call long-distance when it comes to attracting females. *Nature* **417**: 809.

Dahl, C. 1959. Moby Dick's cousin behemoth. *American Literature* **31**:21-29.

Dams, L. 1989. Le 'Sanctuaire des Dauphins' ou 'Salle des Poissons' de la Grotte de Nerja. *Anthropologie et Prehistoire* **100**:165-172.

Dalebout, M.L.; J.G. Mead, C.S. Baker, A.N. Baker & A.L. van Helden. 2002. A new species of beaked whale *Mesoplodon perrini* sp. n. (Cetacea:Ziphiidae) discovered through phylogenetic analyses of mitochondrial DNA sequences. *Marine Mammal Science* **18**:577-608.

De Barral, B.M. 1961. *Guarao Guarata. Lo que cuentan los Indios Guaraos*. Caracas: Gráficas Salesianas.

Ellis, R. 1991. *Men and whales*. New York: Alfred A. Knopf.

Forestell, P.H. 2002. Popular culture and literature, pp. 957-974, In: W.F. Perrin, B. Würsig & J.G.M. Thewissen (Eds.). *Encyclopedia of marine mammals*. San Diego: Academic Press.

Fraser, F.C. 1977. Royal Fishes: The importance of the dolphin, pp. 1-44, In: R.J. Harrison (ed.). *Functional anatomy of marine mammals*, Vol. 3. London: Academic Press.

García, A. 1971. *Cuentos y tradiciones de los indios Guaraúnos*. Caracas: Universidad Católica Andrés Bello.

Hodgson, A. 2007. 'BLIMP-CAM': aerial video observations of marine mammals. *Marine Technology Society Journal* **41**:39-43.

Iwakami, H.; T. Ura, K. Asakawa, T. Fujii, Y. Nose, J. Kojima, Y. Shirasaki, T. Asai, S. Uchida, N. Higashi & T. Fukuchi. 2002. Approaching whales by autonomous underwater vehicle. *Marine Technology Society Journal* **36**:80-85.

Jones IV, G.P., L.G. Pearlstine & H. F. Percival. 2006. An assessment of small unmanned aerial vehicles for wildlife research. *Wildlife Society Bulletin* **34**:750-758.

Matthews, L.H. 1968. *The whale*. London: George Allen & Unwin.

Mellinger, D.K. & C.W. Clark. 1997. Methods for automatic detection of mystecete sounds. *Marine and Freshwater Behavioral Physiology* **29**:163-181.

Montagu, A. 1963. The history of the dolphin, pp. 3-30, In: *The dolphin in history*; papers delivered by Ashley Montagu and John C. Lilly at a symposium at the Clark Library, 13 October 1962. Los Angeles, CA: William Andrews Clark Memorial Library, University of California.

Pachmuss, T. 1979. Prometheus and Job reincarnated: Melville and Dostoevskij. *The Slavic and East European Journal* **23**:25-37.

Papadopoulos J.K. and D. Ruscillo. 2002. A ketos in early Athens: An archaeology of

whales and sea monsters in the Greek world. *American Journal of Archaeology* **106**:187-227.

Philbrick, N. 2000. *In the heart of the sea: the tragedy of the whaleship Essex*. New York: Penguin Books.

Robins, C.R.; R.M. Bailey, C.E. Bond, J.R. Brooker, E.A. Lachner, R.N. Lea & W.B. Scott. 1991. *Common and scientific names of fishes from the United States and Canada*. Bethesda, Maryland: American Fisheries Society Special Publication # 20.

Sachs, V. 1980. The gnosis of Hawthorne and Melville: an interpretation of the scarlet letter and Moby-Dick. *American Quarterly* **32**:123-143.

Slochower, H. 1950. Moby Dick: the myth of democratic expectancy. *American Quarterly* **2**:259-269.

Sweeney, J.B. 1972. *A pictorial history of sea monsters and other dangerous marine life*. New York: Nelson-Crown Publishers.

Van Helden, A.L.; A.N. Baker, M.L. Dalebout, J.C. Reyes, K. van Waerebeek and C.S. Baker. 2002. Resurrection of *Mesoplodon traversii* (Gray, 1874), senior synonym of *M. bahamondi* Reyes, van Waerebeek, Cárdenas and Yáñez, 1995 (Cetacea: Ziphiidae). *Marine Mammal Science* **18**:609-621.

Wada, S.; M. Oishi & T.K. Yamada. 2003. A newly discovered species of living baleen whale. *Nature* **426**:278-281.

Wilbert, J. 1970. *Folk literature of the Warao Indians. Narrative material and motif content. Latin American Studies, Vol. 15*. University of California, Los Angeles.

Chapter 2

History of Marine Mammalogy

2.1. The Ancient World

Ancient cultures had a practical knowledge of nature. There is evidence that humans utilized marine mammals as early as the Upper Paleolithic (40,000-10,000 YBP). This is based on remains of Mediterranean monk seals (*Monachus monachus*), common dolphins (*Delphinus delphis*) and bottlenose dolphins (*Tursiops truncatus*) found in caves off the coast of Gibraltar (Stringer *et al.* 2008) together with the remains of other animals used by Neanderthals. We do not know whether these animals were actively hunted or if the Neanderthals utilized carcasses of stranded animals.

The first evidence of whaling by humans dates back to 3000 YBP when this activity was depicted by two scenes carved in walrus ivory found on the Russian coasts of the Bering Sea (P 2008). Activities like these lead to people in Antiquity to the naming of species, the development of knowledge on behavior in particular and natural history in general, and the acquisition of learning of what was edible or medicinal. They also developed a sense for naming structures such as edible organs. Some even went as far as to speculate evolutionary relationships: a Chinese author, for example, wrote 2,000 years ago about the baiji, the Chinese freshwater dolphin, and speculated that it might be related to the marine dolphins (Nie 1949).

Yet, early civilizations provided little insight on the intrinsic nature of animals in general. Egyptians, Sumerians, and Babylonians, were **animistic**, i.e., they believed in a spiritual force separated from the matter and that natural phenomena produce all life and that objects are alive and have souls. Judaism, Christianity, and Islamism are **monotheistic**, i.e., their beliefs gravitate around a specific book or set of dogmas. These intellectual contexts in those times were not good environments for the development of new ideas.

The Hellenistic culture was different. They were the first to produce scientific writings just for the sake of it. They did not believe in a single god, or revealed 'truth,' or dogmatic books. Greek philosophers came out with different and even contradictory ideas without a sense that they were threatening the establishment. Three different generations of Greek philosophers appeared within a time span of about 250 years:

A) The first generation (from about 600 to 550 BC) was heavily influenced by Eastern cultures that had a natural history tradition as reflected not only in their understanding of

fauna and flora, but also in their success in domesticating animals and plants. These first Greek philosophers concluded that:

1. Creation of the world is the product of the forces of nature.
2. There was no design. What takes place is the result of necessity.
3. They rejected the supernatural explanation in favor of materialistic ones.
4. They considered that the world is eternal (timeless).

This was a fresh start by looking at the world as it presented itself. Therefore, Greek colonies in the Middle East became lively centers for a scientific attitude.

B) The second generation (between 550 and 400 BC) went further and started speculating about biological mechanism and toyed with three ideas:

1. The inheritance of acquired characters.
2. The principle of use and disuse.
3. Spontaneous generation.

C) The third generation started with **Plato**[1] who in many ways represented a step backwards regarding previous achievements. He was the founder of a school called *Academia* and developed a philosophy called **idealism**, i.e., that whatever exists is known to man in dimensions that are chiefly mental: thought and an idea (i.e., a chair is not a chair but it is what we believe it is). For Plato, no true knowledge can be acquired through observation. Yet, it was one of his students who by contradicting his master would produce the first tangible products of biology as a science while generating the first important contributions to marine mammalogy.

His name was **Aristotle**[2] and he was the first philosopher who wrote about marine mammals. Together with Plato and Socrates, he was one of the three most famous Greek philosophers. His father was the royal physician of the Macedonian court. In 345 BC, Aristotle went to Pella, the Macedonian capital, where he became the tutor of the king's young son Alexander, later known as Alexander the Great. In 335, when Alexander became king, Aristotle returned to Athens and established his own school, the *Lyceum*. There he created the **Peripatetic** ('walking' or 'strolling') school, name as such because much of the discussion in his school took place while teachers and students were walking about the *Lyceum* grounds. He broke away from the idealism of his teacher Plato, by insisting that knowledge must derived from direct observations. When asked why he thought so differently from Plato's teachings he replied 'although I loved my teacher Plato greatly, I love the truth more.'

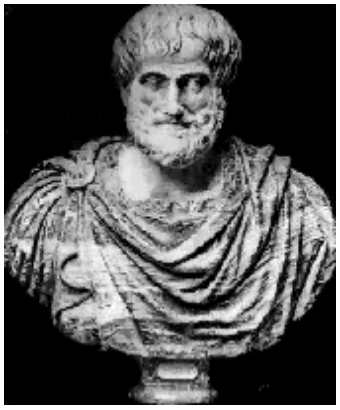


Fig. 2.1 Effigy of Aristotle. Nobody really knows what he looked like.

Unlike Plato, Aristotle saw the world of perceived things as the real world (i.e., a chair is a chair is a chair, period). He was an avid collector of empirical evidence. He

[1] *b*. ca. 427 BCE, Athens (?) – *d*. 347 BCE, (?)
[2] *b*. 384 BCE, Stagira, Macedonia; *d*. 322 BCE, Euboea

was the first to distinguish the different biological disciplines (i.e., zoology, botany). He was also the founder of the comparative method: for him, all structures and biological phenomena have a biological meaning (adaptive significance). Because of this, Aristotle is considered the founder of **teleology** or doctrine of purposiveness in nature. He advanced the idea of *Scala Naturae* or ladder of nature. For him 'Nature passes from inanimate objects through plants to animals in an unbroken sequence' and species were unchanging, fixed, and eternal (neither created nor vanished). Aristotle formalized individual kinds (species) and collective groups (genera). He classified animals into blooded and bloodless (i.e., vertebrates and invertebrates), viviparous and oviparous, hairy and cold-blooded, and flying animals into those with feathered wings (birds), leathered wings (bats), and membranaceous wings (insects). Therefore, he produced the first meaningful biological classification, i.e., based on observations, not just mystical interpretations.

During his trips throughout the eastern Mediterranean world he observed and collected many animals and plants. He actually dissected many of the former and studied their internal anatomy. Adding to this first-hand knowledge, he summarized all that had been observed by other cultures in the region. Aristotle regarded the world as made up of individuals (substances) occurring in fixed natural kinds (species). Because he was able to distinguish between **homology** and **analogy**, he was able to recognize cetaceans as a natural group with many similarities with other mammals. Somehow he grouped together 'viviparous such as man, and the horse, and all those animals that have hair; and of the aquatic animals, the whale kind as the dolphin and cartilaginous fishes' (Book I, Chap V, 'The Parts of Animals' of his book *Historia Animalium*). He also wrote: 'all creatures that have a blow-hole respire and inspire, for they are provided with lungs. The dolphin has been seen asleep with its nose above water as he snores (...) All animals have breasts that are internally or externally viviparous, as for instance all animals that have hair, as man and the horse; and the cetaceans, as the dolphin, porpoise and the whale -for these animals have breasts and are supplied with milk.' He placed marine mammals quite high is his *Scala Naturae* to represent how close they were to what later would be called mammals. Among the species he described were dolphins, orcas, and baleen whales, noting that 'the [latter] has no teeth but does have hair that resemble hog bristle.'

Basic Aristotelian biological ideas were not challenged until Charles Darwin's evolutionary work. Despite this, Darwin admired Aristotle; he said privately that the intellectual heroes of his own time 'were mere schoolboys compared to old Aristotle.'

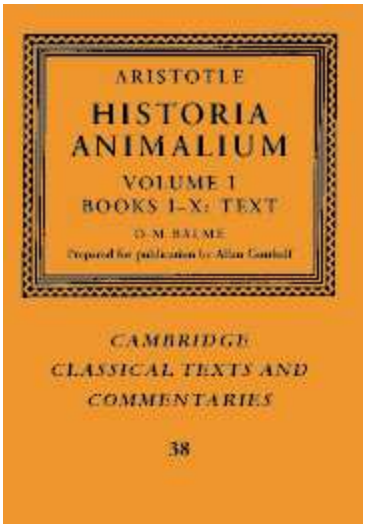


Fig. 2.2 *Historia Animalium* is probably the first Zoological treatise ever written. Although his first writings were in the form of dialogues, most of his surviving work is in the form of lecture notes that were collected and passed on by his students. They are a collection of facts and ideas passed on to his pupils. These writings survived thanks to the continuous copying by Arab scholars (such as the Spanish-Arab philosopher **Ibn Rushd** or **Averroës**[3]) and medieval monks (such as **Saint Thomas Aquinas**[4] who established on it a philosophical foundation for Christian thought). It is believed that no more than 40% of Aristotle works have survived. You can find some portions of this book online at: http://www.knuten.liu.se/~bjoch509/works/aristotle/parts_animals.txt and http://www.knuten.liu.se/~bjoch509/works/aristotle/generation_animals.txt

The next writer to leave written information about marine mammals of his time was **Pliny the Elder**[5]. After serving in the military he became a lawyer but was a failure as an attorney so he decided to become a writer while earning a living as a government bureaucrat. He was a workaholic who wrote a 37-volume *Naturalis Historia* in which according to himself he had compiled '20,000 important facts, extracted from about 2000 volumes by 100 authors.' There he classified animals according to where they live and in consequence he classified marine mammals as 'fish.' This idea would be something that would be perpetuated for nearly 17 centuries. In general he was more interested about what seemed to be curious than what was a fact. He added some mythical comments about these animals such as that 'the dolphin is an animal that is not only friendly to mankind but also a lover of music, and can be charmed by singing in harmony.' His works had great influence for 1700 years, which was unfortunate because he was an uncritical compiler of other people's writings (even if they were contradictory). Pliny also created a number of unfounded impressions about the reality of nature. His only positive contribution was that he established the norm of always citing the sources of his information. He died while watching the eruption of Mount Vesuvius when it destroyed Pompeii and Herculean.

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[3] *b*. 1126, Córdoba, today Spain – *d*. 1198, Marrakech, today Morocco.
[4] *b*. ca. 1225, Roccasecca, today Sicily - *d*. 7 March 1274, Fossanuova, today Italy.
[5] *b*. as Gaius Plinius Secundus in 23 A.D. in what is now Como, Italy; *d*. 79 A.D. near Naples, Italy.

Fig. 2.3 Alleged portraits of Pliny the Elder.

Pliny the Elder represented not only a step backward in our understanding of the natural world as a whole, but also a signal for worse times to come. In the first centuries of our Era, the Western World would see the following cultural events:

1. The replacement of Greek philosophies by Christian beliefs based on dogmatic interpretation of ancient writings.
2. The burn of the Alexandria's library in 390 A.D. the world's most important center of learning
3. Christianity became the official religion of the Roman Empire. Anything looking 'Greek' in thought was suspicious.
4. In 529 AD, the Roman Emperor Junian I closed all Greek philosophical schools because of their pagan character.
5. The history of the world was being fitted into the framework of the ancient Hebrew writings, and the origin of the animals and plants was being traced back to the creation of the world as described in the Book of Genesis.

All these factors kept further scientific inquiry into obscurity and led to a time of intellectual stagnation of the medieval times that would stall all progress in our knowledge of marine mammals.

2.3. Medieval Times

Between the Fifth and the Twelfth centuries there was little intellectual progress. Muslim and Jewish scholars developed virtually all the new knowledge in the Western Hemisphere, while among Christians the monasteries were the only places where western knowledge was kept.

In the Eleventh century we witness the rise of **scholasticism**. This was a set of scholarly and instructional techniques developed in Western European schools. Essentially it meant that people had to believe everything said by the classical authors such as Aristotle. This resulted in no freedom of thought and that truth was determined by logic, not by observation or experiments. In the schools, citations from authorities were accepted in lieu of proof.

Despite scholastic domination there are new developments that will further the development of science. First was the creation of the first cathedral schools and universities in the twelfth century. The first ones were those of Paris (1150-1170) and Oxford (1168). Teaching was done by lecture and disputation (a formal debate). This led to little innovation because it was taught that all the knowledge was in the 'revealed' book, that the 'why' questions were irrelevant, and to the development of **natural theology,** i.e., that God exists because of the order and harmony of the world that requires an intelligent being and, therefore, Nature was subservient of man.

There were two exceptions to these attitudes. One was **Albertus Magnus**[6]. He studied at the University of Padua and joined the Dominican Order. He then was sent to the University of Paris where he read the translations of the Arabic and Greek versions of Aristotle. While in Paris he tried to present the entire body of knowledge, natural science, logic, rhetoric, mathematics, astronomy, ethics, economics, politics, and metaphysics. He called his book *Opera Omnia* ('all the works'). He wrote commentaries on all of Aristotle's works with his own observations and 'experiments,' i.e., 'observing, describing, and classifying.' Albertus Magnus was canonized in 1931 and, in 1941, was made patron of natural scientists. He wrote about marine mammals, but in reality he added nothing new to what Aristotle and Pliny had provided.

Fig. 2.4 One of the four known contemporary portraits of Albertus Magnus.

[6] *b*. ca. 1206, Lauingen an der Donau, Swabia [now Germany]; *d*. 15 November 1280, Cologne, Prussia.

The other exception to scholasticism and intellectual rigidity of the time was **Roger Bacon**[7]. Bacon was critical of the methods of learning of the times, and in the late 1260s, he wrote his *Opus Majus* ('Major Work') in which he advocated a reformation in the sciences through different methods of studying nature. The *Opus Majus* was an encyclopedia of all knowledge in which he popularized the term 'experimental science' and recognized the incompleteness of the knowledge of the time. These ideas were so revolutionary that the Franciscans condemned him for his heretical views, the reading of his books were forbidden, and Bacon himself was arrested and spent ten years in prison after which he returned to Oxford.

Fig. 2.5 Roger Bacon

Despite these points of light, the combined obscurantism of the times with the fervid medieval imagination about monsters and devils, made whales and other marine mammals to be treated as 'monsters' capable of attacking and destroying a ship and swallowing its crew.

[7] *b*. 1214, Ilchester, Somerset, England; *d*. 1294, Oxford, England.

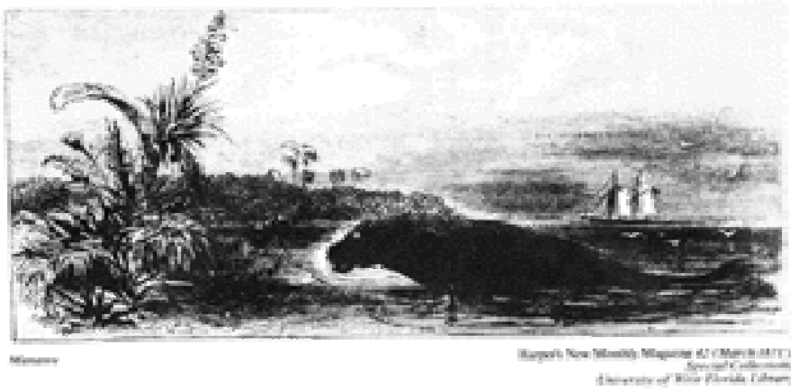


Fig. 2.6 Examples of illustration of 'marine monsters.'

On about 1250 *The King's Mirror* (*Speculum regalae* in Latin; *Konungs skuggsjá* in Old Norse) was written by an anonymous Norwegian. This was an account of Iceland where the whales of those waters were described. This is probably the only written account of medieval times based on actual observation of these animals (you can find the full text at http://www.swt.edu/~bh59648/75years/mirror/).

Yet, probably the most important thing that happened to the scientific study of marine mammals during this era was the 1324 Royal Decree by Edward II of England which stated that '... the crown has the Sovereign dominion and jurisdiction over the sea which encompasses the British isles, and over all creeks and arms of the sea and navigable rivers, it has no general property in the fish therein except whales and sturgeon. These are royal fish and belong to the crown.' What this meant is that from that moment on, the British would very carefully keep records of stranded marine mammals. These records have been used in many subsequent studies of distribution of these animals. This, also, helps explain why so many early British naturalists showed such an interest in

whales and dolphins (see below). The 'royal fish' prerogative was not abolished until 1971.

2.4. The Renaissance (1450-1650)

It began approximately in what is today Italy around 1450 and lasted until about 1650. The Renaissance is characterized by the return to the Greek and Roman cultures. There were five major technological advances that characterize the appearance of the Renaissance:

1. Gunpowder: Developed by the Chinese, gave the ability to blow feudal fortifications, which led to the development of states and nationalism. As a consequence of this, there was a development of secular powers that led to a weakening of the power of the church.

2. Block printing from movable types: The first Guttenberg book (a Bible) was printed in 1455. This led to the propagation of knowledge, secularized learning, reduced the intellectual monopoly of an ecclesiastic elite, and reading of literary and philosophical classics of Greece and Rome.

3. The compass: Invented by the Chinese, it facilitated exploration, conquest, trade, and scientific inquiry.

4. The 'Arabic' numerals (actually from India). They facilitated the development of mathematics. Even Chinese and Japanese numbers are written today in this format.

5. Paper making (developed originally in China). Coupled with printing facilitated the diffusion of knowledge.

Other important historical facts of the time were that in 1488 the Portuguese rounded the southern cape of Africa and opened up a new road to the East and in 1492 Columbus reached America. This meant the observation of many new species that had been described neither in the Bible nor by Aristotle. For example, **Gonzalo Fernandez de Oviedo y Valdes**[8] published *La Historia General de las Indias* (1535) where there is the first illustration of the West Indian manatee.

There was also a revolt against the reign of religion, which translated into questioning the church as an institution, which in turn meant questioning authority, scholasticism, and Aristotle.

During this time we find the first authors writing extensively on marine mammals and returning to the practice of dissecting these animals. For the most part they were uncritical compilers or, at best, naturalists with very little imagination and critical thinking. Here are some examples.

[8] *b*. 1478, Madrid, Spain; *d*. 1557, Valladolid, Spain.

Edward Wotton[9] did general studies at Oxford and medicine and Greek at Padua (1524-6). He was a practicing physician who became famous for his 1552 treatise *De Differentis Animalium.* This was a 10-volume book that in many ways followed Aristotle and Pliny's views that animals should be classified not based on structure but on the medium they inhabit; thus, although he distinguished both kinds, he lumped together cetaceans and fishes.

Guillaume Rondelet[10]. His father was a drug and spice merchant that died while Guillaume was a child and an elder brother brought him up. Among his brothers we find spice merchants and apothecaries. His sister married into a family of surgeons. Therefore, he was surrounded by people interested in nature and an incipient interest on science. He had very little rigorous education in his youth due to illness. In 1525 he went to study humanities at Paris, and transferred to the Medical Faculty at Montpellier in 1529. He returned to Paris in the mid-1530 to study anatomy graduating as a M.D. in 1537 in Montpellier. He was chair of Medicine at the University of Montpellier in France (where Gessner and Aldrovandi were his pupils, see below). Although he was active in several branches of biology, Aldrovandi's reputation effectively depended on his massive compendium on aquatic life, which covered far more species than any earlier work in the field. The *Libri de piscibus marinis in quibus verae piscium effigies expressae sunt* (1554-5) laid the foundation for later ichthyological research and was the standard reference work for over a century. He mentioned six species of true cetaceans: the common dolphin, the porpoise, the blue whale, the right whale, the orca, and the sperm whale. He portrayed them with suspicious round eyes and eyelashes. He wrote the first published account of the external auditory meatus (orifice) of cetaceans. Rondelet was a progressive anatomist who believed in the importance of frequent dissections (he was so interested in anatomy that he himself dissected one of his own dead children!). Although saying that aquatic mammals have testes like terrestrial ones and unlike fishes, he lumped all of them together. His classification of fishes was based on the environment; thus, he classified fishes into sea-fishes, river-fishes, lake-fishes, and marsh-fishes (an even included a few 'monsters' among the first). He included the sawfish among 'cetaceans' (Oppenheimer 1936, Dulieu 1965).

Fig. 2.7 Guillaume Rondelet

[9] *b.* 1492, Oxford, England; *d.* 5 October, 1555, London.
[10] *b.* 27 September 1507, Montpellier, France; *d.* 30 July 1566, Réalmont, Tarn, France.

Conrad Gessner[11] studied theology and medicine in Zurich, Bourges, Paris, and Basel. He was an avid traveler and lived temporarily in Montpellier. He wrote *Historia Animalium* (1551-1558), an encyclopedic (4,500 pages) but uncritical compiler who classified cetaceans among 'aquatic animals,' i.e., including fishes, etc.

Fig. 2.8 Conrad Gessner.

Fig. 2.9 Some of Gessner's depictions of marine mammals.

[11] *b*. 26 March 1516, Zurich, Switzerland; *d*. 13 March 1565, Zurich.

Pierre Belon[12]. He traveled throughout Europe and the Middle East, studied at the University of Wittenberg, and obtained a licentiate in medicine from the University of Paris. He served as a doctor and apothecary for French kings, as well as a diplomat, traveler, and as a secret agent (he was murdered under strange circumstances). In his 1551 *L'Histoire Naturelle des Estranges Poissons Marins* reversed Aristotle's conclusion that the Cetacea were closer to 'quadrupeds' (later known as mammals) than to fishes. He even included the hippopotamus among the fishes. He reached this conclusion despite the fact that he dissected the three most common species of cetaceans in Europe: the common dolphin, *Delphinus delphis* which he called Oye or Bec d'oye, the bottlenose dolphin, *Tursiops truncatus*, which he called Oudre, and the common porpoise, *Phocaena phocaena*, which he called marsouin. It is curious because he described these marine mammals as having a placenta, mammae, and hair on the upper lip of their fetus. He also dealt with issues of breathing and reproduction (although from the description it is clear that he never saw one of these animals giving birth, since he depicted the newborn surrounded with a membrane). Yet, he wrote that apart from the presence of hind limbs, they conform to the human body plan. The porpoises he dissected were acquired at the fish market in Paris and were brought in by Normandy fishers.

Fig. 2.10 Pierre Belon

Ulysses Aldrovandi[13]. He was educated in Bologna and Padua, received the degree of doctor of medicine (1553) and was appointed professor of natural history in the University of Bologna. Because he read Averroës, he was charged with heresy but after producing himself in Rome, he was acquitted. While in Rome he met Conrad Gessner and accompanied him to the fish markets where he became interested in ichthyology (which included the study of marine mammals). He traveled extensively and made a vast collection of zoological and botanical objects (most of them can be found today at the Bologna Museum). He also wrote extensively and his published works fill fourteen volumes in folio. These, together with Aldrovandi's manuscripts, covered the entire field of natural history, making a vast compilation. He was a true encyclopedist whose animal descriptions (poor from the scientific viewpoint) were published in 1613. The fourth volume of his encyclopedia was regarding 'Fish, Cetacea,' and he kept cetaceans and fishes together despite the fact that he recognized that they are air-breathing animals (for some of Aldrovandi's illustrations go to:

Fig. 2.11 Ulysses Aldrovandi

[12] *b*. 1517, Soultière, near Cerans, France; *d*. 1564, Paris, France.
[13] *b*. 11 September 1522, Bologna; *d*. 10 November 1607, Bologna.

http://www.filosofia.unibo.it/aldrovandi/pinakesweb/files/image/VOL001_2_149.jpg). He relied too much on Pliny and added further legends and mistakes

Johann Jonston[14]. He was educated in St Andrews, Cambridge, Leiden, and Frankfurt, graduating with an M.D. from Cambridge in 1632. He traveled extensively throughout Europe teaching. He published *Enchiridion historiae naturalis* (1625-8). He was another encyclopedist who when it came to natural history was more a compiler than anything else, relying heavily on Aldrovandi's work. He gave no hint of biological classification for marine mammals and also added further mistakes and legends (even 'monsters'). He slightly modified Aldrovandi's classification of fishes by adding 'pelagic' fishes and also included some information from the first explorer of Brazil, George Marcgrave. Yet, his books were widely read and translated.

Fig. 2.12. Illustration from Jonston's *Historiae naturalis de piscibus et cetis libri V Amstelodami, apud J.J. fil. Schipper* (1657).

2.5. Modern Science Period (1650-1800)

The concept of 'Modern Science' is applied to the period between 1650 and 1800, in which direct observation and experimentation becomes paramount in the development of science. Now what matters is not what others said, but also what you found out by yourself. In biology, this period is characterized not only by information generated by direct observation, but also by the development of downward classification by logical division, based on similarities, and choice of differentiating characters. Another important characteristic is the fact that the center of gravity of western science moved from the Mediterranean to northern Europe.

There were two precursors of this era. The first one was **Samuel Collins**[15] who published in 1685 his *Systema Anatomicum* in which he described a female porpoise, which he had dissected. The second was **Walter Charleton**[16]. He was an obscure physician who nevertheless wrote a number of works on medicine. In 1668 he published *Onomasticon zoicon* a work more or less on taxonomy that contained anatomical

[14] *b*. 3 September 1603, Sambter, near Leszno, Poland; *d*. 8 June 1675, Liegnitz, Poland.
[15] *b*. 1618, Rutherfield, Sussex, England; *d*. 1710.
[16] *b*. 2 February 1620, Shepton Mallet, Somerset, England; *d*. 24 April 1707, London.

descriptions of two animals that he had dissected. In his *Exercitaciones de Differentiis & Nominibus Animalium* (1677) he classified cetaceans and other aquatic mammals, including the hippopotamus, among fishes (Rolleston 1940, Sharpe 1973).

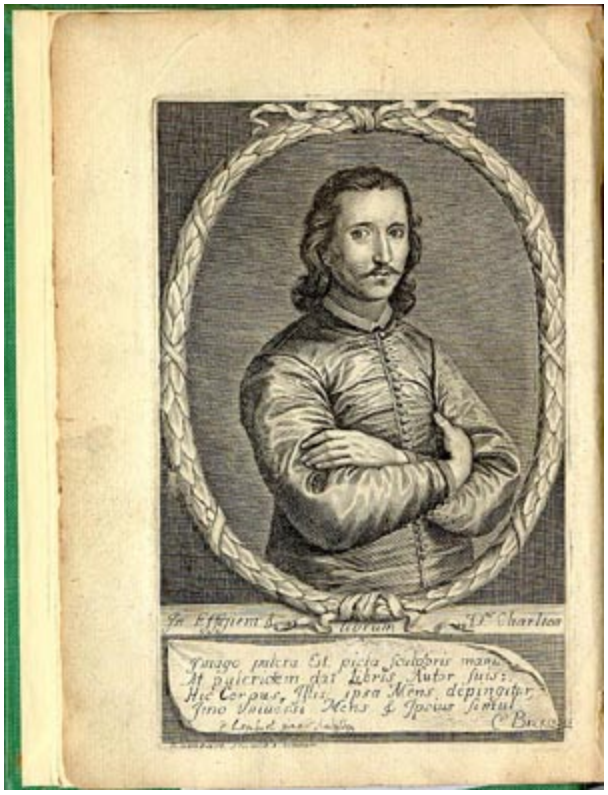
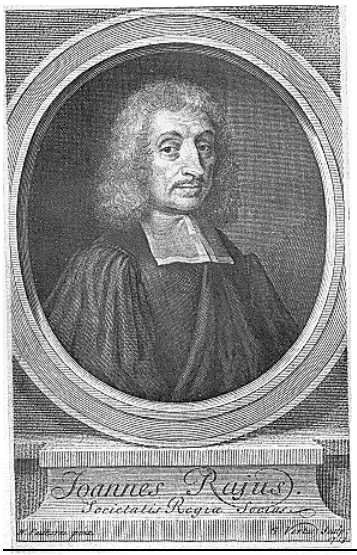


Fig. 2.13 Walter Charleton. This is a portrait from the frontispiece of one of his books.

Fig. 2.13 John Ray



The first naturalist that truly represents this new era of careful observation was **John Ray**[17]. He studied at the University of Cambridge, pursuing comparative anatomy. His main interest was botany. Fairly early he developed a plan with his student and patron, Francis Willughby (see below), to do a joint general natural history. Ray and Willughby then went on an extended tour of the continent (1663-6), clearly at Willughby's expense. When Willughby died, Ray took over his parts of the general natural history. Willughby left him an annuity of £60 and Ray stayed on as tutor to the children until 1675, when Willughby's mother, also his patron, died, and the widow immediately terminated the relationship. Ray inherited a small farm that also contributed to the family's maintenance while he earned money from his industrious publishing. Therefore, Ray had

[17] *b.* 29 November 1627, Black Notley, near Brainton, Essex, England; *d.* 17 January 1705, Black Notley, England.

the financial freedom to pursue his intellectual interests. He published *Historia piscium* in 1686, under Willughby's name, though Ray himself contributed most of the content. He carried out the first serious attempt to achieve a systematic arrangement that served as a basis for the systematic work of the following century. Ray was truly interested in marine mammals. He published three major pieces of work related to these animals: *An Account of the Dissection of a Porpess* (1671), *Historia Piscium* (1686), and *Synopsis Methodica Animalium Quadrupedum et Serpentini Generis* (1693). In the latter he wrote: 'For except as to the place on which they live, the external form of the body, the hairless skin and progressive swimming motion, they have almost nothing in common with fishes, but remaining characters agree with the viviparous quadrupeds' (what we call today mammals). He placed today's terrestrial mammals (including the manatee) among the 'hairy animals' very close to the 'Cetaceum genus' or cetaceans. Yet, he lacked the vision to reunite marine mammals with its terrestrial relatives and still placed the former with the fish 'in accordance with common usage.' John Ray was possibly the best naturalist of the seventeenth century: he established the significance of the generic principle, defined species, and was a leading contributor to the gigantic task of classification.

As mentioned above, one of Ray's students was **Francis Willughby**[18]. He studied at Cambridge University and Padua. With Ray, Willughby undertook to do a complete natural history, he doing the animals, birds, fish, and insects, and Ray doing the plants. Apparently his greatest interest was in entomology. Willughby died at the age of 36, so Ray took his notes and published *Ichthyographia* (1685), which included marine mammals and was beautifully illustrated.

[18] *b.* 22 November 1635, Middleton, Warwickshire, England; *d.* 3 July 1672, Middleton.

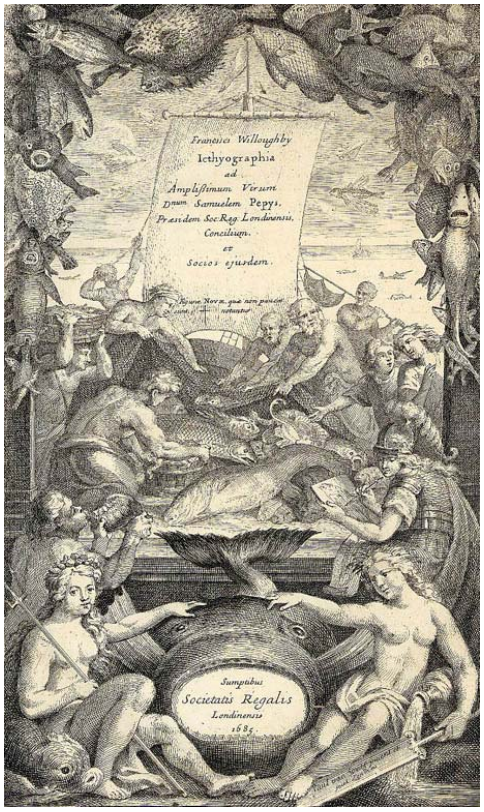


Fig. 2.14 Cover of Francis Willughby's *Ichthyographia*.

Edward Tyson[19]. His father was a wealthy merchant and city magistrate in Bristol, who had inherited a considerable estate from his own father. He studied at Oxford and Cambridge and became a physician. While at Oxford, Tyson became interested in natural history. His manuscripts contain considerable material on this study, including detailed descriptions of a number of plants and of such species as the sea anemone. Tyson published more than two-dozen articles in the *Philosophical Transactions of the Royal Society* on anatomy, natural history, morbid anatomy, and pathology. He was a pioneer in correlating post mortem dissections with specific diseases. He discovered the 'Tyson glands' in the penis. He was a leader in comparative anatomy. He published in 1680 *Phocaena, or the Anatomy of a Porpess*, which contains an extensive discussion of his idea of a natural history of animals based on comparative anatomy. He thought that his 'porpess' was a transitional link between fishes and quadrupeds. He contributed two descriptions of fish to Willoughby's *Ichthyographia*. He did extensive dissections and was the first one in using a microscope as part of his anatomical studies. His manuscripts contain many more descriptions and dissections than he found time from his medical practice to publish. He criticized previous authors (e.g., Aldrovandi and his contemporaries) because they put more emphasis on other authors than in natural objects.

[19] *b.* 20 January 1651, Bristol, England; *d.* 1 August 1708, London.

Peter Artedi[20] was the first 'fish specialist' and considered by many as the father of ichthyology. While in London, he described a whale in November 1734, probably downstream of the London Bridge. After his death, Linnaeus (see below) recovered his manuscripts and published *Ichthyologia* (1738), a fundamental piece of work. He established the basic classification of fishes that lasted for about 200 years and separated cetaceans in a total different order than fishes; he apparently knew that they were different, but still tradition was difficult to break. He also established the basic branching of animal groups into Class, Maniples (Families), Genera, and Species, a system that was to be closely followed by Linnaeus (Wheeler 1987, Broberg 1987).

Pehr Löfling[21], one of Linnaeus' students was very close to make major contribution to the true nature of dolphins and manatees based on his observations of these animals in South America; however, his early death and the fact that his manuscripts were never published prevented him from gaining recognition in the scientific community (Romero *et al.* 1997).

But real changes did not take place until the work by **Carolus Linnaeus (or Linné)**[22]. He based his descriptions of fishes and marine mammals largely on that of Artedi's. However, he had the insight to reclassify all these animals and, in the 10th Edition (1758) of his fundamental book *Historia Naturae*, he introduced the term Mammalia, and included Cete among them. Among his great achievements were:

1. The production of the first fully natural system of classification
2. The consistent use of the binomial nomenclature.
3. The designation of species with Latinized names (genus and species)
4. Telegram-style diagnosis for species descriptions.
5. The standardization of synonymies in order to reach a taxonomic consensus
6. The development of hierchy (class, order, genus, species) as proposed by Artedi.
7. The creation of the Class Mammalia and the inclusion of cetaceans among them.
8. The creation of the Order Primates and the inclusion of humans among them.
9. He defined species as similar individuals bound together by reproduction
10. He observed that individuals tend to multiply in each generation. Species were fixed except for small variations due to climatic/local conditions.
11. He doubled the number of species known to John Ray

[20] *b*. 10 March 1705, Anundsjö, Västernorrland, Sweden; *d*. 27-28 September 1735, Amsterdam, The Netherlands.
[21] *b*. 1729, Valbo, Sweden; *d*. 22 February 1756, Venezuelan Guayana.
[22] *b*. 23 May 1707, Stenbrohult, Småland, Sweden; *d*. 10 January 1778, Uppsala, Sweden.

Linnaeus had a complex personality. He engaged in painstaking descriptive taxonomy, classified anything (even botanists), and was obsessed with the biology of sex. Despite being a scientist he was a mystic: for example he was a numerologist who was crazy about the numbers 5, 12, 365. He also had a pedantic personality epitomized by his phrase 'God creates; Linnaeus classifies' (*Deus creavit, Linnaeus disposuit*), by calling his students his 'apostles,' and by naming ugly, thorny, or poisonous plants after his enemies. Yet, he was, without a question, the founder of systematics and the one who laid the foundations for the naturalists to become specialists and, therefore, opened the door for the first group of marine mammal specialists, now that these creatures were not longer considered 'fishes.'

Fig. 2.15 **(Right) popular portrait of Linnaeus.**

2.6. Nineteenth Century

After 1800 Linnaeus's work it was evident that no taxonomist could cover both plants and animals in detail. Another important factor facilitating the progress of the study of mammals and birds was that the technique for the skin preservation became available in the 1750's; until then plants were easier to preserve than animals. This gave rise to the contributions of comparative anatomist such as Cuvier brothers.

Georges Cuvier[23] was a comparative anatomist and paleontologist who first described species of fossil cetaceans. He made careful anatomical studies and was the first to compare the anatomy of fossil cetaceans with those currently living (called **recent**). His *Le Règne Animal* (1817) and *Recherches sur les Ossements Fossiles* (1823) contain the original descriptions and illustrations of the three species of cetaceans that he named (Cuvier's beaked whale, Risso's dolphin, and the spotted dolphin). His brother, **Frédéric Cuvier**[24] critically synthesized all available cetacean information of his time.

The names of other scientists that contributed to the knowledge of marine mammals are listed alphabetically in Appendix 1 for reference purposes only.

2.7. Conclusions

Marine mammals, particularly cetaceans have fascinated many naturalists throughout history, but because of their extreme adaptations to the aquatic environment they have been a source of confusion and misinterpretation throughout times. It has not been until relatively recent times, when some of the questions about their exact nature in terms of classification and evolutionary history have been answered. All of them have been the result of direct observation, not pure speculation. Yet many other questions remain and we will explore them later in this course.

Key Terms

Analogy
Animistic
Gradualism
Homology
Idealism
Monotheistic
Peripatetic
Scholasticism
Teleology
Uniformitarianism

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[23] *b*. Montbéliard, France, 23 August 1769; *d*. Paris, France, 13 May 1832.
[24] *b*. Montbéliard, France, 28 June 1773; *d*. Strasbourg, France, 24 July 1838.

Critical Thinking Questions

1. Aristotle's idea of classifying cetaceans together with fishes persisted for about 2000 years. That is despite the fact that not only himself but also some other more recent scientists such as John Ray (1627-1705), Edward Tyson (1651-1708), Samuel Collins (1618-1710), and Peter Artedi (1705-1735) had studied cetaceans in detail and had recognized that their internal anatomy was essentially the same of what was called then 'terrestrial quadrupeds' (mammals). What do you think were the main philosophical reasons why they kept classifying whales and dolphins together with fish?

Literature Cited

Abel, O. 1905. Les Odontocetes du Bolderien (Miocene superior) d'Anvers. *Musée Royal d'Histoire Naturelle de Belgium. Memoires*, Bruxelles **3**:1-155.

Abel, O. 1907. The genealogical history of the marine mammals. *Annual reports of the Smithsonian Institutions* **1907**:473-496.

Allen, J.A. 1880. *History of North American pinnipeds, a monograph of the walruses, sealions, seabears and seals of North America*. Washington, DC: Washington Government Printing Office.

Alpers, A. 1961. *Dolphins. The myth and the mammal*. Cambridge: The Riverside Press.

Aristotle. [2000]. *Historia Animalium*. Cambridge: Cambridge University Press. (Available at: http://www.netLibrary.com/urlapi.asp?action=summary&v=1&bookid=1085826

Belon, P. 1551. *L'histoire naturelle des estranges poissons marins avec la vraie peincture & description du daulphin, & de plusieurs autres de son espece*. Paris: De l'Imprimerie de R. Chaudiere.

Broberg, G. 1987. Petrus Artedi in his Swedish context. *Proceedings of the Fifth Congress of European Ichthyology*, Stockholm, 1985:11-15.

Dulieu, C. 1965. Guillaume Rondelet. *Clio Medica* **1**:89:111.

Fraser, F.C. 1977. Royal fishes: their importance of the Dolphin, pp. 1-44, In: R. J. Harrison (Ed.) *Functional Anatomy of Marine Mammals*. Vol. 3. London: Academic Press.

Gruening, E. "Bering" in *The State of Alaska*. New York: Random House, 1954. Pp. 1-16.

La Cépède, M.. 1804. *Histoire naturelle des cétacées*. Paris: hez Plassan.

Nie, G. 1949. *Ju xiang* (Xianggang: Qiu shi chu ban she).

Oppenheimer, J.M. 1936. Guillaume Rondelet. *Bulletin of the Institute of the History of Medicine* **4**:17-34.

P, H. 2008. Signs of the first whale hunters. *Science* **320**:175.

Pilleri, G. 1973. On the representation of A Dolphin Among the Rock Cravings of Khao Kieu, Phangnga, Thailand. *Investigations on Cetacea* **6**:73-74.

Pilleri, G. 1977. The First Iconographic Representation of Plataniusta in the "Babur-Nama: Manuscript from the Babur Period of Miniature Painting. *Investigations on Cetacea* **8**:289-293.

Rodrigues Ferreira, A.1790 [1972]. *Viagem filosofica as Capitanias do Grao-Para, Rio*

Negro, Mato Grosso e Cuiaba. Conselho Federal de Cultura, Rio de Janeiro, Brazil.

Rolleston, H. 1940. Walter Charleton, D.M., F.R.C.P., F.R.S. *Bulletin of the History of Medicine* **8**:403-416.

Romero, A.; A.I. Agudo & S.J. Blondell. 1997. The scientific discovery of the South American freshwater dolphin, *Inia geoffrensis*. *Marine Mammal Science* **13**:419-426.

Sharpe, L. 1973. Walter Charleton's early life, 1620-1659, and relationship to natural philosophy in mid-Seventeenth Century England. *Annals of Science* **30**:311-340.

Steller, G.W. 1743 [1988]. *Journal of a Voyage with Bering 1741-1742*. Stanford, CA: Stanford University Press.

C. B. Stringer, C.B.; J. C. Finlayson, R. N. E. Barton, Y. Fernández-Jalvo, I. Cáceres, R. C. Sabin, E. J. Rhodes, A. P. Currant, J. Rodríguez-Vidal, F. Giles-Pacheco & J. A. Riquelme-Cantal. 2008. Neanderthal exploitation of marine mammals in Gibraltar. *Proceedings of the National Academy of Sciences* (USA) **105**:14319-14324.

Yamase, H. 1760. *Geishi*. Kyoto : Kobunkan kanbon.

Waxell, S. 1962. *The Russian Expedition to America.* New York: Collier Books

Wheeler, A. 1987. Peter Artedi, founder of modern ichthyology. *Proceedings of the Fifth Congress of European Ichthyology*, Stockholm, 1985:3-10.

APPENDIX 1: Short biographical dictionary of marine mammal contributors not mentioned in the previous text

After the acceptance of Linnaeus system of classification and the contributions made by the comparative anatomists, there was steady emergence of specialists of marine mammals, from general zoologist who showed a special interest in marine mammals in the eighteenth century to people specialized in very narrow areas of marine mammalogy. In the Twentieth century a number of new developments helped to accelerate our knowledge of these animals: from the 1924 first scientific expedition (on board of the *Discovery*) to exclusively study whales, to the end of the Second World War when sonar and other acoustic devices were employed to study whales, to the creation of the International Whaling Commission in 1946 (due to the increased scarcity of whales) to promote a great deal on cetacean research, to the enactment of the U.S. Marine Mammal Commission in 1972 that shifted a lot of new research on ecology and conservation issues

The names (in alphabetical order) of some of the most important researchers and major contributions are summarized below. I have also included some other earlier figures prior to 1760 not mentioned earlier. (NOTE: THIS LIST IS INCOMPLETE AND STILL SKETCHY SINCE IT IS A WORK IN RPOGRESS).

Othenio Abel (*b*. 10 June 1875, Vienna, Austria; *d*. 4 July 1946; Pichl am Mondsee, Austria). As the son of a teacher in the horticulture school and the descendant of several generations of gardeners, he was exposed to botany and biology from an early age. He studied at the University of Vienna and became the founder of Paleobiology. He published 275 works, received a variety of honors, and led several paleontological expeditions on three continents. As a paleontologist he worked on several species of fossil cetaceans including the genus *Basilosaurus* (Abel 1905, 1907).

Glover Morrill Allen (*b*. 8 February 1879, Walpole, New Hampshire; *d*. 14 February1942, Cambridge, Massachusetts). He worked on baleen whales of New England and on the conservation of marine mammal species.

Joel Asaph Allen (*b*. 19 July 1838, Springfield, Massachusetts; *d*. 29 August 1921, Cornwall-on-Hudson, New York). He studied first at the Wilbraham academy, and then at the Lawrence scientific school under Agassiz, where he devoted special attention to Zoology, and was one of the assistants that accompanied Agassiz on the Thayer expedition to Brazil in 1865. He visited Florida in 1869, and the Rocky mountain region in 1871, with scientific exploring parties, and in 1873 was the chief of an expedition sent out by the Northern Pacific railroad. In 1870 he became an assistant in ornithology at the Museum of Comparative Zoology at Cambridge. He was the first curator of birds and mammals at the American Museum of Natural History (AMNH) (1885) and later first head of its Department of Ornithology; edited and expanded the museum's *Bulletin*. He published in 1880 a comprehensive bibliography of cetaceans and sirenians as well as other papers on these subjects such as *History of North American pinnipeds, a monograph of the walruses, sea-lions, sea-bears and seals of North America*, in which he provided keys to the families and genera, described the North American species, and gave accounts of pinniped species in other parts of the world. He was an influential neo-

Lamarckian. In addition to naming many species, he carried out important studies on geographic variation and its connection with climate. Allen's recognition of variation within populations and integradation across geographic gradients helped to overturn the typological species concept current in the mid-1800s, setting out the principle that intergradating populations should be treated as subspecies instead of separate species. This idea led to the widespread adoption of trinomial names (i.e., names including subspecies) by American vertebrate zoologists. He established what was later called 'Allen's rule,' i.e., the observation that animals in cold climates had small extremities. He used this kind of evidence to argue that heritable variation was directly caused by the physical environment and was not produced by natural selection. He hired and mentored **Roy Chapman Andrews** at the AMNH.

Roy Chapman Andrews (*b*. 26 January 1884, Beloit, Wisconsin; *d*. 3 June 1960, Carmel, California). A naturalist and explorer educated at Columbia University. Connected with the American Museum of Natural History, New York City, from 1906, he was its director from 1935 to 1942. Between 1908 and 1914 he made several trips to Alaska, along the coast of Asia, and in Malayan seas to study aquatic mammals. He later conducted (1917–30) several expeditions into central Asia to study both fossil and living plants and animals; he discovered some of the world's great fossil fields, which have yielded the remains of many ancient animals. He published a number of papers on marine mammals. He was a master of public relations, creating a dashing, heroic popular self-image. He also published in 1906 a monograph of the Sei whale of the Pacific.

Viktor Aleksandrovich Arsen'ev (1908-1991). A Russian specialist of the northern fur seal.

Wilhelm Barents (ca. 1550-1597) discovered Spitzbergen (island north of Norway) in 1596 and early in the Seventeenth century commercial whalers were sent there by Dutch and English companies to establish a whaling town. Although these expeditions were concerned primarily with whale products, they also generated a number of publications that provided reasonably accurate descriptions of the external appearance of the most common kinds of whales. The best of these are found in *Spitzbergische oder Groenlandische Reisen Beschreibung* (1675) by **Frederich Martens** (1635-1699) and *Bloyeyende Opkomst del Oloude en Hedendaagsche Groenlandsche Vischery* (1720) by **Cornelis Gijsbertsz Zorgdrager** (fl. 1700) both of which contained engravings which continue which continued to be reproduced in books until the early 19th century.

Thomas Bartholin (*b.* 20 October 1616, Copenhagen, Denmark; *d.* 4 December 1680). He studied at the universities of Copenhagen, Leiden, and Padua, particularly medicine in the last one. He published many works on anatomy, physiology, and medicine, from 1645 through 1674. His most important scientific contribution was the discovery of the lymphatic system and in 1670 he published *De Sirene Danica* in which he described marine mammals of the North Sea. His most famous student was Niels Stensen (1638-1686) who also worked on marine mammals.

Thomas Beale (*b*. England, 1807; *d*. 1849). A whaling ship surgeon who published *Natural History of the Sperm Whale* (1839).

Frank Evers Beddard (*b*. 19 June 1858, Dudley; England; *d*. Hampstead, England, 14 July 1925), with the Zoological Society of London. Published *A Book of Whales* (1900).

Alfred Antonovich Berzin (*b*. Rostov-on-Don, Latvia, 1930; *d*. 1996). Famous for his monograph on sperm whales and for exposing true whaling catch data during the Soviet era.

Michael Andrew Bigg (*b*. London, England, 1939; *d*. 18 October 1990). He developed long-termed studies of killer whales by using photo-identification. And discovered two types of orcas in the same area: transients and residents.

William Nigel Bonner (1928-1994). Specialist on the southern elephant seal.

George Louis Leclerc, Compte de Buffon (*b*. Montbard, Cộte-d'Or, France, 7 September 1707; *d*. Paris, France, 16 April 1788). He was a French encyclopedist of natural history; principally known as the author of *Histoire Naturelle* (36 vols - 1749-89); containing the *Epoques de la Nature* (1777), which foreshadowed later theories of evolution. He summarized all the knowledge on marine mammals until his day.

David Keller Caldwell (*b*., Louisville, Kentucky, 1928; *d*. 1990). Discovered together with his wife Melba C. Caldwell, that dolphins have 'signature whistles.' They also made major contributions to the knowledge of Caribbean cetaceans.

Petrus Camper (*b*. 11 May 1722, Leiden, The Netherlands; *d*. 7 April 1789, The Hague, The Netherlands) published *Observations Anatomiques sur Plusiers Especes de Cétacés*, a first rate anatomical atlas of cetaceans.

Douglas George Chapman (*b*. 20 March 1920, Canada; *d*. Seattle, Washington, 9 July 1996). He was a pioneer in the development of mathematical models for the assessment of stock status.

Konstantin Konstantinovich Chapskiy (1906-1984). A noted Russian pinniped biologist.

Philibert Commerson (*b*. 18 November 1727, Châtillon-les-Dombes, France; *d*. 1773). Originally trained as a physician. He sailed in an expedition around the world as a naturalist and never retuned. He was responsible for the description of a new species of porpoise.

Louis Jean Marie Daubenton (*b*. Montbard, Burgundy, France, 29 May 1716; *d*. Paris, 1 January 1799). Study theology and became one of the founders of the Museum Nationale d'Histoire Naturelle de Paris. Made early descriptions of fossil whales.

William Henry Dawbin (1921-1998). New Zealand biologist who pioneered the study of distribution of whales in the Southern Hemisphere

Cristóvâo de Lisboa (*b*. Lisbon, Portugal, 1583; *d*. Santo António do Curral, Portugal, 1652). He was the author of the earliest scientific description of the boto (*Inia geoffrensis*). He was a Capuchin priest that arrived in Brazil in 1624 and stayed there until sometime between 1627 and 1631. Between 1624 he traveled extensively throughout the Maranhâo (lower Amazon) region. He wrote a manuscript titled *História dos animaes e ároveres do Maranhâo* in which he described the boto and provided an illustration of it. The manuscript was rediscovered in 1934 and published in 1967 (Romero *et al.,* 1997).

Henry Dewhurst (?-?). He published *The Natural History of the Order Cetacea* (1834). That was an uncritical repetition of other people's ideas.

Daniel Frederick Eschricht (*b*. 17 March 1798; *d*. 22 February 1863). A Danish naturalist, who discovered the migration of small cetaceans, described different populations of orcas in the Artic as well as the embryo of whales. Together with Richard Owen he was the first to use the concentric layers of teeth to calculate the age of toothed cetaceans. The scientific name of the gray whale was given after him.

Francis Hollis Fay (1927-1994). American biologist who studied the marine mammal fauna of Alaska.

William Henry Flower (1831-1899). British scientist who worked on a wide range of marine mammal species.

Eberhardt Fraas (1862-1915). German paleontologist who work on early whales.

Francis Charles Fraser (1903-1915). Worked on the distribution of cetaceans in British waters, studied cetacean ear anatomy, and the discoverer of a new species, Fraser's dolphin.

David Edward Gaskin (1939-1998). British biologist who worked extensively on cetaceans of the Southern Hemisphere.

Paul Françoise Louis Gervais (1816-1879). He published *Ostéographie des cétacés vivants et fossils*, that described new species of cetaceans, described the anatomy and physiology of several other species as well.

John Edward Gray (1800-1875) who was Keeper of the Zoology Department at the British Museum of Natural History published *Catalogue of seals and whales in the British Museum* (1866). He described three new species of pinnipeds, ons species of whale, two beaked whales, and ten other cetaceans.

John Gulland (1926-1990). British mathematician who worked on defining stocks of whales in the Northern Hemisphere.

Richard Harlan (*b*. 19 September 1796, Philadelphia, Pennsylvania; *d*. 30 September 1843, New Orleans, Louisiana). Studied medicine at the University of Pennsylvania and became professor of comparative anatomy in the Philadelphia museum. He was the collector of the first *Basilosaurus*.

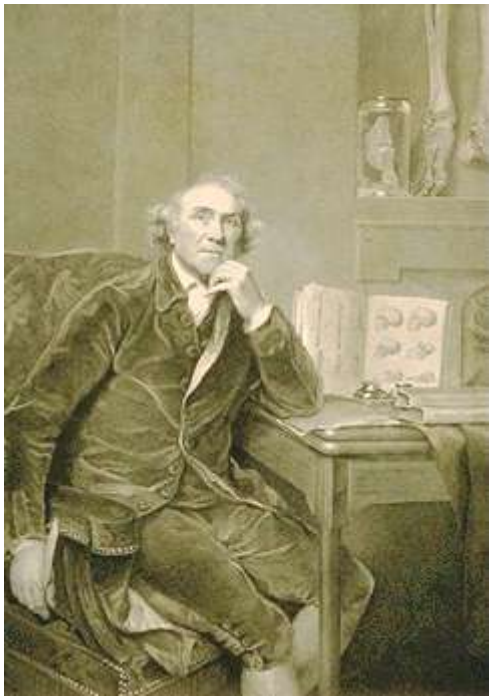
Richard John Harrison (1920-1999). He was a British anatomist who made exceptional work on marine mammals.

Philip Hershkovitz (1909- 15 February 1997). He published the classic work *Catalog of Living Whales* (1966).

Alfred Braziel Howel (1886-?) published in 1929 his well-known comparative study of both phocids and otariids based on the California sea lion and the ringed seal. He followed this with a book on aquatic adaptations in mammals (1930).

Carl Leavitt Hubbs (1894-1979). Mostly an ichthyologist who later in life showed a great interest on cetaceans. He conducted the first aerial survey of gray whales, rediscovered two supposedly extinct species of fur seals. A species of beaked whale was named after him.

John Hunter (*b*. Long Calderwood, Lanarkshire, Scotland, 1728; *d*. 1793). His formal education was scanty, but after service in the army he became a well-known teacher of Anatomy in London. His collection of specimens was the basis of two famous museums. He was surgeon to St George's Hospital and a Fellow of the Royal Society. He is considered, with Ambroise Paré and Joseph Lister, one of the three greatest surgeons of all time. He rejected academic speculation and insisted on experimentation and direct observation. He published 'Observations on the Structure and Oeconomy of Whales' (1787) and he described the thoracic vascular plexus for a sperm whale. This was for many years the main source of information about the anatomy of cetaceans.



Tadayoshi Ichihara (1939-1981). This Japanese scientist is known for his description of the pygmy blue whale and his work on telemetry on marine mammals.

Åge Jonsgård (1916-1997). Norwegian biologist who made major contributions to the study of whales and whaling.

Remington Kellogg (*b*. 5 October 1892, Davenport, Iowa; *d*. 8 May 969, Washington, D.C.). He was a major contributor to the knowledge of fossil marine mammals.

Sergei Evgenyevich Kleinenber (1909-1968). A Russian biologist who study marine mammals of the Black Sea and other seas adjacent to the former Soviet Union.

Bernard Germain Étienne de la Ville La Cépède, later **Compte de Lacépède** (bernär´ zhermaN´ atyen´ de lä vel kôNt de läsaped´) (1756-1825). As a youth he showed considerable talent in both music and physics and won the favor of Buffon, whose work in animal classification he was encouraged to continue. Buffon secured him a position at the Jardin du Roi (later the Jardin des Plantes). His best-known works deal

with the oviparous quadrupeds, reptiles, fishes, and whales; they are frequently printed with Buffon's works, which they supplement. Lacépède was active in politics and was exiled during the Reign of Terror. After his return he gave up scientific work for a political career and held several state offices. He wrote the *Histoire Naturelle de Cétacées* (1804), which was mostly a compilation of information generated y others. Most of the illustrations of this book were copied from previous publications. Lacépède acknowledged that not having ever seen a whale, he had made his descriptions from those of other naturalist.

James Stephen Leatherwood (1944- January 1997). An American biologist who led major conservation projects in developing country.

Neil Alison Mackintosh (1900-1974). A British oceanographer who made major contributions in the exploration of new areas of cetacean distribution.

Leonard Harrison Matthews (1901-1986). A British naturalist that participated in the *Discovery* expedition and who published on the growth and reproduction of many species of whales.

William C. Strettell Miller published in 1888 his report on the marine mammals studied on board of the famous oceanographic ship H. M. S. Challenger expedition to the Antarctic during 1873-1875. He dissected a variety of pinnipeds including southern fur seals, southern elephant seals, and the harbor seals.

James Murie published in 1868 the description of the anatomy of the walrus. On the morbid appearances observed in the walrus lately living in the society's gardens

Takahisa Nemoto (1930-1990). A Japanese scientist who made major contributions to the study of the interactions between plankton distribution and that of whales.

Masaharu Nishiwaki (1915-1984). A Japanese naturalist who did extensive work on marine mammals not only in Japan but if the Far East in general.

Kenneth Stafford Norris (1924-1998). American cetologist who described the Vaquita, demonstrated echolocation among dolphins, and taught a whole generation of marine mammalogists.

Hideo Omura (1906-1993). A Japanese scientist who published extensively on whales.

Seijun Otsuki. He published *Geishi-ko* in 1808. According to the book *The Whale*, this work 'is more accurately scientific' than the following book by Yosei Oyamada.

Yosei Oyamada. He published *Isana-tori-ekotoba* in 1829. According to the book *The Whale*, this work 'describes the different sorts of whales and their structure.'

Antoine Joseph Pernetty (*b*. 13 February 1716 in Roanne, Beaujolais, France; *d*. Valence, Dauphiné, France, 16 October 1801). Originally a Benedictine monk he joined Bougainville's first expedition to the Falklands/Malvinas and he described a number of species he observed during that trip.

Thomas Charles Poulter (1897-1978). Did extensive work on sound production by marine mammals, particularly pinnipeds.

Alexander Rodrigues Ferreira (*b*. Bahia, Brazil, 27 April 1756; *d*. Lisbon, Portugal, 1815). He studied at the University of Coimbra and was commissioned by the Brazilian government to conduct scientific expeditions in Brazil where he spent almost 10 years. Collected the specimen of the 'boto' (*Inia geoffrensis*) that was used as a holotype to describe this species. The specimen was collected in the Lower Amazon sometime no later than 1790. He classified as *Delphinus delphis* and sent it to the Museu de Ajuda in Lisbon, together with a description and a drawing (Rodrigues Ferreira, 1790). The specimen was later plundered by Geoffroy St. Hillaire in 1810 on orders of Napoleon Bonaparte and sent to the Muséum d'Histoire Naturelle de Paris where it is still deposited (de Miranda Ribeiro, 1943; van Bree and Robineau, 1973).

Charles Melville Scammon (1825-1911). An American whaling captain. He published the classical *The Marine Mammals of the North-western Coasts of North America* (1874). It is still a reference for the natural history of the gray whale in California.

William Edward Schevill (1906-1994). American scientist that pioneered the study of bioacoustics in marine mammals.

Per Fredrik Scholander (1905-1980). Norwegian biologist who made major contributions to the diving physiology of marine mammals. He was the first who described the 'diving response.'

William Scoresby (*b*. 3 May 1760, Cropton, Nutholm, England; *d*. 1857) published *Account of the Arctic Regions, with a History and Description of the Northern Whale-fishery* (1820). He was born on. As there was no school within easy walking distance his attendance was not prolific. At the age of nine his father removed him from school to help on the farm. He traveled extensively as both sailor and captain of whaling ships. Preparing himself by study between voyages, he mapped, charted, made deep-sea temperature soundings, noted the flora and fauna, and collected other valuable data along the little-known and hitherto unknown coasts of Greenland, giving special attention to terrestrial magnetism. His last trip to the Arctic was made in 1822. In 1825 he entered the Anglican ministry. He maintained his interest in exploration and encouraged the search for the Northwest Passage. He made a voyage to Australia (1856) to study terrestrial magnetism. Scoresby's several books on his arctic experiences helped laid the foundations of modern arctic geography.

Everhard Johannes Slijper (1907-1968). He was a Dutch naturalist who made major contribution in comparative studies of whales.

Vladimir Evgenyevich Sokolov (1928-1998). He was a Russian scientist who made major contributions to the marine mammal fauna of the former Soviet Union.

Alexander Starbuck (1841-1925). He published *History of the American Whale Fishery* (1874), which is a classical book on the history of whaling.

Georg Wilhelm Steller (originally spelled Stoller) (*b*. 10 March 1709, Windsheim, Franconia, Germany; *d*. 12 November 1746, Tiumen, Russia). He graduated from Wittenberg and Halle universities with degrees in theology and later was certified in botany from the Royal Academy of Sciences in Berlin. In 1737 Steller was appointed an

adjunct professor in natural history at the Imperial Academy of Sciences in St. Petersburg and was accepted as a member of the Great Northern Expedition. He was the ship's naturalist and physician for **Vitus Bering**'s (1681-1741) second expedition to North America on board of the St. Peter. The final two years of his life were miserable: he was recalled from Kamchatka by the Russian Academy of Sciences and was twice arrested on trumped-up accusations of treason. Because of his he had little time for getting his notes published. Others such as Gmelin, Linnaeus, Krasheninnikov, Pallas, and Pennant, made heavy use of the information he had collected. Steller has been compared with Henry David Thoreau for his self-reliance, affinity for nature, disdain for bureaucracy, love of solitude, and respect for native peoples. His notes on marine mammals living in the Bering Sea, *The Beasts of the Sea* (1751), was a natural history of the sea otter, sea lion, fur seal, and the now extinct Steller sea cow, the only first-hand scientific observation of this species (Steller, 1743; Gruening, 1954; Waxell, 1962).

Avenir Grigoryevich Tomilin (1912-2000). A Russian scientist and popularizer on marine mammal issues.

Frederick William True (1858-1914). He was the main American marine mammalogist of his time who carried out numerous studies on many different species. He used a lot of information provided by land-based whaling stations that were used in more modern whaling. An example is his monograph *The Whalebone Whales of the Western North Atlantic* published in 1904.

William Turner (1832-1916). He published *The Marine Mammals in the Anatomical Museum of the University of Edinburgh* (1912). He also wrote the reports about *Challenger* expedition (1873-1876).

Pierre-Joseph Van Beneden (*b*. 19 December 1809, Mechlin, Belgium; *d*. 8 January 1894, Louvain, Belgium). The foremost European cetologist of the second half of the nineteenth century. Educated for the medical profession, he was appointed curator of the natural history museum at the University of Louvain in 1831. Five years later he became professor of zoology and comparative anatomy in the Catholic University at Louvain. Throughout his life he was a most diligent worker, and the list of his contributions to scientific periodicals amounts to over two hundred papers. During the excavations rendered necessary by the fortifying of Antwerp a number of bones of fossil whales were exposed to view. These attracted van Beneden's attention and led him to undertake a detailed study of the group, whose characteristics were at that time very imperfectly known. On the subject of the Cetacea, living and extinct, he published a number of papers and several large works. The most important of these is his *Ostéographie des cétacés vivants et fossiles* which was written in collaboration with Paul Gervais and published between 1868 and 1880 and *Histoire naturelle des delphinides des mers d'Europe* published in 1889. His papers on the extinct species found near Antwerp were published in the *Annales du Musée Royal d'Histoire Naturelle de Bruxelles,* and with them was incorporated a description of the fossil seals which were discovered in the same neighborhood.

Antoni van Leeuwenhoek (b. Delft, The Netherlands, 24 October 1632; d. Delft, 30 August 1723). He is considered as the father of microbiology because his extensive use of the microscope to study living organisms. In order to figure out whether larger animals have larger cells that those in smaller animals, he investigated the crystalline of whales' eyes (and found them not to be that different).

Willem Lodewijk van Utrecht (1926-1994). A Dutch scientist who studied the age and growth of many cetaceans.

Howard Elliott Winn (1926-1995). An American pioneer on the study of bioacoustics in whales.

Harumasa Yamase. (?-?). A Japanese author who affirmed in his 1758 book *Geishi* that whales were not big fish but mammals.

有白班
下反張朝上

Chapter 3

The Principles of Animal and Marine Mammal Classification

Marine mammals, because of their spectacular adaptations to the aquatic environment, present unique challenges to the understanding of their evolution and biological features in general. One of the most useful tools to approach this problem is through the classification of their species within a systematic framework that is consistent with their evolutionary history. To do that, we need to comprehend what those tools are, how they are used, and why we classify marine mammals in the way we do. This chapter is aimed at providing those basic tools and see how they apply to the case of the animals subject of our study.

3.1. Introduction to Animal Classification

Classification is an orderly or systematic arrangement of objects into a number of groups, according to their characteristics. Each group contains organisms that have some characteristics in common with one another. For instance, all animals that belong to the dolphin family must have some characteristics of the dolphin.

Given the huge array of biodiversity on our planet, we need a system that allows us to classify living beings. For that method to work, the system must fulfill three conditions: (a) it must be a system recognizable by all researchers in the world; no system can be accepted as scientific unless it has universal recognition; (b) it must reflect the evolutionary history of the organisms that we are trying to classify; in other words, it must be as non-arbitrary as possible; and, (c) it must be easy to apply, so it does not become so cumbersome that the costs outweigh the benefits of using it.

Humans have been using different methods of classification since antiquity. However, it was not until the eighteenth century that the Swedish naturalist Carl von Linnaeus (or Carl Linné as written in Swedish, see Box 2.1.) established the system of classification universally accepted today. In 1758, Linnaeus published the tenth edition of its book *Systema Naturae*. In there he set out the basic rules that govern biological classification today. Linnaeus used Latin in classifications and Latin was adopted because that was the language used by western scientists then. Thus, he established the tradition of giving animals and plants a simple scientific name avoiding, the great confusion that results from the fact that the same animal or plant may be known by many different common (popular) names in different parts of the world.

Box 2.1.
"God creates, Linnaeus classifies"

There is not a more recognizable name in the field of taxonomy than that of Carl von Linnaeus. He was born in Stenbrohult, Småland, Sweden, on 23 May 1707 (for some recent biographies on Linnaeus see Koerner, 1990; Blunt and Stearns, 2001). His father was a gardener and a Lutheran priest from whom the young Carl inherited a passion for plants and their names. Although he studied medicine, his true passion was botany (in fact, most naturalists up to the nineteenth century used to have some sort of medical training because that was the only career that offered courses in botany and animal anatomy). From early on he mounted botanical expeditions in Scandinavia and published profusely. He sent his students around the world to collect plants and animals for him, so he could expand the world's knowledge of what he considered to be divine creations.
He published in 1758 the tenth edition of his book *Systema Naturae*, which is considered a landmark in the history of biology. Not only did he establish the binomial system of classification that we use today, but also broke off with past traditions by, for example, creating the class Mammalia and including cetaceans among them (which he called "*Cete*") and also created the Order Primates and including humans among them (Stearn, 1959; Linsley and Usinger, 1959). Linnaeus, the creationist, was not thinking in terms of evolution (for him God had created all species and they were "fixed") but in terms of anatomical relationships. He was a presumptuous person, always eager to be honored with titles. When naming new species he used the names of what he considered were his friends and allies for beautiful plants while using the names of his enemies to name plants that were ugly, thorny, or poisonous. He called his students his "apostles" and many died while in their scientific expeditions collecting specimens for him (see e.g., Romero *et al.,* 1997). He felt he was on a mission from God when he declared "Deus creavit; Linnaeus disposuit" ("God creates, Linnaeus classifies"). He died in Uppsala, Sweden, on 10 January 1778. His legacy is still with us.

Fig. 2.1 Carl von Linnaeus.

3.2. Scientific Names and Ranks

Although the dolphin known as the bottlenose in English is also named *delfín* in Spanish and *dauphin* in French, it has only one **Latin or scientific name**: *Tursiops truncatus*. This is the way internationally recognized regardless of the maternal language of the scientists studying it. This method of giving an organism a scientific name, which is made up of two Latin or Latinized words, is known as the **Binomial System of Nomenclature**, or two-name system for naming species. For this reason, species names are known as **binomials** and this type of nomenclature is called **binomial nomenclature**. This is a universally accepted scheme, which for animals is governed by the **International Code of Zoological Nomenclature** (ICZN).

The most important thing to remember about nomenclature is that all species may bear only one scientific name. The scientific name is, by convention, expressed using Latin and Greek words. The first word in the Latin name of an organism is the genus name and the second is the species epithet. Although scientific names are sometimes called Latin names, most generic names are derived from the Greek, either transliterated into the Roman alphabet or Latinized. When writing the species epithet, it must be accompanied by the genus name (or at least its initial), since many species share the same species (second) name. Scientific names are written in italics or underlined. The first letter of the genus is always capitalized, and the second name (species name) is always in lowercase. Sometimes a third name is added and that represents subspecies. Latin names sometimes tell something about the plant or animal it names. For example, *Tursiops truncatus*, comes from the Latin *Tursio* =dolphin-like; *ops* = face; *truncare* = cut (i.e., animal with a similar face to the [common] dolphin, with a cut off beak). In practice, any names are accepted, even barbarous ones. As we mentioned in Chapter 1, a fossil species of cetacean received the genus name of *Basilosaurus*, which means "the King of Lizards," because at the beginning it was thought to be a dinosaur. Although it is not a dinosaur and for the sake of stability of names, that generic name has been maintained.

Biologists classify organisms according to similarities and differences. The groups used in classifying animals are the species, genus, family, order, class, and phylum in order from the smallest to the most inclusive group. These are called **taxa** (singular **taxon**). A taxon is a particular taxonomic group at a given **rank**. The basic taxon or unit of classification is the **species**.

A species is a group of organisms that are so similar that they appear to have had a common ancestor. One or more species are grouped together to form a larger group called the genus. For example, there are several seals that are grouped together to form the genus *Phoca*. The harbor seal (*Phoca vitulina*) and the harp seal (*Phoca groenlandica*), are slightly different seal species, and so belong to two different species. Thus, a **genus** is a group of closely related species. The plural form of genus is **genera**.

A **family** is a group of closely related genera. The names of family-group taxa, which includes all categories from superfamily down to subtribe, are formed from the grammatical stem of the name of an included genus with the addition of an appropriate suffix. The prescribed Latin plural suffixes are:

superfamily:	-oidea
family:	-idae
subfamily:	-inae
tribe:	-ini
subtribe:	-ina

An example of a marine mammal family is the family of oceanic dolphins, known as Delphinidae, which contains approximately 34 species. One genus of this family is *Delphinus*, which includes the common dolphin. Another genus is *Tursiops*, and yet another is *Stenella* (which includes the spotted dolphin, the spinner dolphin, and so on). Even the killer whale or orca of the genus *Orcinus* belongs to this family.

The International Code of Zoological Nomenclature or **ICZN Code** is the system that governs names below the rank of superfamily. The international body in charge of publishing that code is the **International Commission on Zoological Nomenclature**. The ICZN does not govern names above the family-group (Phylum, Class, Order, Suborder, Infraorder, etc.) so their usage is governed by tradition and consensus. There are not generally accepted suffixes for them.

Genus-group (genus and subgenus) names are singular nouns in apposition, attributive nouns, or possessive nouns. If they are Latin adjectives, they must agree in gender with the generic name. Each taxon is followed by: a) the author who first described it and b) the date in which the description of it was first published. If the author and date of the taxon are in parentheses, is because the name has been transferred to another taxon other than the one in which it was originally described. The author's name and the date are not part of the scientific name, and are unnecessary in the text or title of a scientific publication, unless it deals specifically with matters of nomenclature.

The basic principle of the ICZN Code is priority, but if the Principle of Priority would disturb stability or universality, existing usage should be maintained and the case should be referred to the Commission for a ruling (see Box 2.2).

Box 2.2. The Dispute over the Scientific Name of the Sperm Whale

Until the early 1990's we used to see, particularly in books, that the scientific name of the sperm whale used was either *Physeter macrocephalus* or *Physeter catodon*. Which one was right? The confusion about this issue dates back to 1758 when in his *Systema Naturae* Linnaeus described four different species of sperm whales: in addition to the two mentioned above he included *Physeter microps* and *Physeter tursio*. He based his decision on what others had published, not on personal observations. In 1823, the famous French naturalist Georges Cuvier suggested that all sperm whales species described earlier belong to a single species but declined to mention which one. Cuvier had the right insight, so different authors started to use either *P. catodon* or *P. macrocephalus* in the scientific literature.

After a careful examination of the roots of this controversy and a close reading of the rules of the International Commission of Scientific Nomenclature, it was resolved that *P. macrocephalus* was the one that should be used because of both the Principle of Priority

and because that name was being the most used in the literature at that time (for a full discussion of this controversy see Husson and Holthuis, 1974; Schevill, 1986; Holthuis, 1987; Rice, 1989).

Fig. 2.2 An early (1598) portrait of a sperm whale, *Physeter macrocephalus*, by the Dutch painter and mapmaker Gilliam van de GouWen (1669-1713). Notice the "external ear" added by the artist.

An **order** comprises closely related families. The order Carnivora is made up of all the families of mammals that eat meat. Some of the families that make up the Carnivora are (among others) the sea otter and marine otter family (Mustelidae) and the bear family (Ursidae), which includes the polar bear. Other orders in the animal kingdom are the Cetacea (whales, dolphins, and porpoises) and the Sirenia (manatees, dugong).

Class is a group of related orders. The class Mammalia in the animal kingdom, for example, includes all the orders of animals that nurse their young on milk produced by mammary glands.

A group of related classes forms a **phylum** (plural **phyla**) -divisions in the case of plants- and they are part of any of the six **kingdoms** of living organisms recognized today.

Thus, an example would be the classification of the humpback whale:

Kingdom	Animalia
Phylum	Chordata (vertebrates)
Class	Mammalia (mammals)
Order	Cetacea
Suborder	Mysticeti (baleen whales)
Family	Balaenopteridae
Genus	*Megaptera*
Species	*Megaptera novaeangliae*

3.3. Common Names

Nonscientific names are those used by people to name species in their native language. There are two types of these names: vernacular and literary names. **Vernacular, colloquial, or common names** are the "names used by people who are sympatric with" the animals in question (Parkes, 1975). In theory, what that means in the case of marine mammals is that such names are the ones employed by fishers and other mariners that in one way or another have frequent contacts with these creatures (Rice, 1998). The problem, as stated in Chapter 1, is that the majority of marine mammal species have no specific vernacular names because people rarely see them. Also, some species are circumscribed to a particular geographical region, meaning that the only true common name may be in a language other than English. Even when the common name is in English, the name may vary from one area to another as in the case of *Phoca vitulina*, which Americans call the "harbor seal" while the British call the "common seal" (despite being the rarer of the two resident species of seals in the British Isles, Rice, 1998). Also, the same common name may be used for different species in different areas; for example, in Spanish-speaking countries, the name *tonina* (an antique name derived from the alleged similarity between dolphins and tunas), is no longer used in Spain but is widely used in the Caribbean, where it is applied to several species of dolphins, both marine and freshwaters (Romero *et al.*, 2001). The term "bottlenose whales," is employed by whalers in California and British Columbia to mean *Berardius bairdii*, while whalers in Newfoundland when employing that common name mean *Hyperoodon ampullatus* (Rice, 1998).

Another type of non-scientific name is what is called **Literary** or **book name.** These are the names that have never really been employed by people who normally have contact with these animals but rather by either popular or professional writers when publishing either popular or scientific literature. They rise from the need of giving a common name to species that do not have one. This has created some confusion that the practitioners of particular areas of knowledge, have had to convene committees to place some order, as in the case of ichthyologists (the American Fisheries Society's Committee on Names of Fishes, Robins *et al.*, 1991) and ornithologists (the American Ornithologists' Union's Committee on Classification and Nomenclature, AOU, 1998).

For marine mammals in general, an articulation of rules has yet to be fully set. Although for cetaceans, the English names that are the most widely employed are those used by the International Whaling Commission in their Annual Reports (now published as a special volume of the *Journal of Cetacean Research and Management*), they do not specify what the rules should be. The one that has come closest is Rice (1998, pp. 9-10) when he listed a number of considerations about common names for marine mammals such as: a) many distinctive English names have been formed by adding a modifier (often geographic) to the vernacular name (e.g., the "North Pacific bottlenose whale" and the "North Atlantic bottlenose whale"); b) that writer should be considerate the audience they are writing for because, for example, for people familiar with dolphins the common name "susu" means *Platanista gangetica*, but for the rest of the world, "susu" is meaningless, while the name "Ganges river-dolphin" would be comprehensible; c) that writers should be careful in deciding whether or not when to use hyphenation in the formation of compound group names. He cites as examples those of "sea-lion" instead of "sea lion"

because sea-lions are not lions; on the other hand, "elephant seal" should be written as an open compound because it is a true seal; d) that the use of possessives versus attributes for patronyms should be carefully considered. He proposed to ignore consistency "in favor of euphony and common sense" and cites as examples "Ross seal" as obviously better that "Ross's seal" while "True's beaked whale" and "Gray's beaked whale" should be used that way in order to avoid the ambiguity that could arise from "True beaked whale" or "Gray beaked whale"; e) that geographical modifiers may be adjectives such as "Japanese sea-lion" or attributive such as "California sea-lion" and that, similarly, compound modifiers may be adjectives as for the case of the white-beaked dolphin or the longfinned blackfish, nouns in apposition (humpback whale, bottlenose dolphin), or a combination (shortsnouted spinner dolphin; longbeaked saddleback dolphin); so following standard grammatical practice, compound modifiers are always hyphened or closed (bottlenose dolphin, **not** bottle nose dolphin; right-whale dolphin, **not** right whale dolphin); f) that vernacular names should be given preference over book names; g) that the term "common" should be avoided (it should be "harbor" instead of "common seal"), and, g) that patronyms should be rejected in favor of more neutral denominations ; thus, "grampus" is preferred over "Risso's dolphin" (see Chapter 1 on that too). Judging from the recent literature, both general and scientific or peer-reviewed (see for example Reeves *et al.*, 2002 and van Helden *et al.*, 2002, respectively), those recommendations have yet to be followed. Maybe mammalogists in general and marine mammalogists in particular should follow the lead that in this respect has been set by their ichthyological and ornithological colleagues.

3.4. The Practice of Classification

The two major ways to classify organisms are phenetically and phylogenetically. **Phenetic classification** is based on overall similarity while **phylogenetic classification** is based on evolutionary history. The latter should be used when possible, but many times, due to lack of information, we have to settle for phenetic approaches.

Systematics is the study of the biological diversity that emphasizes the reconstruction of **phylogeny**, i.e., the evolutionary history of a particular group of organisms (e.g., species). Its practitioners are called **systematists**. It includes **taxonomy**, the description, identification, and classification of species. Its practitioners are called **taxonomists**. Earlier naturalists classified marine mammals based almost entirely on external characteristics. Today systematists use a wide array of approaches to understand the relationships among marine mammals. Besides external morphology they also use information provided by genetic techniques (such as DNA analysis), fossils, internal anatomy, behavior, and physiology.

Classification is based on the study of **characters** (features) of organisms. Characters are considered to be useful for classification if they are heritable, and include anatomical, physiological, behavioral, and molecular (e.g., DNA sequences) traits. When we find two or more forms of a particular character we refer to them as **character states**. There are two types of character states: the original one referred to as **ancestral**, **plesiomorphic**, or **primitive** and the (new) character that arouse from the original one which is called **derived** or **apomorphic**. For example, Mazzatenta *et al.*, 2001, compared cross sections of the optic nerve of a fin whale and a striped dolphin, with

similar sections of terrestrial mammals and found that the two cetacean nerves share a number of specializations that distinguish them from the optic nerve of terrestrial mammals. For instance, fiber density is approximately two-fold lower than in land mammals. Therefore, they concluded that high fiber density was a plesiomorphic or primitive character while low fiber density was an apomorphic or derived character.

Shared derived characters, known as **synapomorphies**, are usually taken as evidence that the species possessing these features share a common ancestry. For example, Savage *et al.* (1995) analyzed the fossil remains of *Prorastomus sirenoides*, the oldest and the most primitive sirenian known. This extinct species dates back to the early Eocene age (ca. 50 MYA) of Jamaica. They found that this early sirenian shared characteristics with ungulates (hoofed mammals). However, its dental formula contrasted that of other ungulates, while being present in all other Eocene sirenians; thus, the trait was classified as a synapomorphy. However, we must be careful; sometimes, some species will show the same kind of synapomorphies but they will not be directly related. That is the case of the river dolphins; although they all show a reduction of the visual apparatus and pigmentation, they have derived from separate marine ancestors that invaded freshwaters at different times and places in the geological history of the planet. This is a case of what is called convergent evolution, which has also been reported for other unrelated taxa (such as many blind cave fishes, see Romero and Paulson, 2001).

The system that uses this approach is called **phylogenetic systematics** or **cladistics** (from the Greek word meaning "branch") and the relationships among taxonomic groups, whether they are species or families, are commonly represented in the form of a **cladogram** or **phylogenetic tree**. Cladograms are sort of very schematic of branching trees or diagrams that intend to represent the evolutionary history or phylogeny of a group of taxa. The lines of the cladogram are called **clades or lineages** and they represent the sequence of ancestor-descendant populations through time. **Nodes** are the points in which branching takes place and represent **speciation events**. Sometimes three or more branches can come out from a node although it is usually only one. For example, Nikaido *et al.* (2001) studied the sequence of certain amino acids among toothed whales with special emphasis in river dolphins. They built a cladogram (Fig. 2.3) that showed that, based on that genetic information, Ganges River dolphins, beaked whales, and oceanic dolphins had diverged (in that order) after sperm whales.

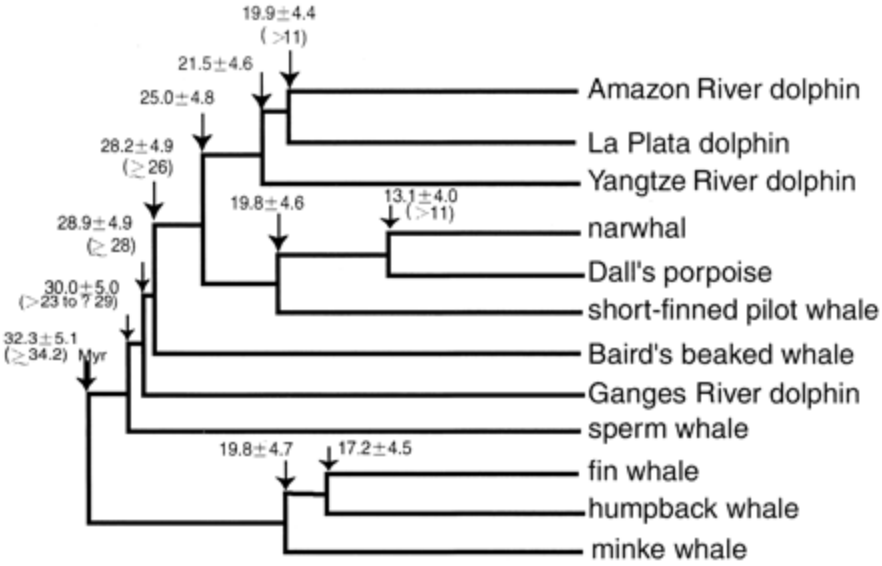


Fig. 2.3 Estimates of branching dates in the cetacean evolution by using the relaxed molecular clock of SINE flanking sequences. Branching times estimated from fossil data are indicated in parenthesis (from Nikaido *et al.,* 2001).

The real difficulty is determining which characters are derived and which are ancestral. To that end an **outgroup comparison** is carried out. This is a method by which we can determine how widespread a particular feature may be: whether it is found only within the group of interest, or beyond that group. For example, if we are interested in determining the relationships among monk seals (our **ingroup**), we would use their closest relatives as the **outgroups**. Once we have determined a lineage, when we see two clades resulting from the splitting of a single lineage we call them sister groups. The primitive state can only be determined if the primitive states for the nearest outgroup are easy to identify and those states are the same for at least the two nearest outgroups. Cassens *et al.* (2000) utilized that approach to study the four species of "river dolphins" which are associated with six separate great river systems on three subcontinents and that have been grouped for more than a century into a single taxon based on their similar appearance. By using phylogenetic analyses of nucleotide sequences from three mitochondrial and two nuclear genes, they demonstrated that extant river dolphins are not **monophyletic** (i.e., they did not have a common ancestor) and suggest that they are relict species whose adaptation to riverine habitats incidentally insured their survival against major environmental changes in the marine ecosystem or the emergence of Delphinidae. Therefore, if "river dolphins" were grouped into a single taxonomic group, that group would be **paraphyletic**, i.e., a group with elements that derived from different direct ancestors (Fig. 2.4).

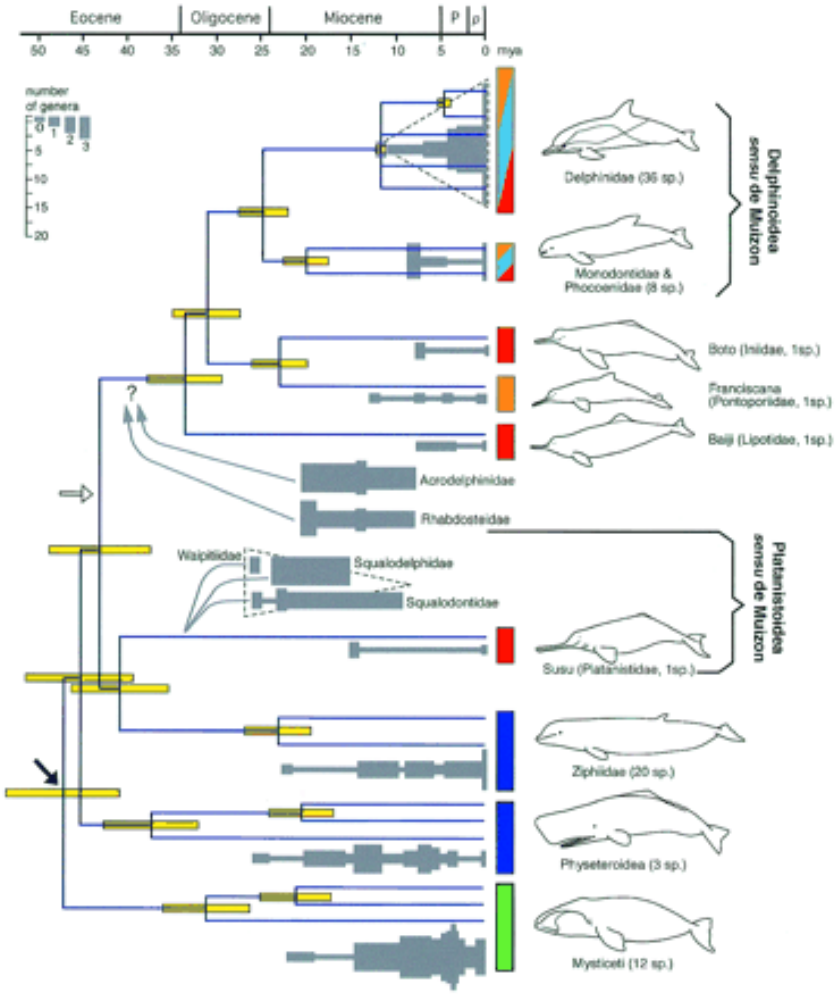


Fig. 2.4. ML tree topology (−lnL = 19019.05697) combined with calculated dates of divergences as well as estimates of generic diversity of relevant fossil taxa (gray-shaded boxes). Only genera considered stable enough and based on diagnostic material are considered. Numbers of extant species are given between parentheses for each group. Vertical colored boxes indicate habitat: green, specialization in filter feeding (baleen whales); dark blue, specialization for deep feeding on squids (beaked and sperm whales); orange, coastal waters; light blue, oceanic waters; and red, fluvial environment (whereas the boto, baiji, and susu are exclusively riverine, some delphinoid species consist of distinct coastal and fluvial populations). Each horizontal yellow bar indicates twice the value of the standard deviation for the age of the corresponding node. Hence, standard deviations are not referring to the *topology* of the tree. Dotted triangles indicate the radiation of Delphinidae and concurrent gradual extinction of Waipitiidae, Squalodelphidae, and Squalodontidae. The black arrow at the base of the tree indicates the position of the root when all nuclear and mitochondrial data are used in a simultaneous ML analysis and by using hippopotamus as an outgroup. This result is, however, unstable because several gene fragments support an alternative root, indicated by the white arrow. P, Pliocene and *p*, Pleistocene.

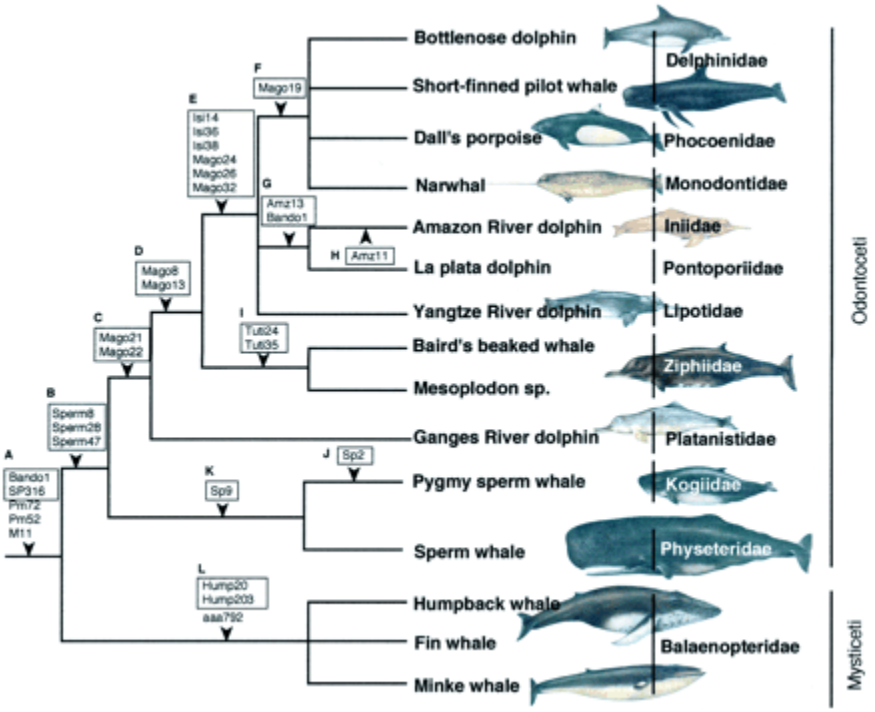


Fig. 2.5 This is a representation of phylogenetic relationships among the major lineages of cetaceans. Newly isolated and characterized loci are boxed (taken from Whitfield, 1998; Copyright 1998, Simon & Schuster).

Other important concepts for phylogenetic reconstruction are those of **homology**, the similarity of features resulting from common ancestry (e.g., flippers among cetaceans) and **analogy**, the similarity of features resulting from different ancestry (e.g., both seals and cetaceans have flippers, but that is the result of their adaptation to the same environment since their ancestors are quite different from one another). The most typical example of analogous characters take place as a result of convergent evolution as noted earlier. The presence of analogous characters is known as **homoplasy** and they can be the result of either **convergence** (flippers in seals and whales) or **reversal** (the appearance of claws among pinnipeds; although claws are common to many terrestrial mammals they are not present among primitive seals, Berta and Sumich, 1999).

Another common concept in phylogenetic studies is that of **parsimony**. The principle of parsimony, based on Okham's razor or principle of simplicity that the simplest explanation is usually the correct one, states that the cladogram that contains the fewest number of evolutionary steps, or changes between character states of a given character summed for all characters, is accepted as the best estimate of phylogeny. For example, Teramitsu *et al.* (2000) analyzed DNA among several species that included whales, dolphins, seals, and sea lions. By applying the principle of parsimony they

clustered the genes of these species and found that, as expected, pinniped (seals, sea lions) genes are more similar to those of dogs (Order Carnivora), which, in turn, were quite different that those from cetaceans, confirming the conservative (and therefore most parsimonious) systematic view that places these two groups separately, despite the fact that both have representatives in the marine environment.

As powerful and useful cladistics has been, this method presents a number of unresolved problems. For example, convergence is not always easy to identify; also, molecular and morphological evidence is not always consistent. That has been the case in some controversies about the origin and evolution of major cetacean groups (which has been the case in some studies of whales, see Milinkovitch, 1995, for a summary). Also, depending upon the weight given to different characters, you can get different results. Finally, complete phylogenies depend upon the fossil record, which is, by definition, incomplete and also gives a glimpse of some characters, not others.

3.5. Mammals

Mammals have been a well-defined clade since the Late Triassic (ca. 220 MY) when they evolved from reptiles. Despite that taxonomic clarity, marine mammals (particularly cetaceans) seem to defy conventional wisdom regarding mammalian characterization. Below are the main mammalian characteristics and explanations of how marine mammals create exceptions to these characteristics.

1. *Body covered with hair, reduced in some.* That is the main differentiating characteristic (as is feathers for birds). Although cetaceans lack hair in their adult stage, they do show a few vibrissae and bristles on the rostrum or around the mouth as fetuses, which they lose around the time of birth. The appendages of some pinnipeds are hairless. On the other extremes, sea otters have the densest fur of any mammal.
2. *Integument with sweat, scent, sebaceous and mammary glands*. Cetaceans and sirenians lack both sweat and sebaceous glands.
3. *Mouth with teeth*. Although baleen whales lack teeth in adult stage, they do show teeth in the fetal stage.
4. *Movable eyelids and fleshy external ears.* Cetaceans and many pinnipeds lack the fleshy external ear.
5. *Four limbs in most, adapted for many forms of locomotion.* In cetaceans, the forelimbs have been modified into paddle-like flippers and the hindlimbs are totally absent. In pinnipeds the limbs have been profoundly modified for swimming and steering, but they are more or less functional for short (but awkward) movements on land. Sirenians forelimbs are modified into flippers and their hindlimbs are reduced to nothing more than a vestigial pelvis.
6. *Four-chambered heart.* In this regard, marine mammals are no different from the rest of mammals although they present some anatomical and physiological adaptations aimed to maximize diving times.
7. *Respiration system with lungs and larynx; presence of muscular diaphragm*. Essentially this is true also for marine mammals. Cetaceans show a drastic

change in the position of the nares by moving them into a dorsal position. Some exceptional physiological adaptations will de discussed in Chapter 7.

8. *Brain highly developed.* That is also true for most marine mammals and particularly true in the case of toothed whales in their auditory areas.
9. *Endothermic and homeothermic*. That is also true for marine mammals. They show a number of physiological adaptations for the low temperatures some species confront in very cold waters.
10. *Internal fertilization; eggs developed in a uterus with placental attachment (except in monotremes) with fetal membranes (amnion, chorion, allantois).* Marine mammals are not particularly different in these basic features.
11. *Young nourished by milk from mammary glands.* The same for marine mammals.

Thus, all these deviations from the "typical" mammal demonstrate how unique marine mammals are by means of convergent evolution.

3.6. Marine Mammals

Early in the evolution of mammals, a variety of forms explored the sea as an alternative to living on land. Many colonization attempts were unsuccessful, and some taxa came and went without making a lasting mark. Others such as otters and seals have partially adapted, while still preserving vital ties to the shore. The cetaceans and sirenians alone are completely and only home in water. Here is an overview of the groups of marine mammals that we will be studying in this book.

Classification of Recent Marine Mammals

Order	Suborder	Family	Typical species	# Spp.
CETACEA				
	Mysticeti			
		Balaenidae	bowhead and right whales	4
		Neobalaenidae	pygmy right whale	1
		Eschrichtiidae	gray whale	1
		Balaenopteridae	rorquals (blue, fin, humpback)	9
	Odontoceti			
		Physeteridae	sperm whales	1
		Kogiidae	pygmy, dwarf whales	2
		Ziphiidae	beaked whales	22
		Platanistidae	Ganges River dolphins	1
		Iniidae	river dolphins	1
		Lipotidae	Baiji	1
		Pontoporiidae	La Plata dolphin	1
		Monodontidae	narwhal and beluga	2
		Delphinidae	oceanic dolphins, orcas	35
		Phocoenidae	porpoises	6

CARNIVORA			
PINNIPEDIA			
	Otariidae	sea lions and fur seals	16
	Odobenidae	walrus	1
	Phocidae	true seals; includes harbor and elephant seals	19
OTHER CARNIVORA			
	Mustelidae	sea otter and marine otter	2
	Ursidae	polar bear	1
SIRENIA			
	Dugongidae	dugong and Steller's sea cow	2
	Trichechidae	manatees	3

Table 3.1 Number of genera and species in the major taxa of marine mammals

Taxon	Number of genera	Number of species	Mean number spp./genera	Number and % monotypic genera
Cetacea	39	87	2.23	30 (77%)
Pinnipedia	21	36	1.71	19 (90%)
Other Carnivora	3	3	1	2 (67%)
Sirenia	3	5	1.67	3 (100%)
Total	66	131	1.98	54 (82%)

Chapter Summary

Animals, like any other living creatures, are classified in order to understand their evolutionary relationships with other animals. That classification is hierarchical with species being the fundamental unit of classification. Each species, as any other systematic rank, is named following a set of rules that are universally recognized by the scientific community. In addition to the scientific names given to species, common or vernacular names are also given. Unlike systematists of other natural groups, marine mammalogists have yet to establish a clearly defined set of rules of how to give common or vernacular names to the different species of marine mammals. Originally, only external features were used in order to classify animals. Today a larger set of information, with emphasis on genetic one, is employed to better understand their phylogeny, i.e., their evolutionary relationships. That information is managed following a set of rules and principles, with their own terminology, within a scientific field called cladistics. The system is not perfect given the inherent complexity of living creatures. Mammals is a very well defined natural group with a number of generalized characteristics; however, because the extreme adaptations to the aquatic environment, marine mammals present (at least during adult stage) a number of exceptions of what

could be called generalized mammalian features. There are a total of 129 species of extant marine mammals within four orders of mammals.

Critical Thinking Questions

1. Do you think that marine mammalogists should establish a set of rules about how to give vernacular or common names to different species? What would be the advantages or disadvantages of such initiative? Should they do it by themselves or should it be a task to be done in concert with other mammalogists?
2. Unlike insects, it is evident that the number of species of marine mammals is very limited and that sooner or later we would discover all the living species that are out there. Do you think that at that time all controversies about their classification will be over? Why or why not?
3. What features exemplify the convergent evolution of marine mammals with other marine vertebrates?

Key Terms

Analogy
Ancestral character
Apomorphic character
Binomials
Binomial nomenclature
Binomial System of Nomenclature
Book names
Characters
Character states
Clades
Cladistics
Cladogram or phylogenetic tree
Class
Classification
Colloquial names
Common names
Convergence
Derived character
Family
Genus (plural genera)
Homology
Homoplasy
Ingroup
International Code of Zoological Nomenclature (ICZN)
International Commission on Zoological Nomenclature
Kingdom (plural kingdoms)

Lineages
Latin name
Literary name
Monophyletic
Nodes
Order
Outgroup
Outgroup comparison
Paraphyletic
Parsimony
Phenetics
Phylogenetic classification
Phylogenetic systematics
Phylogeny
Phylum (plural phyla)
Plesiomorphic character
Primitive character
Rank
Reversal
Scientific name
Speciation events
Species
Synapomorphies
Systematics
Systematists
Taxa (singular taxon)
Taxonomists
Taxonomy
Vernacular names

Further Readings

To learn more about systematics and phylogeny, see:

Adrain, M., G.D. Edgecombe & B.S. Lieberman (Eds.). 2001. *Fossils, phylogeny, and form: an analytical approach*. New York: Kluwer Academic/Plenum Publishers.
DeSalle, R.; G. Giribet & W. Wheeler (Eds.). 2002. *Molecular systematics and evolution: theory and practice*. Boston: Birkhauser Verlag.
MacLeod, N. & P.L. Forey (Eds.). 2002. *Morphology, shape and phylogeny*. New York: Taylor & Francis.

To learn more about mammals in general, see:

Macdonald, D. (Ed.). *Encyclopedia of mammals*. New York: Facts on File.
Clutton-Brock, J. (Ed.). *Mammals*. London: Dorling Kindersley.

Martin, R.E.; R.H. Pine & A.F. DeBlase. 2001. *A manual of mammalogy: with keys to families of the world*. Boston: McGraw Hill.
Vaughan, T.A.; J.M. Ryan & N.J. Czaplewski. 2000. *Mammalogy*. Brooks/Cole, Thomson Learning.

Literature Cited

AOU. The Committee on Classification and Nomenclature of the American Ornithologists' Union. 1998. *Check-List of North American birds. The species of birds of North America from the Arctic through Panama, including the West Indies and Hawaiian Islands*. Lawrence, Kansas: Allen Press, American Ornithologists' Union.

Berta, A. & J. L. Sumich. 1999. *Marine Mammals: Evolutionary Biology*. San Diego: Academic Press.

Blunt, W. & W.T. Stearn. 2001. *Linnaeus, the compleat* [sic] *naturalist*. Princeton, N.J.: Princeton University Press.

Cassens, I.; S. Vicario, V.G. Waddell, H. Balchowsky, D. Van Belle, W. Ding, C. Fan, R.S.L. Mohan, P.C. Simões-Lopes, R. Bastida, A. Meyer, M.J. Stanhope & M.C. Milinkovitch. 2000. Independent adaptation to riverine habitats allowed survival of ancient cetacean lineages. *Proceedings of the National Academy of Sciences* (USA) **97**:11343-11347.

Koerener, L. 1999. *Linnaeus: nature and nation*. Cambridge, MA: Harvard University Press.

Holthuis, L.B. 1987. The scientific name of the sperm whale. *Marine Mammal Science* **3**:87-90.

Husson, A.M. & L.B. Holthuis. 1974. *Physeter macrocephalus*, Linnaeus 1758, the valid name for the sperm whale. *Zoologische Mededelingen* **48**:205-217.

Linsley, E.G. & R.L. Usinger. 1959. Linnaeus and the development of the International Code of Zoological Nomenclature. *Systematic Zoology* **8**:39-46.

Mazzatenta, A.; M. Caleo, N.E. Baldaccini & L. Maffei. 2001. A comparative morphometric analysis of the optic nerve in two cetacean species, the striped dolphin (*Stenella coeruleoalba*) and fin whale (*Balaenoptera physalus*). *Visual Neuroscience* **18**:319-325.

Milinkovitch, M.C. 1995. Molecular phylogeny of cetaceans prompts revision of morphological transformations. *TREE* **8**: 328-334

Nikaido, M.; F. Matsuno, H. Hamilton, R.L. Brownell, Jr., Y. Cao, W. Ding, Z. Zuoyan, A.M. Shedlock, R.; E. Fordyce, M. Hasegawa & N. Okada. 2001. Retroposon analysis of major cetacean lineages: The monophyly of toothed whales and the paraphyly of river dolphins. *Proceedings of the National Academy of Sciences* (USA) **98**: 7384-7389.

Parkes, K.C. 1975. Special review. *Auk* **92**:818-830.

Reeves, R.R.; B.S. Stewart, P.J. Clapham & J.A. Powel. 2002. *Guide to marine mammals of the World*. New York: Alfred A. Knopf.

Rice, D.W. 1989. Sperm whale *Physeter macrocephalus* Linnaeus, 1758, pp. 177-233, In: S. H. Ridgway and R. J. Harrison (eds.)., *Handbook of Marine Mammals*, Vol. 4. London: Academic Press.

Rice, D.W. 1998. *Marine mammals of the world. Systematics and distribution*. Lawrence, KS: Society for Marine Mammalogy.

Robins, C.R.; R.M. Bailey, C.E. Bond, J.R. Brooker, E.A. Lachner, R.N. Lea & W.B. Scott. 1991. *Common and scientific names of fishes from the United States and Canada*. Bethesda, Maryland: American Fisheries Society Special Publication # 20.

Romero, A.; A. I. Agudo & S. J. Blondell. 1997. The scientific discovery of the South American freshwater dolphin, *Inia geoffrensis*. *Marine Mammal Science* **13**:419-426.

Romero, A., A.I. Agudo, S.M. Green, & G. Notarbartolo di Sciara. 2001. Cetaceans of Venezuela: their distribution and conservation status. *NOAA Technical Reports NMFS* **151**:1-60.

Romero, A. & K.M. Paulson 2001. It's a wonderful hypogean life: a guide to the troglomorphic fishes of the world. *Environmental Biology of Fishes* **62**:13-41.

Savage, R.J.G.; D.P. Domning & J.G.M. Thewissen. 1994. Fossil Sirenia of the West Atlantic and Caribbean region. V the most primitive known sirenian, *Prorastomus sirenoides* Owen, 1855. *Journal of Vertebrate Paleontology* **14**:427-449.

Schevill, W. E. 1986. The International Code of Zoological Nomenclature and a paradigm: the name *Physeter catodon* Linnaeus 1758. *Marine Mammal Science* **2**:153-157.

Stearn, W. 1959. The background of Linnaeus's contributions to the nomenclature of systematic biology. *Systematic Zoology* **8**:4-22.

Teramitsu, I.; Y. Yamamoto, I. Chiba, H. Iwata, S. Tanabe, Y. Fujise, A. Kazusaka, F. Akahori & S. Fujita. 2000. Identification of novel cytochrome P450 1A genes from five marine mammal species. *Aquatic Toxicology* **51**:145-153.

Van Helden, A.L.; A.N. Baker, M.L. Dalebout, J.C. Reyes, K. van Waerebeek & C.S. Baker. 2002. Resurrection of *Mesoplodon traversii* (Gray, 1874), senior synonym of *M. bahamondi* Reyes, van Waerebeek, Cárdenas and Yáñez, 1995 (Cetacea: Ziphiidae). *Marine Mammal. Science* **18**:609-621.

Whitfield, P. 1998. *Encyclopedia of Animals*. New York: Simon & Schuster.

Chapter 4

Marine Mammals of the World I: Introduction to Cetaceans

Mysticetes

4.1. Introduction

This chapter is devoted to a descriptive list of all marine mammal species as defined in the previous chapter. I give the basic distinctive features for each species as follows: 1) The scientific name which is encapsulated in a box together with the author of the taxon and the common name (in the case of cetaceans I use the one given by the International Whaling Commission (IWC 2001). 2) The etymology (derivation) of the scientific name and, in case that the origin of the common name is not obvious, I also explain it. For **monotypic** (one species only) families and genera, the etymology is explained within their respective species. 3) Because some species have had a confusing taxonomic past, I provide the most common synonyms for the scientific names (for a more complete treatment of this issue, see Rice 1998). 4) The size of the animal including size at birth (neonate), at weaning (when available), and as adult, the latter including weight in metric tons. 5) Distinguishing features to highlight the kind of (mostly) external characteristics that separate the species from close relatives. 6) Distribution to give a general idea of the worldwide distribution of this species (for a more detailed global account see Rice 1998). 7) Habits to describe the type of habitats in which the species is usually found. 8) The section titled "Remarks" is devoted to give some other interesting information about the biology of the species such as reproduction, feeding, interactions with other species, conservation status, and any other outstanding characteristics. When that information is abundant and specific, I provide a separate heading for each one. These areas of marine mammal biology will be revisited and given a more comprehensive treatment later on in the book.

For the classification I have mostly followed Rice (1998), thought the revisions on the status of some species based on new molecular approaches (e.g., IWC 2001), the renaming of some (e.g. van Helden *et al.* 2002), together with the description of new ones, (e.g., Dalebout *et al.* 2002) has led to some minor modifications.

Order CETACEA Brisson, 1762

4.2. Etymology and Historical Overview

The word Cetacea comes from the Greek *ketos* or its transliteration into Latin *cetos* meaning sea monster or any large marine creature including whales. Historically, whales were lumped together within the realm of "sea monsters" (Sweeney 1972). Today all whales, dolphins, and porpoises, either living or extinct, are classified within the order Cetacea. The Greek philosopher Aristotle (B.C. 384-322) was the first to study these animals through direct observation by performing dissections on them. That approach led him to understand that cetaceans form a natural group, which was possible due to his ability to distinguish between homology and analogy (Mayr 1982, p. 456). He was also able to ascertain that cetaceans are viviparous, breast feed their young, breath air and that some even have hairs. Although Aristotle grouped cetaceans with fish (see critical question 1), he placed these marine mammals very close to quadrupeds (see Book I, Chap V, "The Parts of Animals" of his book *Historia Animalium*). This general classificatory view did not change until the Swedish naturalist Carolus Linnaeus (1707-1778) in the 10th Edition (1758) of his fundamental book *Historia Naturae*, created the group that we know today as mammals and included within it the cetaceans (which he called "Cete"). That, together with the consistent use of the binomial nomenclature (Chapter 2), initiated our modern understanding of the biology of this group. First in 1756 and later in 1762, Mathurin Jacques Brisson (1723-1806) placed these animals under the name "cetacea", their current name. Thus, cetology is the study of cetaceans. Herman Melville in his 1851 novel *Moby Dick* introduced this term in our lexicon (see Box 1.3., Chapter 1).

4.3. Summary Characteristics

Cetaceans and sirenians are the only mammals to live their entire lives in water. Cetaceans comprise an order whose specializations are the most divergent from the rest of the class Mammalia. Although chiropterans (bats and vampires), also show a great deal of specialization because of their flying habits, the number of physiological and behavioral adaptations to the aquatic environment are really extreme, particularly for a group that has evolved such adaptations in just about 50 million years. Because of these unique divergences in morphology, the relationships between cetaceans and other mammals have always been a source of controversy (see, for example, Simpson 1945 and Milinkovitch 1995).

Cetaceans range in size from 1.2 m (the Vaquita, *Phocoena sinus*) to 33.5 m (a female blue whale landed in the Southern Ocean, in 1909) in length. It is generally accepted that the blue whale is the largest species to have lived on earth. These mammals are characterized by having a fusiform, streamlined ("torpedo-shape") body, with paddle-like flippers (modified forelimbs) used for steering, balancing, and stopping, but not for moving forward; that action is powered by the upward and downward motion of the broad horizontal tail or paired flukes. Most species also have a dorsal fin, which serves as a stabilizer. The flukes and dorsal fin are mostly composed of dense connective tissue but no bone. There are a number of other adaptations that further improve the

streamlining among cetaceans: a smooth, rubbery skin, the lack of glands and hairs, and the absence of protruding ears, hind limbs, and external genitalia (even in males). Thus, most of the sensory and reproductive organs of cetaceans have been internalized to reduce drag while swimming. For example, cetaceans rely on an internal system of air sinuses and bones to detect sounds, instead of external ears. In place of hair they have developed a thick layer of fat called blubber under the skin that insulates them from the cold and provides buoyancy, while providing an excellent system for energy storage. The position of the nostrils has shifted to the top of the head creating a blowhole that allows them to more effectively come to the surface for air. Blowholes of cetaceans generally reach the surface before the rest of the body. In modern cetaceans the skull has become "telescoped," i.e., both the upper and lower jaw extending well beyond the entrance of the nasal passages (nares) while the blowholes have migrated to the top of the head.

The order Cetacea is a large one comprising 85 extant species (Jefferson et al. 2008). As it happens with many other living groups, there are more species that have become extinct than the ones that we can find today. The order is further divided into three suborders: the Archaeoceti (which are all now extinct and I describe in the chapter devoted to evolution of cetaceans), the Mysticeti or baleen whales (blue whales, humpback whales, gray whales, and right whales), and the Odontoceti or toothed whales (killer whales, dolphins, porpoises, beluga whales, beaked whales, and sperm whales). The first is an assortment of fossil cetaceans grouped under that name more for convenience than because they represent a natural group. The two suborders of extant cetaceans are grouped based largely on the type of food they eat and the structures with which they eat it. Because of the need for thermoregulation, as well as large size and long migratory routes, many cetaceans consume large amounts of food. The validity of this classification will be reviewed in the chapter dealing with the evolutionary history of these animals. Table 4.1 gives an idea of the diversity of cetaceans down to the family level. This classification is still a matter of controversy and is continuously changing as more molecular and fossil information is gathered.

Table 4.1. A schematic classification of cetaceans down to the family level. Extinct taxa are marked with a (†). Some families that appear as recent (without the "†") also have representatives in the fossil record. Classification is based on Thewissen (1998), Uhen (1998), Williams (1998), and Barnes (2002) for extinct cetaceans and Rice (1998) for living ones with slight modifications. I have avoided the use of intermediate taxa (e.g., infraorder, superfamily) for groups that are exclusively represented by fossils because they tend to be highly artificial.

Order Cetacea

- (†) Suborder Archaeoceti
  - (†) Family Pakicetidae
  - (†) Family Ambulocetidae
  - (†) Family Remingtonocetidae
  - (†) Family Ptotocetidae

(†) Family Basilosauridae

Suborder Mysticeti
(†) Family Llanocetidae
(†) Family Aetiocetidae
(†) Family Mammalodontidae
(†) Family Kekenodontidae
(†) Family Cetotheriidae
Family Balaenidae
Family Neobalaenidae
Family Eschrichtiidae
Family Balaenopteridae

Suborder Odontoceti
(†) Family Agorophiidae

Superfamily Physeteroidea
Family Physeteridae
Family Kogiidae
Superfamily Ziphioidea
Family Ziphiidae
Superfamily Platanistoidea
Family Platanistidae
(†) Family Waipatiidae
(†) Family Squalodelphinidae
(†) Family Dalpiazinidae
(†) Family Squalodontidae
(†) Family Eurhinodelphinidae
(†) Family Acrodelphinidae
Superfamily *incertae sedis*
Family Iniidae
Family Lipotidae
Family Pontoporiidae
Family Platanistidae
Superfamily Delphinoidea
(†) Family Kentriodontidae
(†) Family Albireonidae
(†) Family Odobenocetopsidae
Family Monodontidae
Family Delphinidae
Family Phocoenidae

Suborder MYSTICETI (Gray, 1864) baleen whales

Etymology: *mustax*, genitive *mustakos* (Gr) = moustache; *ketus* (Gr) or *cetus* (L) = sea monster, whale. The reference to moustache is to the baleen plates that characterize this group.
Characteristics: The primary distinguishing characteristic of this group is that all adults lack teeth, which have been replaced by a series of baleen plates on either side of their jaws. Baleen whales are also unique for having two external blowholes. Mysticetes are also different from odontocetes in always having a symmetrical skull (but see Figueroa *et al.* 1997) and by lacking ribs articulated to the sternum. Except for the position of the sexual organ openings, males and female baleen whales are very difficult to identify based solely on external characters. However, adult females tend to be a bigger than their male counterparts. As a group, they are larger in size than most toothed whales, with the pygmy right whale, *Caperea marginata*, being the smallest one at about 6 m in length. The largest toothed whale is the sperm whale, *Physeter macrocephalus*, whose males may reach 18 m in length. That is why baleen whales together with sperm whales are sometimes referred to as the "great whales."
15 species (Jefferson et al 2008).

Family BALAENIDAE (Gray, 1821) right and bowhead whales

Etymology: *balaena* (L) = whale.
This family is characterized by the lack of dorsal fin and by having few or no throat grooves. They have extremely long baleen plates contained in a narrow and hugely arched upper jaw. Their body form is robust with a large head (>25 percent of body length), and broad flippers. This family is represented by two genera and four species.

Genus *Eubalaena* (Gray, 1864) right whales

Etymology: *eu* (L) = true; *balaena* = whale.
They are the least streamlined of all the species of baleen whales. The body is mostly black, often with variable white patches on chin and belly. Their upper jaw is arched. Their lower jaw and head are usually covered with numerous, rough congenital callosities (see page). The patterns of these callosities are unique to each individual, and can be used for individual identification. Their baleen plates (<2.8 m) are dark and narrow with fine bristles, with 200-270 plates/side. Blowholes well partitioned that result in a nearly vertical V-shaped blow, which is used for identification. Flippers large and rounded and flukes are broad (Cummings 1985b). All seven cervical vertebrae are fused. They feed, by means of skimming, on zooplankton with some variation on prey species depending upon geographical and/or ecological circumstances. They are all migratory with feeding grounds in higher latitudes and calving and breeding grounds in lower latitudes. A single female can be courted by as many as 20 males at the same time. There seems to be some

sperm competition, a notion that is supported by the large size of the testicles, which can be as big as two meters in length and weigh up to 500 kg each. The reproductive cycle for a adult female is usually three years with one year for gestation, another year before weaning, and a third year for the female to replenish her energy storage. Their predators include orcas and large sharks. They engaged in breaching, lobtailing, and flippering.

There is genetic evidence supporting the contention that this genus contains three species: the North Atlantic right whale (*Eubalaena glacialis*), the North Pacific right whale (*E. japonica*), and the southern right whale (*E. australis*). Apparently there is more genetic similarity between *E. japonica* and *E. australis* than between *E. glacialis* and any of the other two (Rosenbaum *et al.* 2000). All the populations of the genus have been subject to intense hunting (Reeves *et al.* 1978) and although hunting of these species is prohibited today, they continue to be subject of mortality by ship strikes, entanglements with nets, pollution (including acoustical), pirate whaling, and ecological changes leading to changes in the food source.

Eubalaena glacialis (Müller, 1776) (Plate 000)
North Atlantic right whale, black right whale, black whale

Etymology: *glacialis* (L) = icy, frozen.
Most common synonym: *Balaena glacialis.*
Size: 5.5 m (neonate); 15-19.8 m, weight: 45-60 t (adult).
Distinguishing features: They have a massive head (1/4 to 1/5) of the body length. Mitochondrial DNA analysis has determined that they are three different species of right whales as a result of reproductive isolation, which has led to a number of fixed, genetic differences (Malik *et al.* 2000, Rosenbaum *et al.* 2000, Jefferson et al. 2008).
Distribution: Historically, this species was found from Labrador, Greenland, Iceland and Norway, as south as Florida and northwestern Africa. Today is found only from Nova Scotia to Florida.
Habits: They frequent coastal waters.
Food and feeding habits: They feed by skimming mostly on calanoid copepods and euphasiids.
Reproduction: Their mean age at first parturition is between seven and eight years. The female reproductive cycle is between three and four years (Knowlton *et al.* 1994).
Behavior: They are found as singles or forming unstable groups. They are frequently seeing breaching and lobtailing.
Remarks: The common name of this species derived from the fact that early whalers called them by the "right" whales to kill because they easily floated when dead (fact that has been recently confirmed, Nowacek *et al.* 2001) and produced an exceedingly valuable yield of oil and baleen. Basque whalers took the whale since the eleventh century and other Europeans started to do the same on eastern coats of North America since the sixteenth century. Today it is believed that there are less than 300 individuals alive and there are indications that since the 1980's the population size has been decreasing, deeming this species functionally extinct (Fujiwara and Caswell 2001). The main cause of anthropogenic mortality is collisions with ships (Laist *et al.* 2001). It is probably the most endangered species of baleen whales.

Eubalaena japonica (Lacépède, 1818) (Plate 000)
North Pacific right whale

Etymology: *japonica* (L) = from Japan.
Most common synonym: *Balaena glacialis.*
Size: 5.5 m (neonate); 15-19.8 m, weight: 45-60 t (adult).
Distinguishing features: There is no noticeable morphological difference with the other two species. Only mitochondrial DNA analysis has determined that they are different as a result of reproductive isolation, which has led to a number of fixed, genetic differences.
Distribution: Historically was found from Japan to northern Mexico. This species is now sighted (vary rarely) in the Sea of Okhotsk and in the Gulf of Alaska.
Habits: Frequent coastal waters.
Food and feeding habits: Probably same as for *E. glacialis*.
Reproduction: Probably same as for *E. glacialis*.
Behavior: Probably same as for *E. glacialis*.
Remarks: The actual numbers of individuals for this species is unknown and may be as low as or even lower than for the North Atlantic right whale. High proportion of organochlorine contaminants has been found in the tissues of these animals (Minh *et al.* 2000).

Eubalaena australis (Desmoulins, 1822) (Plate 000)
Southern right whale

Etymology: *australis* (L) = southern.
Most common synonyms: *Balaena glacialis.*
Size: 5.5 m (neonate); 15-19.8 m, weight: 45-60 t (adult).
Distinguishing features: There is no noticeable morphological difference with the other two species. Only mitochondrial DNA analysis has determined that they are different as a result of reproductive isolation, which has led to a number of fixed, genetic differences.
Distribution: This species is found throughout most of the subantarctic waters including eastern South America, South Africa, southern Australia, and subantarctic New Zealand (Rice 1998, van Waerebeek *et al.* 1992).
Habits: Frequent coastal waters.
Food and feeding habits: Probably same as for *E. glacialis*.
Reproduction: Probably same as for *E. glacialis*.
Behavior: Probably same as for *E. glacialis*.
Remarks: The current population estimate is about 7000 animals with an annual increase of 7-8% (Clapham *et al.* 1999, Best 2000).

Genus *Balaena* Linnaeus, 1758

Balaena mysticetus (Linnaeus, 1758) (Plate 000)
bowhead whale

Etymology: *balaena* (L) = whale; *mysticetus* (L from the Gr. *mystakus*) = moustache; *cetus* (L) = whale.
Size: 4-4.5 m (neonate); 6.1 m (weaning); 14-17 m (males) and 16-18 m (females), weight: 70-100 t (adult).
Distinguishing features: They have a very long (one third of the body length) and triangular head (when seen from the side). Their common name derives from the fcat that they have a muscular bulge on the head (hence "bowhead). Proportionally they have the largest heads among baleen whales (Reeves and Leatherwood 1985). Their common name derives from the bowed appearance of their mouth. They have a smooth skin without callosities. Their body is black with white patterns on their chins, undersides, around the tailstocks, and on their flukes. These patterns are unique to each individual and are thus used for identification. Their baleen plates are the longest of any whale (up 5.2 m) usually black, with 230-360 plates/side. Their epidermis can be as thick as 2.5 cm while the blubber underneath can be as thick as 28 cm, which make them the most insulated whale.
Distribution: Restricted to pack-ice zone of the Arctic Ocean and its peripheral seas with four to five disjunct populations (Rice 1998) (Fig. 4.4). It is possible that during warmer periods of the earth history, they move freely between the Atlantic and the Pacific.
Habits: Coastal and offshore, mostly along ice fronts and leads; migratory. Unlike other mysticetes, it spends its life following the advance and retreat of Arctic ice. They can break ice layers of up to 60 cm and can dive for more than one hour, which is very useful when it comes to finding holes in the ice for breathing.
Food and feeding habits: They feed on zooplankton by skimming but also near the sea floor. Orcas are the only natural predator known.
Reproduction: Although sexually active throughout the year, they usually mate in between late winter and early spring. There is sperm competition. Breaching and fluke slapping may play a role in sexual communication. Calves are born during the spring migration the following year.
Behavior: They produce very loud calls at low frequency, which may be used for communicating with other individuals at great distance. They tend to migrate with changes in the ice edge.
Remarks: Probably there are not more than 10,000 bowhead whales throughout the world with some stocks severely depleted (Raftery and Zeh 1998). They are still being hunted under aboriginal provision of the IWC or by direct government permit as in the case of Canada (Harwood and Smith 2002). Some have shown bioaccumulation of contaminants (Hoekstra *et al.* 2002).

Family NEOBALAENIDAE (Gray, 1873)

Etymology: *neo* (Gr) = new or young; *balaena* (L) = whale.
This family is characterized by a unique number of features in their cranial architecture. Unlike other mysticetes, it has a very long supraoccipital bone that extends well forward on the skull. They have a shorter, wider, and less arched mouth to accommodate relatively short baleen plates. They also have a more or less developed dorsal fin, longitudinal furrows on the throat (caused by the mandibular ridges that might be homologous with throat grooves, and a different type of baleen when compared with those of balaenids). Other unique characters are the smaller head size proportional to body length, a short humerus, and four digits in the hand. This family is represented by one species.

Genus *Caperea* (Gray, 1864)

One species.

Caperea marginata (Gray, 1846) (Plate 000)
pygmy right whale

Etymology: *caperea* (L) = to wrinkle (referring to the texture of its ear bone); *marginata* (L) = enclosed with a border (referring to the dark border observed on the baleen of the type specimen).
Size: It is the smallest baleen whale. 2 m (neonate); 3-3.5 m (weaning); 5-6.5 m (female slightly larger than male), weight: 3-3.5 t (adult).
Distinguishing features: The body is streamlined. Dorsal fin set very posteriorly. Color is pale gray or white with dark outer borders. Flippers are dark gray or gray with back and flanks, lightening to white on the belly and lower jaw. The mouth line extends behind and below eye. It has a white gum. The flippers are small and narrow. It has 230 baleen plates on both sides of the upper jaw (Baker 1985).
Distribution: Probably circumpolar in temperate waters of the Southern Hemisphere (Fig. 4.6).
Habits: Mainly offshore.
Food and feeding habits: The feed on copepods and small euphausiids (Kemper 2002). No natural predators are known.
Reproduction: Calving may be year-round. Not much more is known.
Behavior: Largely inconspicuous, but it has yet to be thoroughly studied.
Remarks: Because of their distribution, size, and the fact that they have rarely targeted by whalers, little is known about their biology. There are no reliable estimates about their population status. Despite its common name, because of its resemblance in the arched jaw to the right whale, both species belong to different families and are, thus, not closely related.

Family ESCHRICHTIIDAE (Ellerman and Morrison-Scott, 1951)

This family has one living member, the gray whale. This species is anatomically so distinctive from other mysticete that has been placed within its own family. There are no fossils that can relate them to any other recent cetacean. Molecular and morphological studies have yielded contradictory results in terms to their relationships with modern baleen whales. Thus, its phylogenetic relationships remain unresolved.

Genus *Eschrichtius* (Gray, 1864)

One species

Eschrichtius robustus (Lilljeborg, 1861) (Plate 000) **gray whale**

Etymology: Eschricht after the nineteenth century Danish biologist Daniel Frederik Eschricht (1798-1863); *robustus* (L) = strong.
Size: 4.6-5.0 m, 920 kg (neonate); 8.5 m (weaning); 12-15 m (females are slightly larger), weight: 16-33 t (adult).
Distinguishing features: A mottled gray skin characterizes this species. They have a small dorsal hump (but no true dorsal fin) followed by a series of bumps (7-14) along posterior dorsal midline. They have short (<0.4 m) baleen plates (140-180 plates/side), that differ from those of balaenids by being fewer in number, thicker, and white to yellowish, and by two to five throat creases in comparison to the numerous throat grooves of balaenopterids. Also, there are paired occipital tuberosities on the posterior portion of the skull for insertion of muscles, which originate in the neck region. The head is narrow and tapering, without central ridge. The rostrum has many pits, each with one hair.
Distribution: Originally there were three populations: one in the North Atlantic, another in the western North Pacific, and the third in the eastern North Pacific. It became extinct (sometime between the seventeenth and the eighteenth centuries) in the North Atlantic. The extinct North Atlantic populations are known mainly through subfossil skeletal parts unearthed in the western Atlantic from New Jersey to Florida, the most recent of which dates from about A.D. 1675. Skeletal parts have also been found in the eastern Atlantic from the Baltic coast of Sweden, the Netherlands, Belgium, and the Channel coast of England, the most recent of which dates from about A.D. 1650. There are also convincing historical accounts of living gray whales from New England in the early 1700's and from Iceland in the early 1600's. The one in the western North Pacific ("Korean") population ranged historically from the Okhotsk Sea to southern China and is today severely depleted. The eastern North Pacific ("California") population migrates every year from continental waters of the Chukchi, Bering, Siberian and Beaufort seas to Baja California and adjacent waters (Fig. 4.8) (Rice 1998).
Habits: This is the most coastal and most migratory of all species of whales. It has more coastal habits south of Alaska while being more offshore in northern feeding grounds.

Food and feeding habits: They feed at higher latitudes by filtering sand and mud from the bottom in search of invertebrates, mostly crustaceans (Dunham and Duffus 2002) consuming up to 170,000 Kg in the five months of feeding although the switch preys and tactics depending upon the circumstances (Dunham and Duffus 2001). While feeding, they position their body laterally to the bottom while swimming very close to it. This allows them to suck the sand or mud, which they force by retracting their large and strong tongue. This creates what is called "feeding pits" or mouth-size depressions playing a major role in the entire trophic community of the sea bottom (Bowen 1997). Occasionally they have been seen skimming and engulfing for zooplankton. Among the natural enemies of gray whales are killer whales and white and tiger sharks (Goley and Straley 1994).
Reproduction: Large testes in the males together with multiple copulations may be indications that sperm competition exists among males. Females' reproductive cycle is two years, sometimes with some resting periods. Gestation lasts about 12 months. The mother-calf bond is very strong and the mother is very protective of her young.
Behavior: These whales show very little social behavior beyond the mother-calf relationship, which ends at weaning. The sounds they produce, together with breaching, lobtailing, head and back slaps, jaw claps and flipper slapping, are probably used for short-range communication (Crane and Lashkari 1996).
Remarks: This is the whale species with the larger number of ectoparasites and epizoites. They include barnacle encrustations (particularly on the head) and whale lice. External scars from infestations and abrasions can be used for individual identification (Wolman 1985). There is an aboriginal catching quota allowance by the IWC that until 2002 was of 140 of the "California" population. There are also incidental deaths due to entanglement, ship collisions, and poaching. Recent changes in the ecology of Arctic waters due to decreased in primary productivity, pollution, seasonal ice cover (Perryman *et al.* 2002), and collision with vessels (Leist 2001) has heightened the concerns about the long-range survivability of this species.

Family BALAENOPTERIDAE (Gray, 1864) rorqual whales

Etymology: *balaena* (L) = whale; *pteron* (Gr) = feathers, wings, fins.
This family is the most diverse in species and abundant in population of the living baleen whales. They are collectively known as rorquals (which in Norwegian means "tube whale or "furrow whale"). The family is characterized by long, slender, and streamlined bodies, many throat grooves, a small dorsal fin, head broad and flattened with 1 or 3 dorsal ridges, jaw not highly arched, and narrow flippers. The grooves expand a great deal while feeding to increase their mouth capacity. Their baleen plates are short to moderate in length. This family is represented by eight species ranging from the small (9 m) common minke whale, *Balaenoptera acutorostrata*, to the giant (> 30 m) blue whale, *Balaenoptera musculus*. Nine species.

Subfamily MEGAPTERINAE (Gray, 1864)

Genus *Megaptera* (Gray, 1846)

One species

Megaptera novaeangliae (Borowski, 1781) (Plate 000) **humpback whale**

Etymology: *megas* (Gr) = large; *pteron* (Gr) = wing or fin; *novus* (l) = new; *angliae* (L) = England (the specimen used for the original description was from New England).
Size: 4.0-4.6 m (neonate); 7.6-8.5 m (weaning); 13-17 m, weight: 30-40 t (adults, females are about 10% bigger than males).
Distinguishing features: The most characteristic features in this species are its long and narrow flippers, which correspond to about 1/3 of the length of the animal. The jaws and head have numerous knobs or tubercles, often barnacle encrusted. It has a dorsal fin on hump, at about 2/3 back on the body. It also has long flukes with saw-toothed margin. Body coloration ranges from dark gray to black, with white on the throat. These color variations are related to geographic distribution. Coloration and serration in the tail are used for individual identification. This species has 14 to 24 throat grooves, which are wide and extend to navel. The baleen is short (<0.7 m) and black with dark brownish gray bristles, 270-400 plates/side (Winn and Reichley 1985).
Distribution: All oceans of the world (Fig. 4.10). They spend the summer in high-latitude feeding grounds, and migrate to winter grounds below the tropics in shallow waters around islands, over banks, and along continental coasts. The population of the Arabian Sea does not migrate at all. There is very little difference between the northern and southern populations of humpbacks as well among populations in the same hemisphere. Therefore there is no evidence to support the subdivision of this species into subspecies. For a detailed distributional account see Rice (1998).
Habits: Coastal in many areas; strongly migratory; often in groups of 2-10.
Food and feeding habits: They are generalist feeders eating on small crustaceans and schooling fish. They can use bubbles to corral and trap schooling fish. Then, they open their mouth to engulf the fish at the center of the "bubble trap." Their only known natural enemies are orcas.
Reproduction: Gestation period is 11 months. Lactation lasts until the calf is one year old after which the calf leaves the mother. Thus, the reproductive cycle of females is usually two years. They reach sexual maturity at the age of five. Males forcefully compete for females for hours in corporal behaviors that include ramming, slashing, and head butting. Males prefer to associate with females with high reproductive potential (e.g., without a calf) while becoming progressively less choosy over the course of the reproductive season as females without a calf become increasingly rare on the winter grounds (Craig *et al.* 2002).
Behavior: Males produce some of the most complex and longest sounds produced by any animal species, which are used, apparently, to attract females. These songs vary in structure in both time and space. Non-aggressive behaviors include lobtailing, breaching, and flippering. Since these displays take place under very different circumstances and

times of the year, their function is not always clear and may include play behavior, parasite removal, and even communication.
Remarks: This species were heavily hunted worldwide leading to a severe depletion of some local populations. Although some hunting is allowed under the aboriginal provisions of the IWC, this species is showing signs of recovery worldwide. Collisions with ships (Laist *et al.* 2001), entanglements in nets (Weinrich 1999), chemical pollution (Gauthier 1997), noise pollution (Todd 1996), and illegal whaling continue to be a problem.

Subfamily BALAENOPTERINAE (Gray, 1864)

Genus *Balaenoptera* (Lacépède, 1804)

Etymology: *balaena* (L) = whale; *pteron* (Gr) = wing or fin.
Eight species

Balaenoptera acutorostrata (Lacépède, 1804) (Plate 000)
common minke whale

Etymology: *acutus* (L) = pointed, sharp; *rostrum* (L) = beak, snout, face.
Size: 2.4-2.8 m (neonate); 5.0 m (weaning); 7.8-8.8 m, weight: 6-9 t (adult). Females are always larger.
Distinguishing features: The head is narrow and pointed with a sharp median ridge. The dorsal fin is falcate and prominent. The body is black above, white below and may have chevron markings behind head. The flippers are small with broad white band. Baleens are short (<0.2 m) and white to yellowish with fine white bristles. They have 230-325 plates/side and 50 to 70 throat grooves extending nearly to navel (Stewart and Leatherwood 1985). These are the shortest baleens among all rorquals (Jefferson et al. 2008).
Distribution: It is found in the North Atlantic (including the Caribbean and Mediterranean Sea with rare vagrants occurring in the Black Sea (Rice 1998, Romero *et al.* 2001) and in the North Pacific from the East China Sea to the coast of central Baja California. There is also a population ("dwarf minke whale," probably a subspecies) in the southern hemisphere that appears to be distributed mainly in the lower latitudes including winter localities South America, South Africa and Australia (Rice 1998) (Fig. 4.12).
Habits: Frequent coastal regions, bays, estuaries, and offshore banks; northward shift in summer; often occur singly, sometimes in groups of 2-3.
Food and feeding habits: They feed on a variety of crustaceans and fish although the specific species vary from region to region (Lindstrom *et al.* 2002). Orcas are their main natural predator.
Reproduction: Pregnancy lasts 10 months and lactation 45 months. Reproductive cycle is annual. They reach sexual maturity between the ages of six and eight years old (Olsen and Sunde 2002).

Behavior: They aggregate in coastal and inshore areas for feeding. They also approach stationary vessels (Jefferson et al. 2008)
Remarks: Three subspecies have been proposed: *B. a. acutorostrata* for the North Atlantic, *B. a. scammoni* for the North Pacific, and an unnamed one for the Southern Hemisphere. Some of its stocks have been severely depleted; yet some hunting is being allowed under the aboriginal provisions of the IWC.

Balaenoptera bonaerensis (Burmeister, 1867) (Plate 000)
Antarctic minke whale

Etymology: *bona* (L) = advantage, good; *aerenses* (L) = related to wind.
Size: 2.4-2.8 m (neonate); 5.0 m (weaning); 7.8-9.0 m, weight: 6-9 t (adult).
Distinguishing features: The confirmation that this is a separate species from *B. acutorostrata* comes from genetic analysis (Arnason *et al.* 1993), which confirms also some differentiation from the osteological viewpoint (Rice 1998). Therefore, externally is very difficult to differentiate from the common minke whale.
Distribution: It summers mainly in the Antarctic zone (Fig. 4.14). The distribution is not entirely clear because of past confusion with the "dwarf" minke whale discussed above under *B. acutorostrata*.
Habits: Probably similar to those of *B. acutorostrata*.
Food and feeding habits: Probably similar to those of *B. acutorostrata*.
Reproduction: Probably similar to those of *B. acutorostrata*.
Behavior: Probably similar to those of *B. acutorostrata*.
Remarks: Their basic biology is less known than for the common minke whale but the little we know indicates that there are very similar. This species is being exploited under research provisions of the IWC. Current population estimates are still a matter of conjecture.

Balaenoptera edeni (Anderson, 1879) (Plate 000)
pygmy Bryde's whale

Etymology: *edeni* = after Ashley Eden (1831-1887), Chief Commissioner of British Burma (today Myanmar), who secured the type specimen for Anderson. For explanation of the common name see next species.
Size: 12.5-14 m, weight: 26 t (females larger than males).
Distinguishing features: They have 250 to 410 short baleen plates/side. Their head has three prominent ridges anterior to blowhole. They have a tall, sickle-shaped dorsal fin. They are dark gray in color with white chin and belly; some are light gray between the head and the dorsal fin on the dorsal surface (Cummings 1985a).
Distribution: In the far western Pacific and Southeast Asia (Fig. 4.16).
Habits: Some members are coastal, others offshore. Most are migratory, although some tropical populations may be sedentary.
Food and feeding habits: At least the South African population seems to feed year round on the same grounds (Best 2001). They consume small fish and zooplankton. Orcas have been seen attacking and killing Bryde's whales (Silber 1990).

Reproduction: Apparently gestation lasts one year and the female reproductive cycle is two years.
Behavior: They are usually found alone and groups for reproduction are short-lived while for feeding are just opportunistic.
Remarks: See the remarks section for *B. brydei* below.

Balaenoptera brydei (Olsen, 1913) (Plate 000)
Bryde's whale

Etymology: *brydei* after Johan Bryde, the Norwegian consul who built the first whaling stations in South Africa in 1908.
Size: 4 m (neonate); 7.1 m (weaning); 14 m (adult).
Distinguishing features: Their head has three prominent ridges anterior to blowhole. Their dorsal fin can reach 0.5 m in height and is strongly curved with pointed tip an this is a distinguishing characteristic from sei whales. The body coloration is dark gray. Their baleens are short (<0.4 m), dark gray with coarse bristles. They have 250-370 plates/side and 50 to 70 throat grooves that extend at least to the navel.
Distribution: In the Atlantic Ocean they range from Chesapeake Bay and the Strait of Gibraltar to Buenos Aires in Argentina and South Africa. In the Indian Ocean they have been found in the Red Sea, the Persian Gulf, and India. In the Pacific Ocean, larger Bryde's whales range from the East China Sea and southern California to New Zealand and in Chile (Fig. 4.18) (Rice 1998).
Habits: Variable: some pelagic populations are migratory, some resident in nearshore waters. They can be seen either singly or in pairs.
Food and feeding habits: Probably same as for *B. edeni*. In the Caribbean they take advantage of high productivity areas to consume schooling fish (Romero *et al.* 2001).
Reproduction: Probably same as for *B. edeni*.
Behavior: Probably same as for *B. edeni*.
Remarks: For many decades it was believed that there was only one species of small rorquals, which received the scientific name of *B. edeni* or Bryde's whale. Recently, some molecular (Yoshida and Kato 1999) and morphological evidence seems to point toward the possibility of at least two different species of small rorquals. The main morphological difference seems to be related to size and sexual maturity. One group is made up of small animals that attain sexual maturity at sizes as short as 9.0 m and rarely grow much longer than about 11.5 m; the other group is made up of larger animals that do not attain sexual maturity until they attain a length of at least 11.2 m in males, 11.7 m in females, and sometimes reach a maximum length of 14.6 m in males and 15.6 m in females. The smaller animals are from coastal and shelf waters of the eastern Indian Ocean, the Sunda Shelf, and the Western Pacific. *B. edeni* would correspond to this group. The larger animals have been found in the tropical and warm temperate waters around the world. This would correspond to *B. brydei* (Rice 1998). Genetic separation is possible due to their may be a consequence of their limited seasonal migrations and apparent resource partitioning (Best 2001). Yet, these views have yet to be universally accepted.

Balaenoptera borealis (Lesson, 1828) (Plate 000)
sei whale

Etymology: *borealis* (L) = northern. The common name "sei" derives from the Norwegian "sejhval," because this whale arrives in Norway at the same time than the saithe or cod locally known as "seje" (*Pollachius virens*).
Size: 4.5 m (neonate); 9 m (weaning); 20 m (more typically 15 m, females are larger), weight: 30 t (adult).
Distinguishing features: The dorsal fin is relatively large (0.3-0.6 m) falcate and about 2/3 back on body. They have only one distinctive ridge running the length of the head (Bryde's whales have three). The body coloration is gray to blue-gray above, lighter below, often with light oval scars; the flukes are dark below. Their baleens (<0.8 m) black with fine white to grayish-brown bristles, 220-400 plates/side. The number of throat grooves varies from 35 to 65. They end between flipper and navel (Gambell 1985a).
Distribution: Found in all oceans, but tend to remain in more temperate waters than the other rorquals. Although sei whales migrate considerable distances between higher latitude summer grounds and lower latitude winter grounds, they infrequently venture into cold polar waters and the pack-ice zone, or into hot tropical waters. They have been subdivided into two subspecies: one is *B. b. borealis* for the North Atlantic including the Caribbean and Gulf of Mexico (Romero *et al.* 2001) and the North Pacific from the Sea of Japan to Baja California; the other is *B. b. schlegellii* (Flower 1865) for the Southern Hemisphere (Fig. 4.20). Each one of these subspecies would be further broken into distinct populations (for other distributional information in general see Rice 1998, and for the Caribbean see Romero *et al.* 2001).
Habits: Pelagic; northward shift in summer; occur singly or in small groups.
Food and feeding habits: They feed on copepods, fish, and squids. Orcas prey on them.
Reproduction: Gestation is about one year. Calves are weaned at seven months and sexual maturity is reached at age 10 in both males and females.
Behavior: They are fast swimmers reaching up to 50 km/hr (Nowak 2003). Little else is known except that they rarely form groups and those groups are short-lived.
Remarks: Their body can have numerous scars from healed lamprey bites. Because of whaling, the global population is depleted today. They are easily confused with Bryde's and Eden's whales. Because the general lack of markings, photoidentification is of limited value in the study of this species (Schilling *et al.* 1992).

Balaenoptera physalus (Linnaeus, 1758) (Plate 000)
fin whale

Etymology: *physalos* (Gr) = rorqual whale or toad that puffs.
Size: 6 m, weight: 2 t (neonate); 11 m (weaning); 22-26 m (females 5-10% larger than the males, individuals in the southern hemisphere are also 5-10% larger than the ones in the northern hemisphere), adult weight: 40-50 tons in the northern hemisphere and from 60 to 80 t in the southern hemisphere. This is the second largest species of whale after the blue whale.

Distinguishing features: They have a flattened rostrum with a flattened head that is wedge-shaped. The dorsal fin (to 0.6 m) is falcate and located about 3/4 back on the body. They have a strong dorsal ridge anterior to the tail. The body is gray to brownish above (where the pigmentation is asymmetrical), white below; with the lower right jaw white, left dark. The baleens are no more than <0.7 m in length, being dark gray and yellow striped, but white to yellow anterior right side. The total number of plates varies between 260-470 plates per side. They have between 56 and 100 throat grooves, which extend from the chin to the navel (Gambell 1985b).
Distribution: Nearly worldwide in distribution. There are two allopatric subspecies separated by body size: one is *B. p. physalus* in the North Atlantic, including the Caribbean and the Gulf of Mexico (Romero *et al.* 2001) as well as in the North Pacific from the Sea of Japan to Baja California (there is a year-round resident population in the Gulf of California). The other subspecies is *B. p. quoyi* (Fischer 1829) from the Southern Ocean (Fig. 4.22); for full distributional records see Rice 1998 and Romero et al 2001.
Habits: Generally pelagic, visiting coastal waters in many areas; migratory; may occur singly or in small groups.
Food and feeding habits: This species feeds preferentially on krill, other crustaceans, schooling fishes, and, occasionally, on squids. Its only natural predator is the orca.
Reproduction: Gestation lasts about 11 months. Weaning occurs when the calf is 6-7 months old. Reproductive cycle for the females is two years. Sexual maturity is achieved for males when they are 6-7 years old and for the female when they are 7-8 years old. Hybridization between the fin and blue whale occurs at relatively higher frequencies than among other mysticetes and is geographically widespread (Berube and Aguilar 1998). Hybrid males may be sterile, while females at least reach sexual maturity, although their ability to produce viable offspring has not yet been confirmed.
Behavior: They are migratory and fast swimmers (up to 15 knots or 37 km/h). Only males vocalize (Croll *et al.* 2002).
Remarks: Their conservation status is uncertain, especially for southern hemisphere populations that were more heavily exploited, particularly in the twentieth century. They may further threatened by collisions with vessels (Laist *et al.* 2001), morbillivirus infections (Jauniaux *et al.* 2000), pollution (Hernandez *et al.* 2000), and illegal whaling.

Balaenoptera omurai (Wada, Oishi, and Yamada, 2003)
Omura's whale

Etymology: *balaena* (L) = whale; *pteron* (Gr) = wing or fin; *omurai* (L) = after Japanese cetologist H. Omura.
Size: 11.5 m.
Distinguishing features: They have medially expanded posterior portion of ascending process of maxilla, which conceals posterior end of premaxilla along the adjacent nasal; approximately 200 baleen plates on one side, which is the smallest number among all of its congeners except for *B. edeni*. The skull is relatively broad and flat.
Habits: Pelagic.
Distribution: The Sea of Japan, the Solomon Sea, and the eastern Indian Ocean near the Cocos Islands.

Remarks: This species was described based on eight specimens caught by Japanese whaling ships and a carcass found on a coastal island n the Sea of Japan. Morphological, osteological, and DNA mitochondrial analysis separated it from other balaenopterids.

Balaenoptera musculus (Linnaeus, 1758) (Plate 000)
blue whale

Etymology: *musculus* (L) = little mouse or muscular (?).
Size: 7 m, weight: 3 t (neonate); 21-26 (up to 33.5 m), weight: 80-150 t (adults, females are larger than males; individuals in the southern hemisphere are larger than the ones in the northern hemisphere).
Distinguishing features: They have a broad head with an U-shaped rostrum and a short central ridge. The dorsal fin is small (<0.25 m) and positioned 3/4 back on body. Body coloration is dark blue-gray with pale mottling. In cold waters, blue whales are found covered by a yellow-green to brown film produced by a diatom. The flippers are pointed, white below. The baleens are less than <0.9 m in length, being black with dark, coarse bristles. They are between 270 and 400 plates/side. The tongue and palate are black. The throat grooves (55-88) extend at least to navel (Yochem and Leatherwood 1985).
Distribution: Found almost everywhere in the world's oceans at one time or another. Exceptions may be the Caribbean for which only one record has bee recorded (Romero *et al.* 2001). They ranged from the tropics north and south into the pack ice of the Arctic and Antarctic oceans. Today, there are disjunct populations in the North Atlantic, the northern India, and the North Pacific oceans. Four subspecies have been proposed based on their geographic distribution: *B. m. musculus* for the North Atlantic and North Pacific, *B. m. indica* (Blyth 1859) for the Northern Indian Ocean, *B. m. brevicauda* (Ichihara 1966) or "pygmy" blue whale of the subantarctic Indian Ocean and southeastern Atlantic Ocean, and *B. m. intermedia* (Burmeister 1871), a population that summers in the Antarctic Zone (Fig. 4.24).
Habits: Pelagic, but may frequent coastal waters and shallow banks; migratory. They are usually found in groups of 2-3.
Food and feeding habits: They feed almost exclusively on euphasiids by gulping. Lunging han been observed; throat pleats distend (Jefferson et al. 2008). The only natural predator known is the orca.
Reproduction: Gestation lasts between 10 and 12 months. Calves are weaned when they are 6 to 7 months old. Sexual maturity is reached between 5 and 15 years of age, but most commonly between 8 and 10 years for both sexes. For hybridization with other species see Remarks for the fin whales (p.).
Behavior: They produce powerful songs whose function is not entirely clear. They tend to be solitary but are occasionally found in groups that include fin whales with whom they hybridize.
Remarks: This is the largest animal that has ever lived, reaching 33 m in length and weighing over 60 tons. It was heavily hunted and was brought to the brink of extinction. There is evidence that populations have not recovered since it became protected in 1966 (Clapham *et al.* 1999). Today they are threatened by collisions with ships, entanglements in nets, and pollution (Gauthier *et al.* 1997). Noise pollution is also of concern (Croll *et al.* 2001).

Appendix

A Classification of Extinct and Living Mysticetes

Modified from Bisconti (2007), Steeman (2007), and Bisconti (2008)

Class **MAMMALIA** Linnaeus, 1758
- Order **CETACEA** Brisson, 1762
  - Suborder **MYSTICETI** Gray, 1864a *sensu* Cope, 1869
    - *Mammalodon* spp., incertae sedis (†)
    - ?*Mammalodon colliveri* Pritchard, 1939 (Fordyce, 1982) Late Oligocene
    - Family **AETIOCETIDAE (†)** Emlong, 1966
      - *Chonecetus goedertorum* Barnes and Furusawa, 1994 Late Oligocene
      - *Aetiocetus cotylalveus* Emlong, 1966 (Fordyce, 1982) Early Miocene
      - *Aetiocetus polydentatus*
    - Family **LLANOCETIDAE (†)** Mitchell, 1989
      - *Llanocetus denticrenatus* Mitchell, 1989
    - Infraorder **CHAEOMYSTICETI (†)** Mitchell, 1989
      - Superfamily **EOMYSTICETOIDEA (†)** Sanders & Barnes, 2002a
        - *Mauicetus* Benham, 1939 (Whitmore & Sanders, 1977) Middle Oligocene
        - *"Mauicetus" lophocephalus incerta sedis*
        - *"Mauicetus" waitakiensis incerta sedis*
      - Family **EOMYSTICETIDAE (†)** Sanders & Barnes, 2002a
        - *Eomysticetus*
      - Family **CETOTHERIOPSIDAE (†)** Brandt, 1872 *sensu* Geisler & Sanders, 2003
        - *Cetotheriopsis*
        - *Micromysticetus*
      - Superfamily **BALAENOIDEA** Brandt, 1872 *sensu* Geisler & Sanders, 2003
      - Family **NEOBALAENIDAE** Gray, 1874
        - *Caparea marginata*
      - Family **BALAENIDAE** Gray, 1825

Morenocetus incertae sedis
Balaena montalionis
Balaena mysticetus
Balaenula astensis
Balaenula sp. (Barnes, 1977) Late Miocene - Late Pliocene
Eubalaena glacialis (Müller, 1776, Barnes, 1977) Recent

Superfamily **CETOTHEROIDEA (†)** Steeman, 2007
Mixocetus elysius Kellogg, 1934 (Barnes, 1977) Late Miocene
Cetotherium furlongi Kellogg, 1925 (Barnes, 1977) Early Miocene
"Cetotherium" megalophysum
aff. *Herpetocetus* Van Beneden, 1982 (Barnes, 1977) Late Miocene - Late Pliocene
"Mesocetus" *argillarius*

Family **ESCHRICHTIIDAE** Ellerman & Morrison-Scott, 1951
Eschrichitus robustus (Lilijeborg, 1861, Barnes, 1977) Recent
Eschrichtioides gastaldii **(†)** Bisconti 2008 Early Pliocene

Family **CETOTHERIIDAE (†)** Brandt, 1872 *sensu* Miller, 1923
Cephalotropis insertae sedis
Piscobalaena
Cetotherium rathkei
Metopocetus durinasus
Herpetocetus
Nannocetus eremus Kellogg, 1929 (Barnes, 1977) Late Miocene

Superfamily **BALAENOPTEROIDEA** Gray, 1868 *sensu* Mitchell, 1989
Mauicetus Benham, 1939 (Whitmore & Sanders, 1977) Middle Oligocene
"Mauicetus" lophocephalus incerta sedis
"Mauicetus" waitakiensis incerta sedis

Family **PELOCETIDAE (†)** Steeman, 2007
Parietobalaena palmeri
Pelocetus calvertensis
Halicetus

Cophocetus

Family **AGLAOCETIDAE (†)** Steeman, 2007

Aglaocetus

Isanacetus latycephalus

Pinocetus

Family **DIOROCETIDAE (†)** Steeman, 2007

Amphicetus

"Pleisiocetus" cortesii

cf. *Plesiocetus* Van Beneden, 1859 (Barnes, 1977) Late Miocene – Late Pliocene

Diorocetus hiatus

Thinocetus

Family **BALAENOPTERIDAE** Gray, 1864

Archaebalaenoptera castriarquati Bisconti, 2007 Lower Pliocene

Parabalaenoptera baulinensis

"Balaenoptera" borealina

Megaptera hibachi

Megaptera miocaena Kellogg, 1922 (Barnes, 1977) Late Miocene

Megaptera novaeangliae (Borowski, 1781, Barnes, 1977) Recent

Balaenoptera omurai

Balaenoptera edeni Anderson, 1878 (Barnes, 1977) Recent

Balaenoptera borealis Lesson, 1828 (Barnes, 1977) Recent

Balaenoptera musculus (Linnaeus, 1758, Barnes, 1977) Recent

Balaenoptera physalus (Linnaeus, 1758, Barnes, 1977) Recent

Balaenoptera acutorostrata Lacépède, 1804 (Barnes, 1977) Recent

Mysticeti *incertae sedis*

"*Balaenoptera*" *ryani* Hanna and McLellan, 1924 (Barnes, 1977) Late Miocene

"*Eschrichtius*" *davisonii* Cope 1872 (Barnes, 1977) Late Pliocene

Aulocetus sammarinensis

Eomysticetys whitmorei

Literature Cited

Bisconti, M. 2007. A new basal Balaenopterid whale from the Pliocene of Northern Italy. *Paleontology* **50**:1103-1122.

Bisconti, M. 2008. Morphology and phylogenetic relationships of a new eschrichtiid genus (Cetacea: Mysticeti) from the Early Pliocene of northern Italy. *Zoological Journal of the Linnean Society* **153**:161–186.

Dalebout, M. L, J.G. Mead, G. Baker, C. Scott, A.L. van Helden. 2002. A new species of beaked whale *Mesoplodon perrini* sp. n. (Cetacea: Ziphiidae) discovered through phylogenetic analyses of mitochondrial DNA sequences. *Marine Mammal Science* **18**: 577-608.

Jefferson, T.A, M.A. Webber, and R.L. Pitman. 2008. Marine Mammals of the World: Comprehensive Guide to their Identification. San Diego:Acacemic Press

Milinkovitch, M. C. 1995. Molecular phylogeny of cetaceans prompts revision of morphological transformations. *Tree* **10**: 328-334.

Novak, R.M. 2003. Walker's Marine Mammals of the World. Baltimore: Johns Hopkins University Press

Rice, D.W. 1998. *Marine mammals of the world. Systematics and distribution.* Society of Marine Mammalogy Special Publication Number 4, 231 pp.

Simpson, G.G. 1945. The principles of classification and a classification of mammals. *Bulletin of the American Museum of Natural History* **85**: 100-216.

Steeman, M.E. 2007. Cladistic analysis and a revised classification of fossil and recent mysticetes. *Zoological Journal of the Linnean Society* **150**:875-894.

Chapter 5

Marine Mammals of the World I: Introduction to Cetaceans Odontocetes (I)

Odontocetes

Suborder ODONTOCETI Flower, 1867 toothed whales

Etymology: *odous* (Gr), genitive *odontos*, a tooth; *ketos* (Gr) = a sea monster, whale.
The second suborder of cetaceans are the odontocetes or toothed whales, which includes the majority of living cetacean species such as sperm whales, killer whales, dolphins, porpoises, and many others. It consists of 10 families, 33 genera, and 72 species. It is a much larger and more diverse group than the mysticetes. Its members are usually small to medium size except for the sperm whale and some large beaked whales. Sexual dimorphism is common. Unlike mysticetes, where almost always females are larger than males, odontocetes don't have a general rule for size/gender correlation.

The most distinguishing features of odontocetes are the presence of teeth in one or both jaws, although in some species of beaked whales only adult males display dentition. They also have only one blowhole (naris). All of them have a more or less developed melon, i.e., a region of adipose tissue on top of the skull with connective tissue within it, which is used in their acoustic behavior. Also, they almost always show cranial and facial asymmetry. Generally speaking, odontocetes are more social than mysticetes. In addition to using sounds for communication, they also use them for echolocation, food search, and for navigational purposes. They are mostly marine, but some families travel into rivers or live their entire lives there.

There are three major living odontocete groups: the superfamilies Physeteroidea (sperm whales), Ziphioidea (beaked whales), and Delphinoidea (dolphins, blackfish, porpoises, etc.). Also, the so-called "river dolphins," have always challenged systematists with their convergent features. Now with molecular information at hand, they can be placed together with their respective marine ancestors (see sections below for *Platanista*, *Lipotes*, *Inia*, and *Pontoporia*) within the superfamily Delphinoidea.

There are 10 families of Odontocetes.

Family PHYSETERIDAE Gray, 1821 Sperm whales

One species.

Genus: *Physeter* Linnaeus, 1758

Physeter macrocephalus Linnaeus, 1758
sperm whale

Etymology: *physeter* (Gr) = a blow-pie or tube; *macro* (Gr) = large; *cephalus* (Gr) head. Its common name derives from the belief among whalers that, because of its whitish and dense appearance, the spermaceti oil found in their forehead was actually sperm.
Size: 3.5-5 m, weight: 1 t (neonate); 6.7 m, weight: 2.7 t (weaning); 10.9-12 m, weight: 15-20 t (adult female); 15.8-18.5 m, 45-70 t (adult male).
Distinguishing features: This is one of the most easily identifiable species of marine mammal because of its distinctive huge squarish head occupying at least one-third of its body and projecting often up to 1.5 m beyond its lower jaw. At long-ranges they can be identified by their spout (produced by a single blowhole) because they only show the very upper part of their body above the water. Their large heads contain a cavity called the spermaceti organ, which is a mass of web-like tubes filled with a yellow wax. It has been hypothesized that this organ is used to focus sonar clicks but also possibly for maintaining buoyancy (Cranford, 1999). The sperm whale has a robust body with corrugations in the skin, which may play some role in tactile sensing, in the hydrodynamic characteristics of an animal, or both (Shoemaker and Ridgway, 1991). The skin is dark gray or brownish gray. It is paler at the front of the head and on the belly, with white fringes to the mouth, particularly in the corners. The head is blunt or squarish, with blowhole to left of midline. They have on each side of the narrow and underslung lower jaw conical functional teeth that are not matched in position on the other side of the jaw. In males, the number of teeth ranges between 18 and 26. In females they are fewer and smaller. The upper jaw has up to 10 frequently curved teeth in the male and none in the female. The teeth often erupt only at sexual maturity and then, in males, only in the lower jaw. The throat has short furrows.
The sperm whale has one blowhole which gives a bushy blow projected forwards at a sharp angle to the left. There are two internal openings to the nasal passage divided by an external central septum. The whale has no dorsal fin but it has a distinct triangular or rounded hump two-thirds along the body followed by a spinal ridge, which reaches to its broad, triangular, deeply notched tail flukes. A thick "keel" not seen in many whales runs along the underside of the tailstock. Flippers are small and blunt. This species shows an extreme sexual dimorphism with males up to 50% longer and 3 times heavier than females.
Distribution: The sperm whale is a cosmopolitan species that can be found throughout the world, particularly where there are the deep waters, from the equator to the edges of the polar pack ice. It is most common in submarine trenches at the edge of the continental shelf but may occur inshore anywhere where water is deeper than 200 m (Rice, 1998).
Habits: Generally pelagic; highly social, sexually segregated herds of up to 40- 50; migratory, with larger males moving into higher latitudes, females and juveniles usually remaining south of 50° N; old males solitary.
Food and feeding habits: They feed on squid, octopus and a variety of fish species (Santos *et al.*, 2002). In some areas, they compete with beaked whales and elephant seals for these items.

Orcas and false killer whales have been reported as their natural predators (Palacios, 1996; Pitman *et al.*, 2001).
Reproduction: They are characterized by their low birth rate (only one young born after 14-16 months of gestation and only, on average, once every five years), slow growth and maturation (sexual maturity among females is reached at nine years of age; males continue growing until they are about 30 years old), and high survival rate (females protect the young for several years).
Behavior: Sperm whales may migrate to favored areas for feeding and breeding, although females engage in less extensive seasonal migration than males. Winter is spent in temperate and tropical waters. Some populations are resident year-round. They produce sounds mostly in the form of "clicks" and "creacks" for foraging by means of echolocation, and for communication with other conspecifics (Jaquet, 2001). Females are much more social than males, particularly adult ones (Christal and Whitehead, 2001).
Remarks: A common synonym for this species is *P. catodon*. No subspecies can be recognized. Whaling has reduced the world population size. Collision with vessels (Laist *et al.*, 2001), entanglements with fishing gears (Nolan *et al.*, 2000), pollution (Holsbeek *et al.*, 1999), and illegal whaling continue to be of concern.

Family KOGIIDAE Gill, 1871 pygmy and dwarf sperm whales

Like in Physeterids, they have a large anterior basin in the skull, but kogiids differ markedly in their size (they are much smaller), short rostrum, and other details of the skull.

Genus: *Kogia* Gray, 1846

Etymology: *kogia* is probably a Latinized from of the English word "codger" for "A mean, stingy, or miserly (old) fellow." This is one of those rare cases in which the genus does not mean anything! Gray never explained why or from where he chose it. They have a spermaceti organ, which they use for focusing sounds (Goold and Clarke, 2000). Two species, both rarely seen at sea; most of the information summarized below comes from stranded individuals. Chivers et al. (2005), using mitochondrial DNA (mtDNA) markers and morphologically based species identifications, suggested that *Kogia sima* may be formed by two distinct clades: one from the Atlantic and one from the Pacific-Indian oceans and that those two clades might correspond to two different species.

Kogia breviceps (Blainville, 1838)
pygmy sperm whale

Etymology: *brevis* (L) = short and the genitive *cepitis* (L) = head.
Size: 1.0-1.2 m, weight: 55 kg (neonate); 3.0-3.8 m, weight: 360-450 kg (adult).
Distinguishing features: They have a chunky body, tapering to narrow tailstock. The lower jaw is small with sharp curved teeth. They have a gill-like marking posterior to eye. The dorsal fin is small (<0.2 m) and located about 2/3 back on body. Flippers are short and broad and are located forward on body. Lack throat creases. Body coloration is dark blue-gray, being brownish on back, lighter on sides, white on belly. Teeth: 0/12-16 each side.

Distribution: An oceanic species that lives mostly beyond the edge of the continental shelf in tropical and temperate waters around the world (Rice, 1998).
Habits: Pelagic; occur singly or in small groups.
Food and feeding habits: Mostly cephalopods, but also crustaceans and fish. Remains of this cetacean have been found in stomach contents of orcas and white sharks (Long, 1991).
Reproduction: This species reaches sexual maturity when they are between 2.5 and 5 years of age. Sperm competition has been reported. Gestation lasts between nine and 11 months.
Behavior: Slow moving, usually alone or in small groups. Has been seen standing still with the back of the head above the water and the tail hanging.
Remarks: Scarring suggests that they are attacked by lampreys.

Kogia sima (Owen, 1866)
dwarf sperm whale

Etymology: *sima* (L) = flat-nosed.
Size: 1.0 m, weight: 46 kg (neonate); 2.1-2.7 m, weight: 140-280 kg (adult).
Distinguishing features: Similar to *K. breviceps* but body smaller, dorsal fin taller and near midback; several short creases in throat; upper jaw occasionally with 1-3 pairs of teeth. Teeth: 0-3/8-11 each side.
Distribution: Mainly over the continental shelf and slope off tropical and temperate coasts of all oceans including the Mediterranean Sea (Rice, 1998).
Habits: Pelagic; occur singly or in small groups.
Food and feeding habits: Mostly cephalopods, but also crustaceans and fish.
Reproduction: Gestation lasts between nine and 11 months.
Behavior: Slow moving, usually alone or in small groups. Has been seen standing still with the back of the head above the water and the tail hanging (Scott and Cordado, 1997).
Remarks: Scarring suggests that they are attack by lampreys. This species used to be called *K. simus*.

Family ZIPHIIDAE Gray, 1850 beaked whales

This family, formerly known as Hyperoodontidae, is second only to the delphinids in the number of species (21) (Dalebout et al. 2004). This is a poorly known taxon due to a number of factors: 1) It is composed of essentially deep water species whose specimens have traditionally come from rare strandings and (mostly) accidental captures; therefore, observations of live animals are rare. They range in size between three and 13 m. The most common and also outstanding features are the reduction in dentition with one or two pairs in the lower jaw of males and the elongated rostrum. Other distinguishing characteristics include lower jaw often extending beyond upper jaw, a snout frequently drawn out into a beak, wide crescent-shaped blowhole, one pair of anteriorly converging throat groves forming a “V”, small flippers with short digits, small dorsal fin positioned more than 1/2 way back on body, and median notch in flukes being indistinct or absent. All species show sexual dimorphism. In the past their systematics has been very confusing. Thanks to molecular techniques the relationships among the species have been greatly classified, leading even to the description a new species and the renaming of another

(Dalebout *et al.*, 2002). We have interpreted that work for the taxonomic arrangement presented below.

Subfamily ZIPHIINAE Gray, 1850

Genus *Berardius* Duvernoy, 1851 giant beaked whales

Etymology: After M. Bérard who was the French commander of the vessel that carried the type specimen of the genus from New Zealand to France in 1846.
This genus is composed of two species that differ mostly in size.

Berardius bairdii Stejneger, 1883
Baird's beaked whale; North pacific beaked whale; giant bottlenose whale

Etymology: After Spencer Fullerton Baird (1823-1887), a famous American naturalist.
Size: 4.5 m (neonate); 10-13 m, weight: 10 t (adult, females slightly larger).
Distinguishing features: Their body is long and torpedo-like. The melon is prominent and the beak is cylindrical beak. The dorsal fin is small and triangular and positioned at about 2/3 back on body. Adults have two pairs of laterally flattened functional teeth near the tip of the lower jaw. The anterior pair is visible with the mouth closed. The throat creases are up to 70 cm long, with some showing a small central crease. The color ranges from black to brown to gray with white patches ventrally. They are usually prominent because of the multiple scarring marks.
Distribution: Temperate North Pacific, mainly in waters over the continental slope.
Habits: Pelagic; occur in pods of 2-20 with some segregation of sexes.
Food and feeding habits: Feed on cephalopods and deep-sea fishes.
Reproduction: Males mature faster that females and also live longer with a life span of about 84 years compared to 54 for females. There have been some suggestions of a larger number of males than females as well as male parental care.
Behavior: Usually travel in groups of about 10 individuals.
Food: They prey mostly on squid, particularly *Gonatus fabricii*. They also eat octopus, lobster, crab, rockfish, and herring and occasionally starfish and sea cucumbers.
Remarks: Unlike most other species of beaked whales, most of the knowledge about this species comes from its fisheries since they rarely strand. In the past they were intensively hunted, but since the 1988 that fishery has been regulated and only about 60 individuals are taken every year in Japan (Reeves and Mitchell, 1993). Some are still being killed in by-catches.

Berardius arnuxii Duvernoy, 1851
Arnoux's beaked whale, tsuchi-kujira (J)

Etymology: After M. Arnoux, a French surgeon who was abroad Bérard's vessel that carried the type specimen from New Zealand to France.
Size: 9-9.8 m, weight: 9.8-10.8 t.
Distinguishing features: Prominent, bulbous forehead; long, slender, cylindrical body; adults with 2 pairs of laterally flattened functional teeth near the tip of the lower jaw, anterior pair visible with mouth closed; blue-gray coloration, sometimes with a brownish tint, dark back and

flippers, males dirty white on back from head to dorsal fin; crescent-shaped blowhole; long, tube-like beak.
Distribution: Is found in circumpolar waters of the southern hemisphere.
Habits: Pelagic.
Food and feeding habits: Deep-sea cephalopods and fishes.
Reproduction: Nothing is known.
Behavior: Individuals of this species are seen in groups of 10 or more. This species is capable of swimming up to an estimated 7 km between breathing holes in sea ice, which they find through unbroken ice. These adaptations may enable them to exploit food resources inaccessible to other predators in the region (Hobson and Martin, 1996).
Remarks: This is a rather rare species. No interactions with human seem to occur in any significant way.

Genus; *Ziphius* G. Cuvier, 1823 goosebeak whales

One species

Ziphius cavirostris G. Cuvier, 1823
goosebeak whale; Cuvier's beaked whale

Etymology: *xiphias* (Gr) = *swordfish*; cavus (Gr) = hollow; *rostrum* (L) = beak, rostrum.
Size: 2-3 m (neonate); 6.7-7 m, weight: 2-3 t (adult).
Distinguishing features: Their forehead slopes onto a poorly defined beak. There is a depression behind the blowhole. They show "flipper pockets", indentions in the body cavity for the flippers to fit into. The dorsal fin is about 2/3 back on body; lower jaw of adult males with one pair of conical teeth protruding from tip (unerupted in females and juveniles); color varies from gray to brown to tan to white, getting lighter with age; white scratches and round scars common.
Distribution: All temperate and tropical waters around the world.
Habits: Pelagic; appears to be confined by the 10-degrees-C isotherm and the 1000m bathymetric contour (Houston, 1991).
Food and feeding habits: They seem to feed exclusively on a variety of cephalopod species (Santos *et al.*, 2001) as well as crustaceans and fish..
Reproduction: Almost nothing is known except that their gestation period lasts one year.
Behavior: They have a very elusive behavior. Occur singly or in groups of up to 20-30.
Remarks: These whales are seldom seen alive and are known mainly from occasional stranded specimens. Pollutants have been found in this species (Storelli *et al.*, 1999).

Genus *Tasmacetus* Oliver, 1937

One species

Tasmacetus shepherdi Oliver, 1937
Tasman beaked whale; Shepherd's beaked whale

Etymology: *Tasma* (L) = Tasmanian Sea; *cetus* (L) = whale; the species after G. Shepherd, curator of the Wanganui Museum in New Zealand who obtained the type specimen.

Size: 6-7 m, weight: 5.6 t.
Distinguishing features: They have long, stout body with small head and long, narrow beak. The teeth are small and conical and numbered between 17 and 29 on both jaws. Two of the teeth (at the tip of the lower jaw in males only) are larger. Body coloration is dark gray-brown on back, with lighter flanks and belly almost white. The blowhole is crescent-shaped. The dorsal fin is small and sickle-shaped being position at about 2/3 back on body.
Distribution: Probably circumglobal in the temperate waters of Southern Hemisphere (Rice, 1998).
Habits: Except for sightings south of Tasmania and in the oceanic waters of the South Atlantic it has rarely been observed in nature so it is difficult to discern any habits.
Food and feeding habits: Feed on both fish and cephalopods.
Reproduction: Almost nothing is known.
Behavior: Almost nothing is known.
Remarks: Only known from a few stranded specimens. Its actual external appearance is not known.

Subfamily HYPEROODONTINAE Gray, 1846

Genus *Hyperoodon* Lacépède, 1804

Etymology: *hyper* (Gr) = above; *odon* (Gr) = tooth, because papillae on the palate were confused with teeth.
This genus contains two well-differentiated allopatric species.

Hyperoodon planifrons Flower, 1882
Southern bottlenose whale; flatheaded bottlenose whale

Etymology: *planus* (L) = level or flat; *frons* (L) = front, referring to the unusual forehead.
Size: 6-6.5 m, weight: 6.2 t (adult male); 7-7.5 m, weight: 7.9 t (adult female).
Distinguishing features: They have a long, robust, cylindrical body. Melon is rounded and slopes sharply into a prominent beak. The lower jaw has 1 pair of teeth at tip that erupts in adult males only. Those teeth are not visible with mouth closed. The dorsal fin is hooked, about 30 cm high and positioned about 2/3 back on the body. Body coloration varies from pale gray or brown to blue-black on the back, lightening to bluish- or pale brown on the flanks, and with a paler belly. The head of adults is light.
Distribution: Temperate and Antarctic waters of the Southern Hemisphere.
Habits: Pelagic.
Food and feeding habits: Feed on squids and occasionally on fish and crustaceans.
Reproduction: Almost nothing is known.
Behavior: Found in small groups of about 10 individuals.
Remarks: Seems to be abundant in Antarctic waters.

Hyperoodon ampullatus (Forster, 1770)

North Atlantic bottlenose whale

Etymology: *ampulla* (L) = flask, bottle; *atus* (L) = provided with. All this means "rough papillae on the palate" because those papillae were confused with teeth.
Size: 3.6 m (neonate); 7-8.5 m, weight: 5.8 t (adult female); 9-9.5 m, weight: 7.5 t (adult male).
Distinguishing features: Very similar to *H. planiforns*. Body is black to brown above, lighter below, with various lighter markings in adults, with head of adults being light. It has two conical teeth at the tip of the lower jaw. Males are generally larger than females, which is unusual for beaked whales.
Distribution: Subarctic North Atlantic waters.
Habits: Pelagic, preferentially at deep waters.
Food and feeding habits: Feed on squids, fish, sea cucumbers, and starfishes.
Reproduction: Sexual maturity is reached at 9 years of age in females, slightly older in males. Births take place in spring. Gestation and weaning last one year.
Behavior: Found singly or in groups of 2 to 4. Associations within age/sex classes (female/immature, subadult male and mature male) are significantly higher than associations between different classes. Females and immature bottlenose whales form a loose network of associations. Overall the social organization of northern bottlenose whales is similar to that of some bottlenose dolphins, *Tursiops truncatus*, living in shallow, enclosed bays (Gowans *et al.*, 2001). It has been proposed that their large heads are use for head-butting (Gowans and Rendell, 1999). They can dive at least 800 m and stay underwater for at least 80 min (Hooker and Baird, 1999a).
Remarks: Thousands of North Atlantic bottlenose whales were killed, particularly during the nineteenth century, because of their spermaceti that was used for cosmetics. Now the species is protected but still faces challenges from pollution and entanglement with fishing gear. The Gully, a submarine canyon off eastern Canada, was nominated as a pilot Marine Protected Area (MPA) in 1998 to safeguard the locally vulnerable population of this species (Hooker *et al.*, 2002).

Genus *Mesoplodon* Gervais, 1850

Etymology: *mesos* (Gr) = middle; *hoopla* (Gr) = arms; *odon* (Gr) = tooth, meaning armed with a tooth in the middle of the jaw.

With 15 species, this is the most diversified genus of living cetaceans (Dalebout et al. 2008). These beaked whales are infrequently spotted at sea and even then they are difficult to identify at the species level. Almost all museum specimens are from stranded animals.

General characteristics in addition to those of the Ziphiidae include only one pair of laterally flattened teeth, erupted in adult males only which are used for fighting in dominance bouts. It is believed that the variation in the position and shape of these teeth have evolved to aid species recognition between sympatric and otherwise morphologically similar species of this genus (MacLeod, 2000). In adults size ranges from 3.9 m (*M. peruvianus*) to 6.2 (*M. layardii*). There is no enough data as to make blanket statements on sexual dimorphism regarding females, but it appears that females may be larger than males. Identification of females and immature

males, in which teeth are unerupted, is very difficult. Their body is generally spindle-shaped with a small head and narrow tailstock. They often have an arched prominence on the lower jaw. Flippers are small and narrow and fit within a depression in the body. The dorsal fin is usually small and triangular. Flukes are un-notched. Body coloration is dark above and lighter below. The blowhole is located in a depression behind the melon, which slopes to a long beak. Adults, particularly males, are frequently heavily scarred.

Mesoplodon europaeus (Gervais, 1855)
Gervais' beaked whale; Antillean beaked whale; Gulf Stream beaked whale

Etymology: *europaeus* (L) = Europe, because the type specimen was found floating in the English Channel.
Size: 2.1 m (neonate); 4.5-5.2 m (adult).
Distinguishing features: Body laterally compressed; head extremely small with narrow beak; teeth triangular, about 1/3 back from tip of lower jaw. Dorsal fin small, 2/3 way back from snout tip
Distribution: Warms temperate and tropical waters of the North Atlantic including the Caribbean and the Gulf of Mexico.
Habits: Pelagic; occur in small groups.
Food and feeding habits: Squids (?).
Reproduction: No information available.
Behavior: No information available.
Remarks: No other information available.

Mesoplodon bidens (Sowerby, 1804)
Sowerby's beaked whale; North Atlantic beaked whale, North Sea beaked whale

Etymology: *bis* (L) = two; *dens* (L) = tooth.
Size: 2.4 m (neonate); 3 m (weaning); males up to 5.5 m (adult) and up to 1.300 kg in weight. .
Distinguishing features: Teeth small and pointed, about 1/2 way from tip of lower jaw to corner of mouth. Blows were either invisible or relatively inconspicuous.
Distribution: Temperate North Atlantic from North America to Europe.
Habits: Pelagic, on water depths of 550 to 1500 m.
Food and feeding habits: Squids and fish.
Reproduction: Little information available. Breeding season appears to be late winter to spring
Behavior: It has been seen in groups of up to 10 individuals. Can dive for at least 28 min. During all surfacings the long beak projected from the water well before the rest of the head or back was visible. Tail-slapping has been observed (Hooker and Baird, 1999b). There display male-male combat over access to females using tusks.
Remarks: What we know is from only a handful of sightings and strandings.

Mesoplodon mirus True, 1912
True's beaked whale

Etymology: *mirus* (L) = wonderful.
Size: 5.1-5.4 m, weight 1.4 t (adult).
Distinguishing features: Heavy body, with depression behind blowhole and slightly bulging melon; small, triangular, compressed teeth, located near tip of lower jaw.
Distribution: Warm temperate North Atlantic and southern Indian Ocean. These two represent genetically distinct populations.
Habits: Pelagic.
Food and feeding habits: Squids (?)
Reproduction: No information available.
Behavior: It has been seen in groups of up to three..
Remarks: No other information available.

Mesoplodon hectori (Gray, 1871)
Hector's beaked whale

Etymology: After Sir James Hector (1834-1907), curator of the Colonial Museum in Wellington, New Zealand, who first studied the type specimen (but misidentified it).
Size: 4.3-4.5 m, weight: 2 t (adult).
Distinguishing features: Short beak. Teeth are small and triangular, and located near tip of lower jaw. Blowhole is a crescent with ends pointing forward.
Distribution: Circumglobal in temperate waters of Southern hemisphere.
Habits: Pelagic.
Food and feeding habits: Squids (?).
Reproduction: No information available.
Behavior: No information available.
Remarks: No other information available.

Mesoplodon traversii (Gray, 1874)

spade-toothed beaked whale

Etymology: After William Thomas Locke Travers (1819-1903) A New Zealand naturalist.
Size: Since all specimens known are incomplete portions of the cranium, there is no real estimation of their size.
Distinguished features: It has a large jugal, broad rostrum, and small distance between premaxillary foramina. The male teeth are large and spade-shaped with a strong terminal denticle (van Helden *et al.*, 2002).
Distribution: Known only from three very incomplete specimens. The first is a mandible and two teeth partial remains from the Pitt Island and White Island in New Zealand. The second is a

calvaria (the skull cap made up of portions of the frontal, parietal, and occipital bones) from White Island, New Zealand. The third, also a calvaria, is from Isla Robinson Crusoe (=Isla Más a Tierra) in the Islas Juan Fernández of Chile. The type specimen is a partially damaged mandible and teeth collected in the New Zealand locality and the other one is an incomplete skull from the Chilean locality.
Habits: Presumably pelagic.
Food and feeding habits: No information available.
Reproduction: No information available.
Behavior: No information available.
Remarks: Formerly known as *M. bahamondi* Reyes, Van Waerebeek, Cárdenas, and Yáñez, 1996. This is probably the most poorly known of all mammal species.

Mesoplodon ginkgodens Nishiwaki and Kamiya, 1958
ginkgo-toothed beaked whale

Etymology: *ginkgo* (J) = ginkgo tree; *dens* (L) = tooth, because the teeth of this species are shaped like the leaves of the ginkgo tree.
Size: 2.1 (neonate); 5.2 m, weight: 1.5 t (adult).
Distinguishing features: Upper jaw narrow and pointed; teeth large, wide and flattened, located about halfway between tip of lower jaw and the corner of mouth, on top front edge of prominent arch; area anterior to blowhole neither markedly depressed nor raised; body dark with numerous white blotches and oval scars on belly. The anterior portion of beak is white. Also, dorsal fin small, located 2/3 of way back from snout tip. Un-notched flukes.
Distribution: It has been found in tropical and warm temperate waters of the Indo-Pacific.
Habits: Pelagic.
Food and feeding habits: No information available.
Reproduction: No information available.
Behavior: No information available.
Remarks: Occasionally taken by Japanese ant Taiwanese whalers.

Mesoplodon bowdoini Andrews, 1908
Andrews' beaked whale; deepcrest beaked whale

Etymology: After George Sullivan Bowdoin (1833-1913), a trustee of the American Museum of Natural History (New York) who supported the study of cetaceans at that institution.
Size: 2.20 (neonate); 4.4-4.5 m, weight: 2.6 t (adult).
Distinguishing features: It can be distinguished from all other species of *Mesoplodon* by the shape of its teeth and differences in the morphology of its skull. They have one pair of teeth in the middle of the lower jaw, which protrude outside the mouth in males only. It has a low melon and a short, thick beak. Body coloration is dark gray on back, lightening to pale gray on flanks and belly.
Distribution: Southern circumpolar distribution north of the Antarctic convergence, between 32 degrees and 54 degrees 30'S.
Habits: No information available.
Food and feeding habits: Mostly cephalopods.

Reproduction: The occurrence of fetuses of *M. bowdoini* in May and September, and perinatal juveniles in May and June, indicates a summer-autumn breeding season in the New Zealand region (Baker, 2001).
Behavior: No information available.
Remarks: This species was known until 2001 from about 35 specimens. This species have never been recognized in the wild.

Mesoplodon pacificus (Longman, 1926)
Indo-Pacific beaked whale; Longman's beaked whale

Etymology: *pacificus* (L) = from the Pacific (to distinguish it from *M. mirus* which has been reported only for the Atlantic).
Size: Up to 9 m.
Distinguishing features: Crase between melon and beak, larger dorsal fin than other beaked whales, flipper pockets on sides, single pair of oval teeth at tip of lower jaw
Distribution: Tropical waters on the Indo-Pacific.
Habits: No information available.
Food and feeding habits: No information available.
Reproduction: No information available.
Behavior: Large, coordinated herds, aggressive swimming when moving along surface, long dive times.
Remarks: Known from a few specimens and one live stranding in 2004. Formerly known as *Indopacetus pacificus.*

Mesoplodon layardii (Gray, 1865)
Layard's beaked whale; strap-toothed whale; long-toothed beaked whale

Etymology: After Edgar Leopold Layard (1824-1900) who was curator of the South African Museum and who provided the drawings on which the description of this species was made.
Size: 5-6 m, weight: 3.4 t (adult).
Distinguishing features: A pair of distinctive, strap-shaped teeth which grow out of the middle of the lower jaw in males, and curl over the upper jaw, preventing it from opening completely; coloration black, dark purplish-brown, or dark gray on back and flanks, lightening to white on the belly and light gray forward of the dorsal fin on the dorsal surface. Small dorsal fin, white patch around urogenital area.
Distribution: Circumglobal in the Southern Ocean.
Habits: Pelagic.
Food and feeding habits: Squids.
Reproduction: Calving occurs in southern spring to summer months
Behavior: No information available.
Remarks: Largest in size of the mesoplodonts. Strand at higher rate than other mesoplodonts.

Mesoplodon carlhubbsi Moore, 1963
Hubbs' beaked whale; archbeaked whale

Etymology: After Carl Leavitt Hubbs (1894-1979) a famous American ichthyologist who in his later years showed a great deal of interest in cetaceans.
Size: 2.5 m (neonate); 5.3 m, weight: 1.5 t (adult).
Distinguishing features: Adult males have notable white raised area anterior to blowhole; tip of beak white; teeth massive, flat and wide, protruding from raised arches about 1/2 way from tip of jaw to angle of mouth; throat creases long; body heavily scarred.
Distribution: Temperate waters of the North Pacific from North America to Japan.
Habits: Pelagic.
Food and feeding habits: Squid and fish.
Reproduction: No information available although calving seems to take place in the summer.
Behavior: Occur in small groups. Extensive scarring among males suggests frequent dominance fights.
Remarks: Occasionally killed by Japanese whalers and by catch in drift nets.

Mesoplodon peruvianus Reyes, Mead, and Van Waerebeek, 1991
pygmy beaked whale, Peruvian beaked whale; lesser beaked whale

Etymology: *peruvianus* because the specimens used for describing the species were originally caught in Peru.
Distribution: Eastern Pacific from northern Mexico to northern Chile.
Habits: Pelagic.
Food and feeding habits: Fish, squids, and shrimps caught at moderate depths.
Reproduction: No information available.
Behavior: Group size ranges from 2-5.
Remarks: Specimens obtained in by-catches. It is the smallest of the mesoplodonts.

Mesoplodon perrini Delbout, Mead, Baker, Baker and van Helden 2002
Perrin's beaked whale

Etymology: After noted American marine mammalogist William F. Perrin.
Size:3.9m (M) – 4.4 m (F).
Distinguishing features: Short mandibular symphysis. In males: flattened, triangular tusks just behind tip of lower jaw, splayed outward.
Distribution: All five specimens were found stranded in the coast of California between 1975 and 1977.
Habits: Presumable pelagic.
Food and feeding habits: Squids.
Reproduction: No information available.
Behavior: No information available.
Remarks: Occasionally taken by Japanese whalers.

Mesoplodon grayi von Haast, 1876
Gray's beaked whale, Haast's beaked whale; scamperdown whale; small-toothed beaked whale

Etymology: After John Edward Gray (1800-1876) who was Director of the British Museum.
Size: 5.5-6 m, weight: 4.8 t (adult).
Distinguishing features: One pair of triangular-shaped teeth in lower jaw, erupted in adult males only, 17-22 small teeth on each side of the upper jaw; coloration dark brownish-gray to black on back, gray or mottled gray on flanks, light gray to white belly; long, slender, white or white-flecked beak.
Distribution: Circumglobal in temperate waters in Southern Hemisphere.
Habits: Pelagic.
Food and feeding habits: Squids.
Reproduction: No information available.
Behavior: Groups of up to 6 have been observed.
Remarks: Usually strands of large groups of up to 20 individuals or more.

Mesoplodon stejnegeri True, 1885
Stejneger's beaked whale; Bering Sea beaked whale; saber-toothed whale

Etymology: After Leonhard Hess Stejneger (1851-1943), a curator of the U.S. National Museum of Natural History.
Size: 5-6 m, weight: 1.8 t (adult).
Distinguishing features: Teeth large and flattened, protruding from arches at about middle of the lower jaw and tilting slightly forward; top of head has no raised white area; dorsal side with ridge from dorsal fin to flukes.
Distribution: Subarctic and temperate North Pacific from North America to Japan.
Habits: Pelagic; occur in small groups.
Food and feeding habits: Squids.
Reproduction: Little is known.
Behavior: Seen in groups from 3 to 15 individuals. Scarring and healing fractured jaws in stranded individuals suggest intraspecific fights.
Remarks: Formerly hunted off the coast of Japan. It has been occasionally captured as by-catch of drift nets. Plastic bags have been found in the stomachs of stranded individuals.

Mesoplodon densirostris (Blainville, 1817)
Blainville's beaked whale; densebeak whale

Etymology: *densus* (L) = dense, thick; *rostrum* (L) = beak, face.
Size: 4.5-4.7 m, weight: 1 t (adult).
Distinguishing features: The forehead is flattened with marked depression anterior to blowhole. The rostrum becomes secondarily ossified via high mineralization (Currey, 2001), particularly in males, with age. This ossification produces the densest bone currently known (Zylberberg *et al.*, 1998). It is believed that prevention from damage to the rostrum during aggressive male-male interactions is the most likely function of the ossification (MacLeod,

2002). Their teeth protrude from the front edge of the prominent arch near corner of the mouth and tilt forward. The body coloration is dark on back, lighter gray ventrally and on sides, with blotchy gray to pinkish markings and white oval scars. The skin of adults scarred.
Distribution: Found in tropical and warm temperate waters around the world.
Habits: Pelagic; occur in small groups.
Food and feeding habits: Feed on squid and small fish.
Reproduction: No information available.
Behavior: They have been seen in small groups of seven to 10 individuals. They can dive for at least 22 min.
Remarks: A number of individuals of this species that stranded in the Bahamas in March 2000 may have been victims of a U.S. Navy acoustic experiment.

Family PLATANISTIDAE Gray, 1846

This family is characterized for their very long and narrow beak. Other characteristics include: numerous narrow pointed teeth that increase in length as they approach the snout, broad paddle-like flippers, lack of functional lens in the eyes, and a very enlarged maxillary crest. Two of these characteristics are the result of convergent evolution: 1) the teeth shape and pattern of size is the same as for the crocodilian gavials that are found in the same water which strongly suggests an adaptation for feeding on the same kind of prey, 2) The reduction in functional abilities of the visual apparatus is the same as found for both other river dolphins and other vertebrates that are found living in murky waters.

Genus *Platanista* Wagler, 1830

Platanista gangetica (Roxburgh, 1801)
Indian river-dolphin; blind river-dolphin; susu [Hindi], bhulan [Punjabi and Sindhi] Indus and Ganges river-dolphins

Etymology: *platanistes* (Gr) = fish in the Ganges; *gangetica* (L) = after the Ganges River.
Size: 2-2.5 m, weight: 80-90 kg (adult).
Distinguishing features: In addition to the characters for the family, they have between 27 and 33 pairs of sharp, slender teeth in each jaw. Body coloration is mostly gray-brown with a paler belly. Small dorsal fin. The eye size is much reduced.
Habits: In rivers.
Food and feeding habits: Fish and small fish.
Reproduction: Little is known for certain.
Behavior: Found as solitary or in small, loosely structured groups.
Distribution: Exclusively freshwater. There are two disjunct races.
(1) *P. g. gangetica*. It is found throughout the Ganges-Brahmaputra river system of India, Bangladesh, Nepal, and possibly Sikkim and Bhutan, below an elevation of about 250 m. *(2) P. g. minor* Owen, 1853 is from the Indus River and its tributaries, of Pakistan and India.
Remarks: Until recent historical times there was some faunal exchange among the Indus, Ganges, and Brahmaputra, which explains why this species is found today in a disjunct distribution. Mortality has been and continues to be a problem due to loss of habitat, pollution,

collision with vessels, incidental catches, and intentional captures for oil that is used for a variety of purposes (Senthilkumar *et al.*, 1999; Biswas and Boruah, 2000; Smith *et al.*, 2001).

Family INIIDAE Gray, 1846

This family is characterized for conical front teeth and molariform posterior teeth, very elongated rostrum and mandible, pneumatized maxillae forming a crest, reduced eyes, and a greatly reduced orbital region.

Genus *Inia* d'Orbigny, 1834

Inia geoffrensis (Blainville, 1817)
Amazon river dolphin; boto; inia

Etymology: Inia is a name used by the Guayaro Indians, original inhabitants of the San Miguel River in Bolivia, from where the holotype was taken. The specific name is after the French naturalist Etienne Geoffrey Saint-Hillaire (1772-1850) who took the impounded specimen from Portugal after the French had invaded that country (Romero *et al.*, 1997).
Size: 2-2.5 m, weight: 85-160 kg (adult).
Distinguishing features: 24-34 pairs of teeth in each jaw, conical front teeth and molariform rear teeth; coloration ranges from pinkish to blue-gray on the underside, older individuals may be almost white; broad body with abrupt forehead; long beak lined with stiff hairs; long, low dorsal hump; reduced eyes.
Distribution: The specific and infraspecific taxonomic nomenclature of *Inia* has yet to be fully resolved, with discussion continuing whether all *Inia* populations are a single species. Some authors divide *Inia* into three subspecies depending on geographical distribution: *I. g. geoffrensis* (de Blainville, 1817) for the Amazon, except the upper Madeira river drainage, *I. g. humboldtiana* (Pilleri and Gihr, 1977) for the Orinoco drainage basin, and *I. g. boliviensis* (d'Orbigny, 1834) for the Beni basin (the Madeira River drainage above the Teotonio Rapids). The Beni population has been proposed as a different species, *I. boliviensis* (d'Orbigny, 1834) and there is some controversy on whether *I. boliviensis* is a synonym of *I. geoffrensis* (see Romero *et al.*, 2001 for a summary of references).
Habits: Exclusively freshwater. They are seen most frequently at the junctions of rivers and tributaries (Romero *et al.*, 2001).
Food and feeding habits: Generalist fish feeders.
Reproduction: Calving between May and July (the rainy season). Gestation lasts 10-11 months.
Behavior: They can be found in the Orinoco drainage either as solitary individuals or in groups of up to six (Romero *et al.*, 2001). They produce whistles, which are positively correlated with pre-diving surfaces, suggesting that vocalizations are associated with feeding (Podos *et al.*, 2002).
Remarks: This species is being threatened by intentional captures, habitat disruption, deforestation, and pollution (Romero *et al.*, 2001). This species had been described by at least two pre-Linnean researchers whose works were not re-discovered until late in the twentieth century (Romero *et al.*, 1997).

Family PONTOPORIIDAE Gray, 1870

They have virtually symmetrical cranial vertices and most have long rostra and many tiny teeth.

Genus *Pontoporia* Gray, 1846

One species.

Pontoporia blainvillei (Gervais and d'Orbigny, 1844)
La Plata dolphin; Franciscana

Etymology: *pontos* (Gr) = open sea, high seas; *poros* (Gr) = passage, crossing; Henri-Marie Ducrotay de Blainville (1777-1850) a famous French naturalist. This means that the d'Orbigny thought that this was a dolphin that actually could transverse back and forth from freshwaters to the sea.
Size: 1.5-1.7 m, weight: 32-52 kg (adult).
Distinguishing features: They have between 50 and 60 pairs of slender, finely pointed teeth in each jaw. The beak is long and narrow with straight mouth line. Body coloration is gray-brown coloration with a paler underside.
Distribution: Coastal waters and estuaries of eastern South America, from Brazil to Argentina.
Habits: Despite being included among the "river dolphins," they are estuarine and marine, not freshwater.
Food and feeding habits: Feed on fish, crustaceans, and squids (dos Santos and Haimovici, 2001).
Reproduction: Sexual maturity is reached early on for females. Gestation lasts about 11 months.
Behavior: Seen in small groups, rarely more than 12 individuals (Crespo *et al.*, 1998).
Remarks: They have and continued to be affected by coastal by-catches (Di Beneditto *et al.*, 1998).

Family LIPOTIDAE Zhuo, Qian, and Li, 1978

This family is characterized by: a long, narrow, and upturned beak, low triangular dorsal fin, and broad rounded flippers. Like other true river dolphins they have very small eyes.

Genus *Lipotes* Miller, 1918

Lipotes vexillifer Miller, 1918
Yangtse river-dolphin; baiji; pei c'hi; whitefin dolphin

Etymology: *leipo* (Gr) = left behind; *vexillum* (L) = flag, banner; *fer* (L) = carry, bear. All this means is that this dolphin was left behind (because of its geographic distribution), and that it carries a "white flag" reffering to of its white dorsal fin.
Size: 2-2.5 m, weight: 135-230 kg (adult). Females are slightly larger (Gao and Zhou, 1992).
Distinguishing features: They have between 30 and 35 pairs of uniform, conical teeth in each jaw. Forehead is very abrupt forehead. Body coloration is pale blue-gray with a paler underside.
Distribution: Lower and middle reaches of the Yangtse River, from its estuary upstream for 1,600 km as far as the gorges above Yichang (200 m above sea level).
Habits: Exclusively freshwater.
Food and feeding habits: Feed on fish.
Reproduction: Little is known. Breeding mainly in first half of year
Behavior: Usually found is small groups of up to six. They use clicks for echolocation (Akamatsu *et al.*, 1998).
Remarks: There are fewer than 100 individuals left, maybe as few as 60, which makes this the most endangered species of marine mammal. This is the result of habitat degradation (including pollution), by-catches, and underwater explosions.

Family MONODONTIDAE Gray, 1821

General characteristics: dorsal fin absent, replaced by low dorsal ridge; flippers paddle-shaped; melon prominent; beak indistinct.

Genus *Delphinapterus* Lacépède, 1804

One species.

Delphinapterus leucas (Pallas, 1776)
beluga; white whale

Etymology: *delphinos* (Gr) = dolphin; *a* (Gr) = without; *pteron* (Gr) = wing, fin; *leukos* (Gr) = white.
Size: 1.5-1.6 m (neonate); 3.9-4.9 m (adult), weight: 500-1,600 kg (adult). Males are larger than females.
Distinguishing features: They have a stout body with a well-defined neck, small head, and well-defined, rounded melon. The number of paired teeth varies between 8 and 11 in the upper

jaw and between 8 and 9 pairs in lower jaw. The ones in the upper jaw are often curved. They lack a dorsal fin. Body coloration is slate-gray to reddish-brown at birth, changing to blue-gray at two years of age, white when adult.
Distribution: Distributed discontinuously around the Arctic Ocean and adjacent seas.
Habits: Mainly coastal and estuarine, often found among pack ice.
Food and feeding habits: Feed on fish, cephalopods, crustaceans, and other invertebrates. Polar bears prey on belugas.
Reproduction: Births take place at the end of winter or beginning of spring. Gestation takes between 11 and 14 months. Weaning can last at least two years.
Behavior: They are highly social and can be seen in numbers of up to several hundreds and form aggregations in the thousands. They are highly vocal, producing a great diversity of sounds, reason by which they are called "sea canaries." They can dive for more than 20 min (Laidre *et al.*, 2002).
Remarks: Some local stocks may be depleted. They have been an important source of food for aboriginal populations for centuries (Harwood and Smith, 2002). Today they are being threatened by pollution (Outridge *et al.*, 2002).

Genus *Monodon* Linnaeus, 1758

One species.

Monodon monoceros Linnaeus, 1758
narwhal

Etymology: *mono* (Gr) = one, single; *odon* (Gr) = tooth; *keros* (Gr) = horn.
Size: 1.5-1.7 m, 80 kg (neonate); 4.2-4.7 m, 1000-1600 kg (adult).
Distinguishing features: Body rotund with small head and no beak. Males have a spiral tusk up to 3 m long. Body coloration changes drastically with age: newborns are blotchy gray, juveniles are dark with spots of white, and adults are dark purplish black with white mottling on backs and sides and with white bellies, becoming lighter with age.
Distribution: In the eastern Canadian Arctic and west Greenland.
Habits: Usually associated with pack ice and deep water; occur singly or in small to large groups.
Food and feeding habits: Feed on fish, squids, and crustaceans. Polar bears and orcas prey on them.
Reproduction: Mating takes place during late winter and spring. Gestation lasts about 15 months, so the young are born in the summer. Female reproductive cycle is between two and three years.
Behavior: They are normally seen in homogeneous groups of up to 20 that in summer aggregations result in groups of up to several hundreds. Adult males fight among themselves with their tusks and teeth for social dominance. They can dive down to 1,000 m for about 20 min.
Remarks: They have been hunted for their meat, oil, tusks, and hides.

Literature Cited

Chivers, S.J., R. G. Leduc, K. M. Robertson, N. B. Barros, and A. E. Dizon. 2005. Genetic variation of *Kogia* spp. with preliminary evidence for two species of *Kogia sima*. *Mar. Mamm. Sci.* **21**:619–634.

Dalebout, M.L., C.S. Baer, J.G. Mead, V.G. Cockcroft, T.K. Yamada. 2004. A comprehensive and validated molecular taxonomy of beaked whales, family Ziphiidae. *J. Heredity* **95**:459-473.

Dalebout, M.L.; D. Steel & C.S. Baker. 2008. Phylogeny of the beaked whale genus *Mesoplodon* (Ziphiidae: Cetacea) revealed by nuclear introns: implications for the evolution of male tusks. *Syst. Biol.* 57:857-875.

Jefferson, T.A, M.A. Webber, and R.L. Pitman. Marine Mammals of the World: A Comprehensive Guide to their Identification. Elsevier Publications. 2008.

Nowak R.M. Walker's Marine Mammals of the World. Johns Hopkins University Press, Boston. 2003.

Chapter 6

Marine Mammals of the World I: Introduction to Cetaceans Odontocetes (II)

Family DELPHINIDAE Gray, 1821

This is the largest and most diverse family of marine mammals consisting of at least 36 species. They have radiated to fill many ecological roles, occupying virtually all oceans and major seas as well as some large river systems. Although some species are cosmopolitan, all of them occupy a particular and well-defined niche. This ecological diversification and specialization is reflected into many of their morphological characteristics particular in the rostral length and width, and the number, size, and form of teeth. Except for *Grampus* they have teeth in both jaws. In all of them the teeth are conical. The dorsal fin is usually well developed. The beak is highly variable. Despite being called "small cetaceans," size varies from the Vaquita (1.2 m) to the orca (7 m) within the family.

All dolphins are carnivores. Some feed exclusively on either fish or cephalopods, while others have a more varied diet including fish, squid, crabs, shrimps and lobsters.

Genus *Cephalorhynchus* Gray, 1846

Etymology: *kephale* (Gr) = head; *rhynchos* (Gr) = nose, snout. This means that the large rostrum is very well differentiated from the rest of the skull.
This genus is made up of four species, which are essentially allopatric (the exception is a minor overlap of *C. eutropia* and *C. commersonii* in the Estrecho de Magallanes and Canal Beagle). They are all found in temperate coastal waters of the Southern Hemisphere.

Cephalorhynchus commersonii (Lacépède, 1804)
Commerson's dolphin; piebald dolphin; Jacobite

Etymology: After Philibert Commerson (1727-1773), a noted French medical doctor and botanist whose original description of the species was used by its describer Lacépède.
Size: 1.3-1.4 m, weight: 50 kg (adult).
Distinguishing features: They have between 29 and 30 pairs of small, pointed teeth in each jaw in a conical head. Their coloration is black on head and flippers with a white chevron on the throat and a white or pale-gray cape that extends up over the flanks to the neckline, black dorsal

fin and flukes. Newborns are all brown with small, stout torpedo-shaped bodies, short rounded snouts, and no melon.
Distribution: There are two populations separated by 130° of longitude. The largest one, also named as *C. c. commersonii*, is found in coastal and inland waters of Argentina, from Buenos Aires (as vagrant) to Cabo de Hornos (Falklands/Malvinas), and South Shetland Islands. The second population (of an unnamed subspecies) is much smaller in population size and is found in coastal waters of the Kerguelen Islands (Indian Ocean).
Habits: Coastal.
Food and feeding habits: They are opportunistic feeders that consume crustaceans (mostly krill), squids, and some fish species.
Reproduction: Gestation period is of one year. Most births take place between October and March (austral Spring-Summer).
Behavior: Usually seen in groups of two or three individuals, although up to 100 can congregate under special circumstances. They are fast swimmers that can ride tides and tend to leap frequently.
Remarks: Entanglements in fishing nets may threaten the South American population. They are also taken deliberately off the coast of South America, some for crab bait.

Cephalorhynchus eutropia (Gray, 1846)
Chilean dolphin; black dolphin; Eutropia dolphin

Etymology: *eu* (Gr) = true; *tropidos* (Gr) = keel. This means truly keeled, referring to the skull.
Size: 1.6 m, weight: 45 kg (adult).
Distinguishing features: 30-31 pairs of teeth in each jaw; black back, flanks, and part of belly, with three white areas extending from the white belly to the anal area, behind the flippers, and the throat; small, stout, torpedo-shaped body; short, rounded snout; no melon; low, rounded dorsal fin.
Distribution: Pacific coastal waters of southern South America from Valparaiso, Chile, south to Isla Navarino.
Habits: Coastal.
Food and feeding habits: Their diet includes small fish, squids, and crustaceans.
Reproduction: There is no information available.
Behavior: Usually in small groups of two or three or occasionally up to 12.
Remarks: They are threatened by gillnets. When incidentally or intentionally (using harpoons) captured, their meat is used as bait or for human consumption.

Cephalorhynchus heavisidii (Gray, 1828)
Heaviside's dolphin; hastate dolphin

Etymology: After Captain Haviside (the name was misspelled for the Latinized form) who sent the specimen from the Cape of Good Hope to England.
Size: 1.2-1.4 m, weight: 40 kg (adult).

Distinguishing features: 25-30 pairs of small, pointed teeth in each jaw; black back and flanks, white belly with lobes of white extending in front of the flippers, behind the flippers, and toward the tail; stout, torpedo-shaped body; short, rounded snout; no melon; low, triangular dorsal fin.
Distribution: In southwestern Africa, from northern Namibia south to Cape Point in Cape Province.
Habits: Coastal.
Food and feeding habits: They feed on coastal fish, squids, and cephalopods.
Reproduction: Little is known.
Behavior: It is always in groups of 10 or less individuals. They leap both vertically (as part of their social behavior) or at low angle when swimming at high speed. They have also been observed bowriding.
Remarks: They are incidentally captured in coastal fisheries and sometimes intentionally killed (via harpoon).

Cephalorhynchus hectori (P.-J. Van Bénéden, 1881)
Hector's dolphin; Pied dolphin, whitefronted dolphin

Etymology: After Sir James Hector (1834-1907), who collected the type specimen.
Size: 1.2-1.4 m, weight: 40 kg (adult). Females slightly larger than males.
Distinguishing features: 26-32 pairs of small teeth in each jaw; coloration gray with a black mask from the tip of the beak over the face, flippers, and dorsal fin, black tail flukes; stout, torpedo-shaped body, narrowing at tail stock; short, round stock; no melon; low, rounded dorsal fin. There are two recognizable geographic forms: South Island and North Island, with the North Island form being slightly larger, and having a reduced dark spot around the penile opening in males.
Distribution: Endemic to the main islands of New Zealand.
Habits: Coastal.
Food and feeding habits: This species feeds mostly on small fish and squids.
Reproduction: Gestation period lasts probably one year. Calves are born from November to February, i.e., spring and early Austral summer. Calving interval is usually two years.
Behavior: Usually found in small groups ranging from two to eight individuals. They usually bow ride, like to leap both vertically and in low angle, and play with floating objects.
Remarks: They are threatened by entanglement in gillnets which may have reduced their population size to less than 50% since 1970. They are protected in part of their range by a sanctuary off South Island around Banks Peninsula created in 1988. Some mortality has been reported as result of strikes by boats, while pollution also represents a threat. Large sharks prey them upon.

Genus *Steno* Gray, 1846

Steno bredanensis (G. Cuvier *in* Lesson, 1828)
rough-toothed dolphin

Etymology: *Stenos* (Gr) = narrow; *bredanensis* after Van Breda, the artist who painted the type specimen.
Size: 2.4-2.7 m, weight: 130-160 kg (adult).
Distinguishing features: Forehead sloping without crease to long slender beak; dorsal fin tall and falcate with long base; flippers large and tapered; color dark gray or purple-brown with pink or yellowish white spots on sides; belly and lips white; light scratches, circular scars common. Teeth: 20-27/20-27 each side. Rough-toothed dolphins get their name from the "wrinkled" surface of their teeth, which have many fine vertical grooves running from the gum line to the tip. It is difficult to identify this species from a boat on the basis of this characteristic, but there are several other external features that should prove helpful. Rough-toothed dolphins are dark gray to purplish black in color with pink and white spots and streaks covering their bodies. This unusual speckling led early researchers to refer to it as the "polka dot" or "calico" dolphin. Although their body size and proportion is much like bottlenose dolphins, rough-toothed dolphins can easily be distinguished by their longer and more pointed snouts that are distinctly white underneath and at the tip.
Distribution: They are found in tropical and warm temperate waters around the world including the Caribbean, the Gulf of Mexico, Mediterranean Sea, Gulf of Aden, Arabian Sea, and Hawaiian Islands.
Habits: Pelagic; generally occurs in small groups.
Food and feeding habits: They feed mostly on fish of various sizes and cephalopods. It is possible that they go after larger prey cooperatively.
Reproduction: No information is available.
Behavior: They are usually found in groups of 10-20 individuals although occasionally groups in the hundreds can be observed. Sometimes they mix with other delphinid species; mass strandings are not that uncommon. It is believed to be a deep diver.
Remarks: They are taken in some parts of the world such as Japan, western Africa, and the Caribbean.

Genus *Sousa* Gray, 1866

Etymology: It is not known where the generic name comes from.
These dolphins are largely confined to close inshore waters, tidal creeks, and estuaries in the Old World tropics and subtropics; some populations ascend the large coastal rivers.
Three species.

Sousa teuszi (Kükenthal, 1982)
Atlantic humpbacked dolphin; Teusz's dolphin

Etymology: It is not known where the specific name comes from.

Size: 2 m, weight: weight: 100 kg (adult).
Distinguishing features: 26-31 pairs of peg-like teeth in each jaw; coloration dark gray-white on back and upper flanks lightening on lower flanks to white belly, young are a uniform pale cream color that darkens with age; stout, torpedo-shaped body; long, slender beak; slight melon on forehead; small, prominent dorsal fin.
Distribution: Coasts of West Africa.
Habits: Coastal.
Food and feeding habits: They feed on small benthic fish, squids, and octopus, particularly during the raising tide.
Reproduction: Little is known. Calves are born in spring or summer.
Behavior: They are in groups of three to eight or larger if they feed opportunistically out of fishing boats discards. They do not bowride and are rather slow moving.
Remarks: Being coastal and represented in small populations, they are vulnerable to fishing nets and gear as well as to pollution and strikes by boats; they are also captured intentionally in some areas on Africa.

Sousa plumbea (G. Cuvier, 1829)
Indian humpback dolphin; plumbeous dolphin; speckled dolphin; freckled dolphin

Etymology: *plumbea* (L) = color like lead.
Size: 2 m, weight: weight: 100 kg (adult).
Distinguishing features: They have fatty humps.
Distribution: Coastal waters of the Indian Ocean including Madagascar, the Red Sea, the Arabian Sea, the Persian Gulf, and the western Bay of Bengal; vagrants have been found in the Ganges River 250 km from the sea.
Habits: Coastal wasters.
Food and feeding habits: They feed on small benthic fish, squids, and octopus, particularly during the raising tide.
Reproduction: Little is known. Calves are born in spring or summer.
Behavior: They are in groups of three to eight or larger if they feed opportunistically out of fishing boats discards. They do not bowride and are rather slow moving.
Remarks: Being coastal and represented in small populations, they are vulnerable to fishing nets and gear as well as to pollution and strikes by boats; they are also captured intentionally in some areas on Africa.

Sousa chinensis (Osbeck, 1765)
Pacific humpbacked dolphin; Chinese white dolphin; Bornean white dolphin

Etymology: *chinensis* (L) = from China
Size: 2 m, weight: 100 kg (adult).
Distinguishing features: 29-38 pairs of peg-like teeth in each jaw; coloration dark gray-white on back and upper flanks lightening on lower flanks to white belly; young are a uniform pale cream color that darkens with age; some adults develop yellow, pink, gray, or brown spots; stout, torpedo-shaped body; long, slender beak; slight melon on forehead; small, prominent dorsal fin,

rounded in adults, sickle-shaped in young individuals; dorsal hump in the middle of the back and above and below tail stocks.
Distribution: Discontinuously distributed in coastal waters of the western Pacific.
Habits: Coastal.
Food and feeding habits: They feed on small benthic fish, squids, and octopus, particularly during the rising tide.
Reproduction: Little is known. Calves are born in spring or summer.
Behavior: They make a high roll when surfacing.
Remarks: Levels of pollutants found in their tissues off Hong Kong is very high.

Genus *Sotalia* Gray, 1866

Sotalia fluviatilis (Gervais and Deville, 1853)
tucuxi or tookashee; gray river dolphin

Etymology: Sotalia is probably a coined name; *fluviatilis* (L) = from a river.
Size: 1.4-1.8 m, weight: 36-45 kg (adult).
Distinguishing features: 26-35 pairs of usually raggedly arranged teeth in each jaw; coloration medium to dark gray on back and upper flanks with brownish tinge, lighter gray, sometimes with patches of yellow-ochre on lower flanks and belly, coloration lightens with age, sometimes to creamy white; stout, torpedo-shaped body; pronounced beak; rounded forehead; small triangular dorsal fin.
Distribution: The freshwater Amazonian populations and the coastal marine populations are separable as subspecies; the population in Lago de Maracaibo, Venezuela, also differs somewhat from either. Originally, under what is today the genus *Sotalia*, up to five different species were described: *S. brasiliensis* van Bénéden, 1875 (coastal waters of eastern South America), *S. fluviatilis* (Gervais, 1853) (in the Amazon River and tributaries and in the Tocantins river), *S. guianensis* (van Bénéden, 1864) (coastal waters of the Guayanas and adjacent areas), *S. pallida* (Gervais, 1855) (in the Amazon River, its tributaries, and Tocantins river), and, *S. tucuxi* (Gray, 1856) (Amazon rivers, its tributaries, and Tocantins river). There are three proposed arrangements for this genus. 1) The genus should be divided into two species: *S. fluviatilis* (Gervais, 1853) for the river forms (i.e., *S. fluviatilis*, *S. pallida*, and *S. tucuxi*) and *S. guianensis* (van Bénéden, 1864) for the coastal form (i.e., *S. guianensis* and *S. brasiliensis*) (Rice, 1977; Borobia et al., 1991). 2) The genus is monospecific (*S. fluviatilis*) with two subspecies, *S. fluviatilis fluviatilis* (Gervais, 1853) for the river form and *S. fluviatilis guianensis* (van Bénéden, 1864) for the marine coastal one. 3) It is monospecific but with two distinct populations or stocks (river and marine) that are not differentiated at the subspecific level. The last arrangement is most accepted today (for discussion see da Silva and Best, 1994).
Habits: (see the section on distribution).
Food and feeding habits: They feed on a great variety of fish species.
Reproduction: Reproductive cycle seems to be correlated to the rainy season; gestation period at least 10 months; calves are born in Brazil in January and February (right before the beginning of the rainy season).
Behavior: They form groups of 10 to 12 individuals.

Remarks: Those that are accidentally captured are butchered and some parts are sold for either curative or ornamental purposes; pollution and dam constructions are also a threat to them.

Genus *Tursiops* Gervais, 1855

Etymology: *tursio* (L) = an animal like a dolphin.
The overall range of the genus includes tropical and temperate zones of all oceans and peripheral seas, including the Black Sea.
The two species are reproductively isolated.

Tursiops truncatus (Montagu, 1821)
bottlenose dolphin; common bottlenose dolphin

Etymology: *truncare* (L) = cut off.
Size: 1-1.3 m, 12-25 kg (neonate); 2.2-3.0 m, 140-240 kg (adult coastal form); 3.3-3.8 m, 250-650 kg (adult offshore form).
Distinguishing features: Body robust; head with distinct thick beak; dorsal fin moderately high and falcate, near midback; flippers tapering to point; body gray to black above, becoming lighter ventrally. Teeth: 20-26/18-24 each side. Their backs are medium gray, their sides are lighter gray, and their bellies are white or pink. Offshore animals are darker in color than those found inshore and sometimes appear to be less interested in swimming along with boats.
Distribution: Global distribution except for most polar waters.
Habits: Frequent bays and estuaries in southern regions. These dolphins live in coastal areas of all continents. They are found around most oceanic islands and atolls, and over shallow offshore banks and shoals, in the Gulf Stream of the northwestern Atlantic, and in the Tropical Eastern Pacific.
Food and feeding habits: They feed on a great variety of organisms, including deep-sea species, which suggests that they can perform deep dives. They also feed opportunistically on fishing boat discards. They can fish cooperatively by using their tails, even driving some fish onto mudflats.
Reproduction: Gestation lasts about one year with no marked season for delivery.
Behavior: They are usually in groups between two and fifteen; they form close associations that last for years.
Remarks: Known for their inshore habits, playfulness around vessels, and star performances at oceanaria, bottlenose dolphins are probably the most popular of all cetacean species.

Tursiops aduncus (Ehrenberg, 1833)
Indian Ocean bottlenose dolphin; Indo-Pacific bottlenose dolphin; Red Sea bottlenose dolphin; gadamu [Telugu language of southern India]

Etymology: It is not known where the specific name comes from.
Size: .84-1.12 m, 9-21 kg (neonate); 2.6 m, 230 kg (adults).
Distinguishing features: Smaller and less robust than the common bottlenose species, with a less convex melon and a slender beak. Also, gray coloration is darker on the back.

Distribution: Along the coast of eastern Africa from Cape Province north to the Red Sea, to the Persian Gulf, Arabian Sea, and Bay of Bengal, as far as Taiwan, thence southeast to northern Australia.
Habits: Mostly coastal.
Food and feeding habits: Opportunistic on fish and cephalopods.
Reproduction: Gestation is about one year; calving takes place in late spring and summer.
Behavior: Usually found in groups of five to fifteen individuals, but groups of hundreds have been recorded.
Remarks: Being coastal, it has been affected by by-catching, intentional killing, and pollution. This species is often preyed upon by sharks.

Genus *Stenella* Gray, 1866

Etymology: *Stenos* (Gr) = narrow.
Dolphins of the genus *Stenella* have long slender beaks, many small teeth, and various patterns of stripes and spots. They tend to prefer deeper, clearer off-shore waters, mainly in tropical and subtropical parts of the world. Can swim at speeds of 22-28 km/h; often ride bow waves. There is great variation among stocks, making identification difficult.
The phylogeny of this group has yet to be settled. It is possible that this is a polyphyletic genus. Five species.

Stenella attenuata (Gray 1846)
pantropical spotted dolphin

Etymology: *attenuata* (L) = lessen.
Size: 0.8-1.0 m (neonate); 1.4 m (weaning); 1.6-2.6 m, 90-120 kg (adult).
Distinguishing features: Beak long and sharply defined; dorsal fin tall and curved; flippers pointed; young are unspotted, dark gray above and light gray below; darker spots appear on belly, enlarging and merging with age; lighter spots appear on dorsal cape and sides; peduncle dark above, light below; degree of spotting and details of flipper and eye stripes highly variable among stocks; approx. 80 vertebrae. Teeth: 35-48/34-47 each side. Spotted dolphins are smaller than bottlenose or rough-toothed dolphins, measuring between six and seven feet in length, and weighing about 240 pounds with males being larger than females. Their coloration is dark gray on the back and lighter gray below, with a characteristic dark "cape" extending from the forehead to the dorsal fin. Spotting, if present, consists of light spots on their darker areas or, dark spots on their lighter areas, and is more prevalent in older individuals than in juveniles. This species can also be identified by the slender white-tipped snouts they possess.
Distribution: Tropical and warm temperate waters around the world.
Habits: Pelagic stocks often occur in schools of more than 1000, coastal populations in smaller herds (<100).
Food and feeding habits: They prey upon fish and squid which inhabit the surface/mid-water regions.
Reproduction: Gestation is 11 months with calving being born year round. Calving interval is 2-3 years.

Behavior: Spotted dolphins are extremely social creatures and form herds of a few dozen to more than a thousand.
Remarks: This is one of the most abundant dolphin species in the world The species varies geographically in cranial and postcranial measurements, and in body size and coloration. As a consequence of that three subspecies have been proposed:
S. a. subspecies A. Eastern tropical Pacific from about 145 o W eastward to the immediate offshore waters between Baja California Sur and Colombia ("Eastern Pacific offshore spotted porpoise").
S. a. subspecies B. Inshore waters around the Hawaiian islands ("Hawaiian spotted dolphin").
S. a. *graffmani* (Lönnberg, 1934). Inshore waters within about 25 km from land, between the Golfo de California and Colombia ("Eastern Pacific coastal spotted porpoise/dolphin").

Stenella frontalis (G. Cuvier, 1829)
Atlantic spotted dolphin; bridled dolphin

Etymology: *frontalis* (L) = at the front.
Size: 0.8-1.2 m (neonate); 1.4 m (weaning); 2.0-2.3 m, 100-140 kg (adult).
Distinguishing features: Similar to above, but heavier-bodied; ventral margin of cape obscured by pale blaze extending along sides from head to below dorsal fin; ventral background white rather than gray; adults become heavily spotted, obscuring background pattern; peduncle not divided into upper dark and lower light halves; flipper stripe demarcated above by narrow light line; approx. 70 vertebrae. Teeth: 32-42/30-40 each side.
Distribution: In tropical and warm temperate waters on both sides of the Atlantic.
Habits: Generally pelagic; occur in small groups to schools of several hundred.
Food and feeding habits: Diet includes a variety of epi- and meso-pelagic fishes and squids, with regional differences in the diet.
Reproduction: The gestation period lasts 12 months and calves are born in offshore waters. These dolphins mate and calve in summer.
Behavior: Atlantic spotted dolphins may be seen in groups of up to 50 animals, but smaller groups of six to 10 are more common. These dolphins make a variety of sounds used in echolocation and communication. Sounds are described as loud whistles, chirps, low intensity click trains, squawks, barks, growls, and cracks.
Remarks: There is marked regional variation in the size and shape of the skull, and in adult body size. This dolphin was previously known as *Stenella plagiodon.*

Stenella longirostris (Gray, 1828)
spinner dolphins, longsnouted spinner dolphin

Etymology: *longus* (L) = long; *rostrum* (L) = beak, snout.
Size: 0.7-0.8 m (neonate); 1.8-2.2 m, 75-95 kg (adult).
Distinguishing features: Body slender; head with long narrow beak; dorsal fin triangular to falcate; body dark gray dorsally, lighter on sides, white on belly; beak dark on top, white below, with black tip and black lips; black stripe from flipper to eye. Teeth: 46-65/46-65 each side. Spinner dolphins are the smallest of Hawaii's common dolphins. They are generally between five

and six feet in length and weigh 130 to 200 pounds. Hawaii has its own subspecies that is easy to recognize by its distinctive "three-tone" color pattern which consists of a sharply defined dark gray "cape" on their backs, a stripe of lighter gray on their sides and a white or pink belly.
Distribution: Geographical variation in body configuration and color pattern in more pronounced in spinner dolphins than in any other species of cetaceans. Thee subspecies have been described:

1. *S. l. longirostris* (Gray, 1828). Mainly around oceanic islands in the tropical Atlantic, Indian, and western and central Pacific east.
2. *S. l. orientalis*. Perrin, 1990. Pelagic waters of the Tropical Pacific east ("eastern spinner dolphin/porpoise").
3. *S. l. centroamericana* Perrin, 1990. Coastal waters over the continental shelf from the Gulf of Tehuantepec in southern Mexico southeast to Costa Rica ("Costa Rican spinner porpoise" or "Central American spinner dolphin").

Habits: Pelagic and coastal; daytime in shallow bays; form large herds.
Food and feeding habits: They prey on midwater fish and squid, and are different from other dolphins in that they feed by night.
Reproduction: Their period of gestation is 10-11 months. Females give birth to a single calf at 2-3 year intervals. Calving usually occurs in early summer but can occur in any season.
Behavior: This species gets its common name from its spectacular habit of leaping high into the air and spinning several times on their tails before falling back into the water. Researchers are not sure why the dolphins spin, but most people who have had the opportunity to watch the dolphins don't seem to mind, and find it a real treat.
Remarks: They are often targeted in the purse-seine and yellowfin tuna fisheries of the eastern Pacific Ocean. In other areas many of these dolphins are accidentally killed in gillnets, and also taken in harpoon fisheries. Some individuals have been kept successfully in captivity for at least 10 years.

Stenella clymene (Gray, 1850)
Clymene dolphin; shortsnouted spinner dolphin

Etymology: Clymene (Gr) = daughter of Oceanus and Tethys, mother of Phaetus by Apollo.
Size: 1.8-2.0 m, 75 kg (adult).
Distinguishing features: Similar to spinner, but beak short, caudal peduncle moderately keeled, and coloration pattern more complex, particularly on head (dark band across beak and along top of beak to melon; light band continues over melon to blowhole); black on back not extending to tail stock; white stripe from eye to flipper and darker stripe running forward along flanks from anus. Teeth: 43-58/43-58 each side.
Distribution: Tropical, Subtropical Atlantic.
Habits: Pelagic in small to large groups.
Food and feeding habits: They prey on mid-water fish and cephalopods.
Reproduction: Little is known.
Behavior: They usually form groups of between one to ten animals, but one mass strand of 50 has been recorded. Sometimes they associate with both spinner and common dolphins, but are not as dramatically acrobatic as the former.
Remarks: They have been harpooned in the Caribbean.

Stenella coeruleoalba (Meyen, 1833)
striped dolphin; Euphrosyne dolphin; blue dolphin; blue-white dolphin; Meyen's dolphin

Etymology: *caeruleus* (L) = sky blue; *alba* (L) = white.
Size: 1.0 m (neonate); 1.7 m (weaning); 2.2-2.6 m, 100-130 kg (adult).
Distinguishing features: Body slender; beak long and sharply defined; color pattern distinct with dark back, lighter gray sides, white to gray belly and throat, and black stripes from eye to anus and eye to flipper; tall, curved dorsal fin; fin, flukes and flippers dark. Teeth: 43-50/43-50 each side.
Distribution: Worldwide in tropical and temperate waters.
Habits: Pelagic; form herds up to several hundred.
Food and feeding habits: This species preys mid-water fish and squid.
Reproduction: Like in other areas of the world, males and females reach the sexual maturity at the age of 9 years old. The gestation lasts 12 months, while the births are concentrated in the summer period. The interval between deliveries varies one from 1.5 to 3 years; its longevity is about 30 years.
Behavior: Groups range from a few animals to a few thousand, but most usually between 100 and 500. Within each group there are three segregations: non-mating adults, mating adults and juveniles. They are very active, regularly bowriding and leaping from the water.
Remarks: Stripped dolphins show only moderate geographical variation in skeletal morphometrics, and little if any geographical variation in pigmentation pattern. They were taken in drive fisheries in the western Pacific in numbers of up to 14,000 per year between 1950 and 1969. By the 1980s, these numbers had fallen to between 2,000 and 4,000. Animals in the eastern Atlantic are harpooned from fishing boats to provide the crew with meat. Some individuals have been held in captivity, but have not successfully trained.

Genus *Delphinus* Linnaeus, 1758

Etymology: *Delphinus* (L) = dolphin, porpoise.
The three species have a wide, but disjunct, distribution in tropical and warm temperate waters; their ranges are mostly parapetic, with some local marginal overlap.
Three species.

Delphinus delphis Linnaeus, 1758
short-beaked common dolphin, or saddleback, dolphin; offshore common, or saddleback; dolphin; whitebellly dolphin

Etymology: *delphis* (Gr) = dolphin.
Size: 1.7-2.4 m, weight: 75-85 kg (adult), males slightly larger than females.
Distinguishing features: 40-55 pairs of small, sharp pointed teeth in each jaw; coloration black or brownish-black on back and upper flanks, creamy white to white chest and belly, tan or yellowish-tan hourglass pattern on flanks, becoming gray behind dorsal fin, black stripe from eye

to middle of lower jaw and from eye to base of beak; dorsal fin black or white with a black border and sickle-shaped; slender, torpedo-shaped body; long, slender beak. .
Distribution: Widely but discontinuously distributed in warm temperate and tropical waters of the Atlantic, Pacific, and probably Indian oceans. Its total distribution is uncertain due to taxonomic confusion. The population from the Black Sea is separable from those in the Mediterranean and the eastern North Atlantic and has been described as an endemic subspecies: *D. d. ponticus* Barabash, 1935. In the northeastern Pacific, body length and cranial features can distinguish three populations separated by latitude.
Habits: Pelagic.
Food and feeding habits: They prey on schooling fish (e.g. herring, pilchards) and squid. They have been known to adopt co-operative techniques when hunting (rather like the orca) and have also been observed catching fish in mid-air.
Reproduction: Gestation lasts between 10 and 11 months. Breeding appears to have seasonal peaks in spring and fall. Sexual maturity is reached at approximately 3 years of age, but varies greatly among populations.
Behavior: They are highly social and have been found in groups of up to 2,000 animals, although groups of 10-500 are more usual. They are very active and exuberate, displaying bowriding, breaching, flipper-slapping, and lobtailing. Usually they cannot see well when porpoising for the abundant froth they produce since they leap as a coordinated whole. They are also highly vocal.
Remarks: They have been intentionally captured by fisheries in Japan, South America, and the Azores. Accidental catches in fishing gear take place in the eastern tropical Pacific, the Mediterranean, Europe, China, Sri Lanka, South Africa, West Africa and New Zealand.

Delphinus capensis Gray, 1828
long-beaked common, or saddleback, **dolphin**; neritic common, or saddleback, dolphin; Cape dolphin; Baird's dolphin

Etymology: *capensis* (L) = from the cape.
Size: They range in size from 1.7m to 2.6m, and weigh between 70-135kg.
Distinguishing features: They have a slender with a falcate dorsal fin. Melon is rather flat.
Distribution: Disjunct populations are found in warm temperate and tropical coastal waters around the world.
Habits: Nearshore.
Food and feeding habits: They feed on small schooling fish and squids. Cooperative feeding tactics have been observed with most feeding done in relatively shallow waters.
Reproduction: Reproduction does not seem to be strongly seasonal.
Behavior: School size ranges from 10 up to several thousand individuals with an average of approximately 200. Species highly vocal.
Remarks: They have been intentionally killed in Peru and Venezuela to use their meat as shark bait.

Delphinus tropicalis van Bree, 1971
Arabian common, or saddleback, dolphin; Malabar common, or saddleback, dolphin

Etymology: *tropicalis* (L) = from the Tropics.
Size: They range in size from 1.7m to 2.6m, and weigh between 70-135kg.
Distribution: Coastal waters of the Arabian Sea, from the Golf of Aden and the Persian Gulf, to the Malabar Coast of India, and South China Sea.
Food and feeding habits: Little in known.
Reproduction: Little in known.
Behavior: Little in known.
Remarks: This species was only recently described and has been little studied.

Genus *Lagenodelphis* Fraser, 1956

The one species in this genus was not recognized until 1956, when it was described from a single skull which had been picked up on a beach in Sarawak in 1895. It remained unknown to science until 1971, when the species was "rediscovered." Once its external features became known, it turned out that tuna fishermen in the eastern tropical Pacific were already familiar with it.

Lagenodelphis hosei Fraser, 1956
Fraser's dolphin shortsnouted whitebelly dolphin; Hose's dolphin; Sarawak dolphin;

Etymology: *Lagenus* (Gr) = bottle; *delphis* (Gr) = dolphin; *hosei* (L) = after C. Hose, the Sarawak resident who collected the type specimen in 1895.
Size: 1 m (neonate); 2.4 m (adult).
Distinguishing features: Body heavy; beak short; flippers small; dorsal fin triangular, small and pointed; tail stock with dorsal and ventral keels; back blue-gray, belly white; adults with dark stripe from rostrum to anus. Teeth: 40-44/39-44 each side.
Distribution: Pantropical.
Habits: Pelagic; occur in small groups to large schools.
Food and feeding habits: They prey on a wide variety of fish, squid and crustaceans. It is thought they hunt at night.
Reproduction: Not much information available.
Behavior: This species is normally found in herds of at least one hundred, often mixing up with other cetaceans. Although active at the surface, they do not appear playful.
Remarks: They have been intentionally taken in the Caribbean, Indonesia, and Sri Lanka. Individuals in captivity have done very badly.

Genus *Lagenorhynchus* Gray, 1846

Etymology: *Lagenos* (Gr) = botlle; *rhynchus* (Gr) = beak, snout.
Cold-water dolphins that share short but trenchant beaks, strongly falcate dorsal fins, and complex pigmentation patterns. This is probably a paraphyletic genus.
Six species.

Lagenorhynchus albirostris (Gray, 1846)
white-beaked dolphin

Etymology: *albi* (L) = white; *rostris* (L) = face.
Size: 1.1-1.3 m (neonate); 3.0-3.2 m, 275 kg (adult).
Distinguishing features: Large size; dorsal fin tall and falcate; flippers slightly curved; beak often white or light gray; body dark on back and sides, light gray to white below, with white markings on back and sides; dorsal fin black; dark color of flippers continuous with that of body. Teeth: 22-28/22-28 each side.
Distribution: Immediate offshore waters of the North Atlantic.
Habits: Pelagic; occur in small groups or large schools up to 1500 individuals.
Food and feeding habits: This species takes crustaceans, fish, and squid; often seen feeding with fin whales.
Reproduction: Male white-beaked dolphins become sexually mature at an average length of about 2.6 m and females at 2.59 m. Mating is thought to occur in the warmer months and the calves are probably born in the summer between June and September.
Behavior: It may bow-ride, especially in front of large, fast-moving vessels, but usually loses interest quickly. Sometimes display acrobatic behavior, especially when feeding, and will breach, normally falling onto its side or back. They are powerful swimmers and when swimming at speed, may lift its whole body out of water briefly as it rises to breathe. They have been seen with fin whales and killer whales, and may mix with other species.
Remarks: They have been and are being taken in Norway, the Faröe Islands, Greenland and Labrador. A small number are accidentally trapped in fishing gear every year.

Lagenorhynchus acutus (Gray, 1828)
Atlantic white-sided dolphin

Etymology: *acutus* (L) = sharp, pointed.
Size: 1.0-1.3 m (neonate); 2.4-2.7 m, 200-240 kg (adult).
Distinguishing features: Beak short; dorsal fin tall and sharply falcate; flippers strongly curved and pointed; tail stock with prominent dorsal and ventral keels; sides of body with distinct elongated white patch followed by one of tan or yellow; flippers, back, and short beak black, dorsal fin black and gray, flank lighter gray, belly white; dark stripe from flipper to dark part of body. Teeth: 30-40/30-40 each side.
Distribution: This deepwater species is found across the North Atlantic.
Habits: Pelagic but may feed in deep water close to shore; may occur singly, in small groups, or in schools of hundreds.
Food and feeding habits: They tend to prey upon small schooling fish and squid.
Reproduction: The gestation period is about 10 months long. The calves are usually born in June and July. There is usually one young per a birth, averaging about 25 kg and 107-122 cm in size when born. The young are usually weaned at 18 months. The calving interval is 2-3 years. Males become sexually mature between 2.1 and 2.4 m in length. Females become sexually mature between 1.94 and 2.22 m in length, which probably corresponds to 12 years of age (Klinowska, 1991). The maximum longevity of males is probably 22 years, while female longevity is 27 years.

Behavior: This species is very acrobatic and gregarious. Although small groups are often encountered, herds of several hundred are observed regularly, and they tend to ride the bow waves of larger species (in particular, the fin and humpback whales). They regularly mass strand, particularly along the New England coastline.
Remarks: Norway once hunted Atlantic white-sided dolphins along their south-western coast. At least one thousand animals were taken on two separate occasions in the 1700s. Fishers in Greenland also occasionally hunt this species. The Faröe Islands take hundreds ever year, driving schools (often of 600 or so individuals) ashore in much the same manner as when they cull the larger long-finned pilot whales. A small number are caught in fishing gear every year. Molecular data suggest that this species should be in a separate genus from *Langenorhynchus*.

Lagenorhynchus obliquidens Gill, 1865
Pacific whitesided dolphin; Pacific striped dolphin

Etymology: *obliquus* (L) =sideways; *dens* (L) = teeth.
Size: 0.8-1.0 m (neonate); 2.2-2.3 m, 150 kg (adult).
Distinguishing features: Head short with short beak; flippers long and tapered; dorsal fin at about midback, tall, sharply hooked, and bicolor; color pattern distinct, with black back, elongated light gray area above flipper and light stripe along side, with white belly; beak dark with stripe from mouth to flipper. Teeth: 23-32/24-31 each side.
Distribution: In cold temperate waters of the North Pacific.
Habits: Generally pelagic; nearshore in deep water.
Food and feeding habits: They feed on small schooling fish and squids.
Reproduction: This species' sexual maturity age remains unknown, but may be between three and sixteen years old. Gestation period lasts between nine and twelve months, with an average of 10 months. Female dolphins usually give birth to a single calf once two or three years.
Behavior: They form large schools. They are highly acrobatic and playful. Larger herds feed cooperatively.
Remarks: Japan has taken and continues to take this species for centuries by coastal harpooning fishery, sometimes in the thousands per year. Apart from high numbers that are accidentally caught in fishing gear, these dolphins are also popular as captive performers in Canada, America, and Japan. Between 1966 and 1985, at least 312 individuals were taken for this purpose; fewer than one hundred survived their first year in captivity. Predation by killer whales reported.

Lagenorhynchus obscurus (Gray, 1828)
dusky dolphin

Etymology: *obscurus* (L) = dark.
Size: 1.8-2 m, weight: 115 kg (adult).
Distinguishing features: 24-36 pairs of small, pointed teeth in each jaw; dark gray-black back, large gray area on lower flanks extending from the base of the beak or the eye back to the anus, light gray or white areas on the upper flanks which extend back to the tail stock, white belly; torpedo-shaped body; rounded snout with short black beak; centrally placed, sickle-shaped dorsal fin.

Distribution: Populations in the South American, African, and New Zealand sectors of the range are sufficiently distinct to be regarded as subspecies:
1. *L. o. fitzroyi* (Waterhouse, 1838). Coastal waters of South America from Peru to Falkland/Malvinas Islands; animals of undetermined subspecies occur around Gough Island.
2. *L. o.* obscurus. Coastal waters of southern Africa.
3. *L. o.* subspecies. East coast of New Zealand.
Habits: Mainly coastal.
Food and feeding habits: They prey on fish and squid.
Reproduction: Mating takes place in late winter or early spring. Gestation ranges between 11 and 13 months.
Behavior: This species is a good bowrider that seems to enjoy contract with boats and people. Like many other oceanic dolphins, it breaches in three main ways: performs arc-shaped leaps with clean, headfirst entries, which may be used to look for feeding seabirds; slams body against surface, then lobtails, to signal location of fish to other dolphins or to herd fish into center of school; and high somersaults with twists and turns, which are most common after feeding. It my leap dozens of times in a row, and often when one animal starts, others follow suit.
Remarks: It is exploited in the hundreds every year in Peru, their meat to be sold on the food market. Accidental catches in fishing tackle have been reported in New Zealand. When held in captivity they have survived with low to moderate success.

Lagenorhynchus australis (Peale, 1848)
Peale's dolphin; blackchinned dolphin

Etymology: australis (L) = southern.
Size: 2-2.2 m, weight: 115 kg (adult).
Distinguishing features: 30 pairs of small, pointed teeth in each jaw; dark gray-black back, light gray area on flanks from behind the eye to the anus with a white band above it from behind the dorsal fin to the tail stock, black patch on lower lip, chin, and throat; torpedo-shaped body; short black beak on rounded snout; centrally placed, sickle-shaped dorsal fin.
Distribution: Coastal waters of southern South America including the Falkland/Malvinas Islands.
Habits: Coastal.
Food and feeding habits: Little is known except that octopi have been found in the stomach contents of some individuals.
Reproduction: Almost nothing is known, except that claves have been spotted from spring through autumn.
Behavior: They are seen in groups of between 5-30 individuals. They like to bowride, often porpoising out of the water with long, low-angled leaps. They often speed ahead and leap high into the air, only to fall back into the sea with a loud slapping noise. **Remarks:** They are accidentally drowned in fishing nets and harpooned around the Tierra del Fuego area for use as crab bait. There is concern that the number harpooned may be high enough in such a small range to pose a population problem.

Lagenorhynchus cruciger (Quoy and Gaimard, 1824)
hourglass dolphin

Etymology: *crucis* (L) = cross; *gero* (L) bear, carry.
Size: 1.6-1.8 m, weight: 100 kg (adult).
Distinguishing features: 26-34 pairs of small, pointed teeth in the upper jaw and 27-37 in the lower one; coloration black over back with two white areas forward of dorsal fin on flanks and behind the dorsal fin extending back to the tail stock, white belly; torpedo-shaped body; rounded snout with short, well defined black beak; centrally placed, sickle-shaped dorsal fin.
Distribution: Probably circumpolar in Antarctic and Subantarctic waters, south of the Subtropical Convergence.
Habits: Pelagic.
Food and feeding habits: Prey on small fish.
Reproduction: Calves have been observed in January and February.
Behavior: They are found in groups of one to six animals, sometimes up to 40 individuals. They associate with fin whales and southern bottlenose whales, and are highly active. They are well-known for bowriding, and when porpoising they create a highly visible spray. They are commonly seen traveling through a series of low-angled leaps.
Remarks: Their conservation status is unknown. But given that inhabits one of the most remote marine regions known this species is not being threatened by human activities.

Genus *Lissodelphis* Gloger, 1841

Etymology: *Lisso* (Gr) = smooth; *delphis* (Gr) = dolphin.
The two allopatric species are differentiated by pigmentation patterns. The vernacular name refers to the lack of a dorsal fin in both *Lissodelphis* and in right whales.

Lissodelphis borealis Peale, 1848
northern right-whale dolphin

Etymology: *borealis* (L) = northern.
Size: 0.8-1.0 m (neonate); 2.2-2.3 m (adult female); 2.6-3.0 m (adult male); 90 kg (average adult).
Distinguishing features: Body slender and smooth; no dorsal fin; slender beak demarcated by faint crease; long straight mouthline; body mainly black, some white on the ventral surface and near tip of lower jaw. Teeth: 37-49/37-49 each side.
Distribution: Temperate and subarctic waters of the North Pacific.
Habits: Generally pelagic; nearshore in deep water; forms large (>100) herds.
Food and feeding habits: They prey on small fish and squids.
Reproduction: Their gestation period is a little more than a year with an average calving interval of two years. Some females have been observed to be pregnant at the same time that they are lactating.
Behavior: They form groups as small of five and as large 3,000 individuals, although the average groups size is 200. They also associate with Risso's dolphins and Pacific white-sided dolphins. They travel mainly by porpoising, whipping low over the surface, and like to bowride

boats up to speeds of 35 km/h. They do not appear as vocal as other dolphin species, and are not known to mass strand.
Remarks: Many are caught in Japanese, Korean and Taiwanese fishing gear every year. The populations on the western U.S. coast are considered unthreatened by humans.

Lissodelphis peronii (Lacépède, 1804)
southern right-whale dolphin

Etymology: *peronii* (L) = after F. Peron, the French naturalist that first observed this dolphin off Tasmania.
Size: 1.8-2.3 m, weight: 60 kg (adult).
Distinguishing features: 44-49 pairs of small, pointed teeth in each jaw; black back and flanks, white belly, lower flanks, flippers, beak and forehead forward of the eyes; small, very slender, torpedo-shaped body; rounded snout with short, distinct beak; no dorsal fin.
Distribution: Circumpolar in the Subantarctic Zone.
Habits: Generally pelagic; nearshore in deep water.
Food and feeding habits: They prey on lanternfish and squids.
Reproduction: Their gestation period is a little more than a year with an average calving interval of two years.
Behavior: This species can be observed in groups of two up to 1,000 individuals, and are known to associate with other small cetaceans. They travel by porpoising, whipping low over the surface, or by slow rolling with little surface disturbance. They like to bowride, leap, and flipper-slap, and have been known to strand.
Remarks: Small numbers were taken for meat by nineteenth century whalers, and some are still caught in South America.

Genus *Grampus* Gray, 1828

One species.

Grampus griseus (G. Cuvier, 1812)
grampus, Risso's dolphin; gray grampus; whiteheaded grampus, mottled grampus

Etymology: *Grandis* (L) = great; *piscis* (L) = fish, which combined means “kind of a whale”; *griseus* (L) = gray.
Size: 1.2-1.6 m (neonate); 3-4 m, 300-600 kg (adult).
Distinguishing features: Body heavy anteriorly, tapering to narrow tail stock; head blunt with no distinct beak, but with unique vertical crease in melon; dorsal fin tall and pointed, near midback; flippers long and pointed; color light to dark gray with numerous white scars, becoming lighter with age; flippers, flukes and dorsal fin darker; no teeth in upper jaw. Teeth: 0/3-8 each side.
Distribution: Worldwide in temperate and tropical waters.
Habits: Pelagic; occur singly or in small to large groups.

Food and feeding habits: They prey mostly on squid and octopi as well as some fish. Feeding seems to occur at night.
Reproduction: Their reproductive habits are poorly known. They probably calve in winter. These dolphins may live as long as 24 years. A well-known Risso's dolphin called "Pelorus Jack" was sighted in a New Zealand harbor for over 20 years.
Behavior: They are usually found in groups between three and fifty individuals, although groups of up to 4,000 have been observed. They have been observed mixing with other dolphin species. They often surface leisurely side-by-side in a form of "chorus line" but when moving quickly are aerial acrobats and often breach, bowride and "porpoise". Risso's dolphins create a series of varying sounds including signature whistles. Mass and individual strandings are not uncommon.
Remarks: Both Japan and Peru have taken this species in drive fisheries, and small numbers are also taken in the Caribbean, the Black Sea, and the Indo-Pacific Islands. This is one of the major species, which Sri Lanka catches in its harpoon fisheries and gillnets. A few individuals caught alive and placed in captivity have not adapted well. In 1933 in Ireland, three strange dolphins were beached; it is believed that they were hybrids between Risso's dolphin and the bottlenose. This seems certain as now captive dolphins of the two species have created a hybrid calf.

Genus *Peponocephala* Nishiwaki and Norris, 1966

One species.

Peponocephala electra (Gray, 1846)
melon-headed whale; many-toothed blackfish; little blackfish; Electra dolphin

Etymology: According to its authors, the name *Peponocephala* is derived from the Latin *pepo*, which they say means "melon" - hence the English name; however, *pepo* (genitive *peponis*) actually refers to the pumpkin (*Cucurbita pepo*) whereas melo (genitive *melonis*) is the Latin word for the melon (*Cucumis melo*). Thus "Pumpkinhead whale" would be a more correct Anglicization of the generic name; electra (Gr) = *nymph* in Greek mythology.
Size: 2.7 m (adult).
Distinguishing features: Body slender; head triangular from above; beak indistinct; mouthline long and straight; flippers with convex anterior margin, pointed at tips; dorsal fin falcate, slender, and sharply pointed; color black above with anchor-shaped gray patch on throat, and white areas on abdomen and lips. Teeth: 21-25/21-25 each side.
Distribution: Pantropical.
Habits: Pelagic; occur in small groups to large herds.
Food and feeding habits: They prey mainly upon squid and small fish.
Reproduction: Little is known about their reproductive habits. Calving appears to peak in early spring in the low latitudes of both hemispheres. The length of gestation is not known, but is probably about 12 months.
Behavior: The typical groups are between 100 and 500 individuals, and occasionally can reach as many as 2,000. They are often associated with dolphins. Melon-headed whales are very active species that can swim very fast. Migration is unknown, and strandings occur year round in tropical and subtropical waters.

Remarks: Japanese fishermen have taken a few individuals in the past decades, and many are killed from entrapments in fishing gear. One or two have been taken into captivity, but not for longer than 17 months.

Genus *Feresa* Gray, 1870

One species.

Feresa attenuata Gray, 1874
pygmy killer whale

Etymology: *Feres* is a vernacular name in French for dolphin; *attenuatus* (L) = thin, diminished.
Size: 2.4-2.7 m (adult).
Distinguishing features: Body slender with rounded head, no beak, and straight mouthline; dorsal fin falcate, placed at midback; flippers with convex anterior margin, rounded at tip; color dark on back, lighter on sides and belly; anchor-shaped light area between flippers, white patches on abdomen, lips and chin. Teeth: 8-11/11-13 each side.
Distribution: Pantropical.
Habits: Pelagic; occur in small groups.
Food and feeding habits: They prey mainly upon squid and large fish such as tuna and dolphinfish, but have been known to attack groups of small cetaceans.
Reproduction: Nothing seems to be known regarding reproduction and development in this species.
Behavior: They are usually observed in groups of about 25 although groups of several hundred have been recorded. They are acrobatic at the surface, leaping, spy hopping and tail slapping, this species will occasionally bowride. This is an aggressive species, often eliciting fear from other small cetaceans; if kept in captivity, it will often kill all others in the tank.
Remarks: A few have been taken by Japanese fishermen and in other small local catches. Many are killed from entrapments in fishing gear every year. Between 300-800 are caught annually off Sri Lanka. One or two have been taken into captivity, but without success.

Genus *Pseudorca* Reinhardt, 1862

One species.

Pseudorca crassidens (Owen, 1846)
false killer whale

Etymology: *Pseudos* (Gr) =false, semi; *orca* (L) = kind of whale; *crassus* (L) = thick; *dens* (Gr) = tooth
Size: 1.7-2.0 m, 80 kg (neonate); 5.0 m (adult female); 5.5-6.0 m, 1360 kg (adult male).
Distinguishing features: Body long and slender; head rounded and tapering with no beak and long straight mouthline; flippers long, narrow and pointed, with notable hump at middle of

leading edge; dorsal fin near midbody, moderately high and falcate; color black except for variably distinct gray anchor-shaped area between flippers. Teeth: 8-11/8-11 each side.
Distribution: Worldwide in tropical and temperate waters.
Habits: Pelagic; form large schools.
Food and feeding habits: They prey mainly upon squid and large fish as well as on small cetaceans. They are known for taking bait from fishermen's lines.
Reproduction: Their reproductive habits are poorly known. Breeding probably occurs year round and the gestation period lasts approximately 15 months.
Behavior: The typical group size is between 10 and 50 individuals, although groups in the hundreds have been reported. They are highly social and fast swimmers. They have been seen leaping clear of the water while swimming, bow-riding, and chasing faster vessels. It has adapted well to captivity and is easily trained. Mass strandings are common; in one case, over 800 individuals were found ashore.
Remarks: The false killer whale was assumed to be an extinct species when it was first discovered as a subfossil in the great fen of Lincolnshire, England, in 1846. Not until 1861, when a school stranded at Kiel, Germany, was it realized that it was a presently living species. Hundreds of them were recently slaughtered by Japanese fishermen who drove them ashore, not for food, but because their yields of yellowtail have been decreasing and they blame this on cetaceans in the area. Accidental kills of this species (mainly by entrapment in fishing gear) are also common.

Genus *Orcinus* Fitzinger, 1860

One species.

Orcinus orca (Linnaeus, 1758)
killer whale, orca

Etymology: *Orcinus* (L) = Latin for orca or *Orcynus* (L) = kind of tunny; *orca* (Gr) = kind of a whale.
Size: 2.1-2.5 m, 180 kg (neonate); 4 m (weaning); 7-8 m, 4000 kg (adult female); 8-9.5 m, 8000 kg (adult male).
Distinguishing features: Body heavy with blunt, indistinct beak; dorsal fin at midback, high (to 1.8 m) and triangular in males, smaller and more curved in females; flippers broad and rounded; striking black and white coloration with oval white patch above and behind eye; teeth large, squarish in cross-section. Teeth: 8-11/8-11 each side.
Distribution: Throughout all oceans and contiguous seas, from equatorial regions to the polar pack-ice zones, but most numerous in coastal waters and cooler regions where productivity is high.
Habits: Frequent inshore visitors; occur commonly in pods of 10-40; strong social organization.
Food and feeding habits: Orcas are top predators with the most varied diet of all cetaceans, taking preys of all shapes and sizes, including several species of seals, the dugong, turtles, fish, squid, sea birds, other dolphins, and even whales. They have developed coordinated hunting strategies, working as a team and not as individual units within the pod, just like a pack of wolves. In some areas one orca will hunt but shares the catch with the other members of its pod.

Hunting normally occurs during dives of less than 100 m, with members of the pod cooperating in keeping the prey at or near the surface.
Reproduction: The reproductive habits of these whales are poorly known. The males may mate with more than one female and mating may occur throughout the year, although most calves seem to appear in autumn or winter in shallow waters. Their period of gestation is about 12 months.
Behavior: The typical group size is between three and 25 individuals, although groups of up to 50 are not uncommon. In some areas (e.g., western Canada) there are two types of pods: residents and transients. Transients form smaller pods of between one and seven individuals, roaming over a larger area and feeding mainly on mammals. They vocalize less frequently, often change direction abruptly when swimming, and remain underwater for up to 15 minutes at a time. Residents, on the other hand, form larger pods, have smaller home ranges, and feed mainly on fish. They vocalize frequently, keep to predictable routes, and rarely stay underwater for more than four minutes. Both transients and residents are acrobatic at the water's surface: breaches, spy hops, and tail slaps are common, and there is little aggression within a pod. Mass strandings are rare, but have been known to occur. Studies have also shown that there are differences in vocalizations between pods. It seems each pod (or communities of pod, such as superpods where more than two pods congregate) has its own dialect, and this changes from pod to pod. The degree of difference between pods' dialects reflects the degree of social interaction between the pods; for instance, if two pods' vocalizations are very similar, then they interact with each other, maybe coming together as a "superpod."
Remarks: Orcas have been captured since the times of Yankee whalers although they were never very important as a source of oil. Norway, Japan and Russia took a combined total of 5,537 Orcas between 1938 and 1981, with 916 of those killed in the 1979-80 whaling season. Greenland takes 2-3 every year. Some are captured live for public display. Some calves have been captive-bred, and the annual survival rate of Orcas in Canada and the USA is 91%. Highlighted in the film *Free Willy*, captive Orcas (such as Lolita, Corky, and Keiko) are currently at the center of a major campaign movement around the world, which aims to rehabilitate the animals and release them back into the wild. Since Orcas do prey on fish such as herring and salmon, there is often competition between the cetaceans and fishers for the fish, which most often results in the fishermen (or, in the case of Icelandic Orcas in 1956, the US Navy) "clearing the area". Because they are at the top of the food chain, much of their food is likely to carry high contamination from water pollution.

Genus *Globicephala* Lesson, 1828

Etymology: *Globus* (L) = globe, ball; *kephale* (Gr) = head.
The two species of this genus are largely parapatric: one circumglobal in tropical and subtropical waters, the other bipolar in temperate waters. Their known ranges overlap marginally, without intergradation, off the mid-Atlantic coast of the United States, off southern Europe, off southern Brazil, off South Africa, around Tasmania, and probably elsewhere, but they may be seasonally segregated in these areas.

Globicephala melas (Traill, 1809)
long-finned pilot whale; longfinned blackfish; ca'ing whale

Etymology: *melanus* (Gr) = black.
Size: 1.6-2.0 m, weight: 70-90 kg (neonate); 2.4 m (weaning); 4.5-5.0 m, weight: 800-1200 kg (adult female); 4.5-6 m, weight: 1000-1800 kg (adult male).
Distinguishing features: Head with bulbous melon and indistinct beak; dorsal fin long-based, low, and strongly curved with rounded tip, located forward on the body; pectoral fins long (>1/5 body length) and sickle-shaped; color black with light anchor-shaped patch on throat and variable lighter markings on belly. Teeth: 8-11/8-11 each side.
Distribution: There are two widely disjunct populations, one in the North Atlantic, the other in the Southern Hemisphere. The population of the North Pacific is also different from the one in the Southern Hemisphere.
1. *G. m. melas*. North Atlantic including the western Mediterranean.
2. *G. m.* subspecies. In the North Pacific, there are no historical records of longfinned pilot whales; however, skulls of this species have been recovered from two archaeological sites in Japan.
3. G. m. edwardii (A. Smith, 1834). Circumglobal in Southern Hemisphere.
Habits: Pelagic, moving inshore late summer and fall; highly social, in small groups to large herds
Food and feeding habits: They prey preferentially on squids, but also on fish. In general, they will take any locally abundant schooling prey.
Reproduction: Females mature sexually at six to seven years; males do not until about 12 years of age. As a result, there is an excess of mature females and the species is undoubtedly polygynous. The adults mate in February and March in warm water and the young are born between July and October, 15 to 16 months later, in cooler water; thereafter the young are nursed for about 20 months. The length of lactation is estimated at 21 to 22 months. Since pregnancy and lactation rarely overlap, and a period of ovulation occurs at the end of lactation, the duration of the whole reproductive cycle is deduced to be some 40 months. So, each adult female probably raises one calf about every three years. The young are toothless and will remain with their mother for most of the next two years. Their longevity is between 35-60 years.
Behavior: The typical groups size is between 50 and 100 individuals. They are extremely social. They swim slowly.
Remarks: They have been the main target of shore-based dolphin fisheries off Newfoundland and the Faröe Islands, with the average annual kill in the latter being 1,552 during 1936 and 1978. In 1941 alone, 4,325 were taken by the Faröe Islands, and this number has been steadily rising. There have also been incidental catches in fishery gear where over 100 whales were caught in 1988 alone.

Globicephala macrorhynchus Gray, 1846
short-finned pilot whale; shortfinned blackfish

Etymology: *makros* (Gr) = large; *rhynchus* (Gr) = snout, beak.
Size: 1.5 m, 60 kg (neonate); 4-5 m, 600-1200 kg (adult female); 5-6 m, 1200-1800 kg (adult male).

Distinguishing features: Similar to above, but with shorter pectoral fins (<1/5 body length). Teeth: 7-9/7-9 each side.
Distribution: Probably circumglobal in tropical and warm temperate waters.
Habits: Generally pelagic.
Food and feeding habits: They take mainly squid and octopi, but when none are available, they will take fish.
Reproduction: Breeding and calving take place in winter. Gestation lasts about 12 months. Females are believed to give birth only once every three years.
Behavior: They are highly social; normally found in groups of 40 individuals although occasionally can be found in groups of hundreds. They like to associate with other cetaceans. They swim slowly.
Remarks: This species appears to vary geographically, but no comprehensive study has been undertaken. Of the Pacific coast of Japan, a northern and southern population differs sharply in color pattern and in body size and shape and also in cranial features; thus, their taxonomic status remains unsettled. Short-Finned Pilot Whales were often taken as practice by American whaling crews in the 1800's. Whaling off St Lucia and St Vincent in the 1960's and 1970's claimed 220-225 animals per year. Japan took around 320 per year during the early 1980's. A small number are taken by Canada, USA, and Peru every year through entrapment in fishing gear. At least 140 have been taken for captive exhibits worldwide since 1963, but mortality rates are high.

Genus *Orcaella* Gray, 1866

Two species.

Orcaella brevirostris (Owen in Gray, 1866)
Irrawaddy dolphin; pesut

Etymology: *Orcaella* (L) = little orca; *brevis* (L) = short; *rostrum* (L) = beak.
Size: 2-2.5 m, weight: 100 kg (adult).
Distinguishing features: 12-19 pairs of small, conical teeth in the upper jaw, 12-15 pairs in the lower jaw; blue-gray back and flanks, lighter gray belly; stout body; rounded head with distinct melon; no beak; small, sickle-shaped dorsal fin with a rounded tip.
Distribution: Discontinuously distributed mostly in the shallow, brackish, turbid waters at the mouths of rivers in southeastern Asia and Australasia.
Habits: Mainly coastal, sometimes estuarine or freshwater.
Food and feeding habits: They seem to take fish dwelling in mid-water and on the seabed. Squid and crustaceans may also be taken.
Reproduction: Gestation lasts about 14 months.
Behavior: The typical group size is up to six individuals, but occasionally can number around 15. They can leap, spy-hop, and tail slap. Only one mass stranding of three animals has been reported. They can be quite tame, and do well in captivity.
Remarks: Because of their habitat, they come into contact with humans regularly. They are killed for food in a small area, but in northern Australia they often become entrapped in fishing nets. They are deemed as sacred by fishermen in Vietnam and Kampuchea.

Orcaella heinsohni Beasley, Robertson and Arnold, 2005
Australian snubfin dolphin

Etymology: *Orcaella* (L) = little orca; *heinsohni* (L) = after George E. Heinsohn, who long worked on Australian odontocetes, including the initialanalysis of this species' specimens.
Size: males up to 270.0 cm; females up to 230.0 cm, weight: 114-133 kg (adult).
Distinguishing features: Head rounded in lateral view, usually bounded by distinct neck crease (indistinct in *O. brevirostris*). Dorsal fin higher than in *O. brevirostris*. **Distribution:** Broome, Western Australia, the Northern Territory, and along the Queensland coast as a far south as the Brisbane River. Also in Daru, Papua-New Guinea
Habits: Mainly coastal, in protected, shallow waters, especially adjacent to river and creek mouths.
Food and feeding habits: They seem to take fish dwelling in mid-water and on the seabed. Squid and crustaceans may also be taken.
Reproduction: Gestation lasts about 14 months.
Behavior: The typical group size is up to six individuals, but occasionally can number around 15. Thy can leap, spyhop, and tail slap.

Family PHOCOENIDAE Gray, 1825

Characteristics: Unlike members of the family Delphinidae, porpoises have a small body with triangular or rounded dorsal fin; snout rounded with indistinct beak; teeth spade-shaped. Raised rounded protuberances on the premaxillae. The premaxilla do not extend posteriorly behind the anterior half of the nares. Spatulate-shaped rather than conical teeth
Six species

Genus *Neophocaena* Palmer, 1899

One species.

Neophocaena phocaenoides (G. Cuvier, 1829)
finless porpoise; little Indian porpoise

Etymology: *Neo* (Gr) = new; *phokaina* (Gr) or *phocaena* (L) = porpoise; *eides* (Gr) = like.
Size: 1.4-1.65 m, weight: 35-45 kg (adult), male slightly larger than female.
Distinguishing features: 13-22 pairs of teeth in each jaw, sometimes with spade-shaped crowns; coloration uniform gray with a bluish tinge, lighter lips and chin with a dark "chin strap"; rotund body with rounded forehead; no beak; no dorsal fin; ridged back with small tubercles.
Distribution: There are three distinct subpopulations:
1. N. p. phocaenoides. Coastal waters along the mainland of southern Asia from the Persian Gulf east to the South China Sea.
2. N. p. sunameri Pilleri and Gihr, 1975. Coastal waters of China, Korea, Japan.

3. *N. p. asiaeorientalis* (Pilleri and Gihr, 1972). Lower and middle reaches of the Chang Jiang [= Yangtse River], where it ranges 1,600 km upstream as far as the gorges above Yichang (200 m above sea level).
Habits: Coastal, estuarine, and freshwater.
Food and feeding habits: They prey on fish, shrimp, prawns, and octopi.
Reproduction: Gestation lasts 11 months. They are seasonal breeders. They have a longer life-span than other porpoises: ~33 years.
Behavior: They are usually in groups of between one and four, though aggregations of 20-50 are not uncommon. They are known to spy-hop, and some reports have been made of mothers carrying their calves upon their backs.
Remarks: Pakistan operates a small, directed fishery of finless porpoises, while in China they are under legal protection, though they are declining due to habitat destruction. Some are caught accidentally in fishing gear around Sri Lanka and Japan.

Genus *Phocoena* G. Cuvier, 1816

Etymology: *Phokaina* (Gr) = porpoise.
Four species

Phocoena phocoena (Linnaeus, 1758)
harbor porpoise; common porpoise

Etymology: *Phocaena* (L) = porpoise.
Size: 0.7-0.9 m (neonate); 1.0-1.1 m (weaning); 1.4-1.7 m, 60-90 kg (adult).
Distinguishing features: Dorsal fin broad-based, low and triangular; flippers small and blunt; back, flippers, flukes and tail stock black to brown; sides gray, belly white. Teeth: 23-28/22-26 each side.
Distribution: There are three recognized subspecies.
1. *P. p. phocoena*. North Atlantic Ocean.
2. *P. p.* subspecies. Western North Pacific Ocean.
3. *P. p. vomerina* Gill, 1865. Eastern North pacific Ocean.
Habits: Coastal in bays, estuaries and rivers; frequent offshore banks.
Food and feeding habits: They feed on schooling fish.
Reproduction: Female porpoises are usually larger than males. It is believed that they can live for as long as 20 years. They become sexually mature between three and five years of age. After that time, female porpoises usually produce one calf every year.
Behavior: Occur singly, in pairs or small groups, but groups of 12 are not uncommon. They either swim slowly or remain still, especially at night; it is thought this is a method for remaining undetected by sharks.
Remarks: They are taken in many areas for human consumption, with the largest fishery located in Greenland, where as many as 1,500 are taken annually. They are also accidentally caught in fishing gear, such as in gillnets, trawls, traps and on baited hooks.

Phocoena sinus Norris and McFarland, 1958
vaquita, Golfo de California harbor porpoise; pygmy porpoise; cochito

Etymology: *sinus* (L) = pocket, referring to the very localized distribution of this species.
Size: 0.7 m (neonate); 1.3-1.5 m (adult).
Distinguishing features: Similar to harbor porpoise; range limited to northern Gulf of California.
Distribution: Endemic to the head of the Golfo de California.
Habits: Coastal.
Food and feeding habits: They feed on squid and fish.
Reproduction: Calving seems to be seasonal, with most calves born in the spring; gestation lasts about 10-11 months; females appear to calve every other year.
Behavior: They have only been seen in groups of between one and five individuals.
Remarks: Very little is known of the abundance of vaquita. The latest abundance survey, jointly conducted in 1997 by the National Fisheries Institute of Mexico and the US National Marine Fisheries Service produced an estimate of 567 animals, with a 95% confidence interval of between 177 and 1073 individuals. Vaquita are currently listed in the IUCN Red List of Threatened Species as *Critically Endangered.* The greatest threat to the remaining vaquita is incidental mortality in fishing gear. Vaquita are known to die in gillnets set legally for sharks, rays, mackerels and chano. They are also known to die frequently in illegal and occasionally permitted gillnet sets for an endangered fish called totoaba. Vaquita are also known to die in commercial shrimp trawls. Because vaquita numbers are so low, any significant increases in annual mortality, whether it is through human interaction or through rapid environmental perturbation, pose a serious threat to this species.

Phocoena *spinipinnis* Burmeister, 1865
black porpoise; Burmeister's porpoise

Etymology: *spinna* (L) = with spines; *pinna* (L) = fin, wing, because of the spiny bumps on the dorsal fin.
Size: 1.4-1.8 m, weight: 40-70 kg (adult).
Distinguishing features: 14-16 pairs of small, spade-shaped teeth in upper jaw, 17-19 pairs in lower jaw; coloration dark gray-black on the dorsal surface and flanks, lighter patches on the belly; small, rotund body with a small head; no forehead or beak; low dorsal fin with a convex posterior end.
Distribution: West coast of South America.
Habits: Coastal.
Food and feeding habits: Burmeister's porpoises feed primarily on anchovy and hake throughout most of their range, although squid, mysid shrimp and euphasiids are also eaten. Burmeister's porpoises in Chilean waters also appear to eat mollusks.
Reproduction: They seem to have a high reproductive rate with up to 2/3 of all females pregnant at all time.

Behavior: They are usually seen alone or in pairs. These porpoises are unobtrusive swimmers; they hardly break the surface of the water when they surface to breathe, a reason by which they are considered a "cryptic" species.
Remarks: There are currently no quantitative abundance estimates for this species. They are taken as by-catch in a variety of fisheries throughout their range; the extent of by-catch is not well documented for most regions or fisheries. The largest takes appear to occur in Peru and have been estimated to exceed 450 per year. In some areas they are shot or harpooned for human consumption or for use as bait for crab fisheries. In some areas they are taken in net fisheries and are used for human consumption, blurring the barrier between by-catch deaths and directed fishery mortality.

Phocoena dioptrica Lahille, 1912
spectacled Porpoise

Etymology: *diopter* (Gr) = spectacles.
Size: 1.55-2.04 m; weight: 60-84.
Distinguishing features: 18-23 pairs of small teeth (laterally compressed to give spade-shape) in upper jaw, 16-19 pairs in lower jaw. Black above and white below, with black rim to eyes and lips, and gray stripe from white flippers to jaw angle, rotund body, little forehead, no beak, relatively small flippers with rounded tips, triangular dorsal fin with rounded peak (larger in males).
Distribution: Coastal waters of southeastern South America.
Habits: This is a very poorly known species.
Food and feeding habits: Almost nothing is known about the food preferences of spectacled porpoises. A single stranded animal in Argentina had anchovy and small crustaceans in its stomach.
Reproduction: Very little is known about the ages of sexual maturity for this species; based on a very small sample size it has been estimated at around 4 years for males, and 2-3 years for females.
Behavior: They travel in small groups of one to two individuals. They move by "rolling" slowly forward in the water.
Remarks: There are no abundance estimates available for this species. They are taken in some fisheries including gillnet fisheries in Tierra del Fuego and southeastern Chile. They are also taken in some bottom and mid-water trawls in Argentina.

Genus *Phocoenoides* Andrews, 1911

One species.

Phocoenoides dalli (True, 1885)
Dall's porpoise; True's porpoise; whitesided porpoise; whitefin porpoise

Etymology: Phokaina (Gr) or Phocaena (L) = porpoise; eides (gr) = like; dalli (L) = after William H. Dall, an American zoologist that provided the information to True that led to the description of this species.
Size: 1.0 m, 25 kg (neonate); 1.8-2.2 m, 100-200 kg (adult).
Distinguishing features: Heavy body with small head, mouth, flippers and flukes; tail stock with prominent dorsal and ventral keels; distinct black and white color pattern. Teeth: 23-28/22-26 each side.
Distribution: There are two subspecies:
1. P. d. dalli. In subarctic waters from the southeastern Sea of Okhotsk to north off Baja California Norte, except in the area occupied by the next subspecies. Mainly an offshore deepwater inhabitant, but occurs in narrow channels and fjords where the water is clear and relatively deep.
2. *P. d. truei*. Andrews, 1911. It ranges in a limited area of the western North Pacific immediately east of the southern Ostrova Kuril'skiye, Hokkaido, and the Sanriku coast of Honshu.
Habits: Pelagic; nearshore in deep water; occur in small groups.
Food and feeding habits: These porpoises take fish and squid in the open ocean and schooling fish in coastal areas.
Reproduction: There is some sexual dimorphism in body shape and size. Gestation lasts 10 to 11 months.
Behavior: Dall's Porpoises have been seen in groups of between 10-20 individuals, though aggregations of several thousands are not uncommon. When swimming fast, they create a V-shaped, forwardly directed splash known as a "rooster tail".
Remarks: They are polymorphic for pigmentation pattern. This porpoise is taken in the annual Japanese hand-held harpoon fishery; in 1988 alone 45,000 were taken. In a three -week period in March 1999, 700 were auctioned in Japan; since 1986 over 25,000 have met the same fate. They are also taken accidentally in squid and salmon gillnet fisheries. Only one has been known to survive in captivity, and for only twelve months.

Appendix

A Classification of Extinct and Living Odontocetes

Suborder Odontoceti Flower, 1869

Family **AGOROPHIIDAE (†)** Abel, 1914

Agorophius pygmaeus Müller, 1849 (Fordyce, 1981) Late Oligocene

Family **SQUALODONTIDAE (†)**

Austrosqualodon Climo & Baker, 1972 (Whitmore & Sanders, 1977) Late Oligocene
Eosqualodon Rothausen, 1968 (Whitmore & Sanders, 1977) Late Oligocene
Microcetus Kellogg, 1923 (Whitmore & Sanders, 1977) Late Oligocene
Parasqualodon wilkinsoni Hall, 1911 (Fordyce, 1982) Late Oligocene
Prosqualodon australis Lydekker, 1894 (Fordyce, 1982) Early Miocene
Prosqualodon davidis Flynn, 1923 (Fordyce, 1982) Early Miocene
Squalodon Grateloup, 1840 (Whitmore & Sanders, 1977) Middle - Late Oligocene
Tangaroasaurus Benham, 1935 (Whitmore & Sanders, 1977) Late Oligocene
Metasqualodon harwoodi (Sanger, 1881, Fordyce, 1982) Late Oligocene

Family **RHABDOSTEIDAE** (**EURHINODELPHIDAE**) **(†)** (Myrick, 1979, Fordyce, 1982)

Argyrocetus bakersfieldensis Kellogg, 1932 (Barnes, 1977) Early Miocene
{including *Doliodelphis littlei* Wilson, 1935 and *Eurhinodelphis extensus* Wilson, 1935}
Macrodelphinus kellogi Wilson, 1935 (Barnes, 1977) Early Miocene
{including cetothere of Wilson, 1935)
?*Phocaenopsis mantelli* (Fordyce, 1981, Fordyce 1982) Early Miocene

Family **ZIPIIDAE**

Berardius bairdi Stejneger, 1883 (Barnes, 1977) Recent
Mesoplodon stejengeri True, 1885 (Barnes, 1977) Recent
Mesoplodon carlhubbsi Moore, 1963 (Barnes, 1977) Recent
Mesoplodon densirostris (Blainville, 1817, Barnes, 1977) Recent
Ziphius cavirostris G. Cuvier, 1823 (Barnes, 1977) Recent

Family **PHYSETERIDAE**

Physeter catodon Linnaeus, 1758 (Barnes, 1977) Recent
Kogia breviceps (Blainville, 1838, Barnes, 1977) Recent
Kogia simus (Owen, 1846, Barnes, 1977) Recent
Praekogia cedrosensis Barnes, 1973 (Barnes, 1977) Late Miocene - Early Pliocene
Scaldicetus sp. (Barnes, 1977) Late Miocene - Early Pliocene

Family **DELPHINIDAE**

Steno bredanensis (Lesson, 1828, Barnes, 1977) Recent
Tursiops gilli Dall, 1873 (Barnes, 1977) Recent
Tursiops sp. (Barnes, 1977) Late Miocene - Early Pliocene
aff. *Tursiops* Gervais, 1855 (Barnes, 1977) Late Pliocene
Grampus griseus (G. Cuvier, 1812, Barnes, 1977) Recent
Lagenorhynchus obliquidens Gill, 1865 (Barnes, 1977) Recent
Delphinus delphis Linnaeus, 1758 (Barnes, 1977) Recent

Delphinus sp.? (Barnes, 1977) Late Miocene - Early Pliocene - Late Pliocene
Lissodelphis borealis (Peale, 1848, Barnes, 1977) Recent
Pseudorca crassidens (Owen, 1846, Barnes, 1977) Recent
Globicephala macrorhynca Grey, 1846 (Barnes, 1977) Recent
aff. *Globicephala* (Barnes, 1977) Late Pliocene
Orcinus orca (Linnaeus, 1758, Barnes, 1977) Recent

Family **PHOCOENIDAE**
Phocoena phocoena (Linnaeus, 1758, Barnes, 1977) Recent
Phocoena sinus Norris and McFarland, 1958 (Barnes, 1977) Recent
Phocoenoides dalli (True, 1885, Barnes, 1977) Recent
Loxolithax sinuosa Wilson, 1973 (Barnes, 1977) Late Miocene

Family **PLATANISTIDAE**
Allodelphis pratti Wilson, 1935 (Barnes, 1977) Early Miocene
"*Squalodon*" cf. "*S.*" *errabundus* Kellogg, 1931 (Barnes, 1977) Late Miocene

Family ?**ACRODELPHIDAE** Abel 1905 (Barnes & Mitchell, 1978)
Schizodelphis aff. *S. sulcatus* (Gervais 1861, Barnes & Mitchell, 1978) Early Miocene

Odontoceti *incertae sedis*
Miodelphis californicus Wilson, 1935 (Barnes, 1977) Early Miocene
Lophocetus sp. (Barnes, 1977) Late Miocene
Liolithax sp. (Barnes, 1977) Late Miocene
aff. *Kampholophos* Rensberger, 1969 (Barnes, 1977) Late Miocene
Delphinavus newhalli Lull, 1914 (Barnes, 1977) Late Miocene
Lonchodelphis occiduus (Barnes, 1977) Late Miocene - Early Pliocene
"*Stenodelphis*" *sternbergi* Gregory and Kellogg, 1927 (Barnes, 1977) Late Pliocene
Agriocetus Abel, 1914 (Whitmore & Sanders, 1977) Late Oligocene
Patriocetus Abel, 1914 (Whitmore & Sanders, 1977) Late Oligocene
Xenorophus Kellogg, 1923 (Whitmore & Sanders, 1977) Late Oligocene

Cetacea *incertae sedis*
Archaeodelphis Allen, 1921 (Whitmore & Sanders, 1977) Late Oligocene
Chonecetus Russel, 1968 (Whitmore & Sanders, 1977) Late Oligocene
Ferecetotherium Mchedlidze, 1970 (Whitmore & Sanders, 1977) Late Oligocene
Microcetus Mchedlidze, 1970 (Whitmore & Sanders, 1977) Late Oligocene

Chapter 7

Marine Mammals of the World III: Pinnipeds, other carnivores, and Sirenia

Order Carnivora (Vicq d'Azyr, 1792)

The order Carnivora is comprised of 11 families and about 275 species and includes otters, bears, dogs, cats, raccoons, weasels, and their relatives. All typical carnivores have well-developed claws and a pair of specialized cheek blade-like teeth for cutting hard foods. Those teeth are the carnassials that in pinnipeds are modified as premolars. Five carnivore families have representatives in the marine environment: the Otariidae, the Phocidae, and the Odobenidae (all members of the suborder Pinnipedia), the Mustelidae (sea otter and marine otter), and the Ursidae (polar bear).

Suborder Pinnipedia Illiger, 1811

Some researchers have classified the pinnipeds as a separate order, but currently they are considered part of the Order Carnivora, although some dispute that it should be considered even a suborder. The name Pinnipedia comes from the Latin *pinna* (=feather, wing, fin) and *pedis* (=foot), referring to the paddle-like fore- and hind limbs, which they use in locomotion on and in the water. Pinnipeds spend considerable amounts of time both in the water and on land or ice, differing from cetaceans and sirenians, which are entirely aquatic. In addition to blubber, some pinnipeds have a thick covering of fur.

Three monophyletic families comprise pinnipeds: the Otariidae (eared seals or fur seals and seal lions), the Odobenidae (walruses), and the Phocidae (true, "hair," and earless seals). Pinnipeds comprise slightly more than one-quarter (28%) of the diversity of marine mammals. Thirty-three to 37 different species of pinnipeds are distributed throughout the world: 18 phocids, 14-18 otariids, and the walrus. Roughly 90% of an estimated 50 million individual pinnipeds are phocids; the remaining 10% are otariids and odobenids.

Family OTARIIDAE Gray, 1825 eared seals (fur seals and sea lions)

General characteristics: Body form generally slender with a long neck; small external ear (pinna; pl. pinnae) present; foreflippers long, hairless in most species, with rudimentary nails set back from tips of digits; testis scrotal. They can position their hind flippers forward and use them to walk. The dentary formula is: I3/2, C1/1, PC5/5 or 6/5 on each side.

Other characteristics include:

1. Frontalis extended anteriorly between nasals. That means that the suture between the frontal and nasal bones is W-shaped (in phocids it is V-shaped and in walruses and terrestrial carnivores is transverse).
2. Supraorbital process of the frontal bone is large and shelf-like, especially among adult males.
3. Secondary spine or ridge subdivides the supraspinous fossa of the scapula.
4. Uniformly spaced pelage units (primary hair and its surrounding secondaries).
5. Trachea has an anterior bifurcation of the bronchi (close to the voicebox and associated structures).

The Otariidae are often divided into two subfamilies, the Otariinae (sea lions) and the Arctocephalinae (fur seals). The close relationship between fur seals and the sea lions is revealed by a number of intergeneric hybrids. In the wild *Zalophus californianus* has hybridized with *Eumetopias jubatus* and with *Callorhinus ursinus*, and a possible hybrid between *Arctocephalus townsendi* and *Callorhinus ursinus* has been reported. A lone *Arctocephalus townsendi* male has been seen copulating with *Zalophus californianus* females. In captivity *Zalophus californianus* has crossed with *Arctocephalus pusillus* and with *Otaria flavescens*. These hybridizations may account for the difficulty to discern the true relationships among different species of otariids. In addition, the violent sexual behavior by male sea lions toward females of different species may have resulted in more hybridization and introgression.

The genera of sea lions are widely allopatric, except for *Eumetopias* and *Zalophus*, which occur together in the coastal waters from Vancouver Island south to southern California, and (formerly) in the southern Ostrova Kuril'skiye and northern Hokkaido.

Subfamily Arctocephalinae fur seals

Have thick, dense fur. Two genera.

Genus *Arctocephalus* E. Geoffroy Saint-Hillaire and F. Cuvier, 1826

Arctocephalus means bear head (from the Greek *arktos* = "bear" and *kephale* = head). Fur seals were called bears by earlier explorers because of their bear-like appearance. This genus is represented by eight species.

Arctocephalus pusillus (Schreber, 1775)
Tasmanian and Cape fur-seals; South African fur seal; Australian fur seal; giant fur-seal; brown fur-seal

Etymology: *pusillus* means "little" in Latin. The original description of the species was based on a picture of a pup. There are two subspecies: *A. p. pusillus* for South Africa and *A. p. doriferus*. This latter subspecific name is a composite of the Greek *dora* for "hide" or "skin" and the Latin "*fero*" for "I bear." The two subspecies are undistinguishable in the field. Only examination of the skull yields some differences. They are mostly allopatric populations.
Size: They reach lengths of 1.7 m (females) to 2.2 m (males), And weight from 110 kg (females) to 360 kg (males). Pups weigh 4.5 to 12.5 kg and measure 62-80 cm in length at birth.
Distinguishing features: Adult males are dark grayish to brown, with a dark mane of coarse guard hairs. Mature females are lighter silver gray with a yellowish throat and chest.
Distribution: The South African population is believed to be the parent stock of the Australian one. It occurs along the coasts of South Africa and Namibia. The Australian one is confined to waters off southeastern Australia, primarily along the coasts of Tasmania and Victoria.
Habits: Both subspecies of *A. pusillus* spend most of their year at sea but not too far from land. A maximum of 160 km from land is recorded but is not common. Breeding occurs on the mainland or small islands in the sand or rocks. Both subspecies prefer small rocky islands for mating and pupping.
Food and feeding habits: They commonly eat fish, squid, octopus, and lobsters, along with other crustaceans and cephalopods. Both subspecies of *A. pusillus* dive for their food but they each occupy different depth niches in their respective locations. South African fur seals are surface divers with an average dive of about 45 meters and 2.1 minutes although they can dive as deep as 204 meters and for as long as 7.5 minutes when necessary. While there is extensive overlap, Australian fur seals generally feed at a much lower depths. Their average dive is about 120 meters and they commonly go as deep as 200 meters.
Reproduction: The breeding season for both subspecies of *A. pusillus* begins in the middle of October. At this time males haul out on shore at the breeding grounds, or rookeries, to establish territories by displays, sparring, or actual battle. They do not eat again until they mate in November or December. Females come ashore slightly later and also fight among each other for smaller territories in which to give birth. Female territories are always within male territories and females who are located on a certain male's territory become part of his harem. While harem sizes of both subspecies can reach as many as 50 females, or cows, the average size of the South African fur seal harem is 28 cows, the Australian fur seal harem averages 10 cows. Breeding

occurs between the male and each of his harem members. While copulation occurs within six days after cows give birth to a single pup there is a delay in implantation of the blastocyst. In South African fur seals this delay is approximately 4 months while in Australian fur seals it is about 3 months. Gestation in both subspecies averages 11.75 months.

Pups are borne in late November or early December. They go through two different molts in their first year and a half. Their original coat is black and curly. This coat is replaced between four and five weeks of age with an olive-gray coat. The second molt takes place at about 13 months and replaces the olive-gray coat with a silver one, which later fades in color. Nursing in this subspecies begins immediately after birth and is continuous for the first six days. At this time the mother mates with her male harem leader and then begins going out to sea for food for a few days at a time. By the second month, however, she can be gone for up to two weeks before returning to feed the pup. At four to five months old pups begin supplementing their diet with crustaceans and fish. Lactation does continue, however, until the next pup is born. Pups begin swimming early and continually increase the amount of time that they can spend in the water. At seven months they can swim for two or three days at a time. Females become sexually mature at about three years and males may also follow this trend, but if unable to establish territory at this time, they do not usually mate until several years later.

Behavior: Colonies range in size from 500-3000 bulls, although some have been spotted with over 3000. Australian fur seal colonies tend to range in size from 500-1500. Neither subspecies migrates. When they leave the rookeries, they often travel in small feeding groups. While there is no record of established dispersal some seals have been found in other colonies. There are no true boundaries between colonies, as they all travel separately throughout the year until the breeding season. During the breeding season both subspecies are polygynous but males do not herd the females, who are free to choose their own mates and do so by the value of their territory. In Australian fur seals 82% of the copulations in one breeding season were by males whose harems were located directly on the water. Both subspecies have what is called a pup call: when the mother returns from sea to feed her pup, she emits a loud call. Upon hearing this call, all of the pups on land come to her but she responds only to her own pup. It is suggested that she uses smell, not sight, to distinguish her pup from the others. Pups, when alone, stay in groups and play during the evenings.

Remarks: They are more abundant than are Australian fur seals; yet, they are at the mercy of poachers who disregard the legal hunting seasons for South African fur seals. Much of the poaching danger comes from fishers and large fishing corporations who see the seals as jeopardizing their livelihood by stealing from their nets. These seals are also threatened by pollution: plastic, pieces of netting, and pieces of fishing line kill or injure thousands of these seals a year. Their main predators are killer whales and white sharks. Stingrays can cause some dangerous injuries. Terrestrial predators, such as the black-backed jackal in South Africa, sometimes take pups left on the mainland.

Arctocephalus gazella (Peters, 1875)
Antarctic fur-seal; Kerguelen fur-seal

Etymology: The specimen from which this species was described was carried from Kerguelen Island on the German vessel SMS Gazelle; this species was named in the ship's honor.
Size: Adult males are 1.9 m long and average 188 kg in weight, while adult females average 1.2 m and 35 kg.
Distinguishing features: Both sexes are gray-brown, although females have a lighter belly and adult males have a dark mane. Sexual dimorphism is obvious in both size and coloration.
Distribution: The present breeding range is from about 61° north to the Antarctic Convergence. This species has been expanding its range in the last few years.
Habits: Though the species appears to be capable of traveling long distances over ice, it does not seem well adapted to such an environment. Breeding occurs on rocky beaches sheltered from the sea. The islands they inhabit commonly support lush growth of grass inland. During the months of May and November, there is a general movement out to sea, but specific migration paths are unknown. Some adult males are found ashore or in the general area of the breeding islands year-round.
Food and feeding habits: The main food of the Antarctic fur seal is krill, but individuals also consume squids and even birds. Nursing mothers are almost completely dependent on krill and the reproductive success of this species is, therefore, closely linked with the availability of this food resource. They mainly feed at night in the shallower waters of the ocean.
Reproduction: The breeding season of this species lasts from November to January. The males arrive earlier than the females to compete for territories, which will eventually hold a harem of four or five females. The competition is fierce and males do not feed while defending their territories on shore. Breeding incurs significant costs to the males of the species, which lose an average of 1.5 kg a day throughout the season. Females give birth to a single young approximately two days after arrival on shore. The females become sexually receptive between six and eight days after giving birth and then begin mating. During lactation, females spend up to five days feeding at sea to maintain their supply of milk. This period is followed by one to two days of nursing on shore. This cycle is repeated for 4 months. The lactation period is one of the shortest of all fur seals and is probably due to the harsh weather conditions and strong seasonality of the breeding area. While the female is away, the pup hides in a sheltered area. Both the mothers and the pups use vocalization as a means to relocate each other when the mothers return from the sea.
Behavior: In this polygynous mating system, a dominance hierarchy of males is established through the displays and fights that occur while defending territories. Some subordinate males are forced inland while others assume a completely aquatic lifestyle. Individuals of this species are surprising agile on land, reaching speeds of up to 20 km/hr on smooth surfaces. It is quite probable that they reach even higher speeds in the water. Using time-depth recorders, the dives of several lactating females have been measured: the deepest dives averaged about 181 m and lasted almost 5 min.
Remarks: This species almost became extinct in the eighteenth and nineteenth centuries due to intense commercial sealing for their fur. The population has recovered at a rate of about 10% per year. They are protected under the Convention for Conservation of Antarctic Seals (CCAS) and

the Antarctic Treaty. On a more local level they are protected by the legislation of each of the islands they inhabit. They have also been placed under Appendix II of CITES.

Arctocephalus tropicalis (Gray, 1872)
Subantarctic fur-seal; Amsterdam fur-seal

Etymology: The specific name is from the Greek *tropikos*, "tropical," referring to the location along the north coast of Australia where the first specimen was mistakenly believed to have been collected.
Size: Males reach 1.8 m and attain 131 kg; females grow to about 1.4 m long and average 35 kg.
Distinguishing features: Adults are dark brown dorsally, with a lighter belly and a whitish-orange chest, nose, and face. Males have a tuft of white-tipped hair on top of the head; females lack this tuft.
Distribution: They haul out and breed north of the Antarctic Convergence in the South Atlantic and Indian oceans, mostly on the subantarctic islands of Amsterdam, Saint Paul, Crozet, Gough, Marion, Prince Edward, and Macquarie.
Habits: The males of the species spend most of the year out at sea, hauling out onto the rookeries only during the mating season. Females spend much of their time close to the rookeries, hauling out at regular intervals for nursing and again during the breeding season. Breeding occurs on land and rocky coastal areas are preferred for the rookeries.
Food and feeding habits: The Subantarctic fur seal's diet consists mainly of squid and is supplemented by krill, fish and, at times, penguins or other birds.
Reproduction: The breeding season begins in September when the males haul out on shore at the breeding grounds, or rookeries, to establish territories by displays, sparring, or actual battle. The females come ashore in October and November and choose male territories within which to bear their young. They later mate with the male possessing that territory. It is also at this time that immature animals begin avoiding the rookeries. Pups are born beginning in late November through January. Most pups are born in early December. Cows give birth to a single pup and begin lactation almost immediately. Lactation is almost continuous for the next 8 to 12 days, after which the cow mates and begins returning to the sea. She will spend increasing amounts of time at sea over the next year, returning only to nurse her pup. Lactation continues throughout the pup's first year or until the cow's next pup is born. Copulation occurs between 8 and 12 days after the cow gives birth, but there is a delay of about 4.3 months in the implantation of the blastocyst. The pups are approximately 4.5 kilograms and 60 centimeters at birth, the males being slightly larger than the females. Females reach sexual maturity between four and six years of age while males reach sexual maturity earlier, between 3 and 4 years of age.
Behavior: While the Subantarctic fur seal is basically non-migratory it does exhibit seasonal movements. Males spend most of their year at sea, hauling out at the rookeries only during the mating season. Females, while they will go to sea in order to find food, remain close to the rookery in order to continue nursing their pups throughout the year. The rookery is never fully evacuated because the mothers and pups return to it continually. Males at sea often travel in small feeding groups. Interestingly, some individuals have been found in colonies of other species of seals such as *A. pusillus*, *A. forsteri*, *A. gazella*, and *A. australis*. Most of these individuals are males. While *A. tropicalis* is distinguishable by its coloring and the male's crest,

some variation in these traits have been noted in areas where mixed species groups of seals have been reported, thus it is believed that interbreeding occurs.

This species is facultatively polygynous (solitary most of the year but come together during the mating season). They form harems where one male mates with several females. They also exhibit a "pup call," i.e., when the mother returns from sea to feed her pup, she emits a loud call. Upon hearing this all of the pups on land come to her, but she responds only her own pup which she recognizes by its smell. Cows in other species, such as the northern fur seal, South American fur seal, and the New Zealand fur seal, use similar calls.

Remarks: This species was considered a conspecific of the Antarctic fur seal until recently, when the two were separated based on differences in cranial, dental, and biochemical features as well as geographical distribution. Sealers had taken much of the subantarctic fur seal populations by the 1830s, but enough of the animals survived in order to make a comeback. A majority of the population, which was estimated at 214,000 individuals in 1983, is located on Gough Island. In 1990 the population was estimated at 300,000 individuals. More recently the population was estimated at 310,000 individuals and rising. Currently there are no recognized threats to the subantarctic fur seal population.

Arctocephalus townsendi Merriam 1879
Guadalupe fur-seal

Etymology: It is named after C. H. Townsend, who collected the original specimens (four weatherworn skulls) from a beach on Guadeloupe Island in Mexican waters in 1892, at a time when the species was feared by some to be already extinct.

Size: 0.6 m (neonate); < 2 m, 140 kg (adult male); female smaller.

Distinguishing features: Pelage with dense underfur; fur on forelimb extending onto flipper; snout long and pointed; color grayish black.

Distribution: They now breed only along the eastern coast of Guadalupe Island, approximately 200 km west of Baja California, where they prefer rocky habitats and volcanic caves.

Habits: Coastal, preferring rocky areas and caves; rookeries on land. They can dive to an average maximum depth of 17m for an average of 2.5 minutes.

Food and feeding habits: Guadalupe fur seals eat a variety of fish and squid. During the breeding season, females make 2 to 6 day forging trips to sea, coming onshore in between each trip in order to suckle their pups.

Reproduction: Males have harems that number between 4 and 12 breeding females. They defend their territory for 35 to 122 days. Unlike most other seal species, the males of *A. townsendi* occasionally observe their harems from the water. Female Guadalupe fur seals mate 7-10 days after giving birth to a pup conceived the previous year (post-partum estrus). Females lactate for an average of 9-11 months; it is unclear how this relates to the actual length of time before weaning.

Behavior: Mother seals use olfactory clues to find their pups after foraging trips. They are not migratory, but a male and his females will occasionally disperse to new areas.

Remarks: The Guadalupe fur seal was nearly hunted to extinction in the 1880's, with the known population numbering only 7 individuals in 1892. Other than two males sold to the San Diego Zoo in 1928, only one other was sighted until 1954. Guadalupe Island was declared a seal sanctuary by the Mexican government in 1975. The Guadalupe fur seal was first placed on the

"threatened" list in the US in 1967. By 1984 there were 1,600 seals in the Guadalupe Island population, including around 650 new pups. Current estimates place the population number at more than 7,000 individuals. Despite the bottlenecks of the late 1800's, there still remains a high level of genetic variability in the population. The population of Guadalupe fur seals is growing at the rate of 11.5% per year.

Arctocephalus philippii (Peters, 1866)
Juan Fernández fur-seal

Etymology: The species was named after R. A. Philippi who, in 1864, while director of the natural history museum in Santiago de Chile, collected the skin and skull of a young male from Más a Tierra Island. Peters described the species from this specimen
Size: Adult males are about 2.1 m and females about 1.5 m long.
Distinguishing features: The adult male's heavy mane has silver-tipped guard hairs. Other body parts are a shiny blackish brown. Normally, a male's neck and fore flippers have many scars from fighting.
Distribution: Restricted to the Juan Fernández and San Félix islands off the coast of north central Chile.
Habits: When on land, Juan Fernandez fur seals prefer rocky shorelines with boulders, grottos, and caves.
Food and feeding habits: Diet consists of fish and cephalopods including squid. Food availability is usually low in their habitat.
Reproduction: Breeding occurs from mid-November to January with peak pupping occurring from late November to early December. At birth, male pups weigh 6.8 kg and are 68 cm long; female pups weigh 6.2 kg and are 65 cm long. Pups are nursed for about 7-10 months before being weaned.
Behavior: This species is known for resting in the water with their heads down and hind flippers swaying out of the water.
Remarks: According to the records of the first sailors to encounter these seals at the Juan Fernández Islands, they were very abundant and numbered possibly in the millions. The species was afterwards very heavily exploited for its pelt, blubber, meat, and oil by commercial sealers from the seventeenth to the nineteenth centuries and by the beginning of the twentieth century it was believed to be extinct. After rediscovery, the species was given total protection by national Chilean legislation in 1978. The species is listed as Vulnerable on the IUCN Red List, due to its limited population size and the fact that the species' low genetic diversity may cause problems, and is also listed as an Appendix species under CITES. The IUCN/SSC Specialist group has recommended that research be carried out into the diet of the species in order to determine any potential competition with fisheries. There have been reports of fishermen on Alejandro Selkirk Island using the seal as bait, as well as for food and as a barter commodity. There have been occasional reports of entanglement in fishing nets, while the occurrence of seals with plastic wrapped around their necks has often been reported.

Arctocephalus forsteri (Lesson, 1828)
South Australian and New Zealand fur-seals; New Zealand Fur Seal; Australian fur-seal; Antipodean fur-seal; black fur-seal

Etymology: This species is named after J. G. A. Forster, a naturalist on Captain James Cook's circumglobal voyage 1772-1775. Forster described fur seals encountered at the South Island, New Zealand.
Size: Males reach 2 m in length and up to 200 kg in weight. Adult females reach 1.5 m and 35 kg.
Distinguishing features: Adult coloration is similar in both sexes: dark gray-brown dorsally and lighter ventrally.
Distribution: It is distributed discontinuously throughout the southern ocean.
Habits: New Zealand fur seals oscillate between aquatic and terrestrial habitats. When in the ocean, they are observed both far and near from shore. During the breeding season, however, fur seals spend most of their time along a rocky coastline, especially preferring those areas with an abundance of large boulders, crevices and caves so as to shelter and provide protection for pups. They prefer areas near sheltered water or intertidal pools.
Food and feeding habits: They feed primarily on squid, octopus, and fish on the continental shelf in depths greater than 22 m. Because their prey includes many vertical migrants, fur seals are found to feed almost exclusively during the night, sometimes continuously from dusk to dawn.
Reproduction: Females reach sexual maturity between 4 and 6 years of age, and males become sexually mature near 5-6 years old. The breeding season begins in mid-November and lasts through mid-January. New Zealand fur seals are polygynous, with one male mating with several females. Females give birth to one pup nearly every year until their death at around 14-17 years. Females mate 68 days after the birth of a pup, but due to delayed implantation of the blastocyst (which does not implant for 3 months), gestation periods last nine months. Young are suckled for approximately 300 days before they are weaned.
Behavior: Male fur seals attain and defend territories once they reach approximately 8-10 years of age. Breeding males come to shore in early November to compete for and establish territories, which eventually may support up to 16 females. Adult females begin arriving in mid-November to choose males. Between December and January females give birth to those pups conceived during the last breeding season. Once the young reaches 6-12 days old, the mother begins going to sea to feed. Females alternate between offshore foraging and onshore nursing and caregiving. Foraging trips become longer as the pup gets older. Females and pups can be found at the rookery throughout the year. Adult males remain onshore for the entirety of the breeding season, often not feeding for up to two months. They return to the sea by mid-January. Lactating females are constrained to areas near the breeding site. Further, it has been shown that most dive depths ranged from 12-18m, and the maximum depth observed was nearly 163m. Durations of dives were from 3.2 to 6.2 min, but the average dive length was much shorter (0.7-1.2min). Dives tended to occur nocturnally, and dive depth varied with time of night, with deepest dives being near dusk and dawn (perhaps because prey was just starting to either rise from extremely deep depths, or was beginning to fall back to deep depths after feeding).
Remarks: This species is threatened by pollution, which affects their health in addition to actually physically trapping and drowning them. They are also accidentally caught in nets, as

well as being hunted by Polynesian colonies in New Zealand. Their populations have been increasing at rates near 16-19%, however, and their numbers are quoted at being near 60,000.

Arctocephalus australis (Zimmermann, 1783)
South American fur-seal

Etymology: The specific name is from the Latin *australis*, meaning "southern."
Size: Adult males weigh 150 to 200 kg and are generally about 1.9 m long. Females reach 1.4 m long and weigh 30 to 60 kg.
Distinguishing features: Adult males are blackish gray; females and subadults are grayish black on the back and lighter on the belly.
Distribution: They are found in the Falkland/Malvinas Islands and along the coasts of South America as far north as southern Brazil in the Atlantic and southern Peru, in the Pacific.
Habits: This species prefers rocky shores and islands, especially those with lots of vertical slopes which provide shady areas for them to escape the heat of the sun. During a given day there may be movement from drier rocks to areas close to the sea or in tide pools. They have been found in sea caves in Peru, where some climb up to 15 meters to find a spot to rest. Not much is known about their movements at sea, but a recent study with satellite telemetry has discovered that females will travel 15 to 200 km when foraging at sea.
Food and feeding habits: The diet consists of fish, cephalopods, crustaceans, bivalve mollusks, and gastropods. They forage at night and will dive for 3 minutes to an average depth of 29 meters, but will reach a maximum time of 7 minutes and 170 meters in pursuit of food. El Niño events can affect the reproductive success of females in the Pacific.
Reproduction: Sexual maturity is reached at three years for females and seven years for males. Females begin estrus usually 6 –8 days after they give birth and, though all will mate, only about 15% will give birth the next year if they are nursing a pup. After mating, implantation is delayed for four months. Total gestation time averages 11.75 months. Litter size is limited to one pup. Reproduction is synchronous in rookeries, with a peak birthing period at a time of peak food availability. If rearing takes longer than a year, a second pup will be born, resulting in competition for the mother's milk. After birth, the pup is nursed for anywhere between 7 months and 3 years, depending on environmental conditions. Lactation period may vary and can overlap with pregnancy, resulting in energetic costs that are paid by smaller young being born. It can also result in successful births only occurring every few years, rather than yearly. This phenomenon is unique for *Arctocephalus australis* among otariids. In addition, there is a significant difference in pregnancy rates in *Arctocephalus australis* from year to year, indicating that both environmental and demographic stochasticity play a role in population dynamics. Pups are born throughout November and December along the Uruguayan coast, and a bit earlier in Peru. Pups' average weight is 3-5 kg. Females reach full size in ten years. Both male and female pups are born with a dark coat of fur but, as they mature, females develop lighter coloration ventrally. Mortality of pups can be caused by maternal aggression during times of movement to or from the water and is considered to be higher than in other species of otariids (10 – 48%). Death can also be caused by aggressive males or by males of South American sea lions, *Otaria flavescens*.
Behavior: These seals form rookeries on rocky coasts for breeding purposes. Females remain in the rookery year-round, but not much is known about the movements of males and sub-adults.

Groups of 15 – 20 seals have been observed traveling together offshore, where they compose rafts of animals. They frequently groom while floating on the surface. When pups are still young, mothers stay close, returning daily from foraging for food. As the pups grow, the forays were extended in distance and time. During the breeding season, males compete more for territorial areas than for individual females. In tropical parts of their range, the seals are forced to move between the rookery and the ocean to cool off. The frequent movement of females is a reason that many pups are displaced and become victimized by other aggressive females. In a 1988 study in Peru, it was found that play was an important part of growing for pups, but involved large costs. Though 6.1% of the daily time budget of pups was involved with play, 84.6% of those preyed upon by sea lions were killed while at play.
Remarks: The population of South American fur seals in 1999 was estimated at 390,000, a drop from a 1987 estimation of 500,000. Uruguay has the largest numbers of seals along its coast, numbering over 200,000. Peru's number dropped to only 40 in the 1940's, but subsequent protection has brought the numbers back up to about 20,000 by the 1980s. Because of the El Niño events and general overfishing along the Pacific coast of South America, the population in the Pacific is not recovering as quickly as it could. Peru has had a problem with fishers illegally killing South American fur seals, claiming that the seals interfere with fishing operations and diminish the anchovy numbers. In the Falkland Islands, where commercial hunting greatly reduced their numbers, the population now contains about 15,000 seals. There are approximately 40,000 seals in Chile and 3,000 in Argentina. This species is on Appendix 2 of the CITIES.

Arctocephalus galapagoensis Heller, 1904
Juan Fernández fur-seal, Galapagos fur-seal

Etymology: The specific name refers to the Galápagos archipelago, where this species is endemic.
Size: Adult females are on average 120 cm in length and weigh 27 kg. Males reach 152 cm and 64 kg.
Distinguishing features: The snout is short and pointed; it and the belly are light tan. The sides and back are grayish brown. Their skulls are considerably smaller than those of other fur seals.
Distribution: Endemic to the Galápagos archipelago.
Habits: Southern fur seals live only on the Galapagos Islands and in the surrounding waters. Air temperature is fairly constant year round at an average of 23.8^{o}C.
Food and feeding habits: They feed on fish and cephalopods.
Reproduction: Females are able to have offspring by their fifth year. Pupping takes place beginning in August and lasting until November. Gestation is approximately one year, however, the existence of delayed implantation in this species implies that development time may be less than one year. The unusual birth time in this species may be due to distribution at low latitudes, a more favorable climate throughout the year, and less pronounced seasonal variation in marine productivity than found in temperate and arctic waters. Females go into estrus 8 days after giving birth, and mate during lactation, which lasts from 365-730 days. Peak mating time is during the month of October. If a female gives birth to another pup the next year, it has a 50% chance of survival. The year old pup may kill the new pup or lack of resources may result in their starvation. Female southern fur seals produce a maximum of five offspring in their lifetime.

Behavior: They are the most terrestrial species of Otariidae, spending only 70% of their life in the water. Females dive for an average of 16.4 minutes to a depth of no more than 30 meters at night, but deeper dives have been recorded. Foraging trips have been found to last 50-70 hours at the time of the new moon but only 10-20 hours at the time of the full moon. During the warm months, females will repeat a foraging cycle of 4-6 days in the water and one day on land. After giving birth, females will leave their pups for 1-3 days to dive for food then 1-2 days are spent with the offspring. Pups do not become independent until their 2nd year, and sometimes not until their third. Adult males aggressively hold territories that can extend 200 square meters. Death rate for fighting males is 30% annually. Females hold very small areas, compared to other fur seals, of approximately 100 square meters. They are a polygynous species and males do not offer care for the offspring. Males do not feed while they are defending their territories, and will not abandon them until they have used all of their stored energy and have no choice but to feed. These territories encompass water and rough terrain with overhangs to provide cooling. Other seals do not occupy this type of terrestrial habitat, with most other seals preferring beaches. To keep cool, seals will move to tide pools and wet themselves. Females have to teach this thermoregulatory strategy to their pups or the newborns will suffer from overheating. It is very important at this latitude to keep internal temperatures at approximately 37.7 degrees C; as a result, these seals have evolved methods to accomplish this regulation. They also sweat, depending on individual hydration. Much heat loss is controlled internally by the cardiovascular system in that blood flow is directed away from or toward flippers depending on whether the seal is too cold or too warm, respectively.
Remarks: By the early 1900s the species was said to be extinct due to overhunting for fur, but a population was found in 1932-33. The population had increased to between 30,000 and 40,000 by 1989. Ecuador reports that feral dogs on some of the 15 Galapagos Islands are a threat to current seal populations. Ecuador provides protection by law for southern fur seals.

Genus *Callorhinus* Gray, 1859

One species.

Callorhinus ursinus (Linnaeus, 1758)
Northern fur-seal

Etymology: *Callorhinus* comes from the Greek *kallos* meaning "a beautiful object" and *rhinus* meaning "skin" or "hide," referring to the quality of the seal's fur. The name *ursinus*, which means "bearlike" in Latin, was applied because all fur seals were first called sea bears by Europeans.
Size: 0.7 m, 4.5-6 kg (neonate); 12-14 kg (weaning); 1.3-1.6 m, 35-60 kg (adult female); 1.9-2.3 m, 185-275 kg (adult male).
Distinguishing features: Pelage with coarse outer guard hairs and soft, dense underfur; fur on foreflipper stops at wrist; snout short, down-curved and pointed; males brown, females dark gray and lighter gray or chestnut ventrally; neonates black; extreme sexual dimorphism, adult males with massive neck and bushy mane.

Distribution: Mostly in Pribilof Islands in the eastern Bering Sea and the Commander Islands in the western Bering Sea, although sightings have been reported across the North Pacific and Bering Sea.
Habits: The primary rookeries (breeding sites) are on the Pribilof Islands and the Commander islands in the Bering Sea. They go offshore in winter.
Food and feeding habits: They feed on fish and squid.
Reproduction: Males fast during the breeding season, and can lose 20% of their body weight during the 1 to 2 month period. Bulls have a brief reproductive period, and few breed for more than two seasons. Nearly half the pups die before they are a year old. Females usually give birth a day after arrival at the rookery. Females enter estrus about 5 days after giving birth. Females make considerably longer foraging trips than most other otariids. Pups abruptly weaned at about 4 months old.
Behavior: The males are territorial, and after their arrival on the rookeries beginning in late May, they establish territories by threatening and fighting other males. These territories may contain at least 40 females. Northern fur seals tend to live alone or in pairs, and rarely come to land, except to breed. Sharks, killer whales, and Steller sea lions will all hunt northern fur seals if they get the opportunity.
Remarks: This species has been hunted for fur since the Eighteenth century. In 1911, the North Pacific Fur Seal Convention was founded. Commercial hunting is illegal on many of the islands, but hunting for sustainable use is still allowed. The population is estimated to be at 1,345,000-1,365,000, but is declining. They are classified as Vulnerable (IUCN).

Subfamily Otariinae sea lions

They have sparse pelage. Five genera.

Genus *Zalophus* Gill, 1866

Etymology: The generic name is from the Latin *za*, an intensive prefix, and *lophos*, meaning "crest" and referring to the large sagittal crest on the adult male's skull. Three species.

Zalophus japonicus (Peters, 1866)
Japanese sea-lion

Etymology: *japonicus* refers to its geographic location.
Size: Males grow to 2.4 m 390 kg; females to 2 m and 110 kg.
Distinguishing features: Adult males are generally dark brown to black, but there are some blonds. Both sexes are lighter dorsally than ventrally.
Distribution: Sea of Japan.
Habits: Rockeries?
Food and feeding habits: Fishes perhaps, but little information available.
Reproduction: No information available.
Behavior: No information available.
Remarks: They are believed to be extinct. Last sighting took place in 1951.

Zalophus californianus (Lesson, 1828)
California sea-lion

Etymology: The specific name refers to its geographic location.
Size: 0.7 m, 5.5-6.4 kg (neonate); 25 kg (weaning); 1.5-1.8 m, 50-110 kg (adult female); 2.0-2.3 m, 250-300 kg (adult male).
Distinguishing features: Pelage with sparse underfur; no gap between 4th and 5th postcanines; color dark brown, juveniles and females lighter; extreme sexual dimorphism, males with prominent sagittal crest, more muscular neck; sharp bark-like vocalizations.
Distribution: Originally from Baja California to Canada; today only California coast.
Habits: They are coastal, entering estuaries and rivers. They often congregate on man-made structures such as jetties, piers, offshore buoys and oil platforms.
Food and feeding habits: Male California sea lions assemble at the mouths of fresh water rivers in search for fish. They tend to feed alone or in small groups unless there is a large quantity of food. They can cooperatively hunt with cetaceans, seabirds and harbor porpoises; often one species locates a school of fish and signals the presence of food to the other species. While rare, they can drink seawater while not breeding.
Reproduction: The peak of the breeding season is early July. They usually breed on islands or remote beaches. The total gestation period is about 11 months. Most births occur from mid-May to mid-June with the majority of pups born in mid-June. The time between birth and estrus is about 28 days. California sea lions reach sexual maturity between four and five years. During the breeding season males claim territories. A male consistently occupies a territory until factors change and cause him to be displaced, usually about two weeks. While guarding their territory, males remain present and do not leave even in pursuit of food. As external factors change, males replace other males on the territory. Replacement occurs throughout the entire breeding season. They exhibit moderate to extreme polygyny and tend to live in colonies of a few males and many females. Females exhibit mate choice, by responding differently to the attempts of various males. The lactation period ranges from six months to a year. There are many possible reasons for the variation in lactation periods including availability of food resources, the mother's age and health, the sex of the pup, and the birth of a new pup. They provide more lengthy maternal care for female offspring than for male offspring, yet during lactation both males and females have equal access and receive equal resources.
Behavior: They are capable of diving to depths of 274 meters and can reach speeds of up to 35 km per hour while swimming. They sometimes adopt and foster a pup that has been abandoned by its mother. The normal body temperature is 37.5 degrees Celsius. They thermoregulate by either seeking cooler areas or getting into the water if it is too hot. Pups exhibit many different play behaviors including mock fighting.
Remarks: They are currently protected by the Marine Mammal Protection Act, although may show great natural variation in population size. From 1983 to 1984, for example, this species experienced a decline of 60 percent in pup production from previous years. Food resources declined during these years. During this time mothers left their pups earlier in search of food, which truncated the lactation period, thus reducing the amount of nutrients a pup received and

increasing susceptibility to death. Also, they can be occasionally killed as a result of getting tangled in discarded fishing gear. Legal trapping has been allowed for display in zoos, aquariums, and circuses. Occasionally California sea lions pose a problem for fishermen by stealing fish from commercial fishermen netting.

Zalophus wollebaeki Sivertsen, 1953
Galápagos sea-lion

Etymology: The specific name was assigned for A. Wollebaeki, who in 1925 collected from the Galápagos the sea lion skull from which this species was described.
Size: Males grow to 2.4 m and 390 kg; females to 2 m and 110 kg.
Distinguishing features: Adult males are generally dark brown, but there are some blonds. Both sexes are lighter dorsally than ventrally. Appearance resembles California sea lions, with the only noticeable differences being slightly smaller overall size and smaller sagittal crest among males.
Distribution: Galapagos sea lions inhabit the Galapagos Islands off northwestern South America, as well as a small rookery off the coast of Ecuador.
Habits: They prefer rookeries.
Food and feeding habits: Their diet varies with location and season, but includes several species of fish and squid.
Reproduction: Both males and females reach sexual maturity at 4-5 years. Males defend territories from May to January. Because of the difficulty in defending territories, males are not necessarily successful for extended periods. Instead, females are mated as they move in and out of the water by whichever male is defending that territory at the time.
Behavior: Although not much is known about the seasonal movements of females, it is thought that they remain at the rookeries for most of the year.
Remarks: Ecuadorian legislation that includes an extension of the no fishing zone decreed in the late 1990's protects Galapagos sea lions. In January 2003, 15 sea lions were found dead in the Galapagos Islands as a result of intentional killings. It is thought they had been clubbed to death prior to their genitals being cut out, for which there is a market in the Far East as aphrodisiacs. Even though it was thought likely that the animals had been killed at sea and their bodies washed up on the beach, four of the animals were still alive at the time of being found. Sharks and killer whales are considered to be natural predators. El-Nino events have caused population decreases due to die-offs and cessation of reproduction.

Genus *Eumetopias* Gill, 1866

One species.

Eumetopias jubatus (Schreber, 1776)
Northern sea-lions; Steller's sea-lion

Etymology: The generic name is from the Greek *eu*, meaning "typical" or "well" and *metopion*, "having a broad forehead," referring to the prominent forehead. The specific name is from the Latin *jubatus*, "having a mane," referring to the well-developed mane of adult males.

Size: 1 m, 17-23 kg (neonate); 2.2-2.7 m, 260-330 kg (adult female); 2.8-3.0 m, 560-800 kg (adult male).
Distinguishing features: Pelage with sparse underfur; gap between 4th and 5th postcanines; color light tan to reddish brown, pups darker brown; pronounced sexual dimorphism: adult males with moderately developed sagittal crest, more muscular neck with mane of longer hair; roar-like vocalizations.
Distribution: Coastal and immediate offshore waters of the cool-temperate North Pacific.
Habits: Coastal to pelagic. Colder waters are more preferable than warm waters.
Food and feeding habits: They feed on fish as well as octopi and squid. Males will occasionally kill and consume young northern fur seals.
Reproduction: Mating generally occurs in May. Males establish a harem of 3-20 females and a territory surrounding them. The pups from the preceding season are born from late May to early June. Shortly after giving birth (about 2 weeks), the female is impregnated again. Sixty to sixty seven percent of all females are impregnated every year. Implantation of the fertilized egg is delayed for three months giving Steller's sea lion a twelve-month gestation period. The mothers feed the new pups for a minimum of three months and sometimes up until the next pup is born. The pups are able to swim after one month, and can catch food after approximately three months. The age of maturity is 3-6 years for females, and 3-7 years for males. On average, females live 30 years. Males, which are subject to injury in violent encounters with other males, typically live only 18 years.
Behavior: Bulls are extremely aggressive and territorial. They come to the breeding ground in May, and this is when the fighting begins. They fight by throwing their huge bodies up against one another and biting. The strongest bull is the male with the largest harem. They are rarely found in captivity. Because of their belligerent nature, they are thought to be too dangerous for zoos and un-trainable for circuses. They can dive about 150 m.
Remarks: They are classified as endangered (IUCN). The Western Alaskan population was reclassified as Endangered in April 1997. This is due to a number of causes: First, thousands were killed each year in the nets of fishermen in Alaska. Changes in fishing techniques and gear in 1984 reduced the number killed. Yet, an unknown number are shot each year during commercial fishing because this species is seen as a pest to the industry. The intense commercial fishing of pollock, a major food source, has decreased the Alaskan population from 175,000 animals in 1962 to 40,000 in 1992. They are also caught in plastic trash, which usually leads to death. This species is also hunted on a small scale for subsistence and for trade.

Genus *Neophoca* Gray, 1866

One species.

Neophoca cinerea (Péron, 1816)
Australian sea-lion; white-capped sea lion

Etymology: *Neophoca* means "new seal." The specific name *cinereus* comes from the Latin "ash colored." It refers to the color of females and juvenile males.
Size: Neonates range between 60 and70 cm in length and 6 and 7 kg in weight. Adult males are 2.0 to 2.5 m in length and may weigh up to 300 kg. Adult females are 1.3 to 1.8 m and weigh up to 110 kg.
Distinguishing features: They show sexual dimorphism in terms of both body size and shape and color. Although both males and females are silvery gray to fawn above and creamy below during the first two years of life, maturing males acquire some spotting on the chest and their muzzle darkens to a rich chocolate brown, and the top of the head and nape become whitish (in earlier times this led to its being called the counselor seal).
Distribution: Confined entirely to Australia.
Habits: They are found in cool but not cold waters in temperate and sub-temperate areas. They are generally coastal mammals, spending their time on beaches, offshore rocks, and islands.
Food and feeding habits: Eared seals eat 14-27% of their body weight of food per day. They concentrate in areas where the rising current can bring in an abundance of nutrients. They feed on organisms of the open sea and sea bottom, including fish, lobster, and octopus.
Reproduction: The gestation period is 8-9 months. They are polygynous with the male keeping a harem of over 80 females. From May through October the seals are in the water, after which the mating bulls come ashore. The bulls battle for beaches before the cows arrive; the first cows arrive 2-3 weeks later, two days before giving birth to pups. Cows lactate for 117 days, and will not give birth again for 17-18 months, making this species unusual among the pinnipeds in having a supra-annual pupping interval. Females make frequent trips out to the surrounding waters to collect food for their pups.
Behavior: They are very social, concentrating in groups that become larger during the mating season. Large size is favored not only because a larger bull is stronger and can better defend his harem, but also because larger bulls have a lower metabolic rate. Due to the strain put on a successful bull, he is able to remain dominant for only 2-3 mating seasons. The expected life span of eared seals is 25 years.
Remarks: There are presently only about 3,000-5,000 Australian sea lions in existence, but the population is described as being stable. They are protected by the Australian government, as a substantial sea lion viewing industry has developed there. Historically, they have been taken by native Aborigines as a food source.

Genus *Phocarctos* Peters, 1866

One species.

Phocarctos hookeri (Gray, 1844)
Auckland sea-lion; New Zealand sea-lion; Hooker's sea-lion

Etymology: The name *Phocarctos* derives from the Greek *phoce*, for "seal" and *arktos* for "bear." Sir Joseph D. Hooker, a British botanist, secured the first specimens during the British Antarctic Expedition of 1839-1843.
Size: Adult males are 2.0 to 3.25 m long and weigh up to at least 400 kg; adult females are 1.6 to 2.0 m and can weigh 160 kg.
Distinguishing features: Sexual dimorphism is obvious. Bulls have well developed neck and chest, covered with a mane of hair that is rougher and longer than that on the rest of the body (which females lack). Pups are dark brown with a lighter crown, nape, and nystacial area.
Distribution: In the Auckland islands off New Zealand.
Habits: They inhabit the sandy beaches. The pups explore freshwater creeks and pools behind the beach for about their first six months, until their mothers introduce them to the sea. When not in the sea or on the beach, the sea lions can be found resting deep in the forest or on the tops of grass covered cliffs.
Food and feeding habits: They feed on octopi, small fish, crabs, mussels, and penguins. They swallow pebbles (gastroliths) to aid in digestion. Their intestines may contain numerous gastroliths of irregular shapes. They vomit these gastroliths, as many as 20 at a time, along with squid tentacles and small fish. They do not leave their territory to feed during the breeding season. They opportunistically follow fishing vessels and feed on discarded or escaped fish.
Reproduction: Adult males flock to breeding beaches between October and early November; pregnant females arrive one month later. Cows come into estrus six to seven days after giving birth and matings take place from mid December to mid January. Copulation takes place on the sandy beach and ends when the cow bites at the throat of the bull. All births produce only one pup, which is nursed for about a year. Females produce their first pup around age four. Males become sexually mature around age five, but they do not mate until they are around eight years of age.
Behavior: They establish social hierarchies restricted to subadult and juvenile males. Only these males are able to establish territories, so the conflicts among these males usually occur when defending territories. Adult males are very intolerant of other adult bulls, but they are much more tolerant of the juvenile males and homosexual mounting between the two has been observed. Adult females congregate in large groups on the beach during breeding season. Cows break off into groups of about thirty individuals and depart for the sea. Cows are very tolerant of other females and of their pups.
Remarks: They were abundant at their time of discovery in 1806, but their numbers quickly diminished. They were exploited by settlers and shipwrecked sailors for their hides and oil. There are, at most, 12,500 New Zealand sea lions in existence. They have been legally protected since 1894, but their numbers have remained unchanged in 70 years. ICUN Status is listed as vulnerable.

Genus *Otaria* Péron, 1816

One species.

Otaria flavescens (Shaw, 1800)
South American sea-lion

Etymology: The name *otaria* comes from the Greek *otarion*, meaning "littler ear." It refers of this species' small external ear. The specific name *flavescens* comes from the Latin *flavus*, for "yellowish."
Size: Males grow to a maximum of 2.8 m and weigh up to 340 kg. Females reach 2.2 m and 144 kg. Pups average 0.80 to 0.85 meters in length and 10 to 15 kilograms in weight. Male pups tend to be larger than females.
Distinguishing features: Adult males have a massive neck and a broad head, with a characteristically upturned muzzle and thick mane. The foreparts are so bulky that the hindquarters appear peculiarly feeble by comparison. Females are also powerfully built but are much more evenly proportioned than males, with a smaller head. Pups are black or dark brown above and paler below.
Distribution: They are found along the coasts of South America from southern Brazil, clockwise, to northern Peru, including the Falkland/Malvinas Islands.
Habits: Southern sea lions reside along shorelines and beaches; these beaches usually consist of sand, gravel, rocks, and/or pebbles. They also inhabit flat rocky shelves or cliffs with tidepools and boulders.
Food and feeding habits: They feed on fish, cephalopods, crustaceans, and other invertebrates depending on local abundance. They find their prey in shallower waters to which they travel in schools. When they catch fish, they usually shake the prey in the air and then sometimes eat it whole. In addition, they have been observed eating penguins and female South American fur seals (*Arctocephalus australis*) and their pups.
Reproduction: They are polygynous. Mating season begins from early August to December. Mating behavior includes mutual vocalizations, snout contact, smelling, playful biting, and mouth contact. Males prevent females from leaving the beaches until they have mated. Birth occurs from mid December to early February in the year after mating, with the bulk of births during mid January. The gestation period is about 11.75 months and they usually have only one pup. Mothers seem to not show any gender preference when it comes to nursing, which suggests that the energy spent in development of sons is larger than for daughters during gestation.

In order to nurse their pup, mothers fast for 5 to 7 days. Soon after giving birth, mothers enter estrus and mate again with the male in territory. The mother then leaves her pup behind to find food in the sea. Since they breed synchronously with hundreds of other sea lions, pups are better protected from predators and abduction when the mother is away; this promotes group bonding among pups. However, this group lifestyle also triggers the mother's aggression level toward other female sea lions in defense of her pup. Mothers return from their feeding trips in intervals to nurse the young. They are able to locate their pup by first calling to them and then identifying them by smell. Sometimes mothers are separated from their pup and are not

successful in finding them. Pup mortality can range from 2 to 50%, depending on the size of the population. Larger populations experience higher pup mortality because of the greater risk of pups being trampled to death by adult sea lions. Other causes of pup mortality include terrestrial predators (such as pumas), diseases, parasites, drowning, and starvation when they lose their mothers. Pups spend most of their time in groups or pods playing, sleeping, or residing near the water. They rarely swim into the deeper waters unless accompanied by their mothers. They typically first enter the water at about 3 to 4 weeks of age with other sea lions in a large group. They continue to nurse from their mother for about 6 to 12 months, until the following year when she gives birth to another pup. Even then mothers have been known to nurse both pups simultaneously. Male pups mature later than female pups: male pups reach maturity at 6 years while females mature at 4 years. They both become full sized adults at around 8 years of age.

During development, mothers must be aware of group raids by invading males, who abduct their pups. These raids take place at any time of the day or night but are correlated with the number of females in estrus, their location, and the tide level. The causes may be to obtain female pups soon in estrus, to attract mothers away from their territory for mating purposes, or to signify strength and power. The males kill some pups during these raids. Mothers do not usually leave grounds and try to retrieve the pup if abducted; the mother is helpless in fighting the male because of their much larger size. Some researchers have suggested that males abduct pups to gain practice in controlling females during the mating season.

Behavior: This is a social species. Groups usually consist of multiple females and one to several males who defend the territory. Bulls actively patrol their grounds, threaten intruders, and advertise their territorial boundaries through vocalizations. Fights between the bull and any intruder are rare unless the intruder tries to take over the territory. Bulls let out vocal grunts and attack each other by biting and tearing. Bulls may maintain their territories for 2 to 3 mating seasons. The bull's territory range is highly dependent the presence of cows rather than topological features or size. Each bull typically has 18 cows in their territory. Females tend to choose tidepool areas where temperature is not over 30°C. Young males who have not yet been able to obtain females usually live with other young males in groups of 10 to 40. In these groups, they attempt to raid other male's territories together in order to obtain females. When the temperature gets too cold, they position their bodies so that minimal surface area is exposed to the air; they do this by resting on their belly and covering their forepaws. When it gets too warm, they lie belly up with one hindfoot projected outwards.

Remarks: They experienced a large population decline during the past 70 years in the Falkland Islands for unknown reasons. Though they are not currently threatened, they are protected throughout most of their range.

Family ODOBENIDAE Allen, 1880 walrus

General characteristics: This monotypic family is diagnosed by an obvious ear opening (but without external pinna) and by testes in the inguinal region, between blubber and abdominal muscles.

The most obvious characteristic of the modern walrus, *Odobenus rosmarus*, is a pair of elongated ever-growing upper canine teeth (tusks) found in adults of both sexes. A rapidly improving fossil record indicates that these unique structures evolved in a single lineage of

walruses. The modern walrus is a large-bodied shallow swimmer feeding principally on benthic invertebrates, especially mollusks.

Other diagnostic characters include:
1. Antorbital process formed from both the frontal and maxilla.
2. Distal trochlea (pulley-shaped) of humerus with diameter of medial lip greater than diameter of capitulum.
3, Distal portion of radius with enlarged radial process.
4. Insertion for follicle extensor muscle on first metacarpal developed as a pit or roughened surface.
5. Scapholunar with a distinct pit for the magnum (a wrist bone).

One species.

Genus *Odobenus* Brisson, 1762

Odobenus rosmarus (Linnaeus, 1758)
Walrus

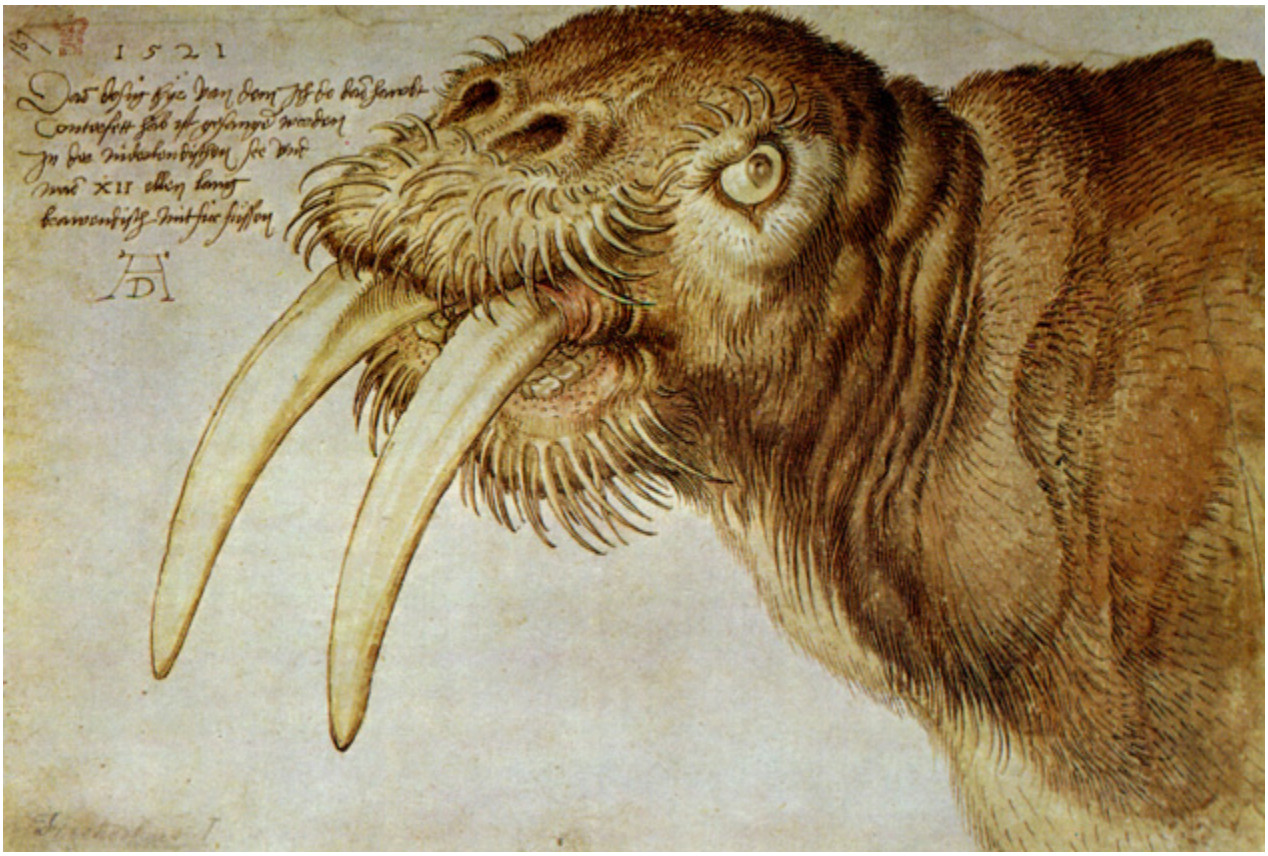
Etymology: *Odonus* or *odonto* (Greek) means "tooth"; *baino* (Greek) means "I walk," referring to the fact that tusks are sometimes used to help the animal to move about, thus, "tooth-walker." *Rossmaal* or *rossmaar* (Norwegian) is derived from the Scandinavian word for walrus.
Size: 1.0-1.4 m, 35-85 kg (neonate); 2 m, 350 kg (weaning); 2.3-2.6 m, 560-1000 kg (adult female); 2.7-3.2 m, 900-1600 kg (adult male)**.**
Distinguishing features: Squarish head with a large moustachial pad and many short stiff vibrissae; enlarged upper canines (tusks); thick, wrinkled skin with short hair; tail contained in folds of skin. Dentary formula: I1/0, C1/1, PC3/3 each side.
Distribution: This species is divided into three species based on their respective distributions:
O. r. rosmarus: In the Atlantic-Arctic from eastern Canada to the Kara Sea.
O. r. laptevi Chapskii, 1940: Eastern part of the Kara Sea, the Laptev Sea, and western part of the East Siberian Sea.
O. r. divergens (Illiger, 1815): In the Pacific-Arctic.
The three subspecies differ slightly in physical characteristics (weight and body length) and in geographic distribution. Pacific walruses are a little larger than their Atlantic counterparts, and the Laptev Sea populations are of intermediate size.
Habits: They usually occupy coastal to offshore areas on sea ice, using shore haulouts in summer and autumn. They prefer areas with ice floes in the shallower regions near the coasts of Arctic waterways. Their seasonal migration patterns coincide with the changes in the ice. In the winter, walruses move south as the Arctic ice expands, and in the summer they retreat north as the ice recedes. This migration can cover distances of 3,000 km. Individuals concentrate where the ice is relatively thin and dispersed in the winter. In the summer time, bulls may use isolated coastal beaches and rocky islets. Cows and young prefer to stay on ice floes in all seasons.
Food and feeding habits: They feed on benthic animals including mussels, snails, echinoderms, and crabs. There are reports of occasionally preying on fish, seals, and young whales. To search

for food they dive to depths of 10-50 m for between 2 and 10 minutes. They swim headfirst along the ocean bottom, rooting about with their stiff beard bristles in a piglike fashion. When encountering soft-bodied organisms they swallow them whole. Two theories on how walruses eat bivalves have been proposed, and it appears that walruses employ both methods. Walruses crack mollusk shells between their flippers and then eat the soft part. More often, walruses hold the shelled organisms in their lips and ingest the fleshy parts by powerful suction, discarding the shells. Walruses are capable of holding down seals and small whales with their flippers and tearing them apart with their tusks. In the winter, when accompanying the females and young, the bulls apparently eat very little. Unlike what has been published in the past, walruses do not use their tusks to dig up food.

Reproduction: They are polygynous with large mature males having exclusive access to a herd of females for 1-5 days at a time. Mating takes place in January and February underwater. Males successful in attracting females usually hold onto their position for 1-5 days, after which other males generally displace them. Males possess a large baculum (penis bone), up to 63 cm in length, the largest of any mammal in both absolute and relative sizes. Walruses swim at an average speed of 7 km/hr, but can reach maximum speeds of at least 35 km/hr. When a female is almost ready to give birth, she often leaves her herd. After giving birth, she joins a group of other mothers and their young. Female offspring remain in their mothers' group, but young males disperse at around 2-3 years old to join a herd of males. Bulls provide no parental care for the young, but community care of offspring by other females has been observed. Adoptions of orphaned calves have also been documented. The implantation of the blastocyst is delayed for 4 or 5 months, until June or July. Birth occurs 10-11 months later, from mid-April to mid-June, meaning that the total gestation period is between 15 and 16 months. Females give birth to a single, precocial offspring. The social bond between the mother and calf is very strong, and cows are extremely protective of their offspring. Lactation generally lasts for two years, but calves are often able to find food before they are finally weaned. Young bulls become sexually mature at 8-10 years, but are often unable to compete successfully for females until they are at least 15 years old. Females become sexually mature at 6-7 years, and are fully-grown at 10-12 years old. Female fecundity is greatest when cows are 9-11 years old, and at this age they can produce a calf every other year. The interval between births is longer in older females. In the wild, walruses have been known to live for over 40 years.

Behavior: Walruses are very gregarious although males and females segregate each other outside the breeding season with dominance hierarchies based on both body and tusk size. Often they haul out on land or ice floes in herds of up to several thousand individuals lying in close physical contact. When an individual hauls out of the water and seeks a resting spot occupied by a smaller animal, it may throw back its head and point its tusks at the smaller animal. If this does not scare the smaller walrus, the larger one may strike with their tusks, and frequently there is bloodshed. Apparently, walruses prefer to lie in the middle of these large congregations. Groups of males gather in large herds and use a variety of tactics to attract females. These tactics include extensive singing and vocal displays, as well as male-male combat. Males make a variety of clicking and bell-like sounds underwater. They also raise their heads above water and emit a series of sharp clucks and whistles. Occasionally, males engage in physical combat, trying to injure each other by stabbing their tusks into the neck region of the other. These fights generally do not last long and usually end with one bull leaving the area. Tusks can be used for cutting through ice, hooking over ice for stability while sleeping, and

helping to pull the body out of the water. Walruses sometimes use their heads to break through ice up to 20 cm thick. Another unusual feature of walruses is the presence of pharyngeal pockets that open on either side of the esophagus. These pockets can hold up to 50 liters of air and provide buoyancy to the animal when filled. This allows walruses to be able to sleep in an upright position. The pockets may even play a role as a resonating chamber and amplifier for the call they produce during mating season, which sounds like the ringing of a bell.
Remarks: Populations have declined drastically since the early Twentieth century. Thanks to legislation and management procedures, some of these populations have rebounded (as in the case of the Pacific). The Atlantic and Laptev Sea populations remain at low levels.



Albrecht Dürer, "Head of a Walrus" 1521.

Family PHOCIDAE Gray, 1821 Hair Seals

This family is characterized by a fusiform and rotund body, with a short, thick neck; pinna absent; hind flippers cannot rotate forward; flippers with hair on both surfaces; claws at tips of flippers; testes in inguinal region, between blubber and abdominal muscles; 2 or 4 mammary teats. Dentary formula: I2-3/1-2, C1/1, PC5-6/5 each side.

The phocids are unable to turn their hind flippers forward and progression over land is accomplished by undulations of the body. They also have a larger body size in comparison with the otariids, averaging as much as two tons in the northern elephant seal. Several phocids, most

notably the elephant seal and the Weddell seal, are spectacular divers which feed on pelagic, vertically migrating squid and fish at depths of 1000 m or more.

Phylogenetically, they are characterized by:

1. Lack of the ability to draw the hind limbs forward under the body due to a massively developed astragalar process (ankle bone) and greatly reduced calcaneal tuber (in the calcaneum, a heel bone). This is what prevents them from bringing their hind limbs forward during locomotion on land.
2. Pachyostic mastoid region. The mastoid (ear) region is composed of thick, dense bone (pachyostosis).
3. Greatly inflated endotympanic bone.
4. Supraorbital processes completely absent
5. Strongly everted ilia (strong outward bending of the ilium, one of the pelvic bones), accompanied by a deep lateral excavation.

19 species.

Subfamily PHOCINAE Gray, 1821

Genus *Erignathus* Gill, 1866

One species.

Erignathus barbatus (Erxleben, 1777)
Bearded seal; squareflipper; ugruk

Etymology: The generic name is from the Greek intensive prefix *eri* in combination with *gnathos*, for "jaw," referring to the relatively deep mandibles and large cheek cavity. The specific name *barba* comes from the Latin for "beard," referring to the array of long, white vibrissae that dominates the animal's face.
Size: 1.3 m, 35 kg (neonate); 1.5 m, 85 kg (weaning); 2.1-2.4 m, 230-340 kg (adult).
Distinguishing features: Hind flipper with 1st and 5th digits slightly longer than middle three; foreflipper broad and squarish with 3rd. digit longest; 4 mammary teats; vibrissae smooth, thick, straight and bushy; head proportionately small; back and sides gray, silver-gray on belly; pups grayish brown with irregular light patches; juveniles are silver-gray; teeth of adults often worn or missing. Dentary formula: I3/2, C1/1, PC5/5 each side.
Distribution: It has a patchy distribution across the Arctic and Subarctic.
Habits: Bearded seals prefer shallow, arctic waters less than 200 meters in depth. They also prefer broken, drifting patches of ice, although they readily adapt to dense, slow moving ice by making breathing holes. During the warmer months they sometimes climb ashore to gravel beaches.
Food and feeding habits: They eat invertebrates and fish which they locate using their whiskers.
Reproduction: Bearded seals are primarily solitary animals, except during breeding seasons or when females are raising their pups. The gestation period is 11 months, including a dormancy

period of 2.5 to 3 months after conception. This dormancy occurs until July when the embryo starts developing rapidly. They give birth on pack ice in mid-March to late April. Shortly after birth, pups are able to swim and can dive 75 meters deep to escape polar bears. Pups put on weight quickly, especially during the 12 to 18 days of nursing. Pups molt into the adult coat around the time of weaning, which occurs when it reaches approximately 85kg. The female's reproductive cycle is annual and they usually breed a fortnight (2 weeks) after their pups are weaned.
Behavior: They migrate northward with the retreating ice in the spring months, returning southward again as the ice advances in autumn and winter. They ram their head into thin ice in order to create breathing holes. They have been known to dive to a depth of 200 meters; however, they mainly feed in shallow waters. Mature males sing an audible, underwater song during breeding season in order to establish a territory. Female life spans can be up to 31 years while males usually live about 25 years. The main predator of the bearded seal is the polar bear. The seals, when on shore, stay close to the edge of the water for a quick escape if disturbed. They are also hunted in the water by killer whales.
Remarks: Bearded seal populations seem to be stable; estimated population size, excluding Canada and Norway, is 500,000. However, there are some concerns that the population may be declining as a result of habitat loss and other disturbances. Their habitats are in danger from global warming, pollution from oil and gas extraction, and boat traffic. Also, there is a potential for conflict between bearded seals and commercial fisheries, particularly in the central Bering Sea.

Genus *Phoca* Linnaeus, 1758

General characteristics include hind flipper with 1st. and 5th digits slightly longer than middle three; foreflipper with 1st. and 2nd. digits longer than 3rd.; two mammary teats; vibrissae beaded, slender and curled; forehead with concave profile and short snout; eyes closer to tip of the nose than to ear opening; nostrils forming V-shape; sexes of nearly same size; neonates usually with white lanugo.

Two species.

Etymology: *Phoca* comes from the Greek *phoce* for "seal," a term said to be derived from the Sanscrit root *Spha*, meaning "to swell up," referring to the animal's plumpness.

Phoca vitulina Linnaeus, 1758
Harbor seal; common seal; Kuril seal; island seal

Etymology: *vitulina* is from the Latin *vitula*, for "calf," and the suffix *inus*, meaning "like."
Size: 0.7-0.9 m, 9-15 kg (neonate); 0.9 m, 20-27 kg (weaning); 1.5-1.8 m, 75-120 kg (adult).
Distinguishing features: Snout blunt; color variable (gray to tan to brownish-black, with darker spotting); pups gray to tan (white lanugo may be shed after birth in northern populations); pelage on back smooth to touch. Teeth: I3/2, C1/1, PC5/5 each side.

Habits: Coastal year-round, entering rivers and some lakes; commonly haul out on land, sandbars and ledges at low tide; form casual small to large groups; pupping season varies with latitude; molt varies with latitude, occurring 2-3 months after pupping season.
Distribution:
P. v. concolor DeKay, 1842: Coasts of western North Atlantic.
P. v. mellonae Doutt, 1942: In certain freshwater rivers and connecting lakes that flow into southeastern Hudson Bay and James Bay.
P. v. vitulina: Coasts of eastern North Atlantic.
P. v. stejnegeri Allen, 1902: Coasts of western North Pacific.
P. v. richardii (Gray, 1864): Coasts of the eastern North Pacific.
Habits: Harbor seals bask and sleep on coastal islands and ledges as well as beaches and sandbars that are uncovered at low tide. They stay close enough to water to facilitate feeding and mating.
Food and feeding habits: The diet varies with the season and region. Their food consists of crustaceans, mollusks, squid, and a variety of fish. Harbor seals do not chew their food; they either tear it into chunks or swallow it whole. Their molars allow them to crush hard objects like shells and crustaceans. Adults consume around 4.5 to 8.2 kg of food per day, which is 5-6% of their body weight.
Reproduction: Males become sexually mature once a weight of around 75 kg is achieved; females mature at about 50 kg. This occurs between 3 and 7 years of age for males and at 2 to 6 years for females. While the mating season varies between the different subspecies, it generally occurs from late spring through fall. About 6 weeks after they give birth to their previous year's pups, the females come into estrus. The gestation period lasts between 9 and 11 months, and usually only 1 pup is born each year. Pre-mating behavior is exhibited by both males and females, such as rolling, bubble-blowing, and mouthing each other's necks. This behavior ends once mating begins. Males initiate behavior by chasing, playfully biting, and embracing females. Females respond, and the act of copulation usually takes place in the water. One male may mate with multiple females. Harbor seals return to the same breeding grounds every year.
Behavior: They are usually solitary animals, with reproduction and "haul outs" being the only exceptions. Seals "haul out" onto land for various reasons including rest, thermoregulation, giving birth, nursing, molting, and digestion facilitation. Another possible reason for haul outs is protection from predators by being in a group. During haul outs, adult individuals do not make physical contact with each other and respond angrily to touching. Younger seals interact with each other along the edges of the group and stay away from the adults. Aggression is shown by growling, snorting, threateningly waving a foreflipper, and head-thrusting (sharp, rapid retraction of the neck). Vocalization occurs only when they feel threatened.
Remarks: In Canada, Norway, and the United Kingdom, it is legal to shoot harbor seals to protect fisheries or fish farms. Seals also become entangled and drown in fishing nets and gear.

Phoca largha Pallas, 1811
Spotted seal; larga seal

Etymology: The name *largha* is from the Tungus word for this species. The Tungus people live along the shores of the Sea of Okhotsk.

Size: Newborns weigh between 7 to 12 kg, and measure from 75 to 90 cm in length; adults reach 1.5-1.6 m and 82-123 kg in weight.
Distinguishing features: Similar to harbor seal; belly light silver-gray, back and head darker and marked with silver rings, brown to black spots scattered over body; neonates with white lanugo. Teeth: I3/2, C1/1, PC5/5 each side.
Distribution: Throughout the Sea of Okhotsk, in the northern Sea of Japan; south to the Shantung Peninsula in the Yellow Sea.
Habits: Spotted seals are strongly associated with sea ice from fall until late in the spring when they gather among the remaining ice packs. They gather on land when no ice is available.
Food and feeding habits: They feed on crustaceans, cephalopods, and fish. Feeding trips may extend hundreds of kilometers before return.
Reproduction: Breeding takes place in the spring. Breeding pairs meet about 10 days before the pregnancy of the last season reaches term, then mate underwater. Implantation of the embryo is delayed until after the current year's pup is born. Spotted seal pups are born between early April and early May; the peak of the pupping season is in the first part of April. Pups are born with a dense coat of whitish hair that provides insulation until blubber is developed; this fur is shed by 4 to 5 weeks of age, the time at which pups are weaned. Pups can swim if forced to, but prefer not to until the time of weaning, at which time they can dive to depths of over 300 meters to feed. Sexual maturity is reached at 3 to 4 years of age in females, and 4 to 5 years of age in males.
Behavior: Being gregarious animals, spotted seals form large groups of up to several thousand when they haul out for pupping and molting season. They are wary animals that crawl on ice floes and are difficult to approach in the open.
Remarks: They are not considered endangered. Their populations have remained relatively stable in the territorial waters of the North American continent countries due to conservation efforts.

Genus *Pusa* Scopoli, 1771

Three species.

Pusa hispida (Schreber, 1775)
Ringed seal; fjord; jar seal; natchik; netsik; floe-rat

Etymology: The specific name is from the Latin *hispidus*, meaning “hairy” or “bristly,” in reference to the coarse pelage of the adult. An obsolete specific name *foetida*, refers to the strong odor characteristic of males during the breeding season.
Size: 0.6-0.7 m, 4-4.5 kg (neonate); 0.8 m, 9-16 kg (weaning); 1.2-1.5 m, 60-100 kg (adult).
Distinguishing features: Head narrow with somewhat pointed nose; back dark gray with light rings, belly silver-gray; neonates with white lanugo; older pups dark gray above, silvery below; pelage on back coarse, harsh to touch. Teeth: I3/2, C1/1, PC5/5 each side.
Distribution:
P. h. hispida: circumpolar in the Arctic Ocean.
P. h. botnica: (Gmelin, 1788): Baltic Sea.
P. h. ladogensis: (Nordquist, 1899): Lake Ladoga, Russia.
P. h. saimensis: (Nordquist, 1899): Lake Saimaa, Russia.

P. h. ochotensis (Pallas, 1811): Western, northern, and northeastern parts of the Sea of Okhotsk.
Habits: They prefer areas that freeze to stable ice in winter. They live in darkness under ice for several months during the year. Ringed seals make lairs in the snow and ice for protection from predators and thermal shelter. They can occupy ice-covered areas by maintaining breathing holes and breathing through cracks in the ice. They make their lairs by rubbing away the ice with their fore flippers.
Food and feeding habits: They feed mostly on small fish and a variety of crustaceans.
Reproduction: Females mature at about 6 years of age and may bear one pup per year. Most mating occurs in late April and early May, which is within one month of parturition. Males are thought to be polygynous and probably hold underwater territories. Although mating occurs in May, the blastocyst does not implant until August or September. The gestation period is approximately 240 days. Ringed seals require solid ice for pupping, which makes the pups more vulnerable to predators. Pups are sometimes preyed upon by bears, foxes, and humans when in the birth lair; as a result, ringed seal pups spend a large proportion of time in the water and learn to dive at an extremely young age.
Behavior: Adult seals are solitary except for loose feeding aggregations in the water in summer. Starting in mid-May, ringed seals haul out onto the ice and bask in the sun. They molt at this time and do not feed very much. Groups of seals at haul out sites are large and seals lying on the ice are vigilant and aggressive.
Remarks: This is a very common species. The population is estimated at 2,500,000-7,000,000.

Pusa caspica (Gmelin, 1788)
Caspian seal

Etymology: The specific name refers to the Caspian Sea, where it lives.
Size: It reaches a maximum length of 1.5 m and 86 kg of weight. The females are slightly smaller.
Distinguishing features: Adults are deep gray on the back and grayish white on the belly. Most individuals are liberally spotted on the back.
Distribution: Isolated to the Caspian Sea.
Habits: They are generally found on rocky islands and floating ice. They can be found less commonly along the shoreline. Because of their seasonal lifestyle, these seals can be found in different parts of the Caspian at different times of year
Food and feeding habits: They eat a wide variety of fish and various types of crabs.
Reproduction: Caspian seals have a gestation period of about 11 months. The pups are born from late January to early February. Females give birth to one pup at a time, which usually weighs about 5 kg at birth. The mother seal nurses the pup for approximately one month before it is weaned, at which time the she mates again. Sexual maturity is not reached until females are at least 5 years old; male seals reach maturity between the ages of 6 and 7 years. Mating season for Caspian seals begins in March and last through early April. There is some evidence that indicates Caspian seals may be monogamous.
Behavior: They spend most of their time in large colonies. In the winter they are found in the northern part of its range while in the summer, when the northern ices melt, they migrate to the

southern parts of the Caspian Sea, where the waters are deeper and therefore cooler at that time of year. From January until the end of April, they pup, nurse, mate, and molt. After the pups are born, adult males are not permitted into the breeding ground until the pups are about two weeks of age, at which point mating takes place (February to mid March). Recently, some females have been observed pupping on islands in the southern portion of the Caspian Sea, where they give birth separately and not in colonies. After breeding, the seals then molt. After molting, the colonies migrate south to feed and form new colonies. A few seals remain in the north to feed, but recent studies show that these seals are usually sick or dying.
Remarks: Pesticides and industrial pollutants that affect their reproductive system threaten them: in 1997, more than 70% of female Caspian seals were infertile. They were hunted extensively in the 19th and 20th centuries and although are now protected by hunting limitations, continue to be a target for poachers. The downfall of the Soviet Union has been particularly hard on the seal population, as many people hunt the seals as a result of economic hardship. The extent of this kind of hunting is unknown. Due to increasing pollution from pesticides and industrial waste, large numbers of dead Caspian seals are found on the Apsheron peninsula on the western shore of the Caspian Sea.

Pusa sibrica (Gmelin, 1788)
Baikal seal

Etymology: The specific name refers to this species relict distribution in Siberia.
Size: At birth, pups weigh around 3 to 4 kg and measure from 65 to 70 cm in length. Males grow to 142 cm and 66 kg of weight, and females to 135 cm and 63 kg.
Distinguishing features: It differs from its close relative the Caspian seal by the unspotted (or rarely spotted) appearance of its pelage. Also, its fore flippers and fore claws are larger and stronger.
Distribution: Essentially confined to the Baikal Sea.
Habits: This is the only seal that lives primarily in freshwater. It is also found in rivers connecting Lake Baikal. Ice conditions in the lake determine the seasonal movements and activities of these seals. In winter the lake is covered by ice that is 80 to 90 cm thick.
Food and feeding habits: They feed on pelagic fish species as well as invertebrates. Most foraging for food occurs at twilight and during the night. Young seals have been observed feeding up to 100 m in depth. They have also been observed doing some short duration dives, most of which last under 10 minutes. Maximum diving time is estimated to be around 20 to 25 minutes, although some seals that are frightened can stay under 2 to 3 times longer.
Reproduction: Mating takes place in the water around the time the last pup is weaned, usually in May. Females experience a short period of delayed implantation. Gestation lasts for about nine months and the pups are born on lake ice from mid-February to March. Twins are possible but uncommon; usually only one pup is born. If there are twins, both of them usually survive to weaning and then stay together for some time. They are covered with a long, white, woolly coat that lasts for the first 6 weeks and then is shed and replaced by an adult coat. Mothers nurse their pups for 2 to 2.5 months, except in the southern part of the lake where the ice breaks up earlier. Pups in the south are weaned prematurely and, as a result, are smaller. They are polygynous. Females tend to reach sexual maturity at 3 to 6 years of age and males at 4 to 7 years of age.

Females can breed until they are about 30 years of age. About 88% of sexually mature females have pups each year.
Behavior: During the winter, these seals are solitary. They usually molt on ice in late spring, but if the ice has already melted they finish their molt on shore. In 1990 and 1991, a number of juvenile seals were radio tagged. This tagging revealed that the seals traveled between 400 and 1600 km around the lake from September to May. During the winter months, when the lake is primarily covered with ice, Baikal seals stay near breathing holes they have made. They keep these holes open by scraping them with their strong claws. Some seals may also use their head, teeth, and rear flippers. Adult seals have one breathing hole, but this hole has many auxiliary openings. Immature seals only use one breathing hole. Baikal seals are most wide ranging during the winter months. Mature males scatter throughout the lake. Mature females are usually found on the east shore. Male and female seals that have not yet reached sexual maturity are found on the west shore. Pregnant females remain on the ice for most of the winter. At around the first of April, Baikal seals begin to come together to feed along new openings where the ice has melted. In May they move to the north end of the lake and stay there until they molt, which usually occurs in late May and early June. During the summer months, Baikal seals move to the southeast corner of the lake to use the rocks and shore for hauling out. When fall returns, they again begin to move to the areas where ice is forming. Baikal seals are solitary animals, but several seals may congregate and share access holes. They will also gather at places where the habitat is most favorable. In spring, when they feed the most, 200 to 500 animals will gather in one area. The first to come are juveniles, then adult males, and, finally, new pups and their mothers. Large groups also form on the shores in the summer.
Remarks: Populations are on the decline, yet hunting is still legal. Pollution from the paper industry is another cause of mortality. In 1987-88 about 5,000 Baikal seals died from an infection caused by a form of Canine Distemper Virus. It is thought this virus was transmitted from dogs or other land mammals.

Genus *Halichoerus* Nilsson, 1820

One species.

Halichoerus grypus (Fabricius, 1791)
Gray seal; horsehead; Atlantic seal; Atlantic gray seal; Baltic gray seal

Etymology: The scientific name comes from the Greek *halios*, "of the sea," *khoiros*, "a pig," and *grupos* "hook-nosed." in reference to its high Roman nose.
Size: 0.8-1.0 m, 11-20 kg (neonate); 1.1 m, 40-45 kg (weaning); 1.8-2.1 m, 100-180 kg (adult female); 2.2-2.4 m, 200-300 kg (adult male).
Distinguishing features: Hind flipper with 1st and 5th digits slightly longer than middle three; foreflippers with long, slender, curved nails and 3rd digit shorter than 1st. and 2nd.; vibrissae beaded, slender and curled; snout long with straight or convex profile; nostrils W-shaped; eye closer to ear than to nose; 2 mammary teats; males distinctly larger than females; pelage coarsely spotted, with dark spots on a tan-gray background in females, and lighter spots on a dark background in males; juvenile coloration less distinct; neonates with white lanugo for 2-3 weeks. Teeth: I3/2, C1/ 1, PC5/5 or 6/5 each side.

Distribution: Confined to the northern North Atlantic.
H. g. grypus: Western Atlantic.
H. g. macrorhynchus Hornschuch and Schilling, 1851: Baltic Sea.
Habits: They prefer remote exposed islands, sandbars and shoals.
Food and feeding habits: They feed on fish, cephalopods, and crustaceans. Occasionally they take seabirds.
Reproduction: Strong sexual dimorphism is observed, with males being up to three times the size of females. Females become mature at ages 4 to 7 and males at ages over 10 years. Gestation lasts 11.5 months including a delay of implantation of 3 months. The pregnancy rate is assumed to be between 80 and 90%. The longevity for females is 46 years, and for males 26 years. Adult female mortality ranges from 6 to 14% per year. First year mortality is, depending on the location, 34-60%.
Behavior: While the young seals disperse widely in the first few years of their lives, the adult gray seal is typically sedentary about the vicinity of its breeding colonies. Colonies are known to range in size from 100 to almost 9,000 individuals. Orcas are their main predator. They have good vision underwater, functional vision in air, and vision is adaptable to the darkness of ocean depths. Hearing is acute both above and below the water's surface.
Remarks: Only the Baltic stock is still in danger, mainly because of the pollution of the Baltic Sea with organo-chlorines (DDT, PCB). Also, net and fishing gear entanglement is a serious problem there.

Genus *Histriophoca* Gill, 1873

One species.

Histriophoca fasciata (Zimmermann, 1783)
ribbon seal

Etymology: The specific name comes from the Latin *fascia*, for "band," referring to the white, ribbon-like bands on the adult's pelage.
Size: 0.9 m, 9-11 kg (neonate); 0.9-1.1 m, 28 kg (weaning); 1.5-1.8 m, 80- 140 kg (adult).
Distinguishing features: Adult males with white bands on dark brown to black background, females with less distinct bands on lighter background; neonates with white lanugo; juveniles blue-gray on back, paler ventrally. Teeth: I3/2, C1/1, PC5/5 each side.
Distribution: Mostly in the Bering, Chukchi, and Okhotsk seas, but also the western North Pacific also, as well as in the Sea of Japan.
Habits: They are restricted to the cold waters of the northern Pacific. In winter and spring they forage and raise offspring on coastal ice flows; the summer months are spent in the open ocean.
Food and feeding habits: They feed on fish, squid, octopi, shrimp, and crabs.
Reproduction: Adult females become pregnant once a year, typically giving birth to one pup sometime in April or May. Nursing lasts up to a month, a time during which the weight of the pup will double. As soon as the pups are weaned, adults will mate again. They employ a delayed implantation of two or three months; this is most likely to assure the presence of ice at the time of birth. After weaning, pups spend a lot of time practicing diving and learning how to move on the ice.

Behavior: They are mostly solitary. They rest on the ice, often very far from the water, apparently unconcerned with the threat of predation, as they will allow their young to wander far from the mother's location for long periods of time. Females shelter their pups. As ice begins to melt in the late summer, some populations move further north with the receding ice-line. Most populations become pelagic in the summer months. Ribbon seals slither along the ice using side-to-side motions to propel them, rather than inching forward with the front flippers as do other seals.
Remarks: The main anthropogenic problem facing ribbon seals is the occasional accidental netting of individuals in Pacific fishing areas. They have an interesting structure on their trachea; the anterior portion is connected to a large air sac. This sac is present in both sexes, although it is much larger in males. There is no similar structure in any other species of seal, and its function is unknown.

Genus *Pagophilus* Gray, 1844

One species.

Pagophilus groenlandicus (Erxleben, 1777)
Harp seal

Etymology: *Pagophilus* means "lover of ice." The specific name refers to Greenland, which is approximately the center of distribution of this species.
Size: 0.8-1.0 m, 7-12 kg (neonate); 1.0 m, 30-35 kg (weaning); 1.7-1.9 m; 120-180 kg (adult).
Distinguishing features: Dark harp-shaped pattern on back and sides, white to tan background (pattern less distinct in females), with dark head; neonates with white lanugo, juveniles gray to tan with darker spots. Teeth: I3/2, C1/1, PC5/5 each side.
Distribution: In the northern North Atlantic.
Habits: They live in the open sea on the edge of the pack ice. They are dependent on the ice for breeding and molting. They prefer rough, hummocky ice at least 25 cm thick, and they maintain natural holes 60-90 cm in diameter for purposes of access to water and breathing. During the breeding season, up to 40 seals may share a breathing hole.
Food and feeding habits: Harp seals are carnivorous. They feed on fish as well as crabs and other invertebrates.
Reproduction: Sexual maturity is reached in males at 6 years and in females at 5 years. The reproductive season for harp seals is from the end of February to the end of March. The seals migrate south to breed and molt. Males fight for access to females by using their teeth and flippers. Mating occurs on the ice and the seals are monogamous for the season. Gestation lasts 11.5 months, with 4.5 months dormancy of the fertilized ovum (delayed implantation). Females give birth to one pup, occasionally to twins. The pups weigh about 10 kg and are suckled for about 12 days. The milk is rich in fat and mostly becomes blubber; pups can gain up to 2 kg a day while nursing. During lactation, the mother feeds on little if anything at all. After weaning, the young spend up to 10 days alone until their embryonic hair is replaced by proper fur.
Behavior: They are solitary animals except during breeding season, when tens of thousands of individuals come together. There is no social organization in these aggregations. The seals seem to be seasonally monogamous. They migrate south in autumn and retreat north in summer with

the receding ice pack. The migration can total 6,000-8,000 km. Harp seals are powerful high-speed swimmers capable of moving quickly on the ice and diving to depths of over 900 ft. Their senses of vision and hearing are very acute, especially under water.
Remarks: Although there are large numbers of these seals, many are killed by hunters each year. Currently, the population is over 2 million. There are 3 populations of harp seals: One breeds in the Gulf of St. Lawrence off the coast of Newfoundland, another breeds north of Jan Mayen Island in the Greenland Sea, and the third breeds in the White Sea. These populations are steady in terms of number of seals, and the species is classified as being of least concern for extinction. Predators of the harp seal include sharks and killer whales.

Genus *Cystophora* Nilsson, 1820

One species.

Cystophora cristata (Erxbelen, 1777)
Hooded seal; bladdernose seal

Etymology: The generic name is from the Greek *kustis*, "a bladder," and *phoros* "carrying," in reference to the inflatable nose and nasal sac that are the most distinctive features of adult males. The specific name comes from the Latin *crista*, "a crest," again in reference to the proboscis.
Size: 0.9-1.1 m, 15-30 kg (neonate); 2.0-2.2 m, 150-300 kg (adult female); 2.3-2.7 m, 200-375 kg (adult male).
Distinguishing features: Hind flipper with 1st and 5th digits much longer than middle three; adult males with inflatable hood extending from crown of head to upper lip and inflatable nasal sac; adult males larger than adult females; 2 mammary teats; body gray with irregular black patches, face dark; neonates blue-gray on back, white on belly, with dark face. Teeth: I2/ 1, C1/1, PC5/5 each side.
Distribution: Over deep waters of the North Atlantic.
Habits: They live mainly at the edge of large ice packs and migrate to deep waters.
Food and feeding habits: They eat deep-sea fish, shrimp, octopus, and mussels. Adults do not feed while breeding or molting, but actively feed during the rest of the year.
Reproduction: Pups are born during March and April after a gestation period of 11.7 months, which may also include a period of four months when the fertilized egg is dormant and does not develop. They usually give birth to one pup at a time. Pups are weaned after only four days of nursing due to the high fat content of the milk (the shortest nursing period for any mammal). They lack an embryonic coat at birth and are blue in color with light gray bellies and black faces.
Behavior: The hooded seal is mainly a solitary animal. The most unusual behavior of the hooded seal is related to the males' trunks: when a male is mating, excited, or threatened, the trunk is inflated. To accomplish this, the male closes one of his nostrils, resulting in the trunk blowing up to as large as twice the size of a football. The inflated trunk forms a crest or a hood on top of the head. This trunk begins to form in young males around 4 years of age and is finished developing at around 12 years. The size of the trunk depends on the body size of the individual, but the average is 6.3 liters.

Remarks: There is evidence for hybridization between *Pagophilus* and *Cystophora*. The total population of hooded seals is not at risk even though it is subject to hunting. The natural predators of the hooded seal are polar bears and sharks.

Subfamily MONACHINAE Gray, 1869

Genus *Monachus* Fleming, 1822

Etymology: The name *monachus* is from the Greek *monakhos*, "a monk, solitary" because J. Hermann, who described it, thought that the smooth, round head resembled a human head covered with a hood, and the shoulders and the short flippers extended like two elbows beyond a scapular covering a frock.

Three species (one recently extinct).

Monachus monachus (Hermann, 1779)
Mediterranean monk seal

Etymology: The same for the genus.
Size: At birth, pups usually measure 80-120 cm and 15-26 kg. Adults may reach 3 m long and 400 kg in weight. There is no major sexual dimorphism in size.
Distinguishing features: There is a considerable variation in color among adults, especially in females. There is a cowl-like effect of the rolls of fat on the neck, seen particularly when the head is drawn back.
Distribution: From an original distribution that included from about 20° N along the Atlantic coast and offshore islands of northwestern Africa, into and throughout the Mediterranean Sea, and in at least the southwestern, southern, and southeastern Black Sea. Today, they are present only in small portions of the original range.
Habits: They are usually found along coastal waters, especially on the coastlines of islands. They are sometimes found in caves with submarine entrances when the female is giving birth or just to get away from other disturbances, such as boats.
Food and feeding habits: They feed in shallow coastal waters on a large variety of fish and cephalopods such as octopus.
Reproduction: They mate between the months of September and November. Mating usually takes place in the water. They reproduce very slowly starting at the age of four. The average time between births is 13 months, and the gestation period is 11 months. When females give birth, they go on the beach or in caves. A female will usually remain on the beach or in the cave nursing and protecting the pup for up to six weeks. During this time, the female must live off of stored fat because she never leaves the pup, not even to feed herself. The pup may remain with its mother for as long as three years even after weaning.
Behavior: They are diurnal and spend most of their time in a limited area, never migrating long distances. There can be up to 20 individuals in a colony of Mediterranean monk seals. On land, the seal is a solitary species. In the water, they are very good divers and swimmers; they swim so well that they can outmaneuver a shark. When communicating with each other they make

very high-pitched sounds. This is done mainly while in the water to let each other know if something is wrong or if danger is approaching.
Remarks: There are between 350 and 450 individuals left today which makes this species the most endangered pinniped. They have been killed by fishers who see them as competition, accidentally by nets, by pollution, and boat strikes.
They are very sensitive to disturbances. Pregnant females are especially sensitive and will often abort when disturbed.

Monachus tropicalis (Gray, 1850)
Caribbean monk seal; West Indian monk seal

Etymology: The name *tropicalis* merely refers to the tropical distribution of this species.
Size: Males reached 2.1 to 2.4 m, and females were slightly smaller.
Distinguishing features: Similar to other monk seals. Pelage brown on the back, with a gray tinge, lighter on the sides, and pale yellow or yellowish white on the undersides and muzzle.
Distribution: Originally throughout the Caribbean and Gulf of Mexico. It is now extinct.
Habits: In small isolated islands and beaches.
Food and feeding habits: No information available.
Reproduction: No information available.
Behavior: No information available except that they were very tame and loud.
Remarks: Last ones seen alive were in 1952.

Monachus schauinslandi Matschie, 1905
Hawaiian monk seal

Etymology: The specific name honors H. H. Schauinsland, a German scientist who in 1899 obtained (from a guano collector on Laysan Island) the skull used in the original description of this species.
Size: 1.0 m, 16-18 kg (neonate); 1.0 m, 56-86 kg (weaning); 2.1-2.2 m, 175 kg (adult male); 2.3-2.4 m, 200-275 kg (adult female).
Distinguishing features: Hind flipper with reduced claws, and 1st and 5th digits much longer than middle three; vibrissae smooth; four mammary teats; females slightly larger than males; pelage dark gray above, lighter below; neonates black. Teeth: I2/2, C1/1, PC5/5 each side.
Distribution: They are now regularly seen on all of the main Hawaiian islands, particularly on Kauai.
Habits: Hawaiian monk seals frequent reefs (for feeding), beaches (for basking and delivering their young), and coves. They spend a great deal of time wallowing in damp sand at the water's edge, presumably to avoid overheating.
Food and feeding habits: They feed mainly on fish, octopus, and lobster. They forage in depths from 10-40m along the slopes of coral reefs.
Reproduction: Females mature at about five years of age. Only 60- 70% of adult females give birth in a given year. Mating takes place underwater. Most births take place from March-June

after a gestation of 11 months (including a period of delayed implantation). Females give birth and suckle their young on sandy beaches with or without shade, and sometimes on rocky shores. They usually give birth to just one pup per gestation. Pups have soft, black hair that is molted after 3-5 weeks into a coat that is silver-blue dorsally and silvery-white ventrally. They are weaned at about six weeks. Males outnumber females 3:1, so when a group of males spots a female in estrus they sometimes mob her, inflicting serious or mortal wounds in their eagerness to mate.
Behavior: They are mostly nocturnal, solitary and do not migrate, although certain individuals may disperse over long distances. In some cases females will sometimes foster another female's youngster. Approaches by large dominant males elicit submissive behavior from other seals. Females with pups are extremely sensitive to disturbances; they will threaten, or if necessary, attack invaders. These aggressive interactions among females often lead to pups switching mothers. Females fast for 2-3 months after weaning their young.
Remarks: It was thought that the last monk seal in the Pacific was killed in 1824. Other factors affecting them since then have been disturbance by humans, shark predation, and disease. They were declared endangered in 1976. Downward counts in the population seemed to be reversed in the 1980's, and the count is now approximately 1400 individuals. The greatest threats are the disturbance of the mother during her breeding season (which causes her to find a new, less preferred site to give birth and nurse), ciguatera poisoning from reef fishes, and shark attacks. All but two of the Leeward Islands are protected from exploitation under the Hawaiian Islands national Wildlife Refuge. Of the protected islands, three are inhabited by humans: Green Island in Kure Atoll, Sand Island in Midway Atoll, and Tern Island in French Frigates Shoal. Hawaiian monk seals are unique because despite being completely tropical phocids they have no obvious anatomical adaptations for a warm habitat. Their blubber content is equivalent to that of polar seals. They appear to have adapted to warm climates by staying inactive during the day. Another unique aspect of the biology of these seals is that their ear structure is very primitive.

***Genus Mirounga* Gray, 1827**

Etymology: *Mirounga* is derived from *miouroung*, the Australian aboriginal name for this species.

Two species.

Mirounga leonina (Linnaeus, 1758) **Southern elephant seal**; southern sea-elephant

Etymology: The specific name is derived from the Latin *leoninus*, for "lion," possibly referring to the male's roarlike threat vocalization.
Size: At birth, size is about 1.3m and 40-50 kg. Adult males measure as long as 5 m and can weigh as much as 3700 kg. Females are considerably smaller, ranging from 350-600 kg.
Distinguishing features: Adults are yellowish brown to dark brown most of the year, slightly darker ventrally than dorsally. Males have an elongated nose, first noticeable at puberty.
Distribution: Throughout the Southern Ocean around the Antarctic continent.

Habits: Oceanic islands.
Food and feeding habits: Deepwater, pelagic fish and squid.
Reproduction: They have a well-developed polygynous breeding system. Males arrive at the beaches in August and pregnant females arrive in September or early October, giving birth within five days. Pups are nursed for about 23 days, with the female entering estrus about four days before weaning.
Behavior: They aggregate in large numbers during the mating season. They migrate over large areas. Both males and females frequently exhibit vocalizations, with males making loud booming calls and females having a high-pitched, yodeling call.
Remarks: They were hunted extensively by Australian aboriginals as well as along the Argentinean and Chilean coasts. They have recovered in some areas. Worldwide population is estimated to be 650,000 individuals, with threat status being of least concern.

Mirounga angustirostris (Gill, 1866)
Northern elephant seal; northern sea-elephant

Etymology: The specific name is derived from *angustus* (Latin) meaning "narrow," and *rostrum* (Latin), meaning "snout," referring to the fact that the snout of this species is narrower than that of the southern elephant seal.
Size: 1.2 m, 30-45 kg (neonate); 135-175 kg (weaning); 2-3.2 m, 900 kg (adult female); 4-5 m, 2000-2500 kg (adult male).
Distinguishing features: Hind flipper with reduced claws and 1st and 5th digits much longer than middle three; adult males with inflatable proboscis that may overhang mouth; 2 mammary teats; males larger than females; color gray to brown with no markings; neonates black; adult males with thick, cracked and scarred skin on the neck and chest. Teeth: I2/1, C1/1, PC5/5 each side.
Distribution: Northeast Pacific Ocean, coastally from Baja California to southern Alaska.
Habits: Northern Elephant Seals reside terrestrially on the sandy, rocky or muddy shores of the coastline, particularly on offshore islands. They spend only 10% of their time on land, during reproduction and molting, and 90% in the water, diving and foraging for food. Only 11% of this time in the water is spent at the surface. These animals can dive exceptionally deep to recorded depths of 500 to 600 meters on average and for extended periods of time (20 to 70 minutes).
Food and feeding habits: They dive into the water repeatedly and continuously to find food, never stopping to rest or sleep for months at a time. Females and males feed separately from each other. Males travel north, remain closer to land, and tend to return to the same locations to feed year after year. Females migrate away from the land, west to the open ocean, and are less accurate in returning to the same places each year. Males forage by benthic dives while females are pelagic foragers. While elephant seals are on land they are fasting; they go for extended periods of time without food while they are reproducing and molting. Hydration comes from food sources and broken down fats. In addition, they have developed physiological methods to retain water, such as producing concentrated urine. Another interesting phenomenon about these mammals is the behavior of eating stones before coming ashore. The true purpose of this behavior is not known. The stones are eliminated when they re-enter the water for migration, so it has been suggested that this phenomenon is in response to the long period of fasting.

Reproduction: Northern Elephant Seals haul out for birthing and breeding from December to March. Females come into heat only 19 days after giving birth. They remain receptive for about four days, during which mating occurs. Females become sexually mature at two years of age, but usually begin giving birth in the 4th year of life. Males are sexually mature at the age of six or seven, but only occasionally are allowed to mate before they reach the nine or ten years due to the hierarchy system of mating exhibited by this species. They experience delayed implantation, which lasts for about 3 months, resulting in a total gestation time of nearly one year. This allows both birthing and mating to occur in the same time frame, during the short period of the year when these animals are aggregated in terrestrial colonies. There is a definitive hierarchy structure to the mating system of these animals because they are polygynous and they aggregate in colonies on land during the breeding season.
Behavior: They are solitary while in the water but highly gregarious during mating season on the shore. Northern Elephant Seals have blood that is rich with hemoglobin and tissues rich in myoglobin, thus increasing their oxygen storing abilities. Another feature of this diving behavior that has perplexed researchers is the lack of rest or sleep for such an extended period of time. Recordings have indicated that these animals conduct dive after dive, 24 hours a day, sometimes for months at a time. It is thought that the dive activity may be a form of sleeping for the seals because their metabolic rate is very low.
Remarks: By the 1880's it was thought that they had been hunted down to extinction. A few animals were then discovered in 1892 which were captured and killed for scientific study. Eventually, it was discovered that a population of about 20 to 100 individuals had survived. Studies have shown that all individuals of the current population, which has grown to over 175,000, are relatives of these few survivors. The population bottleneck that occurred during this time is of concern because genetic variation is reduced, causing the possibility for the population to be vulnerable to disease or reproductive failure.

Genus *Leptonychotes* Gill, 1872

One species.

Leptonychotes weddellii (Lesson, 1826)
Weddell seal

Etymology: The generic name *Leptonychotes* refers to the small size of the claws on the seal's hind flippers. The Greek *leptos* means "small" or "slender"; *onux*, "claw"; *otes* is a suffix indicating possession. The name *weddellii* honors Captain James Weddell, whose book on an Antarctic sealing voyage in the 1820s contains a description and an illustration of this species.
Size: Newborns average 1.5 m and 29 kg. Males reach 2.8-2.9 m, females 3.0-3.3 m; weight averages 400-450 kg.
Distinguishing features: Rotund body and small head; short muzzle; large brown eyes and upturned ("smiling") mouthline.
Distribution: Circumpolar in the Antarctic.
Habits: They live in arctic regions on fast ice areas and in the sea.
Food and feeding habits: Their diet consists of fishes and squids.

Reproduction: Copulation takes place under the water. The female is mounted by the male from behind while her sides are held by his foreflippers. Quite often she is bitten on her neck while copulation occurs. Impregnation occurs between late November to mid-December and implantation occurs about mid-January. Gestation lasts between nine and ten months. Birth (usually of a single pup) occurs onto the sea ice and the babies are born with their permanent dentition. They have a gray lanugo, which after three to four weeks turns to a dark coat. Weaning takes place at six weeks of age and maturity at three years. First breeding of females may be denied for one or two years under some population conditions and males usually do not mate until six to eight years of age.
Behavior: They are nocturnal. They move in slow humping motion on land as well as on ice. They swim at a speed of about 5 to 7 knots, using their fore and hind flippers. Diving has been measured at depths of 600 m, and they can remain under for up to an hour. Drinking seawater as well as eating snow helps this seal meet its water consumption requirements. Fighting consists of continual chest contact, but is ceased when striking of chest, neck, or other areas occurs. Weddell seals sleep in the same position on the stomach or back for hours, but lying on their sides is most common. Vocalization occurs underwater for communication. Overlapped calls are longer than solitary calls, which constitute the varied repertoire of vocal communication in the Weddell seal. Play fighting occurs commonly with subadults. The nails of the foreflipper are used for grooming the head, neck, upper sides, and chest. Other areas are groomed by rubbing back and forth against the ice.
Remarks: The eyes of *Leptonychotes weddellii* are well developed for low light visibility; this helps them to locate breathing holes in the ice. These seals are heavily infested with worms and often reguritate them as a means of expulsion. The louse *Antarctophthirus ogmorhini* attacks the hind-quarters as well as the penile orifice of these seals. Lice also infest subadults.

Genus *Ommatophoca* Gray, 1844

One species.

Ommatophoca rossii Gray, 1844
Ross seal; big eyed seal

Etymology: The generic name *omma* comes from the Greek "eye," because of its very large orbits. The specific name is after James Clark Ross, commander of the HMS Erebus, which entered the Ross Sea during the British Antarctic Expedition of 1839 to 1843. Ross secured two specimens.
Size: Maximum length between 2.3 and 2.5 m with body weights that may exceed 200 kg. Females may be somewhat larger than males.
Distinguishing features: Head small but broad; snout short; prominent eyes.
Distribution: Circumpolar in the Antarctic.
Food and feeding habits: They specialize in feeding on cephalopods, particularly squid, although they can also take fish and krill. They feed at depths of several hundred meters and its large eyes may aid its underwater vision. Killer whales prey on some Ross seals and there is possibly also some predation by leopard seals.

Reproduction: The breeding season probably takes place in November and December. The female nurses her pup alone for a short period, perhaps 2-3 weeks, and breeding may occur about one month after the pup is weaned. Pups are born with dark brown fur, lighter on the underside. Adult Ross seals molt their coat between January and February.
Behavior: Ross seals are the least studied of the Antarctic seals due to their dispersed and isolated distribution. They are usually observed as solitary individuals, appearing to prefer larger and more concentrated ice located further in from the ice pack edge than that preferred by leopard and crabeater seals. Ross seals have a very distinctive "siren-like" call and when approached they often arch their backs and raise their heads near vertically in a recognizable posture.
Remarks: Ross seals have been protected from large-scale commercial hunting due to their inaccessibility and the high cost of operating in the area. They are protected by the Antarctic Treaty and the Convention for the Conservation of Antarctic Seals (CCAS), although 30 were killed in 1986-1987 for commercial purposes under a special permit. In January 1998 the Environmental Protection Protocol to the Antarctic Treaty was ratified, implementing environmental measures such as the banning of mining and oil drilling in Antarctica for at least 50 years, along with the banning of refuse disposal and the use of pesticides in the region. The lesser importance of krill in the Ross seal diet should probably prevent the species from being badly affected by current pressures on krill stocks from the commercial fishery and from increased competition by other Antarctic marine mammals.

Genus *Lobodon* Gray, 1844

One species.

Lobodon carcinophaga (Hombron and Jacquinot, 1842)
Crabeater seal

Etymology: The name *Lobodon* refers to this seal's extraordinary complex dentition. In Greek *lobos* means "lobe"; *odon*, "tooth." The name *carcinophagus* comes from the Greek *karkinos*, "a crab," and *phagein*, "to eat." Despite its name, it does not eat crabs but krill.
Size: Pups are born weighing approximately 20 kg and gain weight while nursing at about 4.2 kg/day. Maximum length is close to 2.6 m and maximum weights of up to 225 kg. Although there is little sexual dimorphism in size, females are slightly larger than males.
Distinguishing features: Body long and slender; they have a noticeable long snout with a distinctly upturned aspect in profile.
Distribution: Circumpolar in Antarctica.
Habits: The crabeater seal lives on the pack ice and the near freezing water surrounding Antarctica.
Food and feeding habits: The crabeater seal does not eat crabs but its primary food is krill, *Euphasia superba*. It probably also eats other invertebrates. The crabeater seal feeds by swimming through a school of krill with its mouth open, sucking them in and then sieving the water out through its specialized dentition. Fish sucking from a distance of 50 cm has been reported.

Reproduction: Reproduction takes place in the austral spring, from October to December. Females give birth in September and cares for her single pup. A male joins the female in her chosen area just before or just after parturition. He defends the female and the newborn pup. He is, in all likelihood, not the father of the pups. Females come into estrus just after weaning and the male's only apparent interest is in waiting for the female to be sexually receptive. Physical contact between the mother and pup during this period is necessary. If either the pup or the mother strays, the other immediately follows. Pups are weaned at about 3 weeks of age. By the end of lactation the mother's body weight may be reduced by half, rendering her unable to defend herself adequately. She becomes sexually receptive shortly after weaning and, unlike most seals, copulation appears to occur on the ice floes instead of in the water. Gestation lasts about 11 months and probably includes a period of delayed implantation. Crabeater seals become sexually mature between 3 and 4 years of age and females may have successful pregnancies between 5 and 25 years old.
Behavior: Crabeater seals are mainly nocturnal and may be found in large aggregations of up to 1,000 animals, but are usually solitary or in small groups. Once in the water, diving occurs nearly continually for approximately 16 hours. Those dives include foraging, traveling, and exploratory dives. Most dives are for traveling and are less than a minute long and less than 10 m deep. Foraging dives are slightly deeper, up to 30 m, and appear to vary throughout the day, with crepuscular dives being deeper. This is most likely in response to krill distribution. Exploratory dives are the deepest and presumably for navigation as they usually occur just before a traveling or foraging dive. Their main predators are the orca and the leopard seal. They may use breathing holes created by Weddell seals, sometimes chasing them away. At the end of the summer, crabeater seals disperse northward as the ice freezes. It appears that some seals, usually young ones, become disoriented and head farther south over the pack ice. As they are particularly mobile on land for pinnipeds, they may travel hundreds of kilometers inland. When sprinting, it lifts its head high and swings its head from side to side in synchrony with its pelvis. Its foreflippers move alternately across the snow and its hind flippers are lifted off the ground and held together. These seals almost always die and are well preserved as "mummies" in the ice throughout Antarctica. Most seals, however, successfully travel north to oceanic islands, Australia, South America, and even South Africa.
Remarks: The crabeater seal is the most numerous species of pinniped in the world, with a population estimated at between 15 and 40 million. The large population of crabeater seals has been associated with the near-extinction of the large baleen whales. This is because the whales, like the crabeater seal, eat krill; now there is probably more krill available to the crabeater seal. It is hypothesized that changes in sexual maturity and other reproductive characteristics correlate with large ecological changes such as this. The age of sexual maturity of the crabeater has significantly decreased since the 1950's. Since its habitat is remote, the only concerns for conservation are indirect. Trace amounts of chemicals such as DDT have been found in some populations.

Genus *Hydrurga* Gistel, 1848

One species.

Hydrurga leptonyx (Blainville, 1820)
Leopard seal

Etymology: The name *Hydrurga* means "water worker," from the Greek *hudor* for "water" and the Greek *ergo* (a misspelling of the Latin *urgeo*, "I work"), "I drive," a reference to the animal's aquatic life. The species name *leptonyx* comes from the Greek *leptos* "small" or "slender," and *onux*, "claw."
Size: Pups weigh about 30 kg and are about 160 cm long. Females grow larger than males, reaching 3.6 and 3.15 m, respectively. Very large individuals may weigh 450 kg.
Distinguishing features: Body long and slender; huge head with massive jaws and tremendous gape. Their appearance is almost reptilian. Color pattern is counter-shaded, being dark gray above and light silvery below.
Distribution: They have a wide distribution in high latitudes of the Southern Hemisphere.
Habits: *H. leptonyx* is most common in antarctic and subantarctic waters, along the outer edges of the pack ice, hauling out on ice and land (Jefferson et al. 1993).
Food and feeding habits: They are the only pinniped in which warm-blooded vertebrates make up a large portion of the diet; this includes crabeater and fur seals. They also feed on krill, penguins, fish, and cephalopods. Leopard seals have also been known to scavenge the carrion of whales and other seals.
Reproduction: Male leopard seals reach sexual maturity around their fourth year, females in their third. Mating occurs in the water from November to February, and males are probably serially polygynous. Gestation lasts around 11 months, but implantation seems to be delayed for about two months. Parturition occurs from September to January, with the concentration of births in October and November. Lactation can persist for up to four weeks. The pup's coat is soft and thick, dark gray above with a dorsal stripe, pale on the sides and with black spots below.
Behavior: The leopard seal is primarily a solitary species. Adults normally occur on the outer fringes of the pack ice. Young animals disperse to subantarctic islands during the winter, and it is debated whether or not these movements are migrations or periodic dispersals due to intraspecific competition. Leopard seals are capable of producing a variety of vocalizations, used in intraspecific aggression. They have been correlated with different body movements and postures.
Remarks: Their populations are abundant. Humans do not exploit this species. Leopard seals are protected by the Antarctic Treaty and the Convention for the Conservation of Antarctic Seals (CCAS).

Order SIRENIA Illiger, 1811

The Greek name for this order is derived from the sirens of Greek mythology.

Like cetaceans, sirenians spend their entire lives in water. They have relatively large stout bodies and downturned snouts. Their forelimbs are modified to form flippers, their hindlimbs are reduced to a vestigial pelvis, and their tail is enlarged and flattened horizontally to form a fluke or paddle. Sirenians are massive, sometimes weighing more than 1150 kg. Their body is streamlined and nearly hairless. Their ears have no pinnae. Their eyes lack obvious eyelids, but are closed by a sphincter-like mechanism. Their bones are unusually dense, a condition called **pachyostosis**; the extra mass probably helps them remain suspended at or below the surface of the water. Their nostrils are located on top of their snouts and closed by valves. The lips are large and mobile, and they are covered with stiff bristles.

The sirenians' skull is unique with large premaxillae that are deflected downward. Nasals are reduced or absent, and the nasal opening extends posteriorly nearly to the orbits. The dentary is very broad. In the region of the ear, the tympanic bone is semicircular, and the petrosal is massive and only loosely bound to the basicranium. The teeth of manatees and dugongs are unusual, but they are very different from each other and are described in the accounts of each family.

Manatees can be readily distinguished from dugongs by their smaller size, a rounded rather than notched tail, and a less pronounced deflection of the snout. The latter feature enables the manatees to feed at any level in the water column rather than being obligate bottom feeders, unlike the dugong with its strongly downturned snout.

Sirenians are strict vegetarians, feeding on a variety of marine algae and higher plants. Members of both families are social, occurring in large aggregations and interacting frequently with one another.

The living sirenians or sea cows consist of one species of dugongs (family Dugongidae) and three species of manatees (family Trichechidae). A fifth species, the Steller's sea cow, (also a Dugongidae) was hunted to extinction by 1768.

Family DUGONGIDAE Gray, 1821

It includes the dugong (subfamily Dugonginae), the Steller's Sea Cow (subfamily Hydrodamalinae), and the paraphyletic extinct "Halitheriinae."

Subfamily: Dugonginae Gray, 1821

Genus *Dugong* Lacépède, 1799

Dugong dugong Lacépède, 1799
Dugong

Etymology: The term dugong comes from the Malayan and Javanese word *duyong*.
Size: Adults range in length from 2.4 to 4 meters and weigh 230 to 908 kg.
Distinguishing Characteristics: Dugongs are born a pale cream color, but they darken with age to a deep slate gray dorsally and laterally. The short hair is sparsely distributed over the body, save the bristles on the muzzle. The skin is thick, tough and smooth. The front-limbs have evolved into flippers that are 35-45 cm long. The young use these for propulsion, but the adults use the fluke-like tail for locomotion, using the flippers for steering. Despite its diet, the dugong has a relatively simple stomach. The muscular upper lip is cleft and protrudes over the down turned mouth. The lower lip and distal parts of the palate have horny pads used to grasp vegetation, which is then uprooted with the strong upper lip. They have a total of 10-14 teeth in adults. Sexual dimorphism is either absent or females may slightly outsize males. Nasals absent, constant presence of juveniles of a deciduous first incisor, frequent presence in adults of vestigial lower incisors, sexual dimorphism in size and eruption of permanent tusks (first incisors), and functional loss of enamel crowns on cheek teeth and persistently open roots of M 2-3 and m 2-3.
Distribution: They are distributed in the western Pacific and Indian oceans.
Habitat: Dugongs inhabit shallow, tropical marine coastal waters and are more strictly marine than manatees.
Food and Feeding Habits: Dugongs are aquatic herbivores and feed on sea grasses in water 1-5 m deep. They are reported to occasionally eat algae, and crabs have been found in the stomachs of dugongs. Wear on the tusks and trails through grass beds suggest that some digging or rooting is part of the feeding behavior. Head shaking during feeding appears to be used to clean sediment from the food before ingesting as little sediment is reported in the stomach contents of animals examined. The timing of feeding seems to be most closely related to tides, not photoperiod.
Reproduction: Breeding occurs throughout the year and peak months for birth vary geographically. The exact length of gestation is unknown, but it is presumed to be about 1 year. Single calves are the norm and twins are rare. Parturition takes place in shallow water, and newborn calves are able to swim immediately to the surface for their first breath of air. Newborn calves are about 100-120 cm long and weigh 20-35 kg. Newborns cling to the mother's back and ride from the surface to grass beds along with the feeding mother. The young suckle underwater beneath the mother in an inverted position. Lactation lasts approximately 18 months, but offspring are known to eat grass at 3 months. Calves may remain with the mother for a year. Sexual maturity is reached in both sexes by an age of 9-10 years, though it can occur as late as 15 years.
Behavior: Frightened animals make a whistling sound and calves have a bleat-like cry. Though now rare, herds of several hundred animals were formerly known. Calves formerly left the herd during the day to form nurseries in shallow water. Groups of six animals are most common now. Males are not known to stay with the stable mother-calf social units. Long distance migration is unknown, but daily and seasonal movements do occur in some populations. Tides, water temperature, and food abundance are probably the main factors involved in these movements. Average swimming speed is 10 km/hr, but this can be doubled quickly. Dives typically last between 1 and 3 minutes.
Conservation: Dugongs are hunted throughout their range for meat, which has been likened to veal. They are also hunted for oil, hides for leather, and for their bones and teeth, which are made into ivory artifacts and charcoal for sugar refining. Some Asian cultures prize dugong

products for medicinal purposes. Dugongs are listed as endangered under the Endangered Species Act of the U.S.A. and as vulnerable by the IUCN. All populations are in CITES Appendix I except the Australian populations, which are in Appendix II.

Subfamily: Hydrodamalinae Palmer, 1895

Genus *Hydrodamalis* Retzius, 1794

Hydrodamalis gigas (Zimmermann, 1780)
Steller's Sea Cow

Etymology: The generic name is from the Greek *hydro* for "water" and *damalis* for "a young cow"; the specific is from the Greek *gigas* for "giant."
Size: It measured at least 7.6 m in length and was estimated to weigh between 4 and 10 tons.
Distinguishing characteristics: It had rough, bark-like skin. Its flippers were covered with short, coarse hairs and did not have finger bones. The tail had two lateral lobes with a deep notch in-between. The head was small. Adults had no teeth, the mouth bearing horny oral plates which crushed and ground the vegetarian diet. The sea cow had small eyes and aural apertures. In his notes, Steller wrote, "From the structure of the eyes and ears, I do not venture to confirm that they could definitely see and hear and, since the head was repeatedly submerged in water, it seems that the animal itself neglected and scorned the use of these organs."
Distribution: In the Pacific/Arctic Ocean: In the Pleistocene this species inhabited the northern rim of the Pacific Ocean from Japan to Baja California. In the 18th century they were restricted to the shallow, cold waters off of a few small islands in the Bering Sea.
Habitat: Shallow waters and kelp-beds.
Food and Feeding Habits: They had no functional teeth and ate algae exclusively. The stomach Steller measured was reported to be six feet long and five feet wide. The stomach, he wrote, "When full of seaweed and attached to a rope, could hardly be moved by four strong men. Herds of sea cows were fond of gathering at the mouths of rivers. They were docile and could be stroked. They ate constantly, gathering the seaweed with bristled lip flaps."
Reproduction: Steller's sea cows had a gestation period of over a year. Copulation took place in early spring with births in autumn of the following year. Only single young were born. Steller described the sea cows as monogamous, mating in the spring after extensive courting behavior. The single calf was born in about a year.
Behavior: Steller's sea cows are thought to have been monogamous with cohesive pair bonding. They grazed almost constantly. Half of the body was generally out of the water. When their heads were submerged, they pulled themselves along the shallow bottom with their hook-like forelimbs. They were totally unafraid of predators and were easily approached by boat. This fact led to their eventual extinction due to hunting. They had no known predators other than man.
Remarks: Vitus Bering was a Danish navigator who entered the Russian navy in 1704 and served in the war against Sweden. Twenty years later, Peter the Great appointed him to conduct an expedition to northeast Siberia to determine if Asia and America were, indeed, divided. After Peter's death, Empress Anne sent Bering on a second expedition. This time Bering sailed southeast, and as he headed back to Russia, he was almost parallel to the Aleutian Islands - but

was not aware of it. Unfortunately, he became lost and was shipwrecked on an uninhabited island in 1741. He died there a month later. Bering Island and the cold Bering Sea were named in his honor.

On board the second Bering expedition was Georg W. Steller, a German naturalist whose duty was to record the fauna of these cold waters. After the death of Bering, Steller and a Lt. Waxel headed the marooned explorers. Noting the abundance of seals and otters in the surrounding seas, they are credited with establishing the important fur trade of the northern Pacific that, in time, threatened the existence of many animals and nearly brought war to America and Britain on one occasion. As the little band of mariners settled into the discomforts of the isolated island, Steller became fascinated with the odd, air-breathing mammals that lived in the shallow waters. He initiated an intensive study of the huge creatures. Though his resources were limited, he conducted a thorough investigation of their feeding habits, biology and behavior, making copious notes.

The animal had been determined to be a sea cow, related to the manatees and dugongs of warmer seas. Steller had plenty of specimens to study since they were easily captured as a prime source of food for the stranded seamen; the milk was also sweet and rich, and the fat could be burned in a lamp without an odor or taken as a drink to settle the stomach. Steller was the only scientist to see or study this animal. From his notes, however, we have derived some facts regarding its morphology and biology.

The lethargy of these animals along with its limited distribution range probably contributed to its demise. It was easily captured. Steller's sea cows were infested with parasites in the rough, cracked skin, which he described as “insects.” Later scientists concluded the parasite was a crustacean that probably became extinct along with the sea cow. After six months of isolation, Steller and the remaining seamen were rescued from Bering Island. Due to crowding on the vessel, Steller was forced to leave behind many of his observations and all of his specimens. He never sketched the whole animal and most of what we know has been deduced from his notes and later writings. As the fur trade blossomed, the traders hunted the sea cow for sustenance. Also, Steller described the sea cow’s blubber (3-4 inches thick) as tasting something like almond oil, which led to it becoming a prime source of food for Russian hunters. By 1768, 27 years after its discovery, it had been exterminated leaving a host of questions unanswered. Its downfall may have been set, though, by a combination of predation, competition, and decline in food supplies that occurred when aboriginal human populations colonized mainland coastlines and islands along the North Pacific. It has been estimated that at the time Steller made his study of the Arctic sea cow, the population was about 2,000 animals.

Family: Trichechidae Gill, 1872 (1821)

All three species of manatees belong to this family.

Genus *Trichechus* Linnaeus, 1758

Trichechus manatus Linnaeus, 1758
West Indian Manatee, sea cow, lamantin

Etymology: The generic name is from the Greek *trichos* for "hair" and *ekho* for "have," referring to the facial hair and bristly moustache. The specific name is said to have originated from the Carib *manati*, referring to a woman's breast.
Size: 1.1-1.5 m, 30 kg (neonate); 3.5-4.1 m, 1000-1620 kg (max. adult). Females tend to be slightly larger than males.
Distinguishing features: Large, torpedo-shaped, thick-skinned animals with bulky body tapering to a spatulate tail; mobile forelimbs with 3- 4 nails; body gray to brown, nearly black in newborn; thick, wrinkled skin; prominent facial vibrissae.

Two paddle-like front "flippers" are tipped with three or four "finger-nails." There are no hind limbs, but manatees have undeveloped pelvic bones suggesting they are descendants of wading animals; they are distantly related to elephants. The broad, rounded tail is flattened like a spatula and used to propel the animal through the water. Sparse hairs are scattered over the body, but are especially noticeable around the face and mouth. A layer of blubber beneath the wrinkled skin provides buoyancy for the large body, plus insulation. Small, beady eyes are almost buried on either side of the face. Although depth perception is thought to be limited, manatees can differentiate colors, shapes and patterns. Their vision in air is also thought to be acute. Tiny ear openings are located just behind the eyes. Two nostrils are located on the upper surface of the snout. They are securely sealed by fleshy flaps while under water and are only opened when the animal surfaces to breath. Manatee bones are very dense. The brain is relatively small for such a large animal. As warm-blooded mammals with a metabolic rate lower than that of a cow in the field, they are sensitive to sudden temperature drops.
Distribution: *Trichechus manatus* has at times been considered divisible into two subspecies: *Trichechus manatus manatus* ranging from Mexico south through Central and into South America, as far south as Recife, Brazil, including the West Indies, and *Trichechus manatus latirostris* from the Southeastern United States. Thus, West Indian manatees live in the rivers, estuaries and coastal areas of tropical and subtropical regions. Though they can be found occasionally in the summer months as far west as Louisiana in the Gulf of Mexico and as far north as Virginia in the Atlantic, they congregate in southern Florida during the winter.
Habits: Protected shallow coastal waters, estuaries, rivers, and canals where vegetation is abundant. They move freely between fresh and salty waters and may be found in either clear or muddy environments. Because of their size, water depths of at least one meter are preferred. It is rare to find them in waters exceeding depths of seven meters. They often travel great distances up coastal rivers.
Food and Feeding Habits: Manatees consume a wide variety of aquatic and semi-aquatic plants. While showing some preference for submerged succulent forms, they will feed on floating mats of seaweed, overhanging and emergent vegetation, and even algae, detritus, and salt-marsh grasses when preferred plant species are depleted. Manatees consume from 10 to 15 percent of body weight in vegetation daily for which they feed for six to eight hours per day. The split upper lip is used to maneuver food into the mouth, assisted by the flippers. Several molar-like teeth arise at the back of the jaw. They gradually move forward and are worn down

by the grinding action of the teeth as the fibrous diet of vegetation is consumed. The worn teeth eventually fall out but are replaced as new teeth arise. To accommodate the diet of vegetation, the digestive system includes bacterial breakdown of cellulose in the hindgut; to accommodate the large volume of high-fiber food, the intestines are long, measuring 45 m in some cases.

Reproduction: Manatees breed primarily during the non-winter months in Florida, so most calves are born during warmer weather, after a gestation period of about 12-13 months. Cows apparently seek sheltered waters in which to give birth to their single calf. The nursing period is normally 1 to 1.5 years, although the young may begin to graze at 2 to 3 months. The interval between births is at least 2 to 3 years, and likely 3 to 5 years for some individuals. Both females and males may reach sexual maturity as early as 3 to 4 years of age, although they may not breed successfully until they are about 5 to 8 years old. The lifespan may surpass 50 years.

Behavior: They are essentially solitary animals, other than the firm association between a cow and her calf. They often form loose aggregations, however, with individual animals moving freely in and out of the group. Manatees rest from ten to twelve hours a day. When manatees surface to breathe, only the tips of the snout are visible. With each breath they renew 50% of their lung air. Manatees remain submerged an average of four minutes, depending on how active they are. When resting, they may not surface for air for ten minutes or more. They also are quite playful, executing somersaults, barrel rolls and other agile maneuvers. They move through the water by undulating their tails and steering with the flippers or tail. Manatees have no known natural enemies. Their only defense mechanism is to swim away when threatened. Mothers have been seen maneuvering between their calves and a threat, however.

Remarks: When Christopher Columbus first saw manatees in the New World in 1493, he attested to the manatee's lack of beauty, noting that these '"mermaids" were not quite so handsome as they had been painted.

Natural mortality is highest among calves, especially when abandoned or orphaned. These are called **perinatal deaths**, which includes the mortality of newborn and infant manatees. Extreme low temperatures and red tides are also the causes of natural deaths among manatees. The main causes of anthropogenic mortality are strikes by boats, drowning or crushing in navigation locks or flood-control gates, entanglement in fishing gear, ingestion of foreign material such as fishhooks or plastic, and vandalism. Despite regulations, hunting pressure was strong until the 1930's and 1940's, and poaching continues to be a matter of concern, particularly in remote areas of Florida and Georgia. Habitat alteration is also a matter of serious concern.

Trichechus inunguis (Natterer, 1883)
Amazonian Manatee, vaca marina, peixe-boi

Etymology: The specific name comes from the Latin *in* for "without" and *unguis* for "nails," referring to the lack of nails on the flippers.

Size: At birth: 85-105 cm, adults: less than 3 m. Weight: at birth is 10-15 kg, adults up to 450 kg. It is the smallest of the manatee species.

Distinguishing features: It is similar to the Florida manatee, but has no "finger nails" on the flippers. Body cylindrical with fewer ribs and shorter rib cage. It has a smooth, rubber-like skin. Most have a conspicuous white or bright pink ventral patch.

Distribution: It is found only in the Amazon and Orinoco river basins of Brazil.
Habits: They inhabit the dense vegetation in blackwater lakes, oxbows, and lagoons.
Food and feeding habits: They feed upon aquatic vegetation such as grasses, water lettuce, and water hyacinths. It is also known to eat floating palm fruits. Captive animals eat up to 15 kilograms of leafy vegetables per day, i.e., up to 8% of their body weight. Most feeding occurs during the wet season, when the manatees graze upon new plants in seasonally flooded backwaters. When the animals return to the main water courses during the dry season, they may not eat for weeks. Adults have seven to eight fully erupted teeth, which are continuously replaced horizontally throughout the animal's life.
Reproduction: They breed throughout the year and gestate for approximately one year. Usually one young is born. Lactation lasts approximately two years. The mother and calf have a long-lasting bond. The mother may carry the young on her back or clasped to her side. The lifespan of this animal is unknown but believed to be between 60 and 760 years old. Individuals have lived past twelve and a half years in captivity.
Behavior: They are gregarious and active at both night and day time. Only their nostrils protrude from the surface of the water as this animal searches river and lake bottoms for lush vegetation. They are preyed upon by jaguars, sharks, and crocodiles.
Remarks: This species is listed as Vulnerable by the IUCN and is in Appendix I of CITES. They have been hunted by Amazonian peoples with nets and harpoons for centuries. In the 1930's and 1940's they were killed by the thousands for their hides, which were used to make water hoses and machine belts. Today the species is protected in nearly every range country, but enforcement is not strict.

Trichechus senegalensis Link, 1795
West African Manatee

Etymology: The specific name comes from Senegal, West Africa, where this species reaches its northern limit of distribution; the Latin suffix *-ensis* denotes locality or country.
Size: At birth they are 1 m long. Adults are generally 2.5 to 3.4 m (maximum, 4 m) long and weigh 400 to 500 kg.
Distinguishing features: It is very similar to the West Indian manatee in appearance. The two probably share a common recent ancestor. It has nails on the dorsal surface of its flippers.
Distribution: In West Africa from Senegal in the north to the Cuanza River in Angola to the south.
Habits: It is found in the coastal waters (estuaries, rivers, swamplands, and coastal lagoons).
Food and feeding habits: They feed primarily on aquatic vegetation, and adults may consume up to 8,000 kg per year. They may also feed on overhanging bank growth, and populations living in estuarine environments are reported to feed exclusively on mangroves. There are unconfirmed (and unlikely) reports of this species consuming fish out of fishing nets.
Reproduction: They are capable of reproducing throughout the year, while a peak in calving tends to occur in late spring or early summer. Females are sexually mature as early as three

years of age. A dozen or more males join a female in estrus. Together they form a mating group in which copulation appears to occur at random. Gestation lasts about 13 months and usually a single calf is born, but twins do occur occasionally. Calves are born tail first, and they can swim on their own. They feed from a pair of pectoral mammary glands. Calves may remain dependent on their mothers for up to two years. They can live up to about 30 years of age, and females can bear young every three to five years.
Behavior: They are active at both night and day time. They are seen living singly or in family groups of up to four to six individuals. They have few natural predators.
Remarks: They are usually seen in conflict with local human populations and there are a number of myths about different parts if their bodies having aphrodisiac properties. There are no current population estimates. It is considered the most seriously threatened of the sirenians.

Other Carnivores: Otters and the Polar Bear

Family MUSTELIDAE Fischer, 1817

Although sea otters are the smallest marine mammals, they are the largest members of the Family Mustelidae, which includes 70 species of river otters, skunks, weasels, and badgers, among others.

Subfamily LUTRINAE Bonaparte, 1828

Genus *Enhydra* Fleming, 1822

One species.

Enhydra lutris (Linnaeus, 1758)
Sea otter

Etymology: The generic name is from the Greek *enhydris*, for "otter," while the specific epithet is from the Latin *lutra*, "otter."
Size: A pup weighs 3 to 5 pounds (1.4-2.3 kg) at birth, and measures 0.6-1.1 m in length. Adults reach a length of 1.4 m. On average, male sea otters weigh between 32 and 41 kg. Females weigh between 18 and 27 kg.
Distinguishing features: The sea otter is one of the 12 different species of river and sea otters worldwide. It is the only exclusively marine mustelid in the Northern Hemisphere, being the smallest, most recently evolved, and least "marine" marine mammal. Its lack of a blubber layer and absolute dependence on fur for insulation, unique among temperate marine mammals, suggests an incomplete adaptation to its environment. Vestiges of a more terrestrial existence may have left the sea otter with a narrow range of environmental tolerance.

They have a dense pelage, light buff to brown to nearly black; head and shoulders often lighter, sometimes almost white in adults; newborn with light brown wooly coat, darkening by about three months of age; canines blunt, molars and premolars rounded and flattened; fully webbed hind feet, 5th digit the longest. Males are distinguishable from females by the penile and testicular bulge and more muscular head and neck; females have abdominal mammae. Adult dental formula: I3/2, C1/1, P3/ 3, M1/2.

Like seals, the hind feet are webbed and are adapted for swimming. The toes on the forefeet are short and stiff, enabling the animal to deftly handle food. On land their gait is clumsy. Probably because of this vulnerability, they are seldom found more than a few yards from water.

For warmth, the sea otter relies on its very dense (100,000 hairs/cm^2, or about 600,000 per square inch), long, silky fur to trap an insulating layer of air. The fur, which is possibly the finest in the world, consists of a very dense underfur of inch-long fibers and sparse guard hairs. For this reason, otters spend much time grooming their fur to keep it clean. It forces air bubbles down next to their skin, acting as insulation for warmth and providing buoyancy. When the fur is soiled, water penetrates to the skin and the animal becomes chilled. The underfur ranges from brown to almost black. Guard hairs may be black, pale brown, or silver, often giving a veiled effect of silvery hairs on a dark background. Older animals often develop a silvery head. This, combined with the prominent whiskers, leads to the nickname, "Old Man of the Sea."

Sea otters have external ears like a sea lion. Also, they have flattened tail flipper-like hind feet for propulsion and forepaws with retracting claws like a cat for grooming and eating. Their lungs are 2.5 times the size of those found among terrestrial mammals of the same size.

Distribution: Sea otters live in shallow water areas along the shores of the North Pacific. They once inhabited the entire northern rim of the Pacific Ocean, from southern California north, then west through the Aleutian Islands, to the Kamchatka Peninsula, and south to the northern islands of Japan. Three subspecies are recognized based on differences in morphology and distribution:

E. l. lutris: Large wide skulls with short nasal bones. Kuril Islands, the east coast of the Kamchatka Peninsula, and the Commander Islands.

E. l. kenyoni: Longer mandibles than either other subspecies. For other characteristics, they are intermediate. Aleutian Islands to Oregon.

E. l. nereis: Narrow skulls with a long rostrum and small teeth. Lacks the characteristic notch in the postorbital region found in most specimens of the other two subspecies. From northern California to approximately Punta Abrejos, Baja California.

Habits: This is a coastal species, often associated with kelp beds and rocky bottom habitats.

Food and Feeding: Sea otters feed on up to 40 different species of invertebrates, but mainly on sea urchins, although mussels, clams, octopus, crabs, limpets, snails, and fish are also taken. They consume food equivalent to 20-33% of their body weight per day. Because sea urchins contain little nourishment, the sea otter must eat 35 to 40 urchins a day, the equivalent of one quarter its body weight, to produce enough heat to survive the cold Pacific waters. In the wild, sea otters never eat on land. In order to obtain the 4 to 7 kg of solid food needed, an otter may have to bring up 18 to 23 kg of whole shellfish. Their feeding habits may result in conflicts with subsistence, recreational, and commercial fishers when otters move into areas that support important shellfish resources. They have strong canine teeth for tearing food and flat molars for crushing.

The search for food is one of the most important daily activities of sea otters. They forage in shallow, nearshore waters often characterized by rocky bottoms and kelp beds. Prey selection varies with individual tastes, foraging ability, and prey abundance and diversity. Under favorable conditions, they select calorie-rich prey such as abalones, sea urchins, crabs, and clams. In habitats where preferred species are depleted, otters must change their eating habits spend more than half the day searching for food, or move on. Some long-established populations in Alaska have exhausted the supply of bottom-dwelling invertebrates and now feed primarily on fish.

One of the most striking characteristics of the sea otter is its ability to use tools. They dive to the bottom down to 60 meters looking for hard-shelled mollusks and retrieve a flat stone from the ocean floor at the same time. Feeding dives generally last less than one minute although some otters are capable of staying underwater for five minutes or more. Then, floating on its back, the otter props the stone on its chest and bangs the mollusk or the sea urchin against it until the shell or the sea urchin breaks.

Reproduction: Female sea otters reach sexual maturity at 3 to 4 years and males at 5 to 6 years, although neither may breed successfully until they are older. Pupping occurs throughout the year, with a peak from January to March in California and later in the spring in Alaska. The pregnancy period, including a phase of delayed implantation, is about 6 to 7 months, perhaps varying with environmental conditions. They have only one pup during each breeding cycle. In areas where food is limited, they may produce pups every other year. The female seldom leaves her pup during the first 5 to 8 months except when diving for food. When traveling, sleeping, or preening, the pup usually rides its mother's chest as she floats on her back. The pup may weigh 30 pounds (14 kg) when weaned and look almost as big as its mother.

Male and female sea otters often live apart. In expanding populations and along the California coast, females predominate in the central, more established portions of the range. Breeding males defend territories within the female areas, while other males, juveniles and non-breeding adults occupy the periphery. These males are typically the first to colonize new areas. Although most otters travel less than a few kilometers daily, juveniles and adult males can cover hundreds of kilometers in a matter of days. The life span of sea otters is about eight years in the wild. Many sea otters live up to 15 to 20 years.

Behavior: The sea otter is a superb swimmer, undulating its whole body while alternating strokes with its paddle-like flippers. They seldom travel far unless an area has become overpopulated and food is scarce. They are gregarious and may become concentrated in an area, sometimes resting in pods of fewer than 10 to more than 1,000 animals. Breeding males will drive non-breeding males out of areas where females are concentrated. In some areas, the non-breeding males will concentrate in “male areas” that are usually off exposed points of land where shallow water extends offshore. Much of the sea otter's day is spent cleaning and grooming its fur coat. Bald eagles prey on newborn pups and killer whales may take a few adults, but predation is probably insignificant. Orcas are adult sea otters’ major predator.

Remarks: In 1742, Vitus Bering's men returned with sea otter pelts from the historic voyage of discovery of Alaska. Interest in these rich furs initiated an era of exploitation, which almost wiped out the sea otter. The early Russian settling of Alaska was largely a result of the sea otter industry. In 1867, when Russian exploitation had greatly reduced the numbers of sea otters, Alaska was sold to the United States. The Americans dropped the few conservation measures that had been instituted by the Russians in their final years of occupation, and hunting

intensified. Sea otters became alarmingly scarce. By 1900 excessive hunts had completely wiped out the Canadian sea otter population. By 1911, when only 2,000 animals were left that it was no longer profitable to hunt them (in many areas they were completely exterminated), sea otters were given full protection under the Fur Seal Treaty. The treaty was signed by the United States, Great Britain, Russia, and Japan. Sea otters are hunted by Alaska Natives for subsistence and products used in handicrafts. Many otters accidentally drown in fish traps of various kinds. Some experts believe the lack of growth in the California sea otter population is due to otters being trapped in coastal fishing nets. Tourists and pleasure boats may also be disturbing the otter's habitat. As the human population increases, so do threats to the sea otter.

Oil pollution, even in small amounts, poses extreme danger to sea otters. Oil contaminates the otter's fur, increasing heat loss and leading to death from hypothermia. Oil also reduces the otter's ability to float and, if swallowed through grooming, can cause death from stomach bleeding. Many otters died from these causes after the tanker Exxon Valdez ran aground in Prince Edward Sound, Alaska, in March 1989, causing a tragic oil spill. More than 1,000 carcasses were found after the spill, and it is likely that the total number that died was several times greater. High concentrations of chlorinated hydrocarbon pesticides have been found in sea otter individuals.

Sea otters play an important role in maintaining the ecosystem of the coastal waters where they live. If they disappear, the kelp beds are soon overwhelmed by a rising population of purple sea urchins whose numbers are no longer controlled by the sea otter's feeding. The urchins soon overgraze the seabed, disturbing the kelp bed's anchors. The kelp then breaks loose and is swept away, exposing to predators all the fish, crabs, mussels, oysters, clams and other creatures that live in the kelp forest.

Genus *Lontra* (Gray, 1843)

One (marine) species.

Lontra (=Lutra) felina (Molina, 1782)
marine otter; chungungo

Etymology: The Latin name *Lutra* is for "otter"; *felina* is from the Latin *felis*, for "cat." Also known in English as marine otter, this species is called chungungo, gata de mar, gato marino, huallaque, nutria de mar, and chinchmen in different coastal regions of Chile and Peru.
Size: The maximum body length (head to tip of tail) is about 1.15 m, and adults weigh only 4 to 4.5 kg. The tail is relatively short. This is the smallest species of the genus *Lutra*.
Distinguishing features: Tail relatively short. Guard hairs are dark brown overall, lightened at the tips. The underfur is brownish gray. The chin cheeks and throat may be somewhat lighter than the rest of the foreparts, and the ventral region is generally lighter than the dorsal. Individuals in Peru and northern Chile are said to be lighter than those from father south. Feet are well-webbed, claws are strong.
Distribution: It is found in the coast and coastal islands of Chile and Peru. It has been eliminated from the coasts of Argentina.

Habits: They are coastal, preferring rocky shores. Occasionally they can be seen in estuaries and lower ranges of rivers.
Food and feeding habits: Diet includes crabs, shrimps, mollusks, and fish.
Reproduction: It is believed that its breeding season is between December and January every year, and that pupping occurs from January to March. Gestation lasts between 60 and 70 days. Litters average 2 offspring. Pups remain with the mother for the first 10 months of life.
Behavior: They have secretive habits and are difficult to observe. They are apparently diurnal and may be territorial. Usually seen singly or in groups of up to three.
Remarks: Although legally protected in several parts of its range, there are no population estimates. Poaching, incidental netting, and habitat modification threaten them. Population fragmentation is also a serious problem. The species is considered to be endangered.

Family URSIDAE Fischer, 1817

All bears belong to this family. The family is divided into three subfamilies, Ursinae (black bears, brown bears, polar bears, sloth bears, and sun bears), Tremarctinae (spectacled bears), and Ailuropodinae (giant pandas). There are six species in the genus *Ursus*: polar bears, brown bears, American black bears, Asiatic black bears, sun bears, and sloth bears. Species can be distinguished by size, build, coloration, and habitat.

Genus *Ursus* Linnaeus, 1758

One (marine) species.

Ursus maritimus Phipps, 1774
polar bear

Etymology: The generic name is the Latin word for "bear"; *maritimus* refers to the maritime habitat of the species. They are also known as the white bear and Nanuk or nanook by Eskimos and Inuit.
Size: Polar bears are the largest land carnivores. Male polar bears (boars) grow two to three times the size of female polar bears (sows). Boars weigh from 350 to more than 650 kg and are about 2.5 to 3 m long. Sows weigh about 150 to 250 kg and are about 2 to 2.5 m long. Pregnant females can weigh as much as 500 kg. The largest polar bear ever recorded was a male weighing 1,002 kg and measuring 3.7 m long.
Distinguishing features: Compared to other bears, polar bears have elongated bodies and long slender necks. The coat can vary from pure white to creamy yellow to light brown depending upon season and angle of light. The hind limbs are longer than the forelimbs. This makes the large, muscular hind end stand higher than the shoulders. Polar bear legs are large and stocky. They have large paws compared to body size, reaching 30 cm in diameter. The large paws of a polar bear act like snowshoes, spreading out the bear's weight as it moves over ice and snow. The forepaws are round, and the hind paws are elongated. Each toe has a thick, curved, nonretractable claw. The claws are used for grasping prey and for traction when running or

climbing on ice. The sole of a polar bear's foot has thick, black pads covered with small, soft papillae (dermal bumps). The papillae create friction between the foot and ice to prevent slippage. Long hairs growing between pads and toes also help prevent slippage.

A polar bear's head is oblong and relatively small. The muzzle is elongated with a "Roman-nosed" (slightly arched) snout. The nose is broad and black. Polar bears have 42 teeth, which they use for catching food and for aggressive behavior. Polar bears use their incisors to shear off pieces of blubber and flesh. Canine teeth grasp prey and tear tough hides. Jagged premolars and molars tear and chew. Polar bears swallow most food in large chunks rather than chewing. A polar bear's eyes are dark brown, set relatively close together, and look forward. The ears are small and rounded, and lay flat when under water. The tail is small, about 7 to 12 cm (2.8-4.7 in.) long. Polar bears are completely furred except for the nose and footpads. A polar bear's coat is about 2.5 to 5 cm (1.2 in.) thick. A dense, woolly, insulating layer of underhair is covered by a relatively thin layer of stiff, shiny, clear guard hairs.

Polar bear fur is oily and water repellent. The hairs do not mat when wet, allowing the polar bears to easily shake free of water and any ice that may form after swimming. Ice forms when the wet fur is exposed to air temperatures at or below freezing. The hairs reflect light, giving a polar bear its white coloration. Oxidation from the sun, or staining, can make the hairs look yellow or brown. Polar bears completely molt (shed and replace their fur) annually, in May or June. The molt can last several weeks.

Distribution: Polar bears are found throughout the circumpolar Arctic. Their tracks have been reported almost as far north as the pole; however, scientists believe few bears frequent areas north of 82° north latitude. The northern Arctic Ocean has little food for them. The polar bears' southern range is limited by the amount of sea ice that forms in the winter.

Habits: Polar bears inhabit Arctic sea ice, water, islands, and continental coastlines. Polar bears prefer sea ice habitat with leads, next to continental coastlines or islands. Leads are water channels or cracks through ice, which may remain open (ice free) for only a few minutes to several months, depending upon weather conditions and water currents. Polar bears hunt seals in the leads, using sea ice as a platform. The "Arctic ring of life" is a biologically rich system of leads and polynyas. It runs parallel to the polar basin coastline. Polynyas are areas of water, surrounded by ice, that remain open throughout the year due to winds, upwellings, and tidal currents. Polynyas are important breathing and feeding areas for wintering or migrating marine mammals and birds. Some polar bears spend part of the year on land. Polar bears in warmer climates may become stranded on land. In summer, sea ice melts along the coastlines, and pack ice (floating sea ice, or floes, not connected to land) moves north. Most pregnant females spend the autumn and winter on land in maternity dens.

Food and Feeding Habits: Polar bears feed mainly on ringed seals and bearded seals. Depending upon their location, they also eat harp and hooded seals and scavenge on carcasses of beluga whales, walruses, narwhals, and bowhead whales. When seals are unavailable, polar bears eat other marine mammals, reindeer, small rodents, sea birds, ducks, fish, eggs, vegetation (kelp), berries, and human garbage. On occasion, polar bears kill young walruses and belugas. A polar bear's stomach can hold an estimated 15-20% of its body weight. They need an average of 2 kg of fat per day to survive.

A polar bear's sense of smell is acute, and it is the most important sense for detecting prey on land. A polar bear can smell a seal more than 32 km away. The polar bear remains motionless beside a breathing hole or lead edge waiting for a seal to surface. When a seal

surfaces, the polar bear bites onto the head or upper body, then flips the entire seal onto the ice. Hunting usually takes less than one hour, but polar bears will wait much longer. Stalking is a hunting method used in summer when seals haul out on sea ice. The polar bear swims toward a hauled-out seal. At 15 to 30 m away (or once the polar bear reaches the ice edge), the polar bear suddenly charges the seal. The bear quickly emerges from the water and grabs the seal with its claws or teeth. Once a seal is captured, a polar bear bites it several times on the head and neck before dragging it several meters from the water to feed. The skin and fat are eaten first, followed by the meat. Polar bears often stop to wash during feeding, using nearby water or rubbing in the snow. Polar bears don't always eat the entire kill; carcass remains are scavenged by other bears, arctic foxes, and gulls.

Stalking ringed seals at their birth lairs is a hunting method polar bears use in spring, when ringed seals give birth to their pups. Ringed seal birth lairs are caves built under snowdrifts next to a hole in the ice. The snowdrifts are on stable sea ice attached to land. Once a polar bear identifies a birth lair, it slowly and quietly positions itself next to the lair. If a polar bear smells or hears a seal in the lair, it slowly rises up on its hind legs and crashes down with its front paws to break through the lair roof. To break the roof's hard surface, several tries are sometimes needed. Mother seals and pups have the high fat content needed for hungry polar bear mothers and their growing cubs. Male polar bears that may attack young polar bear cubs don't normally hunt seals in birth lairs. Birth lairs are usually on sea ice attached to land, allowing young cubs (who have little protective blubber) to avoid crossing water.

Reproduction: Female polar bears reach sexual maturity at about 4 years; male polar bears reach sexual maturity at about 6 years. Most male polar bears don't successfully mate until 8 to 10 years and older. Breeding takes place in April and May on the sea ice. During the breeding season, males and females find each other by congregating in the best seal-hunting habitats. Male polar bears have been seen following the tracks of breeding female polar bears for more than 100 km. It is uncertain what signals males use to track breeding females. Competition for females is intense. Females breed about once every three years; therefore, there are about three adult males to every breeding female.

Before mating, a female polar bear may be accompanied by several males. The males fight fiercely among themselves until the strongest or largest male succeeds in chasing the others away. A polar bear threatening to attack another polar bear usually lowers its head, flattens its ears back, and gives an open mouth threat with a hisslike roar. Fights are rarely fatal, but do result in broken canines and scars on the head, neck, and shoulders. Dominant males may succeed in breeding several females in a season. Once paired, the male and female stay together for a week or more. Females are induced ovulators; this means the act of mating causes a female to release an egg for fertilization. Several days of mating interactions may be required to stimulate ovulation and guarantee fertilization of the egg. Polar bears may have many different mates over their lifetime.

The total gestation period is about eight months. Gestation includes a period of delayed implantation. The fertilized egg divides into a blastocyst, then stops growing and lies free-floating in the uterus for about four months. The blastula then implants in the uterine wall and continues to develop. Delayed implantation assures that the cub is born during the best time of the year for survival and allows the female to get into good physical condition and use her energy for nursing her newborn cubs.

Once mated, females begin depositing fat in preparation for cubbing. Females need to gain at least 200 kg for a successful pregnancy. Some females may seek out maternity dens as early as late August, but most enter dens in mid to late October. Dens protect newborn cubs from winter's temperature extremes. Females usually dig dens in snowdrifts on southerly facing slopes. Some dig earthen dens that later become covered by snow. Most dens are on land, within 16 km of the coast. In some areas, dens are more than 100 km from the coast. A few polar bears make dens on the sea ice. Den elevations range from sea ice level to 548.6 m above sea level. Most dens consist of a single chamber slightly elevated from a short entrance tunnel. On average, the chamber is 2 m long, 1.5 m wide and 1 m high. Polar bears maintain a ventilation hole through the chamber ceiling to provide fresh air. Because of body heat and snow insulation, the den stays warmer than the outside air temperature.

Polar bear cubs are born November through January in a den. Mother and cubs emerge from their den in late March or April. During their first few weeks of life, polar bear cubs nurse most of the time and stay close to their mother to keep warm. Most adult females give birth once every three years. In some populations, birth occurs once every two years. The most frequent litter size is two, followed by litters of one. Litters of three are less common than twins or singles, and litters of four are rare. At birth, polar bear cubs weigh about 454-680 g and are about 30 cm long. Males are born slightly larger than females. Polar bear cubs are born small and helpless, with their eyes closed. The fur is very fine at birth, making the cubs look hairless.

Female polar bears have four mammary glands. Mothers nurse their cubs in a sitting position, or lying down on their side or back. During their first few weeks of life, polar bear cubs nurse most of the time and stay close to their mother to keep warm. For the next three or four months the cubs nurse as often as six times a day. The length and number of nursings gradually decreases as the cubs grow older. Mother polar bears nurse their cubs for as long as 30 months. Some cubs stop nursing as young as 18 months of age, but remain with their mothers for survival until they are 30 months old. The average fat content of polar bear milk is 33%, similar to the milkfat of other marine mammals. Mother polar bears are extremely protective of their young, even risking their own lives in their cubs' defense.

Cubs open their eyes within the first month. The cubs begin walking while in the den at about two months. By this time, they also have thick, whitish fur and their teeth have erupted. By the time the mother and cubs emerge from the den in late March or April, the cubs weigh 10 to 15 kg (22-33 lb.). Mother and cubs remain around the den for about 12 more days, sometimes longer. This enables the cubs to acclimate to the colder weather and develop their walking muscles. During this time the cubs still spend about 85% of their time in the den, sleeping there at night. When ready, the mother polar bear leads her cubs to sea ice. Travel is slow with frequent rest and nursing stops. A mother will sometimes carry her cubs on her back through areas of deep snow or water. Cubs begin eating solid food as soon as their mother makes her first kill on the sea ice (about three to four months of age). The cubs grow quickly on their mother's fat rich milk and on seal blubber. By eight months of age, they weigh over 45 kg.

Polar bear cubs learn to hunt by watching their mother. Cubs will try hunting in their first year, but don't seem to be successful until they are over one year old. Even then, they only spend about 4% of their time hunting. By the time they are two years old they spend about 7% of their time hunting and can catch a seal every five or six days. When her cubs are about 30 months old, a female polar bear is ready to breed again. At this time, an adult male may begin following her. Either the mother bear or the male chases away the cubs.

Polar bears can live 20 to 30 years, but only a small proportion of polar bears live past 15 to 18 years. The oldest known polar bear in the Arctic lived 32 years. The oldest known polar bear in a zoological park lived 41 years. Each year, as a polar bear grows, a thin layer of cementum is added to the outside of each tooth. Age can be estimated by examining a thin slice of tooth and counting the layers. To estimate the age of a live polar bear, researchers can extract one small, vestigial premolar tooth. Adult polar bears have no natural predators.

Behavior: Polar bears are basically solitary. Usually, only two social units exist: (1) adult females with cubs and (2) breeding pairs. Polar bears will aggregate to feed on large whale carcasses and at dumpsites. In some southern regions, like Hudson Bay, bears aggregate on land during the ice-free summer and autumn months. On occasion, adult and sub adult (ages 30 months to five or six years) polar bear males will feed and travel together for short periods of time. Polar bear males will feed and travel together for short periods of time.

The most constant social interaction occurs between mother and cubs. Polar bear mothers are attentive, frequently touching and grooming their cubs. Polar bear breeding pairs remain together for one week or more, mating several times. Aggression occurs between males during the breeding season and when males attempt to steal food caught by other polar bears. Play fighting has been observed between aggregating sub adult and adult male polar bears. Young polar bear cubs chase and tackle their siblings.

Polar bears do not enter deep hibernation. Deep hibernation applies to an animal whose body temperature drops to 5°C for a period of days or weeks. Deep hibernators also show a marked drop in heart rate, and are slow to wake up when disturbed. Only pregnant female polar bears hibernate. Polar bears are not deep hibernators, but enter a state of carnivore lethargy. Though hibernating females sleep soundly, they are easily and quickly aroused. The female polar bear's heart rate slows to about 27 beats per minute from a normal resting heart rate of about 46 beats per minute. When hibernating, a female's body temperature may drop slightly, perhaps to 35°C, or it may remain normal at 37 ^{o} C. Unlike most other hibernators, female polar bears give birth while hibernating. High body temperature is needed to meet the demands of pregnancy, birth, and nursing. Researchers have found that non-hibernating polar bears, during times of food scarcity, can efficiently utilize their energy reserves much like hibernating bears.

Adult polar bears vocalize most when they are agitated or threatened. Sounds include hissing, growling, champing of teeth, and soft chuffing. Cubs vocalize more often and for diverse reasons. Sounds include hissing, squalling, whimpering, lip smacking, and throaty rumblings. Mothers warn cubs with a chuffing or braying sound. Polar bears also communicate through sight, touch, and smell. A male polar bear initiates play fighting by approaching another male with its head down, mouth closed, and eyes averted. The bears usually make contact by gently touching or “mouthing” each other around the face and neck. They then proceed to rear up on their hind legs and try to push each other over with their forepaws. A mother polar bear can comfort, protect, or punish her cubs by using her body, muzzle, or paws.

Polar bears are most active the first 1/3 of the day and least active the final 1/3 of the day. When not hunting, polar bears are often sleeping or resting. On warm days polar bears sprawl out on the ground or ice, sometimes on their backs with their feet in the air. They may also make temporary snow or earthen pits to lie in. On cold days polar bears curl up and often cover their muzzle area. During the winter, some polar bears excavate temporary dens or find natural shelters to stay warm. They may use these shelters for several months at a time.

Polar bears walk on the soles of their feet with their heels touching the ground first. Like other bears, they can also stand on their hind feet and walk upright for short distances. Polar bears generally walk with a steady, lumbering gait. The front paws swing outward with each step, landing slightly pigeon-toed. The head swings gently from side to side. The walk has a four-beat pattern; first the right front foot touches the ground, then the left hind foot, then the left front foot, and lastly, the right hind foot. The bulky build and swinging gait cause polar bears to use more than twice energy to move at a given speed than most other mammals. The average walking speed of a polar bear is 5.5 kph. When being chased or charging prey, polar bears can run as fast as 40 kph for short distances. Polar bears are capable of traveling 30 km or more per day for several days. One polar bear was tracked traveling 80 km in 24 hours. Another polar bear traveled 1,119 km in one year.

Polar bears travel throughout the year within individual home ranges. Home range size varies among individuals depending upon access to food, mates, and dens. Home ranges tend to be larger than for other mammal species because sea ice habitat changes from season to season and year to year. A small home range may be 50,000 to 60,000 square km. Small home ranges can be found near Canadian Arctic islands. A large home range may be in excess of 350,000 square km. Large home ranges can be found in the Bering or Chukchi Seas. Polar bears do not mark or defend their home ranges. Polar bears show "seasonal fidelity": they remain in the same area during the same season.

Remarks:

1. Adaptations to the marine environment:

(A) Swimming and Diving: Polar bears are strong swimmers; they swim across bays or wide leads without hesitation. They can swim for several hours at a time over long distances. They've been tracked swimming continuously for 100 km. Front paws propel them through the water dog-paddle style. The hind feet and legs are held flat and are used as rudders. A thick layer of blubber, up to 11 cm thick, keeps the polar bear warm while swimming in cold water. Polar bears can obtain a swimming speed of 10 kph. The hair of a polar bear easily shakes free of water and any ice that may form after swimming. A polar bear's nostrils close when under water. Polar bears make shallow dives when stalking prey, navigating ice floes, or searching for kelp. Polar bears usually swim under water at depths of only about 3 to 4.5 m. They can remain submerged for as long as two minutes. No one knows how deep a polar bear can dive. One researcher estimates that polar bears dive no deeper than 6 m.

(B) Thermoregulation: Air temperatures in the Arctic average -34°C in winter and 0°C in summer. The coldest area in winter is northeastern Siberia, where the temperature has been recorded as low as -69°C. The warmest areas in summer are inland regions of Siberia, Alaska, and Canada where temperatures can reach as high as 32°C. The ocean temperatures in the Arctic are about -1.5^{o}C in summer. In winter the ocean's temperatures can drop to -2°C, at which point seawater freezes. Body temperature in polar bears, (normally 37°C), is maintained through a thick layer of fur, a tough hide, and an insulating layer of blubber. This excellent insulation keeps a polar bear warm even when air temperatures drop to -37°C. Polar bears are so well insulated they tend to overheat. Polar bears move slowly and rest often to avoid overheating. Excess heat is released from the body through areas where fur is absent or blood vessels are

close to the skin. These areas include the muzzle, nose, ears, footpads, inner thighs, and shoulders. Polar bears will also swim to cool down on warm days or after physical activity.

2. Conservation:

(A) Hunting: Polar bears have been hunted for thousands of years. Evidence of human polar bear hunts have been found in 2,500- to 3,000-year-old ruins. Arctic peoples have traditionally hunted polar bears for food, clothing, bedding, and religious purposes. Commercial hunting of polar bears for hides began as early as the 1500's and flourished by the 1700's. Kills increased substantially in the 1950's and 1960's when hunters began using snowmobiles, boats, and airplanes to hunt polar bears. Public concern about these hunting methods led to an international agreement in 1973 banning the use of aircraft or large motorized boats for polar bear hunts. Hunting is the greatest single cause of polar bear mortality. Today, polar bears are hunted by native Arctic populations primarily for food, clothing, handicrafts, and sale of skins. Polar bears are also killed in defense of people or property. Hunting is government-regulated in Canada, Greenland, and the United States. Hunting is currently banned in Norway and Russia.

(B) Environmental threats: Oil spills from drilling platforms or tankers potentially threaten polar bears. A polar bear's fur loses its insulating properties when covered with oil. Oil spills could diminish or contaminate polar bear food sources. The presence of toxic chemicals in polar bears may have long-term effects on their health and longevity. Toxic chemicals from worldwide industrial activities are carried to the Arctic by air, rivers, and oceans. Arctic animals in higher food chain levels concentrate greater amounts of toxic chemicals in their tissues than those below them. Polar bears, at the top of the food chain, develop the highest concentrations of all. Human-made toxic chemicals such as polychlorinated biphenyls (PCBs), dichloro-diphenyl-trichloro-ethane (DDT), and chlordanes are present in the Arctic. These chemicals have been found in significantly high levels in the tissues of polar bears. Scientists continue to monitor the levels of toxic chemicals in polar bears to determine their long-term effects. Radionuclides, from nuclear waste dumping in the Russian Arctic, may have detrimental effects on polar bears, and the Arctic ecosystem as a whole.

(C) Starvation: Starvation is the greatest threat to subadult polar bears. Subadults are inexperienced hunters, and often are chased from kills by larger adults. Older, weaker bears also are susceptible to starvation.

(D) Disease and parasitism: As in any animal population, a variety of diseases and parasites can be responsible for polar bear illnesses. Polar bears are especially susceptible to the parasitic worm *Trichinella*, which they contract by feeding on infected seals. *Trichinella* larvae encyst in various parts of the polar bear's body, usually muscle tissue. If enough larvae encyst in one area, such as the heart, the tissue becomes severely damaged and they may die.

3. Ecology: The world polar bear population is estimated to be between 21,000 and 28,000 individuals. Due to governmental regulations on hunting, the population has increased from an estimated 10,000 polar bears in 1968. The ratio of males to females is approximately one to one.

4. Polar Bears and Humans:

(A) Tracking: Scientists use radio collars to track the movements of polar bears. Once a polar bear is fitted with a radio collar, the collar sends signals to a receiving station via satellite. Then data is entered the data into a computer program that plots the polar bear's path. Only female polar bears can be tracked using radio collars. Male polar bears have necks wider than their heads, and the collars simply fall off. The movements of polar bears are also studied by following their tracks in the snow, usually by aircraft. Other behaviors are recorded by

observing polar bears directly, or finding evidence of polar bears, such as a partially eaten seal. Most polar bear research is conducted in the spring or summer when weather conditions are more favorable to humans.

(B) Attacks on Humans: Humans may encounter polar bears wherever human and polar bear habitats overlap. Polar bear attacks occur most often at sites of human habitation, such as hunting camps, weather stations, and towns. Compared to other bears, polar bears are more willing to consider humans as prey. Consequently, the person attacked is usually killed unless the polar bear is killed first. Polar bear subadults and females with cubs attack most often. They are also the chief scavengers (among polar bears) of human dumpsites. Both groups tend to be thinner and hungrier; subadults are inexperienced hunters, and females with cubs must feed themselves and their young.

5. Conservation:

(A) First International Scientific Meeting on the Polar Bear, 1965: Growing public concern about polar bear hunting and other human activities in the Arctic, such as oil exploration, led to the First International Scientific Meeting on the Polar Bear in 1965. Attending were representatives from all five polar bear countries: Canada, Greenland (territory of Denmark), Norway, the United States, and the former Union of Soviet Socialist Republics. The meeting set the stage for additional international conferences and research efforts, which eventually led to an international agreement on polar bear conservation.

(B) The International Agreement on Conservation of Polar Bears and Their Habitat, 1973: This agreement states that the five polar bear nations (Canada, Greenland, Norway, the United States, and the former Union of Soviet Socialist Republics) shall protect polar bear habitat, especially denning areas, feeding areas, and migratory routes; ban hunting of bears from aircraft and large motorized boats; conduct and coordinate management and research efforts; and exchange research results and data. The agreement allows the taking of polar bears for scientific purposes, for preventing serious disturbances in the management of other resources, for use by local people using traditional methods and exercising traditional rights, and for protection of life and property. Each nation has voluntarily established its own regulations and conservation practices using the knowledge gained from the international community as a whole.

(C) United States Marine Mammal Protection Act, 1972: Polar bears are protected under the U.S. Marine Mammal Protection Act (MMPA). The primary objective of the MMPA is to maintain the health and stability of the marine ecosystem and to obtain and maintain an optimum sustainable population of marine mammals. The MMPA prohibits taking and importing marine mammals unless a permit is issued for the purposes of public display, native subsistence, scientific research, or sustaining a depleted species. MMPA revisions in 1994 allow U.S. citizens to import polar bear "trophies" acquired in Canadian hunts. Polar bears in Alaska can be hunted only by Alaskan natives.

(D) Convention on International Trade in Endangered Species of Wild Fauna and Flora: In 1975, the polar bear was placed on Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). Appendix II includes species identified as threatened, or likely to become endangered if trade is not regulated. International trade of polar bears, or their parts, is permitted with proper documentation issued by the government of the exporting country.

(E) International Union for the Conservation of Nature and Natural Resources/World Conservation Union: The IUCN/World Conservation Union is a worldwide conservation

organization. This organization links together government agencies, non-government agencies, and independent states to encourage a worldwide approach to conservation. The Polar Bear Specialist group works under the guidance of the IUCN/World Conservation Union's Species Survival Commission. This group helps to coordinate and identify the management and research efforts of the five polar bear nations (Canada, Greenland, Norway, the United States, and Russia). The IUCN/World Conservation Union categorizes animal species they feel are threatened. The polar bear is listed as vulnerable by the IUCN/World Conservation Union. This means the species is likely to move into the endangered category if the negative factors affecting the population continue at their present rate.

(F) Zoological Parks: Having polar bears at zoological parks provides the opportunity for the public to learn about these animals and how human activities may impact their survival. In the protected environment of a zoological park, scientists can examine aspects of polar bear biology that are difficult to study in the wild. Areas of study include polar bear reproduction, birth and care of young, physiology, and communication. However, to keep wild animals in artificial enclosures raises a lot of questions that many animal-rights groups are quick to point to. The whole issue of captivity will be reviewed later in this course.

Chapter 8

General Concepts on the Evolution of Marine Mammals

8.1. Introduction

The marine mammals as we know them today are the result of evolutionary processes highly influenced by both natural selection and the phylogenetic history of their taxa.

Since shortly before (in geological terms) the marine mammals we know today started to evolve, there were a number of changes in the configuration of the oceans and land masses that directly affected the current composition of marine mammals in terms of both species and distribution.

On the other hand, marine mammals are extraordinary because of their exceptional adaptations to the aquatic environment. Those adaptations baffled scientists for centuries. That is one of the reasons why they classified whales and dolphins as "fish" while recognizing that they shared many characteristics with the so-called "quadrupeds," i.e., mammals. Those adaptations to the aquatic environment come in many ways and are not always similar. For example, although cetaceans and pinnipeds share some similar adaptations when it comes to physiology of deep diving, whales and dolphins lost (for the most part) their hair and the hindlimbs; yet, both characters have been retained, to certain extent, by marine carnivores; even in some cases they have augmented them as is the case of the fur among the sea and marine otters.

This chapter is aimed at reviewing the major changes that occurred on earth that shaped the marine mammal fauna composition and its distribution, while exploring some of the main evolutionary mechanisms that played some role in the major phenotypic changes that characterize marine mammals today.

8.2. The Geological Setting

8.1.2. Plate Tectonics

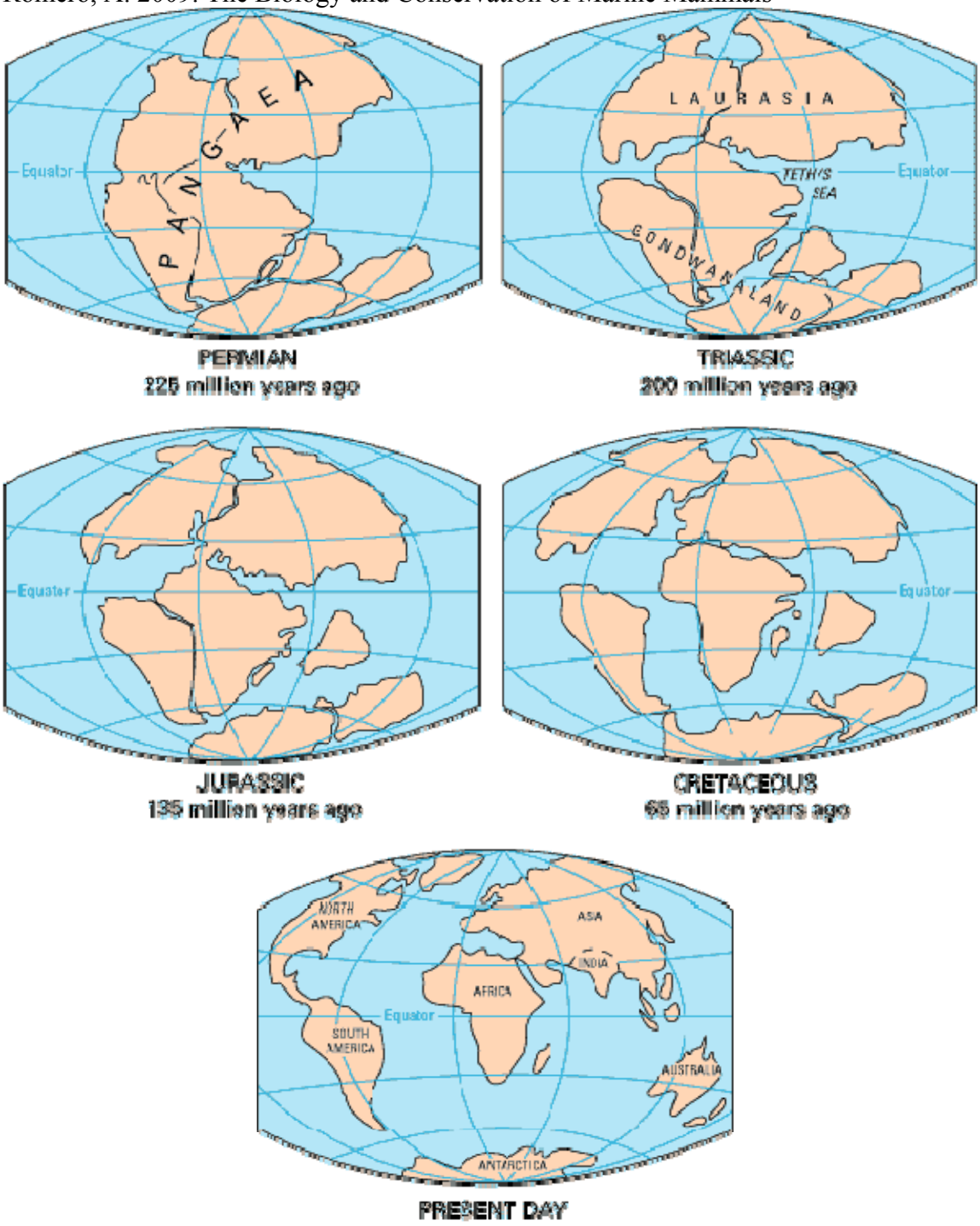
The Sun, the Earth, and the other planets formed from a cloud of interstellar dust about 4.6 billion years ago. A region of the interstellar dust became progressively denser due to gravitational attraction between the particles. Ultimately, it became dense enough so that collisions produced larger and larger bodies, which ultimately included the sun and the planets. Probably, the oceans formed as soon as the Earth cooled enough for water to become liquid, about 4 billion years ago. That is the time at which life appears on earth.

First mammals (together with birds) appeared more than 200 My (million years ago). However, reptiles including dinosaurs occupied most ecological niches for large terrestrial vertebrates. About 65 My, a big meteorite (or a comet) hit the earth and caused the extinction of dinosaurs and many other reptiles, leaving open niches for both, mammals and birds to diversify in terms of species and expand their ranges.

GEOLOGIC TIME					
EON	**ERA**	**PERIODS AND SYSTEMS**	**EPOCHS AND SERIES**	**BEGINNING OF INTERVAL***	**BIOLOGICAL FORMS**
Phanerozoic	Cenozoic	Quaternary	Holocene	0.01	
			Pleistocene	1.6	Earliest humans
		Tertiary	Pliocene	5	
			Miocene	24	Earliest hominids
			Oligocene	37	
			Eocene	58	Earliest grasses
			Paleocene	65	Earliest large mammals
	Cretaceous-Tertiary boundary (65 million years ago): extinction of dinosaurs				
	Mesozoic	Cretaceous	Upper	98	
			Lower	144	Earliest flowering plants; dinosaurs in ascendance
		Jurassic		208	Earliest birds & mammals
		Triassic		245	Age of Dinosaurs begins

	Paleozoic	Permian		286	
		Carboniferous			
		Pennsylvanian		320	Earliest reptiles
		Mississippian		360	Earliest winged insects
		Devonian		408	Earliest vascular plants (as ferns & mosses) & amphibians
		Silurian		438	Earliest land plants & insects
		Ordovician		505	Earliest corals
		Cambrian		570	Earliest fish
Proterozoic	Precambrian			2500	Earliest colonial algae & soft-bodied invertebrates
Archean				4000	Life appears; earliest algae & primitive bacteria

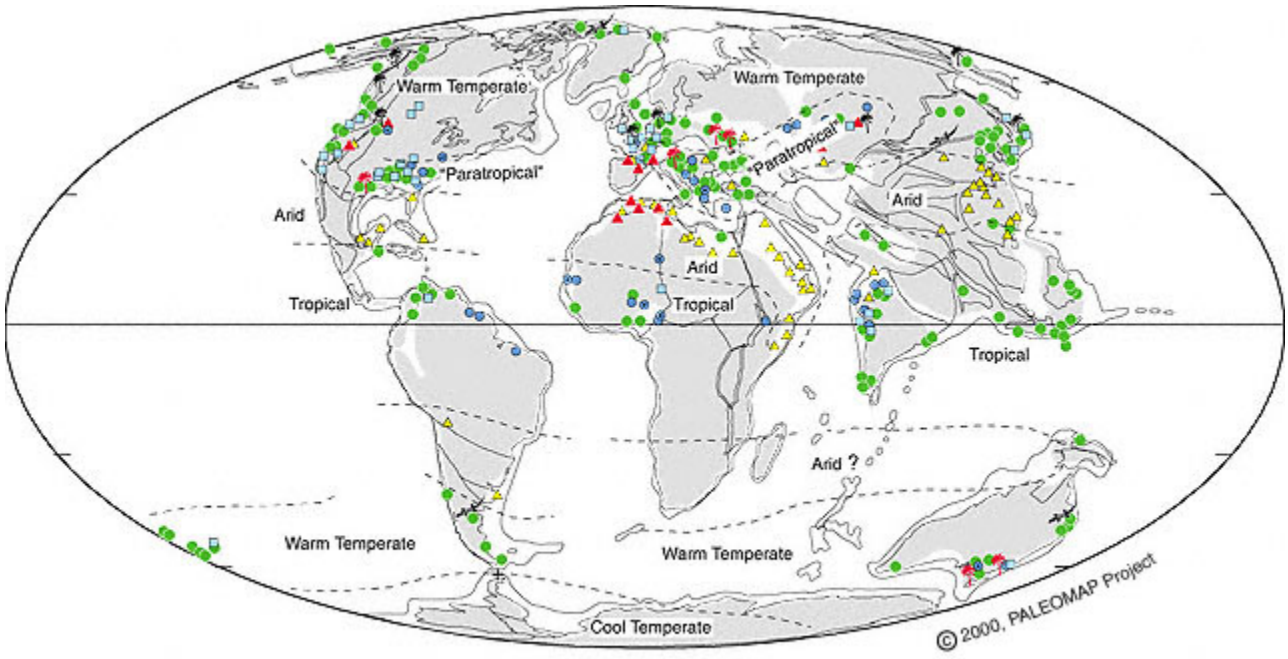
At the same time that these changes in terrestrial vertebrates were taking place, a number of changes in the shape of oceans and emerged land occurring that would strongly influence the evolution of marine mammals. The supercontinent Pangaea began to break up about 225-200 million years ago, eventually fragmenting into the continents, as we know them today.


PANGAEA
Equator
PERMIAN
225 million years ago
LAURASIA
TETHYS SEA
Equator
GONDWANALAND
TRIASSIC
200 million years ago
Equator
JURASSIC
135 million years ago
Equator
CRETACEOUS
65 million years ago
NORTH AMERICA
ASIA
INDIA
AFRICA
Equator
SOUTH AMERICA
AUSTRALIA
ANTARCTICA
PRESENT DAY

8.1.3. The Tethys Sea

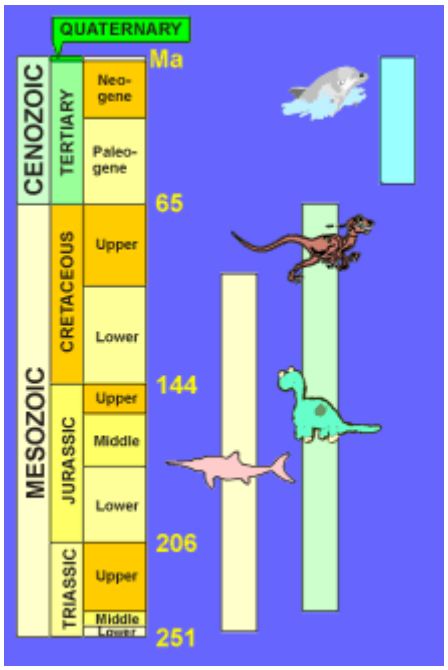
Between the Triassic and the Cretaceous there was a big sea between what is today Africa and Europe and western Asia. That was called the Tethys Sea.

The Austrian geologist Eduard Suess named the Tethys Sea in 1893 after the sister and consort of Oceanus, the ancient Greek god of the ocean. As presently understood, there were actually at least two maybe three Tethys Seas. In Permian times, the continents were, roughly speaking, assembled into one, enormous, C-shaped landmass, known as Pangea. The Paleo-Tethys was the body of water enclosed on three sides (and at times, almost four sides) by Pangea. By the Early Triassic, a long sea-floor spreading ridge developed along the southern shore of the Paleo-Tethys. This extended all the way from Australia, at the extreme southeast end of Pangaea, northwest to the point where the plates of Europe, North America and Africa met, roughly at the center of the "C". As the sea floor spread, it created a basin bordered on the south and west by the Gondwanan continental plates of the Pangean landmass (the bottom half of the "C") and on the north and east by the new microplates of Tibet, Iran and Turkey. These microplates were pushed rapidly northward towards Eurasia and China, eventually closing the Paleo-Tethys. The new Tethys basin expanded behind them to become the Mesozoic Tethys Sea. The Tethys Sea also expanded westward, splitting Pangaea into the supercontinents of Gondwana (in the South) and Laurasia (in the North). By Late Triassic and Jurassic times, the Tethys extended a long, shallow arm through what is now Central Asia and Southern Europe, known as the Tethys Seaway (yet a third "Tethys"). This Seaway became the home of many unique marine reptiles; mostly coastal and shallow water dwellers.



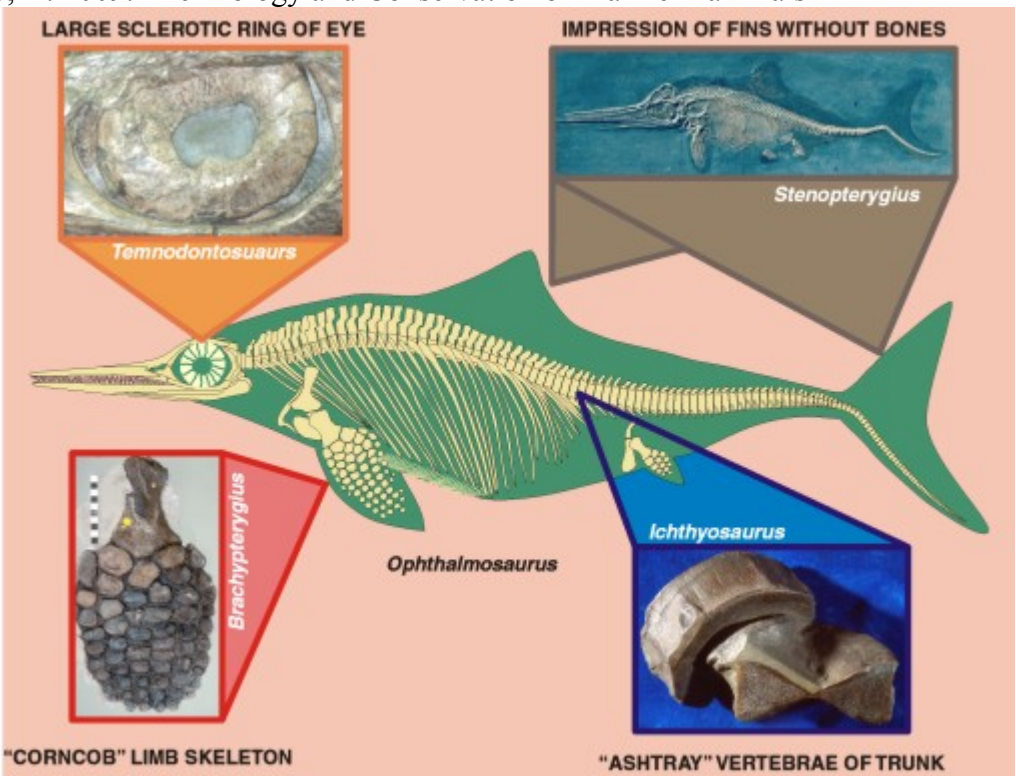
Lower Eocene

8.3. Convergence in the Tethys Sea

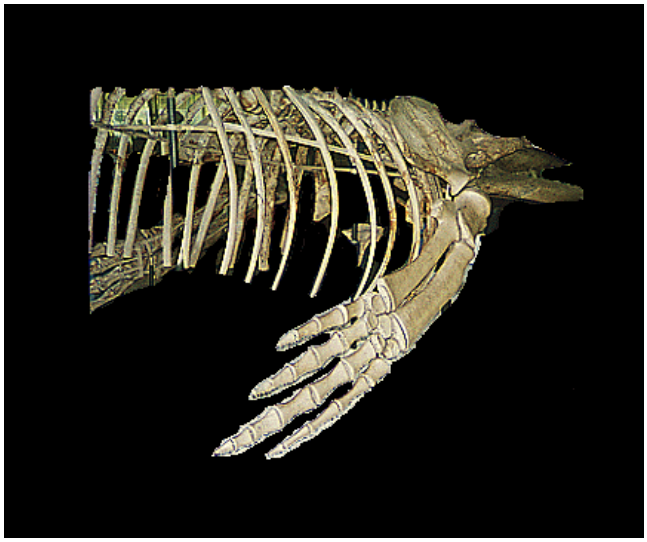


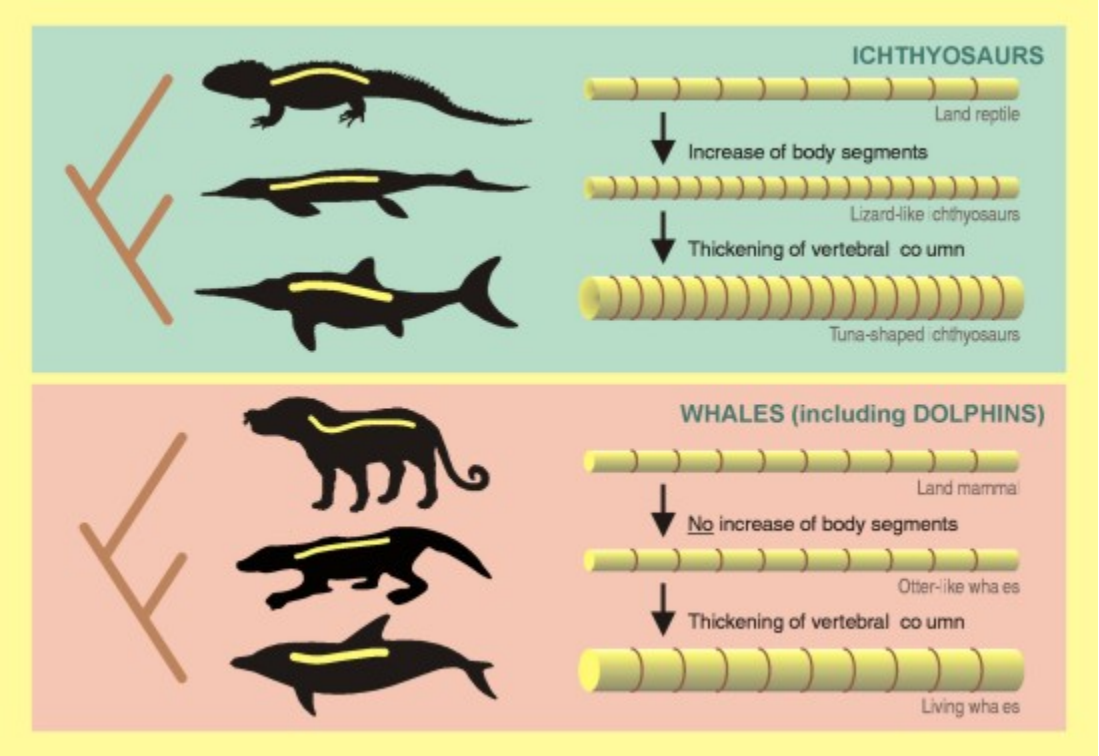
Some of the most common marine reptiles were the ichthyosaurs whose external resemblance to today's dolphins is uncanny, certainly an example of convergent evolution.

However, if we take a closer look at these reptiles we can see that there are also important differences between them and today's marine mammals.

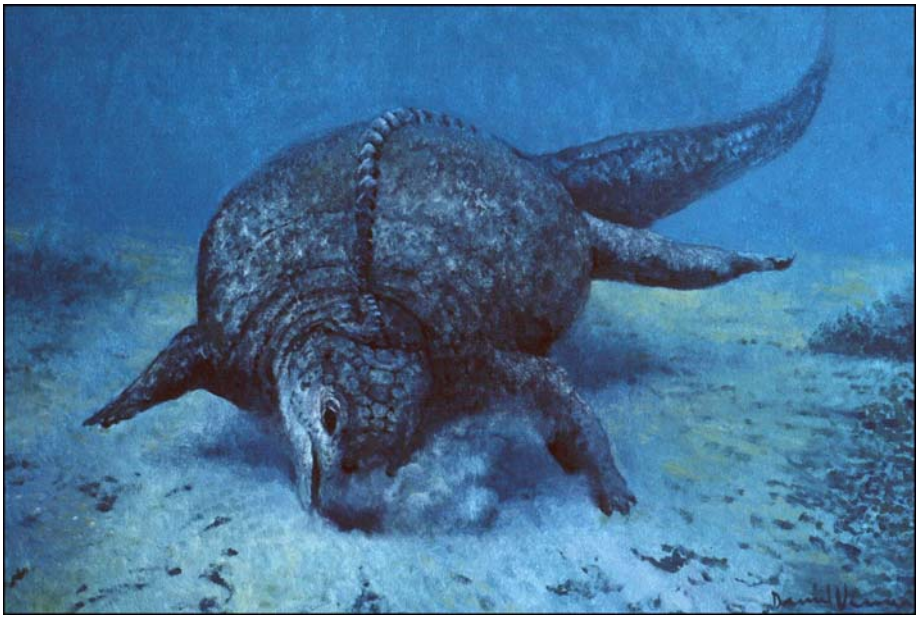


For example, today's marine mammals do not have skeletal structures reaching all the way into the flukes as marine reptiles did. Additionally, ichthyosaurs retained hindlimbs, a structure totally lost among odontocetes. Ichthyosaurs also had a "corncob" limb skeleton, while flippers in cetaceans have much less developed skeletal structures. Also, ichthyosaurs had a large sclerotic ring around the eye, something that never occurred among marine mammals. Finally, ichthyosaurs increased the number of vertebrae as they developed from terrestrial reptiles, while such phenomenon did not occur among cetaceans in relation to their terrestrial mammalian ancestors.





Other characteristics are very similar like, for example, the homodont dentition, which makes sense given that both types of animals ate the same type of food: fish. Other marine reptiles included the *Mixosaurus*, which in many ways, fed like some marine mammals such as the walrus.



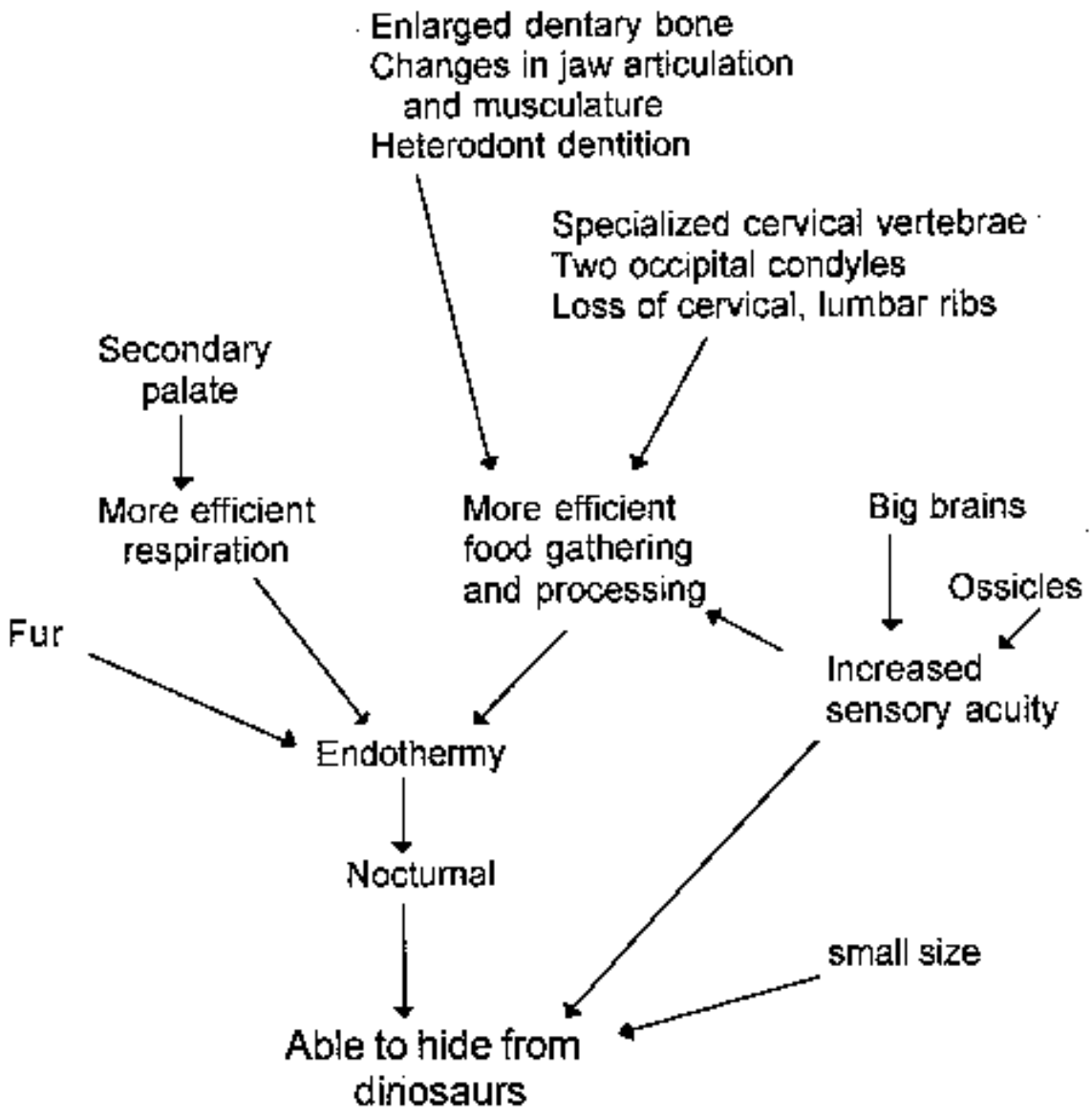
Two major events took place that eventually led to the opening of an ecological opportunity for marine mammals: one was the extinction of these large marine reptiles toward the beginning of the upper Cretaceous and, then, the extinction of large number of large terrestrial reptiles which open the opportunity for mammals and birds to diversify.

8.4. The Origin and Diversification of Mammals

Prior to the rise of dinosaurs, the ancestors of the mammals began diverging from the reptiles. These were reptiles that had mammal-like characteristics (at first subtle) that distinguished them from other contemporaneous reptiles, such as well-differentiated teeth, an upright posture, as well as numerous other mammal-like skeletal modifications.

These first mammals developed **endothermy**, i.e., the ability to generate and efficiently maintain heat. These true mammals first appeared in the fossil record at about the same time as the first dinosaurs. The dinosaurs were more successful, especially as large animals.

The original mammals apparently were forced into roles as small animals (i.e., the big ones went extinct, natural selection favored smaller varieties) since their evolution prior to (and following) the presence of dinosaurs certainly does not suggest an inability to assume roles as large, dominant, terrestrial fauna. Thus, for the 150 million years while the dinosaurs dominated the landscape, the mammals were mostly relegated to body sizes rarely larger than that of a house cat.


Enlarged dentary bone
Changes in jaw articulation
and musculature
Heterodont dentition
Specialized cervical vertebrae
Two occipital condyles
Loss of cervical, lumbar ribs
Secondary
palate
More efficient
respiration
More efficient
food gathering
and processing
Big brains
Ossicles
Fur
Increased
sensory acuity
Endothermy
Nocturnal
small size
Able to hide from
dinosaurs

The dominance of the dinosaurs ended with the collision of a large extraterrestrial body with the Earth, either a meteorite or a comet. The impact of this object combined with associated temporary climatic changes apparently led to the extinction of the majority of the dinosaurs and other large reptiles. Both events define the end of the Cretaceous period and the beginning of the Tertiary period, in what it known as the K-T event. Only a dinosaur lineage, which we call today birds, retained some aspects of the terrestrial dominance exhibited by the dinosaurs prior to the K-T boundary.

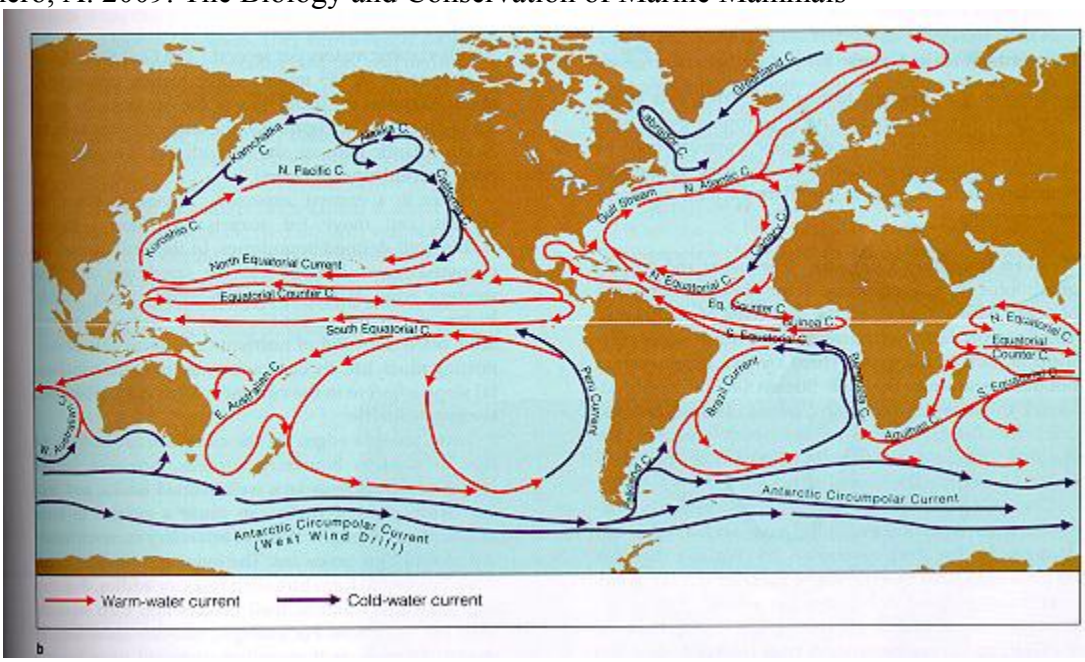
The reasons for the replacement of dinosaurs and other reptiles by mammals and birds, may be found on two facts: (1) both of these groups were endotherms, and thus, more prone to survive drastic climatic changes following the K-T event; and (2) these small mammals were generalists, i.e., more capable to survive to fluctuation to food resources.

After the extinction of the dinosaurs and other reptiles, mammals became the dominant terrestrial vertebrates and they underwent an extensive **adaptive radiation**. **Adaptive radiation** is the rapid evolutionary differentiation of a single or a few species to fill many ecological niches via mutation and natural selection. Adaptive radiation often occurs when a species is introduced to a new ecosystem, or when a species can survive in an environment that was unavailable before. That was the case for mammals while dinosaurs and other reptiles dominated earth's terrestrial environment.

Three major evolutionary innovations provided mammals with a competitive advantage to dominate the terrestrial environment: milk secreted from **mammary glands, hair** for conserving body heat, and **specialized teeth** for cutting (incisors), tearing (canines) and grinding (molars) their food.

8.5. Implications of Geological Changes in the Evolution of Marine Mammals

Oceans cover about 70% of Earth's surface, with an average depth of 3,800 m. There are four major basins: Atlantic, Pacific, Indian, and Arctic. Two thirds of the landmasses are in the northern hemisphere and oceans cover 80% of the southern hemisphere. The deepest point of the ocean is the Mariana's trench (W. N. Pacific Ocean) 11,022 m. The continental shelf has a depth that ranges between 120 and 200 m.



With that huge space and diversity of environments, no wonder that marine mammals have been, for the past 50 million years or so, so diverse and abundant in our planet. However, the landmasses whose location dictates a number of oceanographic phenomena such as upwelling have changed in size and position through millions of years. That has had a major influence on the evolution and past and present distribution of marine mammals. The science that studies those distributions is called **biogeography**.

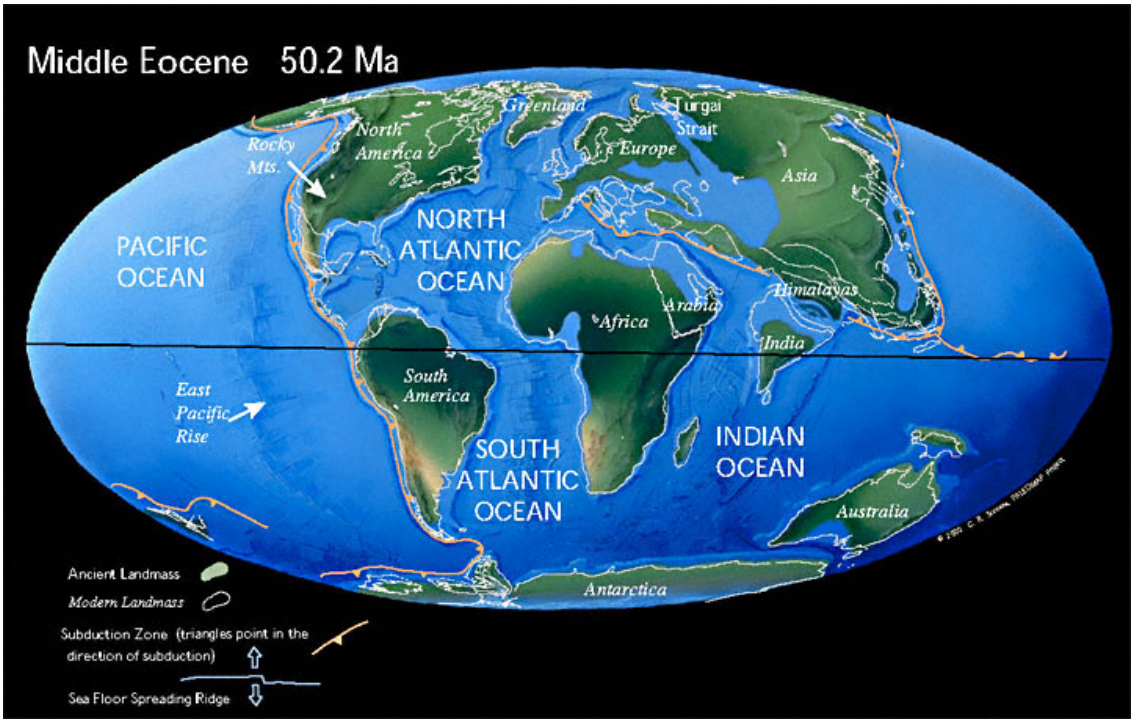
For example, some marine mammals have a **cosmopolitan** distribution, i.e., can be found in every ocean of the world, in both pelagic and coastal waters. Examples are the sperm whale, the killer whale or orca, and the harbor seal. Some are found in all oceans but only in tropical waters. This is called a **pantropical distribution**. There are others that are found only throughout polar waters. They are called **circumpolar**. Examples are the narwhal and the beluga. Some have a very **restricted distribution**. Examples are river dolphins, and the Caspian and the Baikal seals restricted to either a specific watershed or a particular interior sea or lake (Caspian Sea or Lake Baikal, respectively.).

Species that are found in two or more areas that do no overlap are said to have a **disjunct distribution**. An example of that are **antitropical** groups of species found in both Arctic and Antarctic waters but not in the tropical seas in between. That is typical of porpoises and elephant seals. Other examples are certain species that are found in different oceans (e.g., the Pacific and the Atlantic) but without any contact of individuals between the populations of those oceans; that is the case of the harbor porpoise, the walrus, the fin whale, and the humpback whale. In some cases, disjunct populations exist even within the same ocean. In the Pacific, for example, the West and East Pacific populations of the gray whale and the sea otter are disjunct.

One major source of information to explain today's distribution is by looking at past events in the Earth's geological history, particularly in the last 50 million years.

The way the oceans look today is the result of the breaking up of the original, single continent called **Pangea**, about 190 million years ago (MYA). About 150 MYA the landmasses

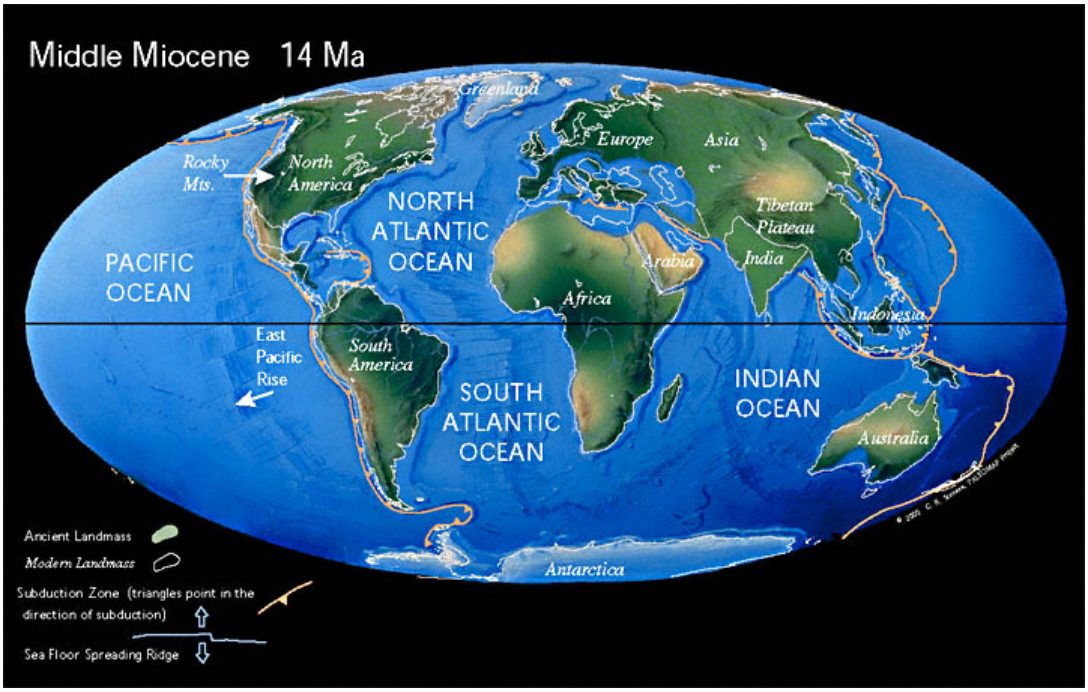
of the north (**Laurasia**) started to separate from the landmasses of the south (**Gondwana**). About 95 MYA Laurasia still remained as a single continent, but South American and Africa separated from each other. One of the seas at that time was the **Tethys Sea**. This was a sea between central Asia and the then migrating Indian subcontinent that had broken off from Gondwana and was moving north. This sea, which lasted for about 500 million years, disappeared as the Indian subcontinent collided against the Asia landmass forming the Himalayas. The oldest fossils of cetaceans as well as those of their reputed ancestors, the mesonychids, have been found in the shallow, coastal environments of that ancient, in what is today Pakistan and northern India, which leads us to believe that the first whales evolved in that part of the world, which makes the Tethys Sea the **center of origin** for cetaceans.



There was also the Paratethys Sea as a northern arm of the Tethys Sea stretching between western Russia and Siberia. As this sea and the Mediterranean started to dry out (a process completed between six and five million years ago), a number of inland bodies of waters such as the Caspian Sea and the Lake Baikal remained which explains why some species of seals were "trapped" in those regions.

About 45 MYA, when cetaceans and sirenians started their evolutionary path toward what we know today as whales and dolphins and manatees and dugongs, Australia started to separate from Antarctica (pinnipeds did not appear until about 30 MYA). By about 5 MYA South America and North America were connected and Antarctica had moved further south. The fact that the oldest and most primitive fossil pinnipeds are found in the Pacific northwest of the U.S., leads us to believe that such area was the **center of origin** for this group. Also, this means that the actual separation between the Atlantic and the Pacific in the tropic took place only

recently in geological history, which explains why today we find populations of species of whales and dolphins on both sides of the American continent.



Other current biogeographical patterns are the consequence of exploitation by humans. For example, the gray whale that used to be found on both sides of North America became extinct in recent times in the Atlantic side due to human overexploitation.

Chapter 9

The Evolution of Cetaceans

9.1. Introduction

9.1.1. The Uniqueness of Cetaceans

Cetaceans, together with sirenians, are the earliest recorded marine mammals, appearing in the Eocene about 54-53 MYBP Cetaceans are also the most diverse mammalian group to adapt to a marine existence.

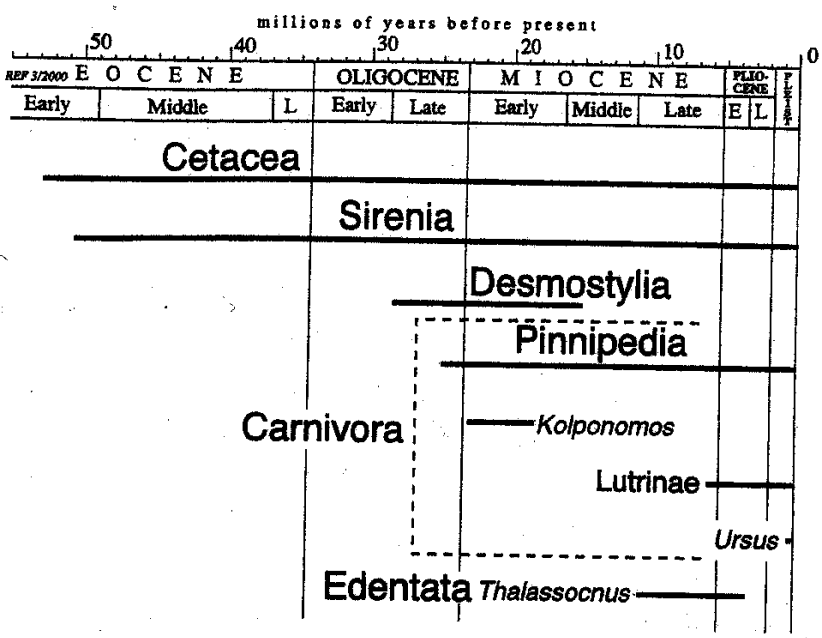
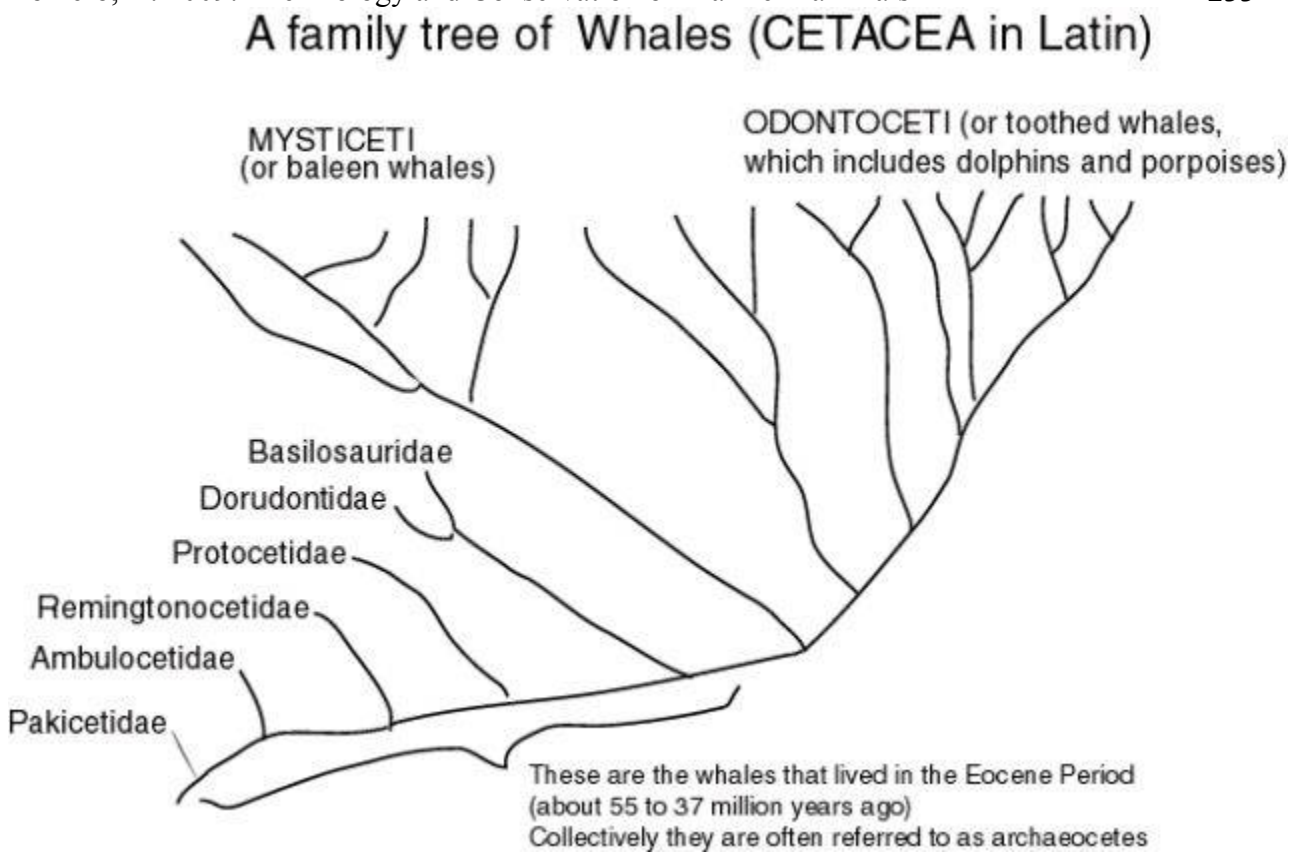
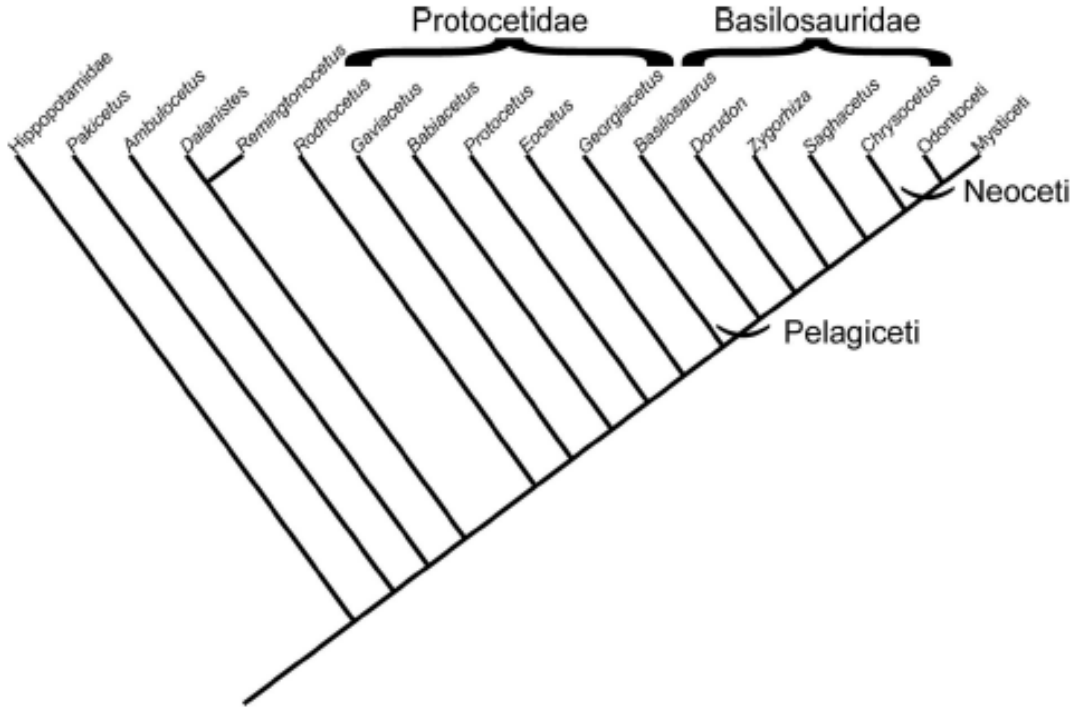


Figure 1 *Summary of geological age ranges for the main groups of fossil marine mammals.*

Throughout their evolution cetaceans have become perfectly suited to the aquatic environment and are virtually incapable of leaving it. They illustrate an example of **adaptive radiation** among mammals.


A family tree of Whales (CETACEA in Latin)
MYSTICETI
(or baleen whales)
ODONTOCETI (or toothed whales,
which includes dolphins and porpoises)
Basilosauridae
Dorudontidae
Protocetidae
Remingtonocetidae
Ambulocetidae
Pakicetidae
These are the whales that lived in the Eocene Period
(about 55 to 37 million years ago)
Collectively they are often referred to as archaeocetes


Protocetidae
Basilosauridae
Hippopotamidae
Pakicetus
Ambulocetus
Dalanistes
Remingtonocetus
Rodhocetus
Gaviacetus
Babiacetus
Protocetus
Eocetus
Georgiacetus
Basilosaurus
Dorudon
Zygorhiza
Saghacetus
Chrysocetus
Odontoceti
Mysticeti
Neoceti
Pelagiceti

9.1.2. Cetacean Phylogenetic Characters

Cetaceans are monophyletic. They have the following derived characters that diagnose the group:

1. Presence of a sigmoid process, an elongated protuberance of the tympanic bone anterior to the external auditory meatus (ear opening). It may serve as a buttress for the malleus (a middle ear bone) and may have assisted in the reorientation of the middle ear that cetaceans underwent. Subsequently, the sigmoid process has been found to be morphologically variable among archaic cetaceans, and a related feature of the tympanic bone, development of the involucrum (pachyostosis of the medial part of the bulla), is now recognized as an unequivocal cetacean synapomorphy.

2. Pachyosteosclerotic ectotympanic and incus. The lateral portion of the auditory bulla (ectotympanic bone) and the middle ear bone (incus) of cetaceans consist of dense, thick (pachyostotic), and osteosclerotic (replacement of spongy bone with compact bone) bone, referred to as pachyosteosclerotic bone. Pachyosteosclerosis occurs in the ear region of all cetaceans. This condition is absent among archaic hoofed mammals.

3. Rotation of the middle ear bones. In cetaceans, the position of the middle ear bones has become rearranged; evolutionarily the ear bones have rotated. The rotation is unique in cetaceans and is only partly developed in the archaic cetacean *Pakicetus*.

4. Incisors set anteroposteriorly. In cetaceans the incisors (front teeth) are arranged in parallel with the toothrow. In most fossil relatives of cetaceans (except *Andrewsarchus*), the incisors are transversely aligned in front of the canines.

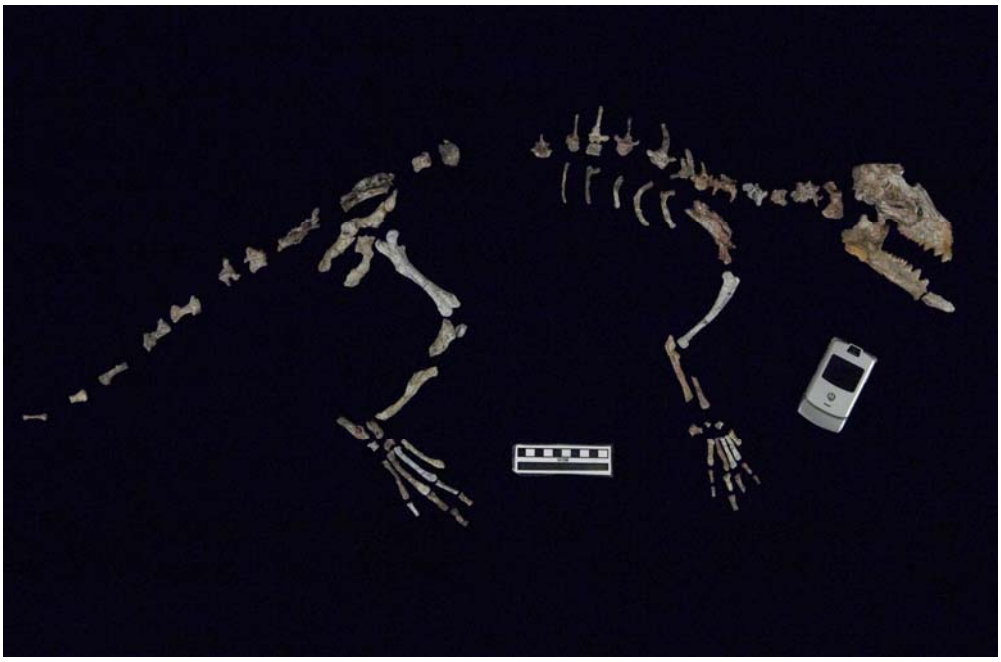
5. Fourth upper premolar paracone height twice that of first upper molar. In archaic cetaceans (e.g., *Pakicetus* and *Ambulocetus*), the upper fourth premolars have an anterior cusp (paracone) that is elevated twice as high as that of the first upper molar. In fossil relatives of cetaceans the paracone is not higher than in the first upper molar.

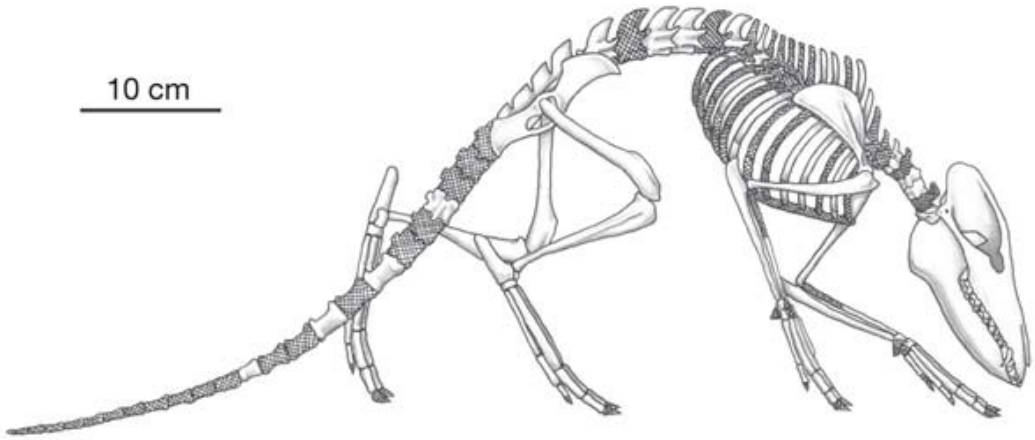
9.2. The Precursors to Cetaceans

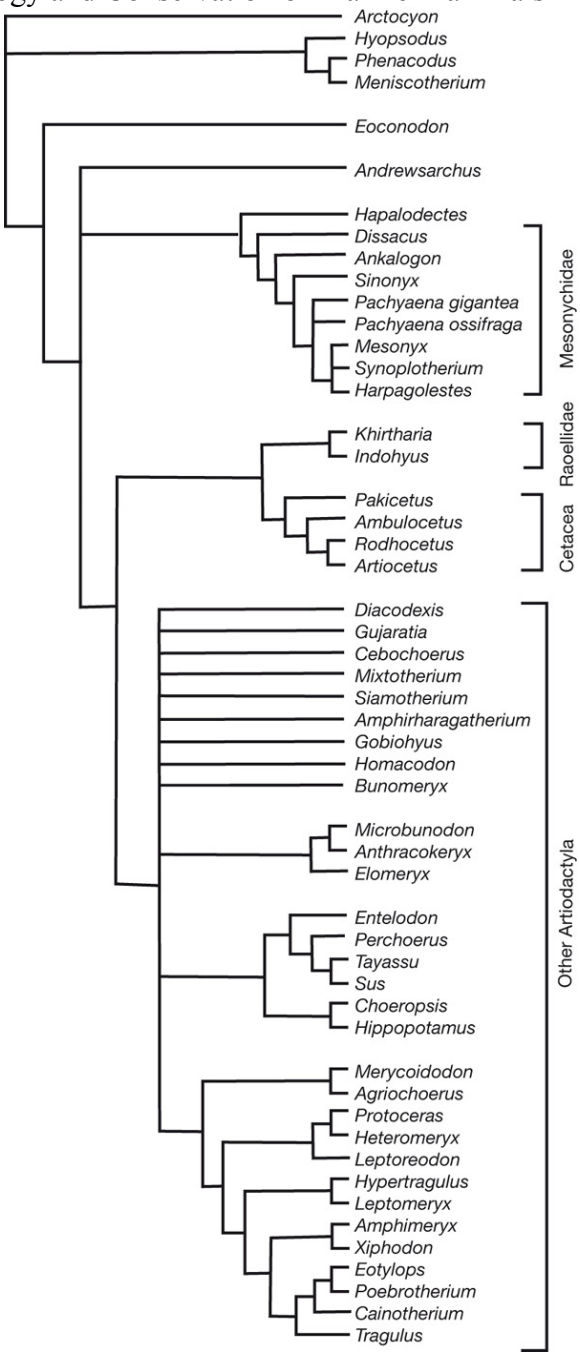
There is a growing fossil record of cetaceans despite the fact that fossilization of any organism is a chance process. Our knowledge comes from fossils found in sediments that were deposited in shallow waters near shore. Since cetaceans are almost exclusively marine animals, it is likely that key events in their history occurred in open waters from which there is almost no fossil. There are a few fossil records of freshwater fossils in South America, China, and Australia.

Although the first ten million years of whale evolution are documented by a remarkable series of fossil skeletons, the link to the ancestor of cetaceans has been missing. It was known that whales are related to even-toed ungulates (artiodactyls), but until now no artiodactyls were

morphologically close to early whales. Thewissen et al (2007) suggested that the Eocene (ca. 48 MYBP) roellid from the Kashimir region of India are the sister (closest) group to whales. The raoellid *Indohyus*, a fox-sized animal, is similar to whales, and unlike other artiodactyls, in the structure of its ears and premolars, in the density of its limb bones and in the stable-oxygen-isotope composition of its teeth. They also suggested that a major dietary change occurred during the transition from artiodactyls to whales and that raoellids were aquatic waders. This indicates that aquatic life in this lineage occurred before the origin of the order Cetacea. Two species og this genus have been described: *Indohyrus indirae* and *I. major*.



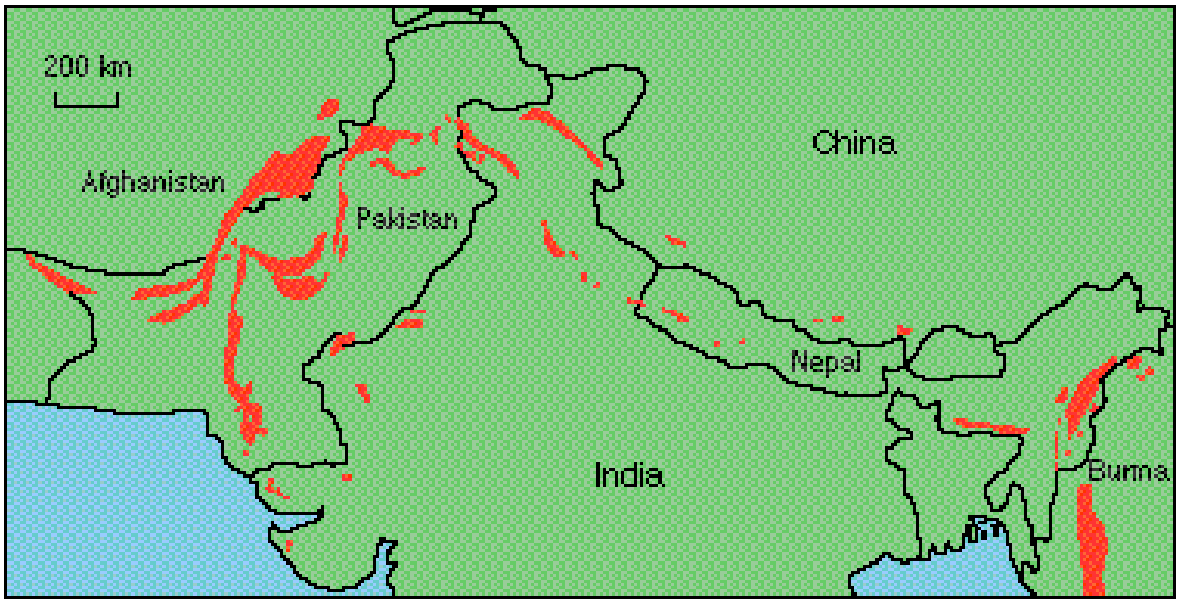



Arctocyon
Hyopsodus
Phenacodus
Meniscotherium
Eoconodon
Andrewsarchus
Hapalodectes
Dissacus
Ankalogon
Sinonyx
Pachyaena gigantea
Pachyaena ossifraga
Mesonyx
Synoplotherium
Harpagolestes
Mesonychidae
Khirtharia
Indohyus
Raoellidae
Pakicetus
Ambulocetus
Rodhocetus
Artiocetus
Cetacea
Diacodexis
Gujaratia
Cebochoerus
Mixtotherium
Siamotherium
Amphirharagatherium
Gobiohyus
Homacodon
Bunomeryx
Microbunodon
Anthracokeryx
Elomeryx
Entelodon
Perchoerus
Tayassu
Sus
Choeropsis
Hippopotamus
Merycoidodon
Agriochoerus
Protoceras
Heteromeryx
Leptoreodon
Hypertragulus
Leptomeryx
Amphimeryx
Xiphodon
Eotylops
Poebrotherium
Cainotherium
Tragulus
Other Artiodactyla

Artist's rendition of *Indohyus*

9.3. Suborder: Archaeoceti

The Suborder Archaeoceti is defined solely by virtue of it containing cetaceans lacking the derived characters marking the two highly distinctive lineages of living cetaceans: mysticetes and odontocetes. The archaeocetes is a paraphyletic group. As such, Archaeoceti is a taxonomic wastebasket on a par with "invertebrates" (Metazoans that are not vertebrates) and fish (vertebrates without legs). Like modern cetaceans they have dense ear bones, space around the bones for fat deposits, air sacs to isolate the air from the skull, a long palate, and nostrils located on top of the snout, elongated body with long tail, short neck, reduced hind limbs, paddle-shaped forelimbs, and a point of flexion in the tail vertebrae that allows up and downs (as opposed to side to side, like fishes) movements. They are primitive Eocene cetaceans with non-telescoped crania. All archaeocetes have elongated jaws and well-developed teeth, but there is no suggestion that they could echolocate or filter-feed.



The red areas represent regions of remaining deposits of the Tethys Sea where may remains of archaeocetes have been found.

The earliest archaeocetes were small, amphibian species that lived in productive fresh and brackish waters of the warm subtropical Tethys Sea between Eurasia, India, and Africa, particularly in what is today Pakistan and India. Archaeocetes diversified greatly not only in terms of species but also in size and occupied all oceans of the world. They were the only cetaceans for about 40 million years until they became extinct. They were ecologically replaced by mysticetes and odontocetes both of which have been around for 34-35 MYBP.

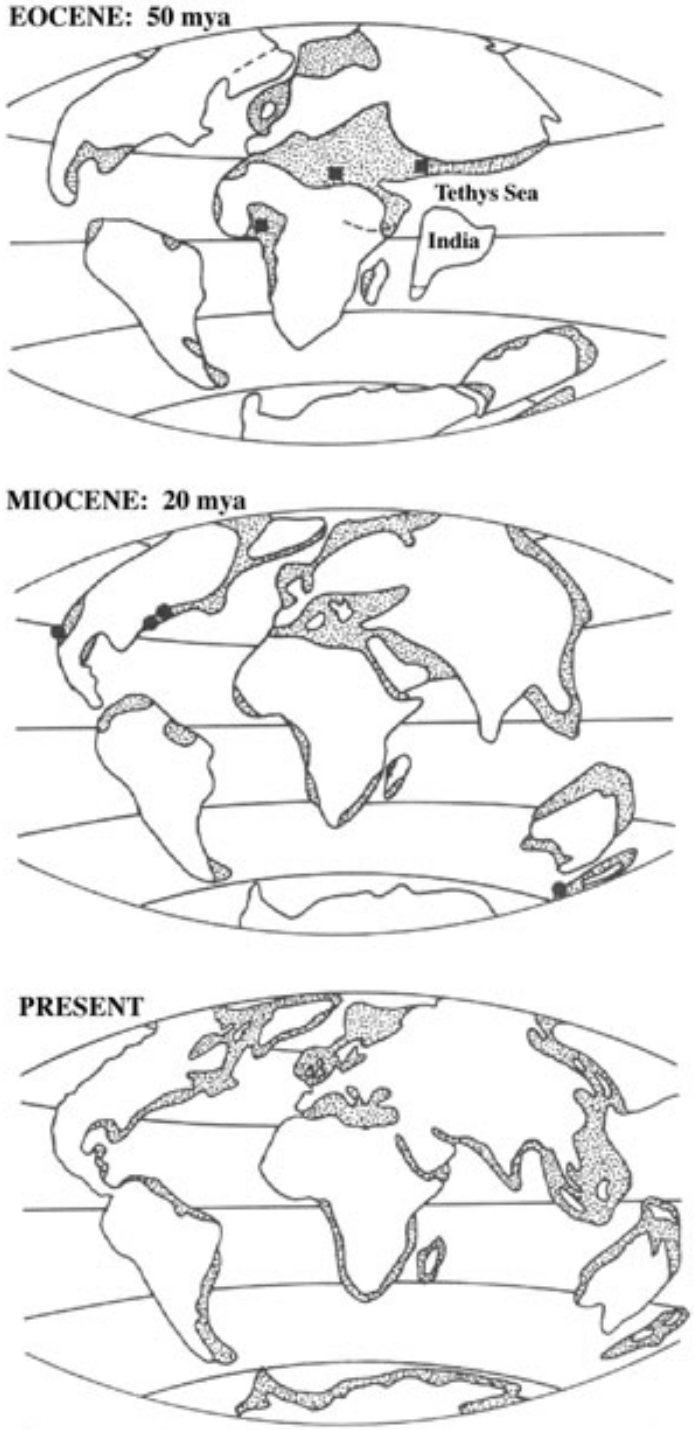
Both molecular and morphological evidence suggest that archaeocetes are related to ungulates such as the hippopotamus, with the roellids, and with the mesonichyds.

Archaeocetes have been divided into six families: Pakicetidae, Ambulocetidae, Remingtonocetidae, Protocetidae, Durodontidae, and Basilosauridae.

9.3.1. Family: Pakicetidae

Pakicetids were predominately land mammals and, except for features of the ear, had few adaptations consistent with aquatic life. The earliest skull if that of *Pakicetus* (ca. 49.5 MYBP from Pakistan) but the Pakicetidae is also represented by a fragmentary jaw of *Himalayacetus subathuensis* from India, dated back to 53.5 MYBP. This was a marine, rather than a freshwater organism. Other genera include *Ichthyolester* and *Nalacetus*, also from the eastern Tethys. It is quite possible that the Pakicetidae family is a paraphyletic one because the different genera seem to contain a number of primitive and derived characters including small mandibular foramina (for passage of blood vessels and nerves), primitive dental morphology, and the lack of peritympanic sinuses (air filled sinuses in the ear).

CONTINENTAL DRIFT CARRIES INDIA INTO ASIA MAKING THE TETHYS SEA MORE SHALLOW

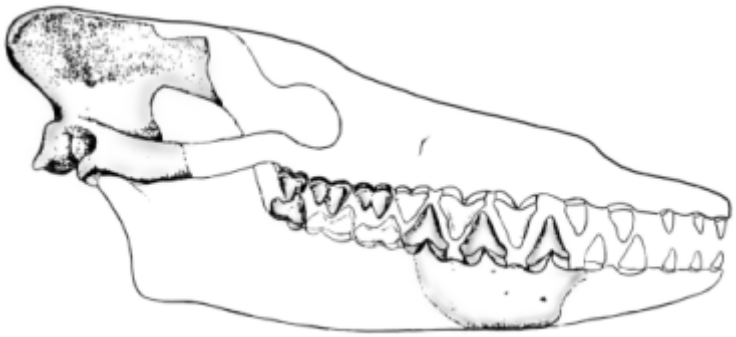


from Peter Evans, 1987
The Early History of Whales & Dolphins

9.3.1.1. *Pakicetus*

The earliest archaeocetes found so far are *Pakicetus attocki* and *P. inachus*, from the early Eocene (ca. 49.5 MYBP) in the Himalayan region of Pakistan. It was discovered in 1983 by Philip D. Gingerich and Neil A. Wells (University of Michigan), Donald E. Russel of the Muséum National d'Histoire Naturelle of Paris, and S.M. Ibrahim Shah of the Geological Survey of Pakistan. *Pakicetus* occurs with a land-mammal fauna in fluvial sediments bordering epicontinental Eocene remnants of the eastern Tethys seaway.

Although it is known only from fragmentary skull remains, those remains are definitely intermediate between the mesonychid *Sinonyx* and later whales. This is especially the case for the teeth. The upper and lower molars, which have multiple cusps, are still similar to those of *Sinonyx*, but the premolars have become simple triangular teeth composed of a single cusp serrated on its front and back edges. The teeth of later whales show even more simplification into simple serrated triangles, like those of carnivorous sharks, indicating that *Pakicetus*'s teeth were adapted to hunting fish.



Reconstruction of the skull of *Pakicetus inachus* (redrawn for RNCSE by Janet Dreyer).

Pakicetus had a narrow braincase, a high, narrow sagittal crest, and prominent lambdoidal crests. The nostrils were still at the front of the head, so they did not have a blowhole. The skull was about 35 centimeters in length and it has been calculated that it may have been 2.5 m in length. We have no remains of limbs.

The hearing organ in *Pakicetus* is intermediate between that of land mammals and modern cetaceans. It possessed neither dense tympanic bullae nor sinuses isolating the left auditory area from the right one, an adaptation of later whales that allows directional hearing under water and prevents transmission of sounds through the skull. All living whales have foam-filled sinuses along with dense tympanic bullae that create an impedance contrast so they can separate sounds arriving from different directions. Further, the lower jaw of all described cetacean (except *Pakicetus*) have a great enlarged mandibular foramen which lodges (in odontocetes) a fat pad and foramen are often assumed to be involved in underwater hearing: sound vibrations received by the lower jaw are transmitted by the fat pad to the middle ear. There is also no evidence in *Pakicetus* of vascularization of the middle ear, which is necessary to regulate the pressure within the middle ear during diving.

The incus and mandible of *Pakicetus* indicate that the path of sound waves to its ear resembled that of land mammals. *Pakicetus* has a small mandibular foramen as is the case of all terrestrial mammals. Sounds reached its eardrum following the external auditory meatus as in terrestrial mammals. The incus is rarely found in fossil mammals. No incus is known for any condylarth, but in recent artiodactyls the incus is similar to *Pakicetus*. There are similarities between pinnipeds and *Pakicetus* in hearing apparatus.

These fossils indicate that this primitive whale was amphibious. *Pakicetus* was probably incapable of achieving dives of any significant depth. This paleontological assessment of the ecological niche of *Pakicetus* is entirely consistent with the geochemical and paleoenvironmental evidence. When it came to hearing, *Pakicetus* was more terrestrial than aquatic, but the shape of its skull was definitely cetacean, and its teeth were between the ancestral and modern states.

9.3.2. Family: Ambulocetidae

The Ambulocetidae is a monophyletic family that contains the genera *Ambulocetus* and *Gandakasia*. They have been found in deposits of the Early to Middle Eocene of eastern Tethys.

9.3.2.1. Ambulocetus natans; *ambulo* (Gr) walking, *cetus* (L) = whale; *natans* (L) = that swims.

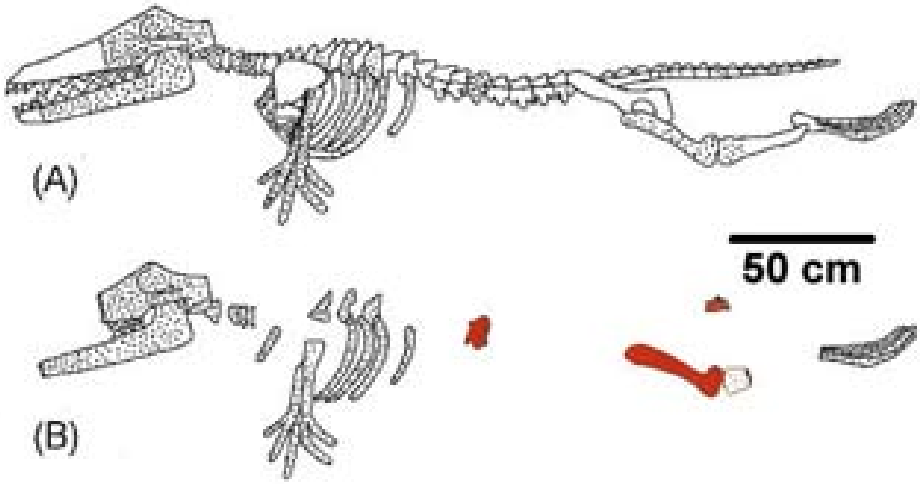
J.G.M. Thewissen of North Eastern Ohio University, S.T. Hussain of Howard University in Washington, D.C. and M. Arif from the Geological Survey of Pakistan unearthed in 1992 a new species of cetacean from the lower to the middle Eocene (49 MYBP) of Pakistan, which they named *Ambulocetus natans*. The associated fauna indicates that this species was buried in shallow seas. *Ambulocetus* was found in the same area that *Pakicetus*, but in sediments about 120 meters higher. It weighed some 1,000 kilos and was the size of a hefty sea lion.

It was clearly a cetacean, but it also had functional legs and a skeleton that still allowed some degree of terrestrial walking. The conclusion that *Ambulocetus* could walk by using the hind limbs is supported by its having a large, stout femur. However, because the femur did not have the requisite large attachment points for walking muscles, it could not have been a very efficient walker. Probably it could walk only in the way that modern sea lions can walk, i.e., by rotating the hind feet forward and waddling along the ground with the assistance of their forefeet and spinal flexion. When walking, its huge front feet must have pointed laterally to a fair degree since, if they had pointed forward, they would have interfered with each other.

The forelimbs were also intermediate in both structure and function. The ulna and the radius were strong and capable of carrying the weight of the animal on land. The strong elbow was strong but it was inclined rearward, making possible rearward thrusts of the forearm for swimming. However, the wrists, unlike those of modern whales, were flexible.

It is obvious from the anatomy of the spinal column that *Ambulocetus* must have swum with its spine swaying up and down, propelled by its back feet, oriented to the rear. As with other aquatic mammals using this method of swimming, the back feet were quite large. Unusually, the toes of the back feet terminated in *hooves*, thus advertising the ungulate ancestry of the animal. The only tail vertebra found is long, making it likely that the tail was also long. The cervical vertebrae were relatively long, compared to those of modern whales; *Ambulocetus* must have had a flexible neck.

Ambulocetus's skull was cetacean (Novacek 1994). It had a long muzzle, teeth that were very similar to later archaeocetes, a reduced zygomatic arch, and a tympanic bulla (which supports the eardrum) that was poorly attached to the skull. Although *Ambulocetus* apparently lacked a blowhole, the other skull features qualify *Ambulocetus* as a cetacean. The post-cranial features are clearly in transitional adaptation to the aquatic environment. Thus *Ambulocetus* is best described as an amphibious, sea-lion-sized fish-eater that was not yet totally disconnected from the terrestrial life of its ancestors.



Unlike extant cetaceans, it retained a long tail instead of flukes. No pelvic bones have been found but most elements of large and powerful hind legs were recovered, including a complete femur.

The forelimbs, smaller than the hind limb and limited in motion, were probably used in maneuvering and steering while swimming, as in extant cetaceans, as they lacked major propulsive force in water. Hands were long and broad with five digits suggesting the possibility for a webbed-like hand. They had flexible elbow, wrists, and digits. Toes are terminated by a

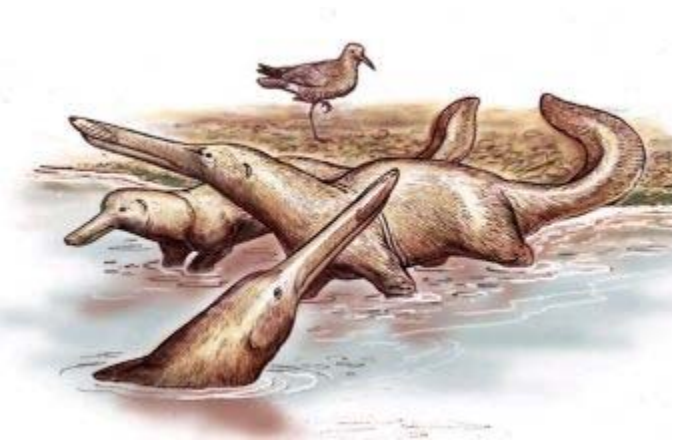
short phalanx carrying a convex hoof, as in mesonychids, and leave no doubt that they were used in locomotion.

The long, spinous processes and the transverse processes with deeply excavated caudal sides of the cervical vertebrate, suggesting undulating vertebral column. The nature of the hips and well-developed articulation of the limbs and large feet suggest that they were able to walk. Thus, *Ambulocetus* was able to both, walk on land a swim in water by undulating its body like current cetaceans.

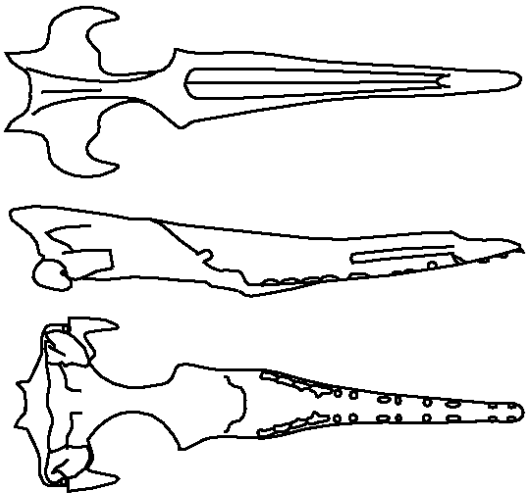
Body size estimates suggest that *Ambulocetus* weighed between 141 and 235 kg and was similar in size to a female Steller's sea lion. *Gandakasia* is distinguished from *Ambulocetus* mostly by its smaller size.

9.3.3. Family: Remingtonocetidae

This was a short-lived archaeocete clade (middle Eocene of India-Pakistan) containing the genera *Remingtonocetus*, *Dalanistes*, *Andrewsiphius*, *Kutchicetus,* and *Attockicetus*. They are characterized by long, narrow skulls and jaws. Morphology of the jaws for this family suggests a diet of fast-swimming aquatic prey. The middle ear is large and shows some specializations for underwater hearing. Their skeletons are similar to ambulocetids in retaining large hind limbs. They differ from ambulocetids in having smaller orbits (and eyes), long slender snouts, and a wide basicranium which places the ear regions far from the midline. The widely separated ears, combined with the small eyes, may have been an adaptation for enhanced emphasis on hearing to locate prey. Unlike earlier suggestions this family are not ancestral to odontocetes.



Reconstruction of *Kutchicetus.* Illustration by Carl Buell and taken from http://www.neoucom.edu/Depts/Anat/Remi.html.



Remingtonocetus **cranium (dorsal, lateral, and ventral views)**

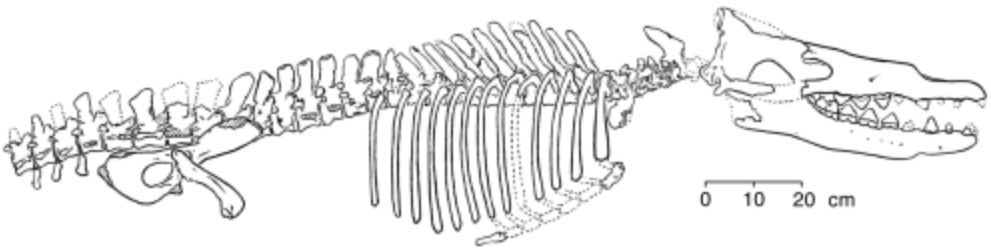
9.3.4. Family: Protocetidae

The family lived from the Early to the Middle Eocene from western Tethys to the western central Atlantic. They had a skull with enlarged supraorbital shield, mandible with a large mandibular foramen, and reduced hindlimbs. They also showed a lack the complex teeth and the pterygoid sinuses of other cetaceans. They have short neck vertebrae and more posterior vertebrae adapted for dorso-ventral oscillation.

This family shows a wide distribution both geographically and in habitats, including both offshore and near shore, shallow water representatives. The best-known members of this family are *Rodhocetus* and *Indocetus.* Other genera of this family are: *Babicetus* and *Gaviacetus* from India-Pakistan, *Protocetus* and *Eocetus* from Egypt; *Pappocetus* from Nigeria; *Geogiacetus* from Georgia and possibly North Carolina, and *Natchitochia* from Louisiana. Two more (but unconfirmed) Protocetidae are *Gaviacetus* and *Takracetus*.

9.3.4.1. *Rodhocetus kasrani*

Gingerich and Pakistani paleontologists discovered *Rodhocetus kasrani* in Pakistan (Middle Eocene, 46-47 MYBP). This is the first archaeocete with complete thoracic, lumbar, and sacral vertebral column. It has short cervical vertebrae, a reduced femur, and a flexible sacrum, robust tail and high neural spines on lumbars and caudals required for dorso ventral oscillation of a heavily muscle tail. This is the oldest fossil whale described from deep-neritic shelf deposits implying early colonization of offshore habitats, and it shows that tail swimming evolved early in the history of cetaceans. This is the earliest archaeocete of which all of the thoracic, lumbar, and sacral vertebrae have been preserved.



Reconstruction of the skeleton of *Rodhocetus kasrani*

Elsewhere along the spine, the four large sacral vertebrae were unfused. This gave the spine more flexibility and allowed a more powerful thrust while swimming. They also had a shortened cervical vertebrae, heavy and robust proximal tail vertebrae, and large dorsal spines on the lumbar vertebrae for large tail and other axial muscle attachments that are associated in modern whales with the development and use of tail flukes. It must have been a very good tail-swimmer, and it is the earliest fossil whale committed to this manner of swimming.

The pelvis of *Rodhocetus* was smaller than that of its predecessors, but it was still connected to the sacral vertebrae, meaning that *Rodhocetus* could still walk on land to some degree. However, the ileum of the pelvis was short compared to that of the mesonychids, making for a less powerful muscular thrust from the hip during walking, and the femur was about 1/3 shorter than *Ambulocetus'*s, so *Rodhocetus* probably could not get around as well on land as its predecessors.

Rodhocetus's skull was rather large compared to the rest of the skeleton. The premaxillae and dentaries had extended forward even more than its predecessors', elongating the skull and making it even more cetacean. The molars have higher crowns than in earlier whales and are greatly simplified. The lower molars are higher than they are wide. There is a reduced differentiation among the teeth. For the first time, the nostrils have moved back along the snout and are located above the canine teeth, showing blowhole evolution. The auditory bullae are large and made of dense bone (characteristics unique to cetaceans), but they apparently did not contain the sinuses typical of later whales, making it questionable whether *Rodhocetus* possessed directional hearing underwater.

9.3.4.2. *Indocetus ramani*

This whale was found in shallow-water marine deposits of India and Pakistan. It dates back to 46.5 MYBP being intermediate in age between the *Pakicetus* skull and the *Basilosaurus* hind legs. Its discovery was reported in 1993 by Gingerich, M. Raza, M. Afif, M. Anwar and X. Zhou who found hind legs of substantial size. They found pelvic bones, and the ends of both femur and tibia, but not foot bones, and insufficient evidence for reconstructing the full limb and its articulations. The leg bones are large and presumably functional on both land and sea (the tibia, in particular) differs little in size and complexity from that of the related and fully terrestrial mesonychid *Pachyaena ossifraga*. *Indocetus* was probably able to support its weight on land, and it was almost certainly amphibious as early Eocene *Pakicetus* is interpreted to have been. *Indocetus* probably entered the sea to feed on fish, but returned to land to rest and to birth and raise its young.

9.3.5. Family: Basilosauridae

This is a family with ample representation in terms of species and geographic range. The most current approach to its classification is that it is composed of two subfamilies: Basilodaurinae and Dorudontinae.

9.3.5.1. Basilodaurinae

This subfamily was characterized for having cheek teeth with complex denticles and expanded basicranial air sinuses. They had large size, elongate vertebral bodies, although probably too specialized to be direct ancestors of either mysticetes or odontocetes. This is a paraphyletic family. Sometimes basilosaurids and dorudontinids have been grouped within the family Basilosauridae but with two different subfamilies. Yet, the latter are very different in that they lack elongated vertebral bodies. Some basilosaurids were as large as 25 m in length and can be found from the Middle to Late Eocene and probably also from the early Oligocene in the northern hemisphere.

9.3.5.2. *Basilosaurus*

The particularly well-known fossil *Basilosaurus* is represented by two species: one found in SE United States, *B. cetoides*, and another one discovered in Egypt, *B. isis*. New specimens of middle Eocene 45 My *B. isis* (of which hundreds of specimens have now been excavated) were discovered in 1990 by Phillip Gingerich and Holly Smith of the University of Michigan and E. L. Simons of Duke University, from north-central Egypt (Wadi Hitan, also known as the Valley of Whales or Zeuglodon Valley). This species lived during the late Eocene and latest part of the middle Eocene (35-45 million years ago). *Basilosaurus* was a long, thin, serpentine animal that was originally thought to have been the remains of a sea serpent (hence it is name, which actually means "king lizard"). Its extreme body length (about 15 meters) appears to be due to a feature unique among whales; its 67 vertebrae are so long compared to other whales of the time and to modern whales that it probably represents a specialization that sets it apart from the lineage that gave rise to modern whales.

Basilosaurus is unique because of the distinctive anatomy of its hind limbs. It had a nearly complete pelvic girdle and set of hindlimb bones. The limbs were too small for effective propulsion, less than 60 cm long on this 15-meter-long animal, and the pelvic girdle was completely isolated from the spine so that weight-bearing was impossible. Reconstructions of the animal have placed its legs external to the body, a configuration that would represent an important intermediate form in whale evolution.

Although no tail fluke has ever been found (since tail flukes contain no bones and are unlikely to fossilize), *Basilosaurus* vertebral column shares characteristics of whales that do have tail flukes such as that the tail and cervical vertebrae are shorter than those of the thoracic and lumbar regions.

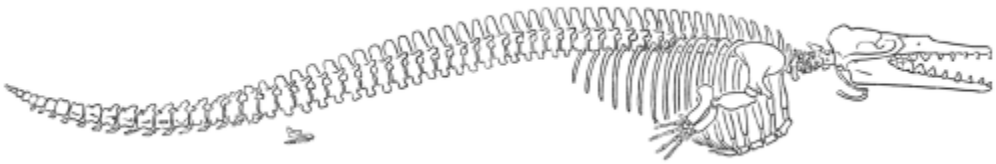
Basilosaurus had a large single nostril that had migrated a short distance back to a point corresponding to the back third of the dental array. The movement from the forward extreme of the snout to a position nearer the top of the head is characteristic of only those mammals that live in marine or aquatic environments.

The presence of functional pelvic limb and foot bones are important in corroborating the intermediate evolutionary position of Archaeocetes between generalized Paleocene land mammals that used hind limbs in locomotion and Oligocene-to-Recent whales that lack functional, pelvic limbs. These legs were very small (3% of the animal's length) and they did project from the body wall. The foot is paraxonic, consistent with derivation from mesonychid Condylarthra. Hind limbs of *Basilosaurus* are interpreted as either copulatory guides or vestigial structures. Hind limbs in *Basilosaurus* appear to have been too small relative to body size to assist in swimming, and they could not possibly have supported the body on land.

9.3.5.2. Family: Dorudontinae

The durodontines were smaller dolphin-like species that were taxonomically and ecologically very diverse. They are known from the late Eocene in Egypt, southeastern North America, Europe, and New Zealand. Among the abundant fossil cetaceans from Egypt are the remains of *Durodon atrox*. *Dorudon* lacked the elongated vertebrae of *Basilosaurus* and was much smaller (about 4-5 meters in length). *Dorudon*'s dentition was similar to *Basilosaurus*'s; its cranium, compared to the skulls of *Basilosaurus* and the previous whales, was somewhat vaulted. *Dorudon* also did not yet have the skull anatomy that indicates the presence of the apparatus necessary for echolocation.

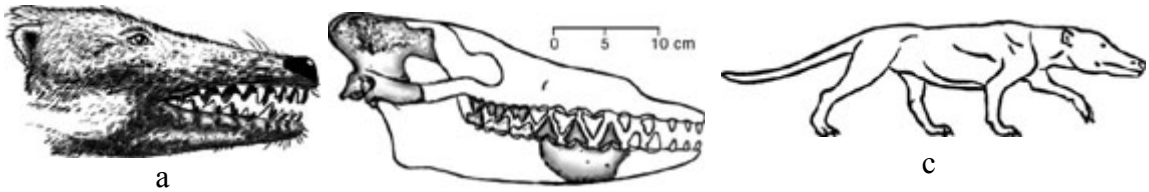
Also from Egypt, there is a new genus and species of dorudontidae, *Ancalecetes simonsi*, which differs from *Dorudon atrox* in several peculiarities of the forelimb including fused elbows that indicate very limited swimming capability. Modern whales, including both odontocetes and mysticetes, likely diverged from durodontids. *Prozeuglodon* (Late Eocene, 40 MYBP) still carried a pair of vestigial 10 cm hind legs on its 5 m body. *Eocetus* and its relatives were advanced whales have lost their hind legs entirely, but retain a primitive whale skull and teeth, with unfused nostrils. They grew to larger body size (up to 25 m by the end of the Eocene), had an elongate, streamlined body, flippers, and a cartilaginous tail fluke. The ear was modified for hearing underwater.



R*econstruction of the skeleton of Dorudon atrox*

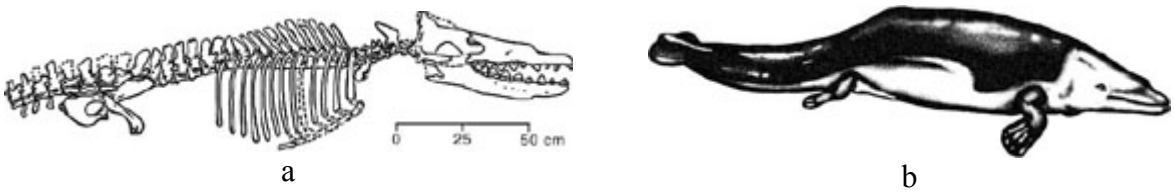
Thus, the fossil record of archaeocetes can be summarized in the graph below:

1. *Pakicetus inachus* ~ 50 MYBP, Pakistan, Riverine, Partially aquatic, but no directional hearing



2. *Ambulocetus natans* ~ 48 MYBP, Pakistan, shallow/marine, long femur and feet=seal-like propeller swimmer

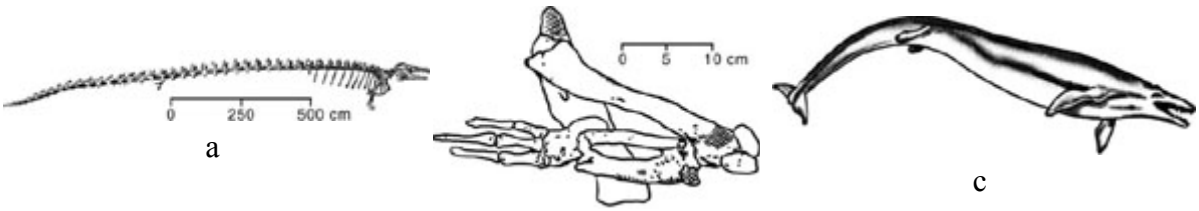
3. *Rodhocetus kasrani* ~ 46 MYBP, Pakistan, deep neritic, tail swimming



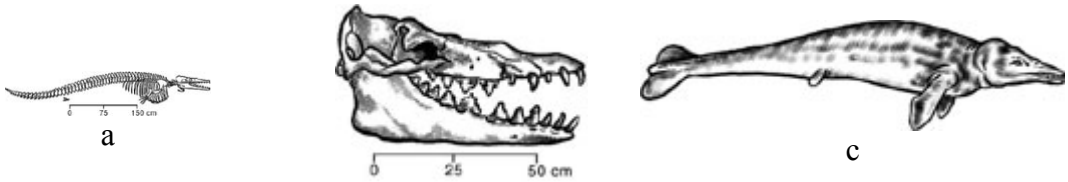
4. *Indocetus remani* ~ 46.5 MYBP, Pakistan, shallow/marine, robust sacrum = caudally propelled

5. *Protocetus atavus* ~ 46 MYBP, Egypt, deep/neritic, sacrum not articulated w/pelvis = fully aquatic

6. *Basilosaurus* spp. ~ 37-45 MYBP, U.S., Egypt, deep/neritic, fully aquatic (*Basilosaurus isis*, below)



7. *Dorudon, Prozeuglodon* ~ 36 MYBP



9.4. Hypotheses of Origin

Charles Darwin first hypothesized about the origin of whales from bears. At that time, when fossils were non-existent, that was the best possible explanation available. Thanks to recent finding of fossils (particularly since the 1980's) and the development of molecular techniques, now we have a much better picture of how cetaceans evolved from terrestrial ancestors.

In recent years three mammalian groups have been proposed as possible cetacean ancestors: the mesonychids, the hyppopotamidae, and the family roellids (artiodactyla). Let us analyze these hypotheses.

9.2.1. The Mesonychids

From insectivorous mammals in the early age of mammals a carnivorous group called Condylarthra evolved which ranged in size and appearance from small catlike animals to bear-like ones. One Condylarthra family was the mesonychids, an extinct group of large-bodied, wolf-like proportions, terrestrial animals of the Paleocene and Eocene. Mesonychids were the first group of mammals to become specialized meat-eaters, appearing in the middle Paleocene (approximately 62 million years ago), before more specialized carnivorous mammals (the creodonts and eventually the true carnivores) occupied that niche. Members of this group had a heavy robust skull armed with sharp canine teeth and huge round-cusped molar teeth, suitable not only for eating meat but also for crushing bone. The body was also very wolf-like, with a long tail and limbs. Mesonychids walked on the tips of their long toes, rather than flat-footed, like many modern carnivores. Despite all these carnivorous adaptations, however, mesonychids were derived from hoofed mammals. The proof is in their toes, which had hooves rather than claws.

Some of them were fish eaters and their remains have been found in sediments of estuaries and lagoons suggesting that they actively used the aquatic environment. Mesonychids have been found in some of the same rock units that have produced the earliest whales in Pakistan and India and have skull characteristics similar to those of the earliest Archaeocetes. The mesonychids were running carnivorous animals that when swimming probably paddle by flexing and extending their hindlimbs alternately as in extant land mammals. The mesonychids were characterized by long limbs, a digitigrade stance (walking on their fingers and toes), and probably had hoofs. In addition, most genera had massive, crushing dentition. They spanned a great range of habits from eating fishes at river edges to crushing bones of carrion. This is a group yet in need of systematic revision.

There are so many morphological similarities between the mesonychids and the cetaceans that some authors have grouped them under the denomination of Cete (a name proposed by

Linnaeus even before the mesonychids were known). The evidence is based in the skull, dentition, and vestigial hind limbs between the mesonychids and earlier cetaceans such as *Basilosaurus* and *Ambulocetus*. The hind limbs of these two genera show a paraxonic arrangement, a condition where digits symmetrically extend about a plane located between digits III and IV. This paraxonic arrangement bears striking resemblance of that of mesonychian condylarths as well as that of the artiodactyls (even-toed ungulates that include the antelopes, deers, camels, pigs, giraffes, and hippos).

By the Early Eocene (approximately 55 million years ago), mesonychids had reached their peak of diversity, with wolf-sized beasts such as *Mesonyx* and *Harpagolestes* reigning as the largest carnivorous mammals of their time. However, they had to share their world with two other groups of carnivorous mammals: the creodonts (which soon surpassed them in size and diversity) and the true carnivores (which were still weasel-sized and which did not become large dog-sized or cat-sized predators until the Oligocene (approximately 30 million years ago). By the Middle Eocene (approximately 50 to 47 million years ago), the mesonychids had declined rapidly in North America and Eurasia, where once they had dominated. The reasons for this decline are unclear. They disappeared from North America at the end of the Middle Eocene (approximately 37 million years ago) and from Asia in the Late Eocene (about 34 million years ago).

The connection between mesonychids and whales first was suggested by William Diller Matthew in 1937 and revived by Leigh Van Valen in 1968 and by Fred Szalay in 1969. The earliest whales have many features of the braincase and skull, and especially their distinctive, triangular-bladed teeth, that are very similar to the condition found in mesonychids. *Ambulocetus* still has a mesonychid skull and teeth but its front and hind feet are both adapted for swimming.

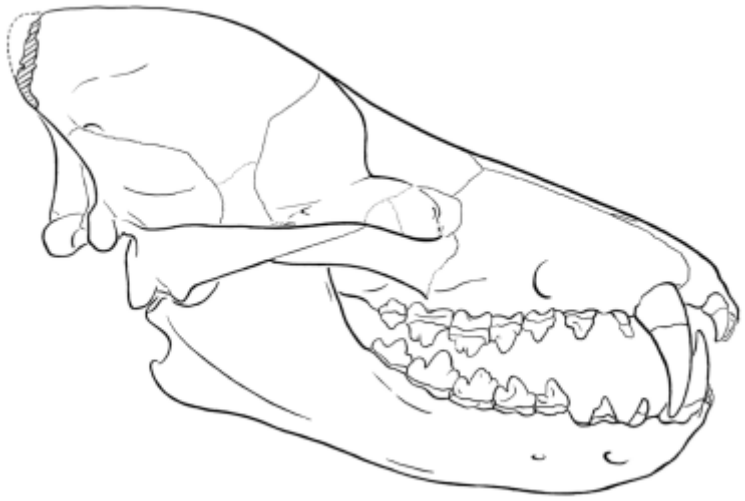
a c

Mesonychids had whale-like teeth, e.g. *Pachyaena*, *Sinonyx,* ~ 55 mya

Sinonyx

A good example of mesonychids is represented by *Sinonyx*, a wolf-sized animal from the Late Paleocene, about 60 MYBP. The characters that link *Sinonyx* to the whales, thus indicating that they might be relatives, include an elongated muzzle, an enlarged jugular foramen, and a short basicranium. The tooth count was the primitive mammalian number (44); the teeth were differentiated as are the heterodont teeth of today's mammals. The molars were very narrow shearing teeth, especially in the lower jaw, but possessed multiple cusps. The elongation of the

muzzle is often associated with hunting fish. These features were atypical of mesonychids, indicating that *Sinonyx* might have already developing the adaptations that later became the basis of the whales' specialized way of life.



Reconstruction of the skull of Sinonyx jiashanensis

Many considered that the Mesonychids as the ancestor because there is a lot of evidence linking them to artiodactyls (cloven hoofed ungulates) which in turn are linked to cetaceans based on fetal blood sugar, blood composition, chromosomes, insulin, uterine morphology, and tooth enamel microstructures. Here is the evidence:

1. *Morphological:* Fossil whales and living ungulates share many characters. For example, the anatomy of the foot of *Basilosaurus* allies whales with artiodactyls. The axis of foot symmetry in these fossil whales falls between the 3rd and 4th digits. This arrangement is called paraxonic and is characteristic of the artiodactyls, whales, and condylarths, and is rarely found in other groups.

Another example of shared characters is the incus (the "anvil" of the middle ear). In *Pakicetus* the incus is morphologically intermediate in all characters between the incus of modern whales and that of modern artiodactyls. Additionally, the joint between the malleus (hammer) and incus of most mammals is oriented at an angle between the middle and the front of the animal (rostromedially), while in modern whales and in ungulates it is oriented at an angle between the side and the front (rostrolaterally). In *Pakicetus*, the first fossil cetacean, the joint is oriented rostrally (intermediate in position between the ancestral and derived conditions). Thus the joint has clearly rotated toward the middle from the ancestral condition in terrestrial mammals.

Recent cetaceans move in the water by vertical tail beats and cannot walk on land. Their hindlimbs are not visible externally and the bones are reduced to one or a few splints that commonly lack joints. The two fully marine orders of mammals: Sirenia and Cetacea swim by

beating horizontal tail flukes up and down. Fishes beat their vertical tail flukes and beat from side to side. Many mammals run by flexing the spinal column up and down. River and sea otters move in water by powerful vertical bending propels the body forward both by itself (and by driving the tail up and down) and by sweeping the hind limbs back and forth in paddling as the body undulates. Thus, horizontal tail flukes may evolve in fully marine mammals because inherited spinal flexibility for movement up and down (rather than side to side) directed this pathway from terrestrial past. We may infer from the vertebra of *Ambulocetus* that it retained a long, thin mammalian tail, and had not yet evolved the horizontal fluke. We know from the spinal column that this transitional whale retained its mammalian signature of flexibility for up-and-down movement-and from the large hind legs that undulations of the back must have propelled the powerful, paddling feet, as in modern otters. *Ambulocetus* shows that spinal undulation evolved before the tail fluke. Cetaceans have gone through a stage that combined hind limb paddling and spinal undulations, resembling the aquatic locomotion of fast swimming otters.

2. *Molecular:* Molecular studies show that whales are more closely related to the ungulates than they are to all other mammals. These studies examined myoglobin, lens alpha-crystallin A, and cytochrome c, alpha- and beta- hemoglobins and ribonuclease in a large number of species. This pattern of biochemical similarities must be present if the whales and the ungulates, especially the artiodactyls, share a close common ancestor. The fact that these similarities are present is therefore strong evidence for the common ancestry of whales and ungulates.

3. *Vestigial evidence:* Modern whales often retain rod-like vestiges of pelvic bones, femora, and tibiae, all embedded within the musculature of their body walls. These bones are more pronounced in earlier species and less pronounced in later species. As the example of *Basilosaurus* shows, whales of intermediate age have intermediate-sized vestigial pelves and rear limb bones. Whales also retain a number of vestigial structures in their organs of sensation. Modern whales have only vestigial olfactory nerves. Furthermore, in modern whales the auditory meatus (the exterior opening of the ear canal) is closed. In many, it is merely the size of a thin piece of string, about 1 mm in diameter, and often pinched off about midway. All whales have a number of small muscles devoted to nonexistent external ears, which are apparently a vestige of a time when they were able to move their ears - a behavior typically used by land animals for directional hearing. The diaphragm in whales is vestigial and has very little muscle. Whales use the outward movement of the ribs to fill their lungs with air. Similarly, dolphins have been spotted with tiny pelvic fins, although limb bones as in those rare sperm whales probably did not support them. And some whales, such as belugas, possess rudimentary ear pinnae - a feature that can serve no purpose in an animal with no external ear and that can reduce the animal's swimming efficiency by increasing hydrodynamic drag while swimming.

4. *Embryological evidence:* Many whales, while still in the womb, begin to develop body hair. Yet no modern whales retain any body hair after birth, except for some snout hairs and hairs around their blowholes used as sensory bristles in a few species. The fact that whales possess the genes for producing body hair shows that their ancestors had body hair. In other words, their ancestors were ordinary mammals. In many embryonic whales, external hind limb buds are visible for a time but then disappear as the whale grows larger. Also visible in the embryo are

rudimentary ear pinnae, which disappear before birth (except in those that carry them as rare atavisms). And, in some whales, the olfactory lobes of the brain exist only in the fetus. The whale embryo starts off with its nostrils in the usual place for mammals, at the tip of the snout. But during development, the nostrils migrate to their final place at the top of the head to form the blowhole (or blowholes). We know that the baleen whales evolved from the toothed whales: some embryos of the baleen whales begin to develop teeth. As with body hair, the teeth disappear before birth. Since there is no use for teeth in the womb, only inheritance from a common ancestor makes any sense; there is no reason for the intelligent designer or special creator to provide embryonic whales with teeth. So we have yet another independent field in complete accord with the overall thesis - that whales possess features that connect them with terrestrial mammalian ancestors, in particular the hoofed mammals.

5. *Geochemical evidence:* The earliest whales lived in freshwater habitats, but the ancestors of modern whales moved into saltwater habitats and thus had to adapt to drinking salt water. Since fresh water and salt water have somewhat different isotopic ratios of oxygen, we can predict that the transition will be recorded in the whales' skeletal remains, the most enduring of which are the teeth. Fossil teeth from the earliest whales have lower ratios of heavy oxygen to light oxygen, indicating that the animals drank fresh water. Later fossil whale teeth have higher ratios of heavy oxygen to light oxygen, indicating that they drank salt water. This absolutely reinforces the inference drawn from all the other evidence discussed here: the ancestors of modern whales adapted from terrestrial habitats to saltwater habitats by way of freshwater habitats.

6. *Paleoenvironmental evidence:* The morphology of *Sinonyx* indicates that it was fully terrestrial. It should be no surprise, therefore, that its fossils are found associated with the fossils of other terrestrial animals. *Pakicetus* probably spent a lot of time in the water in search of food. Although the mammalian fauna found with *Pakicetus* consists of rodents, bats, various artiodactyls, perissodactyls and probiscideans, and even a primate, there are also aquatic animals such as snails, fish, turtles and crocodilians. Moreover, the sediment associated with *Pakicetus* shows evidence of streaming or flowing, usually associated with soils that are carried by water. The paleoenvironmental evidence thus clearly shows that *Pakicetus* lived in the low-lying wet terrestrial environment, making occasional excursions into fresh water. Interestingly, both deciduous and permanent teeth of the animal are found in these sediments with about the same frequency, supporting the idea that *Pakicetus* gave birth on the land.

The sediments in which *Ambulocetus* was found contain leaf impressions as well as fossils of the turret-snail *Turritella* and other marine mollusks. Clearly, the presence of such fossils must mean that the Ambulocetus fossil was found in what was once a shallow sea - although leaves can be washed into the sea and fossilize there, marine mollusks would not be found on the land. *Rodhocetus* is found in green shales deposited in the deep-neritic zone (equivalent to the outer part of the continental shelf). Because green shales are associated with fairly low-oxygen bottom waters, *Rodhocetus* must have lived at a greater water depth than any previous cetacean. The fact that it is found in association with planktonic foraminiferans and other microfossils agrees with this determination of water depth. *Basilosaurus* and *Dorudon* have been found in a variety of sediment types, indicating that they were wide-ranging and capable of living in deep as well as shallow water.

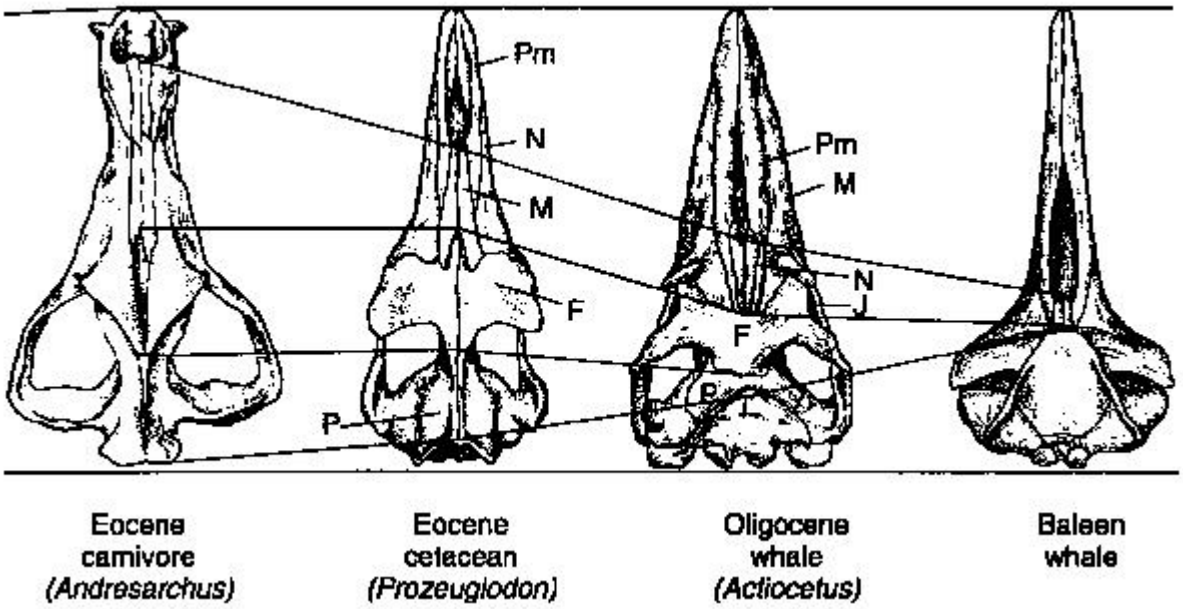
7. *Paleobiogeographic evidence:* The geographic evidence is also consistent with the expected distributional patterns for the whale's first appearance and later geographic expansion. We would expect terrestrial species to have a more restricted geographic distribution than marine species, which have essentially the whole ocean as their geographic range. The range of *Sinonyx* is restricted to central Asia. Specimens of *Pakicetus* have only been found in Pakistan; Ambulocetus and *Rodhocetus* seem to be similarly restricted. In contrast, *Basilosaurus* and *Dorudon*, representing the whales more adapted to living in the open sea, are found in a much wider area. Their fossils have been found as far away from southern Asia as Georgia, Louisiana, and British Columbia. During the Eocene, most of the areas in which fossils of the later whales have been found were fairly close to one another. In fact, most of them are along the outer margin of an ancient sea called the Tethys, the remnants of which today are the Mediterranean, the Caspian, the Black, and the Aral Seas. The biogeographic distribution of fossil whales matches the pattern predicted by evolution: whales are initially found in a rather small geographic area and did not become distributed throughout the world until after they evolved into fully aquatic animals that were no longer tied to the land.

8. *Chronological evidence:* Before the late-Cretaceous extinctions, the Mesozoic marine reptiles such as the plesiosaurs, ichthyosaurs, mosasaurs, and marine crocodiles might well have feasted upon any mammal that strayed off shore in search of food. Once those predators were gone, the evolution quickly produced mammals, including whales that were as at home in the seas as they once were on land. The transition took some 10-15 million years to produce fully aquatic, deep-diving whales with directional underwater hearing. Whales could not have successfully appeared and radiated before the Eocene, and that mammals should have radiated into marine environments as they did into a wide variety of other environments vacated by the reptiles at the end of the Cretaceous.

9.5. Fossils of Modern Whales

Estimates of the divergence time for the mysticete-odontocete split based on gene rates are clearly in conflict with the known fossil record. According to the fossil record, mysticetes and odontocetes diverged from a common archaeocete ancestor about 35 MYBP. On the basis of rates of evolution in mitochondrial ribosomal genes of ungulate mammals, a 10-13 MY divergence has been postulated. This figure has been revised to 25 MYBP based on a slower rate of evolution for whale mitochondrial DNA and the recognition that sperm whale fossils are older than 15 MYBP.

Modern whales differ from archaeocetes because they possess a number of derived features not seen in archaeocetes. Arguably one of the most obvious features is the relationship of the bones in the skull to one another in response to the migration of the nasal openings (blowholes) to the top of the skull. Termed **telescoping**, the modern whale skull has premaxillary and maxillary bones that have migrated far posteriorly and presently form most of the skull roof resulting in a long rostrum (beak) and dorsal nasal openings. The occipital bone forming the back of the skull and the nasal, frontal, and parietal bones are sandwiched between the other bones.



Another derived feature of modern whales is a fixed elbow joint. The laterally flattened forelimbs are usually short and rigid with an immobile elbow. Archaeocetes have flexible elbow joints, capable of rotation.

9.5.1. Earlier Mysticetes

Although all extant mysticetes lack teeth (except in the embryonic stage) and possess baleens, this is not true for some fossil toothed mysticetes. Major evolutionary trends within the group include the loss of teeth, development of large body size and large heads, shortening of the intertemporal region, and shortening of the neck.

Among the characters used to diagnose mysticetes are the following:

1. "Telescoped" skull in which the maxilla extends posteriorly under the orbit to form a plate-like infraorbital process.

2. Antorbital process of maxilla present.

3. Mandibular symphysis (connection between the lower jaws) unfused, with only ligamental or connective tissue attachment.

Living mysticetes lack the form of maxilla seen in odontocetes. The upper jaw bone expands outward to the roof of the mouth, then backward, extending down below the level of the eye. This characteristic form of maxilla seems to be an adaptation to filter feeding in living mysticetes. Since a similar structure of maxilla is present in early Oligocene fossils, filter-feeding may have been used successfully by mysticetes for some 30 million to 35 million years.

By 25 million years ago, early members of the right whale family appeared. Archaic toothed mysticetes have been grouped into four families: the Aetiocetidae, the Llanocetidae, the Mammalodontidae, and the Kakenodontidae.

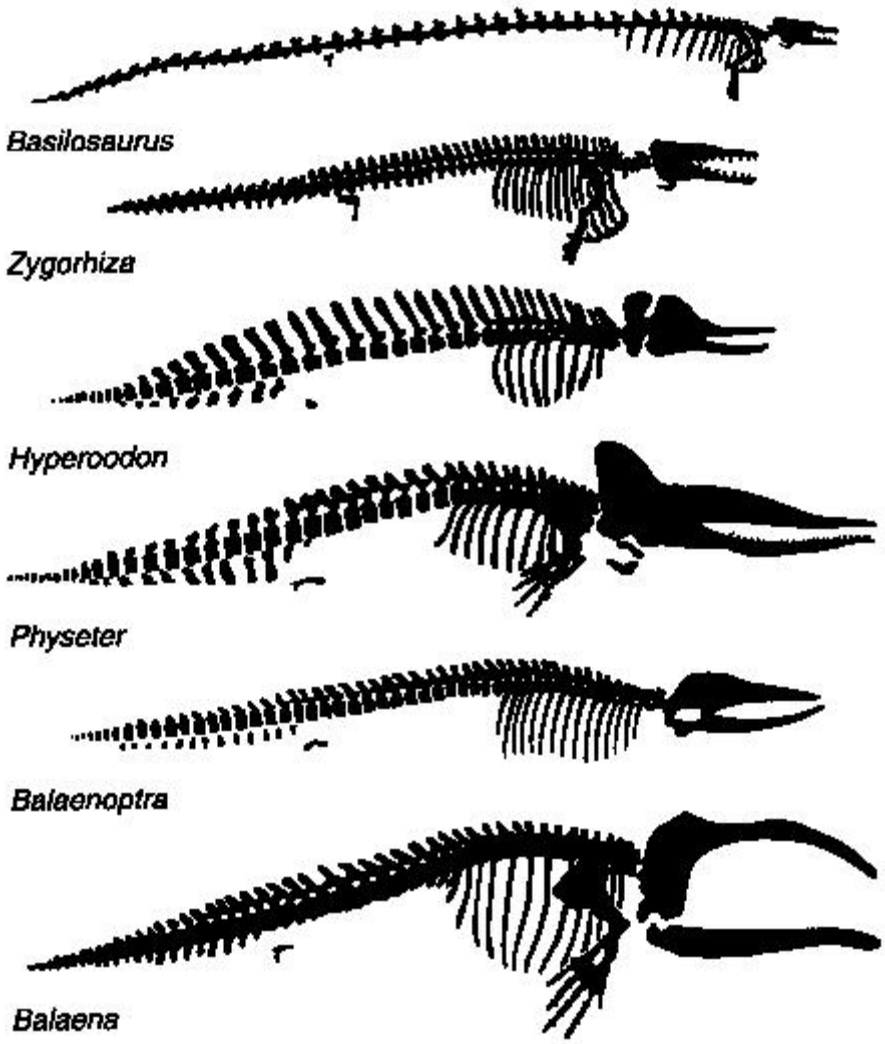


FIGURE 8.40 Axial skeletons of whales in lateral silhouettes. Shown are two fossil species (*Basilosaurus*, *Zygorthiza*), two odontocetes (*Hyperoodon*, *Physeter*), and two mysticetes (*Balaenoptera*, *Balaena*). Notice the reduction in size of the limbs and girdles and the proportionate increase in size of the vertebral column compared with the size of limbs, girdles, and vertebral columns of quadrupeds.

The Aetiocetidae lived during the Late Oligocene (29-23 MYBP) in the North Pacific. They are in many ways intermediate between the primitive toothed Archaeocetes and filter-

feeding, baleen-bearing mysticetes and supporting theories of cetacean monophyly. They probably originated in the North Pacific and were a short-lived transitional group. This family includes *Aetiocetus cotylalveus* from the late Oligocene of Oregon, *A. polydentatus* and *A. tomitai* from the late Oligocene of Japan, and *Chonecetus sookensis* from the northeast Pacific. *Aetiocetus* and *Chonecetus* possess multicuspid teeth and nutrient foramina (openings for blood vessels) for baleens. They have a flattened triangular rostrum. Another species is *Morawanocetus*.

The oldest described mysticete is the toothed *Llanocetus denticrenatus*, the only member of the family Llanocetidae. It is known only from a fragment of a large inflated mandible of late Eocene of early Oligocene age in Antarctica. The holotype skull and skeleton represent a large individual with a skull with a skull length of 2 m. Its multicuspided teeth may have functioned in filter feeding, like those of the modern crabeater seals, contrasting with the long pincer-like jaws and teeth typical of other fish-eating archaeocetes.

Another archaic toothed mysticete, *Mammalodon colliveri*, represents the Mammalodontidae from the late Oligocene or early Miocene in Australia, and has a relatively short rostrum, flat palate, and heterodont teeth.

Another archaic mysticete is the enigmatic *Kekenodon onamata* of the family Kekenodontidae.

The Cetotheriidae is a large, diverse, nonmonophyletic assemblage of extinct baleen-bearing, toothless mysticetes that have been grouped together primarily because they lack characters of living mysticetes. This is a paraphyletic family. "Cetotheres" range in age from the late Oligocene to the late Pliocene of North America, South America, Europe, Japan, Australia, and New Zealand. At least 60 species of "cetotheres" have been named, although many of them are based on plates. And have been implicated in the ancestry of balaenopterids and balaenids. Species of this family include *Cetotherium rathkii* from Ukraine (Paratethys), *Herpetocetus* from Japan, *Cetotheriopsis*, *Mauicetus*

9.5.2. Later Divergent Mysticetes

The relationships among the four families of mysticetes have yet to be resolved.

Balaenopteridae: Members of the rorqual family appeared about 15 My, including the modern genus *Megaptera*. The modern genus *Balaenoptera* appeared about 5 to 10 MYBP Fossils for this family have been found in all continents except Africa and Antarctica. They are distinguished by a skull structure with the frontal bone above the eye depressed to house the large muscles that close the lower jaw. *Megaptera miocaena* from California indicate that Megaptera derived from the *Balaenoptera* in the Late Miocene (ca. 12 MYBP). *M. hubachi* and others show that it is a very divergent from Balaenoptera.

Balaenidae: The oldest fossil balaenid is *Morenocetus parvus*, from the early Miocene (23 MYBP) of South America. It had an elongated supraorbital process and a triangular occipital shield that extends far anteriorly; both characters are developed to a lesser extent than in later balaenids. Relatively abundant fossils of later diverging balaenids are known, especially from Europe. The modern genus *Balaena* appeared about 5 million years ago.

The **Eschrichtiidae**, the modern gray whale family, appeared two million years ago. Fossils of the extant species have been dated back to the Pleistocene (100,000 YA).

Neobalaenidae: The one reported fossil record for this family, *Caperea simpsoni*, from Chile, is dubious. They may have derived from balaenids.

Living mysticetes lack the form of the maxilla seen in odontocetes. The upper jaw bone expands outward to the roof of the mouth, then backward, extending down below the level of the eye. This characteristic form of a maxilla seems to be an adaptation to filter feeding in living mysticetes. Since a similar structure of maxilla is present in early Oligocene fossils, filter-feeding may have been used successfully by mysticetes for some 30 million to 35 million years.

9.5.3. Earlier Odontocetes

Asymmetry is a condition in which bones (=cranial asymmetry) and soft structures (=facial asymmetry) on the right side of the facial region are larger and more developed than equivalent structures on the left side. Cranial asymmetry is not universal among odontocetes, in either presence or extent. Both cranial and facial asymmetries are found in all modern odontocetes of the seven extant odontocete families, but fossil evidence indicates that cranial asymmetry is less pronounced in the more basal members of these groups and totally absent among the extinct taxa. When present, however, this asymmetry is always skewed to the left side.

Regarding the presence of a melon, mysticetes have a fatty structure just anterior to the nasal passage that may be homologous to the melon of odontocetes. Assuming that the melon developed among odontocetes, one might hypothesize that this structure first evolved in archaeocetes. It has been suggested that the vestigial melon of mysticetes might be a hint of more generalized paedomosphism of their facial anatomy, seen for example in a fossil delphinoid which has dramatically reversed telescoping of the skull.

Odontocete monophyly is supported by numerous synapomorphies. The most important are:

1. Concave facial (sagittal) plane.
2. Asymmetric cranial vertex (elevated region of the skull posterior to the bony nares)
3. Premaxillary foramen present
4. Maxillae overlay supraorbital process
5. Anterior notch present at the base of the rostrum where the maxillae expand laterally to cover the supraorbital process of the frontals. They allow for the passage of the facial nerves. Thus, the presences of a melon, together with cranial and facial asymmetry could be interpreted as part of the development of echolocation abilities, originated in archaeocetes and that baleen whales have greatly reduced these characters. However, there is no empirical evidence for this hypothesis since early mysticetes show neither a large melon not ear bones of echolocating cetaceans. The earliest known odontocetes, from about the middle of the Oligocene (30 MYBP), show the same pattern of maxillary structure, suggesting that they too could echolocate.

The oldest odontocete is *Archaeodelphis patrius.*

Agorophiidae are chronologically and morphologically intermediate between the primitive Archaeoceti and more typical Odontoceti.
Agorophius pygmaeus Late Oligocene > 24 My, South Carolina. This family is not the basal clade of Odontocetes.
Agorophius (late Oligocene)
Skull partly telescoped, but cheek teeth still rooted. Intermediate in many ways between archaeocetes and later toothed whales.

The most primitive one still extant is Physeteridae with a 23 million-year fossil found in Argentina.

Archaic "dolphins": Archaic dolphins of the Miocene are grouped into one of three extinct families: the Kentriodontidae, the Albeirodontidae, and the Eurhinodelphidae.
The earliest diverging lineage, the Kentriodontidae, were small animals approximately 2 m or less in length and with numerous teeth, elaborate basicranial sinuses, and symmetrical cranial vertices. They had a widespread distribution. This group's monophyly has been questioned because of relatively diverse species and widespread distribution ranging from the late Oligocene to late Miocene in both the Atlantic and Pacific oceans.
Prosqualodon (late Oligocene)
Skull fully telescoped with nostrils on top (blowhole). Cheek teeth increased in number but still have old cusps. Probably ancestral to most later toothed whales (possibly excepting the sperm whales?)
Kentriodon (mid-Miocene)
Skull telescoped, still symmetrical. Radiated in the late Miocene into the modern dolphins and small toothed whales with asymmetrical skulls.

Eurhinodelphidae: dramatic long rostra and specialized skulls. Oligocene, central Australia.

9.5.4. Modern Odontocetes

Morphological and molecular data point out as Physeteridae and Ziphiidae as basal odontocetes.

Physeteridae: Their fossil record goes back to at least the Miocene (21.5-16.3 MYBP) and earlier is *Ferecetotherium* from the late Oligocene (29-23 My) of Azerbaijan is included. By the middle Miocene, physeterids were moderately diverse and the family is fairly well-documented from fossils found in South America, eastern North America, western Europe, the Mediterranean region, western North America, Australia, New Zealand, and Japan. They show the characteristic basined facial bones of later sperm whales but retain the more primitive braincase of earlier odontocetes. Many species are based just on teeth.

Kogiidae: The oldest kogiids are from the late Miocene (8.8-5.2 MYBP) of South America and early Pliocene (6.7-5 My) of Baja California.

Ziphiidae: This family is known in the fossil record from the Miocene and Pliocene of Europe, North and South America, Japan, and Australia. A freshwater fossil ziphiid has been reported

from the Miocene of Africa. There is generally a poor fossil record, probably due to the fact that this is a pelagic family.

Waipatiidae: This is a small heterodont family. Late Oligocene, 25-26 My, New Zealand. Skull characteristics with the ability to echolocate.

Squalodontidae: Shark-toothed, geographically widespread, medium to large size. Related to the platanistoids.

Platanistidae: They have no fossil record and the time of invasion into freshwater in unknown. Middle to late Miocene marine species of *Zarhachis* and *Pomatodelphis* are closely related to *Platanista*, although they differ in rostral profiles and cranial symmetry.

Pontoporiidae: Fossil *Pontoporia*-like taxa include species of *Pliopontos* and *Parapontoporia* from temperate to subtropical marine settings in the east Pacific. Late Miocene *Pontistes* and *Pontoporia* species come from marine sediments of Argentina.

Iniidae: Their fossil record goes back to the late Miocene of South America and the early Pliocene of North America. The North American records of iniids, however, have been disputed. The phylogenetic history and fossil record of iniids indicate that they originated in South America in the Amazonian basin, entering river systems along the Pacific coast.

Lipotidae: The only fossil closely related to *Lipotes* is *Prolipotes*, based on a fragment of mandible from China.

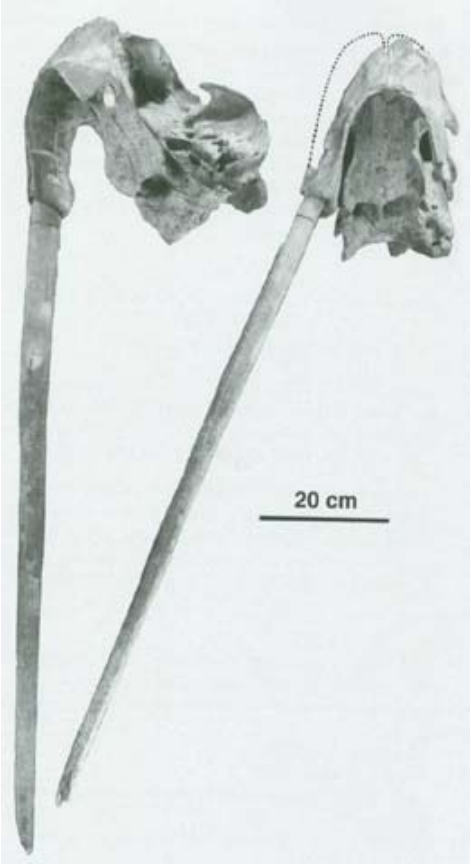
Delphinidae: The oldest delphinid is of the latest Miocene age, probably 11 MYBP They have a highly asymmetrical skull.

Phocoenidae: They have a fossil record that extends back to the late Miocene and Pliocene in North and South America. No clear ancestors identified.

Monodontidae: During the late Miocene and Pliocene, monodontids occupied temperate waters as far as Baja California. No clear ancestors identified.

9.5.5. A Remarkable Fossil

A walrus-like dolphin has been found for the early Pliocene in Peru. The delphinoid *Odobenocetops peruvianus* has a skull convergent to the walrus. Is possible that in both animals, the tusks and/or tusk sheaths served as orientation guides in bottom-feeding, to help maintain proper orientation of the mouth and vibrissal array relative to the substrate as the animal swims forward. Social functions of the tusks are doubtless also important, but historically secondary.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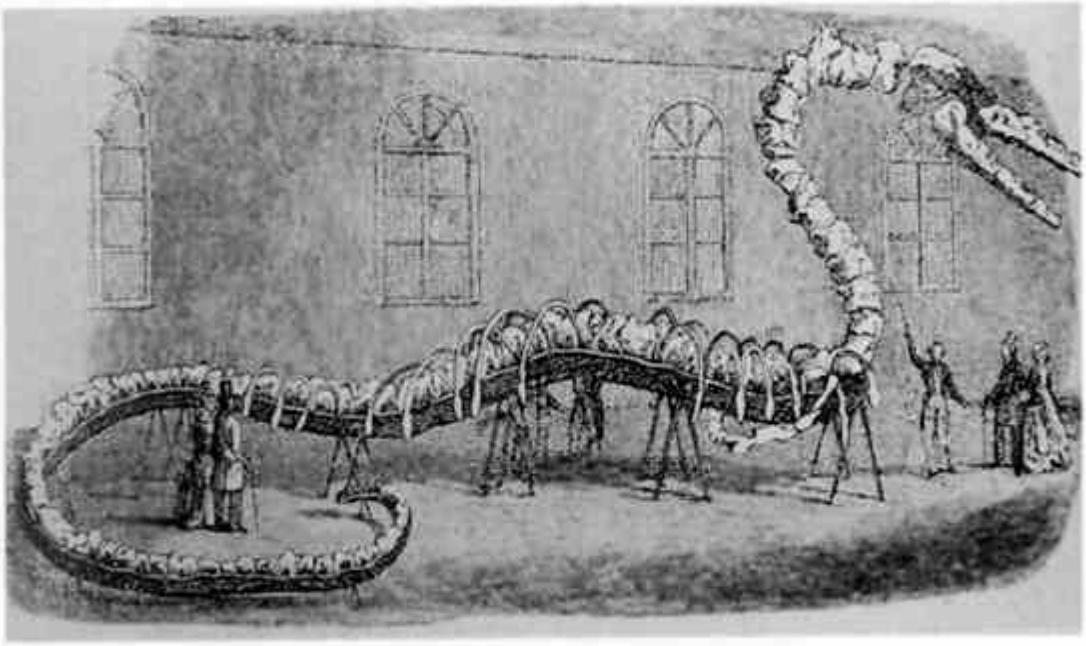
9.6. Footnote: The Discovery of the First Fossil Whale

9.6.2. The First Fossils

In 1832, judge H. Bry sent one of 28 vertebrae that had been washed out of a marl bank belonging to the upper Eocene Jackson formation in near the Ouachita River in Louisiana, to P.S. Du Ponceau, president of the American Philosophical Society, who in turn instructed **Richard Harlan** (1796-1843), the first American to devote most of his career to paleontology, to publish an account of the discovery. Because of its supposed reptilian affinities, Harlan in an article published in 1834 in the *Transactions of the American Philosophical Society*, proposed to call the animal represented by this bone "the king of lizards" or *Basilosaurus*. This discovery created a worldwide controversy in terms of the affinities.

In January 1839, Harlan arrived to London which additional fossil remains of similar animals found in Alabama in 1834 and 1835. Among those fossils remain there were teeth and Prof. **Richard Owen** (1804-1892), Hunterian Professor at the Royal College of Surgeons and a superb anatomist, examined them, and found to them to be mammalian; furthermore, he found that the vertebrae structure was like the one of whales, reason by which Owen in a paper published in 1839 in the *Transactions of the Geological Society of London*, proposed a new name: *Zeuglodon* (yoke-like appearance of the cheek teeth) *cetoides* (whale-like structure of the vertebrae).

In 1842 an excavated skeleton of *Basilosaurus* was obtained from Alabama: it had a partial skull the forelimb and a vertebral column extending 65 feet. This discovery prompted the German collector, **Albert Koch**, to visit Alabama in 1845. He collected remains of at least five different individuals of two different genera of Archaeocetes. He put all the bones together and "reconstructed" a single specimen that happened to be 114 feet long (about 30 feet longer than the Blue Whale, the largest animal believed to have ever lived on Earth). He claimed that such a skeleton belonged to a "sea serpent" which he called "Hydrargos sillimanii." The "skeleton" was exhibit in the Apollo Rooms of Broadway, New York, and later shipped to Germany and exhibit in Europe's main cities.



Dr. Koch's Hydragos sillimanii, *1845* *Reprinted from Bernard Heuvelmans,* In the Wake of the Sea Serpents *(New York, 1968)*

Later more careful examination by Europe's most outstanding paleontologists such as Wyman, Lister, Lyell, and Muller, showed that the skeleton in question was a composite despite the fact that the collector denied it. He sold the skeleton to the King of Prussia, and with the proceeds he went back to Alabama to successfully continue his fossil hunting.

Further Reading

Barnes, L.G. 1984. Search for the first whale. *Oceans* **17**:20-23.

Carroll, R.L. 1988. *Vertebrate Paleontology and Evolution*. New York: Freeman.

Flower, W.H. 1883. On the arrangement of the orders and families of existing Mammalia. *Proceedings of the Zoological Society of London* **1**:178-186.

Gatesy, J., C. Hayashi, M.A. Cronin & P. Arctander. 1996. Evidence from milk casein genes that cetaceans are close relatives of hippopotamid artiodactyls. *Molecular Biology and Evolution* **13**:954-963.

Gingerich P. 1994. The whales of Tethys. *Natural History* **103**:86-88.

Gingerich, P., S.M. Raza, M. Arif, M. Anwar & X. Zhou. 1994. New whale from the Eocene of Pakistan and the origin of cetacean swimming. *Nature* **368**:844-847.

Gingerich, P., B.H. Smith, E.L. Simons. 1990. Hind limbs of Eocene *Basilosaurus*: evidence of feet in whales. *Science* **249**:154-157.

Gingerich, P., N.A. Wells, D.E. Russell & S.M.I. Shah. 1983. Origin of whales in epicontinental remnant seas: new evidence from the early Eocene of Pakistan, *Science* **220**:403-406.

Goodman, M., J. Czelusniak & J. Beeber. 1985. Phylogeny of primates and other eutherian

orders: a cladistic analysis using amino acid and nucleotide sequence data. *Cladistics* **1**:171-85.
Gould, S.J. 1995. Hooking leviathan by its past. In: *Dinosaur in a Haystack*, New York: Harmony Books p. 359-76.
Graur, D. & D.G. Higgins. 1994. Molecular evidence for the inclusion of cetaceans within the order Artiodactyla. *Molecular Biology and Evolution* **11**:357-364.
Irwin, D.M. & U. Arnason. 1994. Cytochrome b gene of marine mammals: phylogeny and evolution. *Journal of Mammalian Evolution* **2**:37-55.
Irwin, D.M., T.D. Kochner & A.C. Wilson. 1991. Evolution of the cytochrome b gene of mammals. *Journal of Molecular Evolution* **32**:128-144.
Kellogg, R. 1936. *A Review of the Archaeoceti*. Washington DC: Carnegie Institute.
Milinkovitch, M.C. 1992. DNA-DNA hybridizations support ungulate ancestry of cetacea. *Journal of Evolutionary Biology* **5**:149-160.
Milinkovitch, M.C., G. Orti & A. Meyer. 1993. Revised phylogeny of whales suggested by mitochondrial ribosomal DNA sequences. *Nature* **361**:346-348.
Miyamoto, M.M. & M. Goodman. 1986. Biomolecular systematics of eutherian mammals: phylogenetic patterns and classification. *Systematic Zoology* **35**:230-240.
Novacek, M. 1992. Mammalian phylogeny: shaking the tree. *Nature* **356**:121-125.
Novacek, M. 1994. Whales leave the beach. *Nature* **368**:807.
Osborn, H.F. 1924. *Andrewsarchus*, giant mesonychid of Mongolia. *American Museum Novitates* **146**:1-5.
Prothero, D.R., and R.M. Schoch. 1998. *Horns, Tusks, Hooves, and Flippers: The Evolution of Hoofed Mammals and Their Relatives*. Baltimore, Maryland: Johns Hopkins University Press; Princeton, New Jersey: Princeton University Press.
Savage, R.J.G., and M.R. Long. 1986. *Mammal Evolution: An Illustrated Guide*. London: British Museum (Natural History); New York: Facts-on-File.
Scott, E.B. 1888. On some new and little known creodonts. *Journal of the Academy of Natural Sciences of Philadelphia* **9**:155-85.
Shimamura M, H. Yasue, K. Ohshima, H. Abe, H. Kato, T. Kishiro, M. Goto, I. Munechika & N. Okada. 1997. Molecular evidence from retroposons that whales form a clade within even-toed ungulates. *Nature* **388**:666-669.
Szalay, F.S. 1969. Origin and evolution of function of the mesonychid condylarth feeding mechanism. *Evolution* **23**:703-720.
Szalay, F.S. 1969. The Hapalodectinae and a phylogeny of the Mesonychidae. *American Museum Novitates* (2361):1-26.
Szalay, F.S. and S.J. Gould. 1966. Asiatic Mesonychidae (Mammalia, Condylarthra). *Bulletin of the American Museum of Natural History* **132**:127-174.
Thewissen JGM, Hussain ST. 1993. Origin of underwater hearing in whales. *Nature* **361**: 444-445.
Thewissen, J.G.M., S.T. Hussain & M. Arif. 1994. Fossil evidence for the origin of aquatic locomotion in Archaeocete whales. *Science* **263**:210-212.
Thewissen, J.G.M., S.I. Madar & S.T. Hussain. 1996. *Ambulocetus natans*, an Eocene cetacean (Mammalia) from Pakistan. *Courier Forschungs-Institut Senckenberg* **190**:1-86
Thewissen, J.G.M., L.J. Roe, J.R. O'Neill, S.T. Hussain, A. Sahni & S. Bajpal. 1996. Evolution of cetacean osmoregulation. Nature 381:379-380.

J. G. M. Thewissen, Lisa Noelle Cooper, Mark T. Clementz, Sunil Bajpai & B. N. Tiwari. 2007. Whales originated from aquatic artiodactyls in the Eocene epoch of India. Nature **450**:1190-1194.

Van Valen, L. 1966. Deltatheridia, a new order of mammals. Bulletin of the American Museum of Natural History **132**:1-126.

Wyss, A. 1990. Clues to the origin of whales. *Nature* **347**:428-429.

Zhou, X., R. Zhai, P. Gingerich & L. Chen. 1995. Skull of a new Mesonychid (Mammalia, Mesonychia) from the late Paleocene of China. *Journal of Vertebrate Paleontology* **15**:387-400.

Appendix

A List of Archaeoceti species

Archaeoceti Flower 1883

Pakicetidae Gingerich and Russell 1990
- *Ichthyolestes* Dehm and Oettingen-Spielberg 1958
  - *I. pinfoldi* Dehm and Oettingen-Spielberg 1958
- *Pakicetus* Gingerich and Russell 1981
  - *P. attocki* (West 1980)
  - *P. inachus* Gingerich and Russell 1981
- *Nalacetus* Thewissen and Hussain, 1998
  - *N. ratimitus* Thewissen and Hussain, 1998
- *Himalayacetus* Bajpai and Gingerich, 1998
  - *H. subathuensis* Bajpai and Gingerich, 1998

Ambulocetidae Thewissen *et al*., 1996
- *Ambulocetus natans* Thewissen, Hussain, and Arif 1994
  - *A. natans* Thewissen, Hussain, and Arif 1994
- *Gandakasia potens* Dehm and Oettingen-Spielberg 1958
  - *G. potens* Dehm and Oettingen-Spielberg 1958

Remingtonocetidae Kumar and Sahni 1986
- *Andrewsiphius* Sahni and Mishra 1975
  - [*A. kutchensis* Sahni and Mishra 1975] subsumed into *A. sloani* (Gingerich et al., 2001)
  - [*A. minor* Sahni and Mishra 1975] subsumed into *A. sloani* (Gingerich et al., 2001)
  - *A. sloani* (Sahni and Mishra 1972)
- *Remingtonocetus* Kumar and Sahni 1986
  - *R. harudiensis* (Sahni and Mishra 1975)
  - *R. domandaensis* Gingerich *et al*., 2001
- *Dalanistes* Gingerich, Arif, and Clyde 1995
  - *D. ahmedi* Gingerich, Arif, and Clyde 1995
- *Attockicetus* Thewissen and Hussain 2000
  - *A. praecursor* Thewissen and Hussain 2000
- [*Kutchicetus* Bajpai and Thewissen, 2000]
  - [*K. minimus* Bajpai and Thewissen, 2000] subsumed into *A. sloani* (Gingerich et al., 2001)

Protocetidae Stromer 1908
- Protocetinae (Stromer 1908)
  - *Protocetus* Fraas 1904
    - *P. atavus* Fraas 1904
  - *Eocetus* Fraas 1904
    - *Eocetus schweinfurthi* (Fraas 1904)
    - *Eocetus wardii* Uhen, 1999
  - *Pappocetus* Andrews 1920
    - *P. lugardi* Andrews 1920
- *Babiacetus* Trivedy and Satsangi 1984

B. indicus Trivedy and Satsangi 1984
B. mishrai Bajpai and Thewissen 1998
Takracetus Gingerich, Arif, and Clyde 1995
T. simus Gingerich, Arif, and Clyde 1995
Georgiacetus Hulbert et al., 1998
G. vogtlensis Hulbert et al., 1998
Natchitochia Uhen, 1998
N. jonesi Uhen, 1998
Cross Whale Geisler, Sanders, and Luo, 1996
Indocetinae Gingerich et al., 1993
Indocetus Sahni and Mishra 1975
I. ramani Sahni and Mishra 1975
Rodhocetus Gingerich *et al*. 1994
R. kasrani Gingerich *et al*. 1994
Qaisracetus Gingerich *et al*., 2001
Q. arifi Gingerich *et al*., 2001
Basilosauridae Cope 1868
Basilosaurinae (Cope 1868)
Basilosaurus Harlan 1834
B. cetoides (Owen 1839)
B. isis (Andrews 1904)
B. drazindai Gingerich *et al*., 1997
Basiloterus Gingerich *et al*., 1997
B. hussaini Gingerich *et al*., 1997
Gaviacetus Gingerich, Arif, and Clyde 1995
G. razai Gingerich, Arif, and Clyde 1995
G. sahnii Bajpai and Thewissen 1998
Dorudontinae (Miller 1923)
Dorudon Gibbes 1845
D. serratus Gibbes 1845
D. atrox (Andrews 1906)
Zygorhiza True 1904
Z. kochii (Reichenbach 1847)
Z. sp. (Köhler and Fordyce, 1997)
Saghacetus Gingerich, 1992
S. osiris (Dames 1894)
Cynthiacetus Uhen, 2005
C. maxwelli Uhen, 2005)
Ancalecetus Gingerich and Uhen, 1996
A. simonsi Gingerich and Uhen, 1996
Chrysocetus Uhen and Gingerich, 2001
C. healyorum Uhen and Gingerich, 2001

Chapter 10

The Evolution of Marine Carnivores and Sirenians

10.1. Pinniped Evolution

Although pinnipeds constitute an entire suborder of (mostly) marine mammals, they took a route to aquatic adaptation that in many cases is quite different than those of cetaceans.

Pinnipeds are diagnosed by a suit of derived characters. They are:

1. Large infraorbital foramen: It is located below the eye orbit and allows passage of blood vessels and nerves. It is large in pinnipeds contrasting with its small size in most terrestrial carnivores.

2. Maxilla makes a significant contribution to the orbital wall. This is unique among carnivores. The upper jaw forms part of the lateral and anterior walls of the orbit of the eye. In terrestrial carnivores, the maxilla is usually limited in its posterior extent by contact of several facial bones (jugal, palatine, and/or lacrimal).

3. Lacrimal absent or fusing early in ontogeny and does not contact the jugal.

4. Greater and lesser humeral tuberosites (rounded prominences on the proximal end of the humerus) enlarged.

5. Deltopectoral crest of humerus strongly developed (for insertion of the deltopectoral muscles).

6. Short and robust humerus.

7. Digit I (thumb) on the hand elongated

8. Digit I and V (big and little toe) on the foot elongated.

All pinnipeds, fossil and recent, possess the characters described above, although some of these characters have been modified or lost secondarily in later divergent taxa.

10.2. Pinniped Fossil Record

The fossil record indicates that extant pinnipeds represent only a small fraction of what was once a much greater diversity. For example, only a single species of walrus exists today whereas no less than 10 genera and 13 species existed in the past.

The earliest well-documented record of pinnipeds is from the later Oligocene (27-25 My) although a slightly earlier record (29 My) is less well substantiated.

Most researchers today agree that pinnipeds are monophyletic and that they originated in what is today the North Pacific ocean.

10.2.1. Pinniped Affinities

Since Illeger proposed the name Pinnipedia in 1811, there have been debates on the relationships of pinnipeds to one another and to other mammals. Two hypotheses have been proposed. The monophyletic hypothesis proposes that the three pinniped families share a single common evolutionary origin. The diphyletic hypothesis (pinniped diphyly) proposes that pinnipeds originated from two different carnivore lineages, with odobenids and otariids deriving from a dog-bear looking animal in the ursid (bear) family and the phocids deriving from an otter-like animal in the mustelid (weasels, skunks, otters, etc.) family. According to this hypothesis, convergent evolution to meet environmental constraints would then account for shared characteristics such as streamlined body shape, limbs modified as flippers, simple grasping teeth suitable for catching fish, and diving and thermoregulatory mechanisms.

Most recent morphological and molecular studies support the monophyletic hypothesis. This evidence indicates that their closer relatives are arctoid carnivores which include procyonids (racoons and their allies) and ursids, although which specific arctoid group forms the closest alliance with pinnipeds is still a mater of controversy. Most of the evidence points out to a close relationship with the Ursidae (bears and their extinct relatives the Amphicyonidae), with the Musteloidea (Procyonidae and Mustelidae) forming the next closest outgroup. The other studies argue that the closest relatives are the Lutrinae (otters).

Although this supporting evidence for monophyly among pinnipeds, the relationships among the different families is still problematic. Most of the controversy lies in the debate on whether the walrus is most closely related to the phocids to or the otariids, being the former the one with the most support.

10.2.2. Early "Pinnipeds"

The earliest "pinnipeds" are actually members of the Pinnipedimorpha clades and appear to have originated in the eastern North Pacific (Oregon) during the late Oligocene (27-25 My). It is represented by one genus (*Enaliarctos*) and five species. The oldest one (*E. barnesi*) dates back to 27-18 My and others, most recent ones have been reported for California and, possibly, Japan. These animals possessed heterodont dentition with large blade-like cusps on the upper cheekteeth well-adapted for shearing, which indicate close similarity with archaic bears. They were medium size, about 1.5 m in length and possibly between 73-88 kilos in weight, roughly the size and weight of a small male harbor seal. As this genus evolved, we can see a decrease in the shearing function of the cheekteeth (e.g., reduction in the number and size of cups). This is

in the trend of developing of the simple peg-like, homodont dentition characteristic of most living pinnipeds.

They seemed to have considerable lateral and vertical movement of the vertebral column. Both limbs were modified as flippers and used in aquatic locomotion. Some features of the "Californian" species (*E. mealsi*, from which nearly complete skeletons have been recovered), indicates that it was highly capable of maneuvering on land and probably spent more time near the shore than extant pinnipeds

A later diverging lineage of fossil pinnipeds more closely allied with the pinnipeds than with *Enaliarctos* is *Pteronarctos goedertae* from the late Miocene (19-16 MY) of coastal Oregon. A striking osteological feature in all pinnipeds is the geometry of bones that comprise the orbital region. In *Pteronarctos*, the first evidence of the uniquely developed maxilla is seen. Also, in *Pteronarctos* the lacrimal is greatly reduced or absent, as it is in pinnipeds. A shallow pit on the palate between the last premolar and the first molar, seen in *Pteronarctos* a pinniped, is indicative of a reduced shearing capability of the teeth and begins a trend toward homodont.

10.2.3. Modern Pinnipeds

Otariidae

In addition to the extant fur seal genera *Callorhinus* and *Arctocephalus*, several extinct otariids are known. The earliest otariid is *Pithanotaria starri* from the late Miocene (11 My) of California. It is a small animal characterized by double rooted cheekteeth and a postcranial skeleton that allies it with other otariids. A second extinct late Miocene taxon (8-6 My), *Thalassoleon*, is represented by three species: *T. mexicanus* from Cedros Island, Baja California, Mexico; *T. macnallyae* from California, and *T. inouei* from central Japan. *Thalassoleon* is distinguished from *Pithanotaria* in its larger size and in lacking a thickened ridge of tooth enamel at the base of the third upper incisor. A single extinct species of northern fur seal, *Callorhinus gilmorei*, from the late Pliocene in Southern California, Mexico, and Japan has been described on the basis of a partial mandible, some teth, and postcranial bones. Several species of the southern fur seal genus Arctocephalus are known from the fossil record. The earliest known taxa are *A. pusillus* from South Africa and *A. townsendi* from California from the late Pleistocene.

The fossil record for sea lions is less known. Two species have been reported: *Eumetopias* aff. *E. jubatus* (early Pliocene of Japan) and *Neophoca palatina* (middle Pleistocene of New Zealand).

Odobenidae

There are two monophyletic lineages: The Dusignathinae that includes the extinct genera *Dusignathus*, *Gomphotaria*, *Pontolis*, and *Pseudodobenus*. This subfamily is characterized by enlarged upper and lower canines.

The Odobeninae includes in addition to the modern walrus *Odobenus*, the extinct genera *Aivukus*, *Alachtherium*, *Gingimanducans*, *Prorosmarus*, *Valenictus*, and *Protodobenus*. These evolved only the upper canines.

At the base of walrus evolution are *Proneotherium*, *Prototaria*, *Imagotaria*, and *Neotherium* from the middle Miocene (16-9 My) of the eastern North Pacific. They are characterized by unenlarged canines and narrow, multiple rooted premolars with a trend toward molarization, adaptations suggesting retention of the fish diet hypothesized for archaic pinnipeds rather than the evolution of the specialized mollusk diet of the modern walrus. The dusignathine walrus, *Dusignathus santacruzensis*, and the odobenine walrus, *Aivukus cedroensis*, first appeared in the late Miocene of California and Baja California, Mexico. Early diverging odobenine walruses are now known from both sides of the Pacific in the early Pliocene. *Prorosmarus alleni* is known from the eastern U.S. Virginia and *Protodobenus* japonicus from Japan.

A new species of walrus, possibly the most completely known fossil odobenine walrus, *Valenictus chulavistensis*, was described as being closely related to modern *Odobenus* but distinguished from it in having no teeth in the lower jaw and lacking all upper postcanine teeth. The toothlessness of this species is unique among pinnipeds but parallels the condition seen in modern suction feeding whales and the narwhal.

Remains of modern walrus *Odobenus*, date back to the early Pliocene of Belgium; this taxon appeared approximately 600,000 years ago in the Pacific.

Phocidae

The oldest fossil phocid is from the late Oligocene (29-23 My) of South Carolina. Other fossils date from the middle Miocene (15 My) when both phocinae and "monachine" seals became distinct lineages in the North Atlantic. The extinct phocine seal *Leptophoca lenis* and the "monachine" seal *Monotherium*? *wymani* are known from under Maryland and Virginia during this time. *Leptophoca lenis*, or a closely related species represented in the eastern Atlantic, from deposits in the Antwerp Basin, Belgium. Another addition to the fossil record of phocids is a new genus and species of phocine seal, based on an articulated skeleton (lacking the skull, neck, and part of the hind limbs) reported from the middle Miocene of Argentina. Other fossil seals are represented by well preserved skeletal material. For example, *Acrophoca longirostris* and *Piscophoca pacifica* from the late Miocene and early Pliocene were found in the Pisco Formation of Peru, and *Homiphoca capensis* was discovered in South Africa. Although originally considered "monachines" (i.e., lobodontine seals), ongoing studies indicate that *Acrophoca*, *Piscophoca*, and new material from the Pliocene of Peru may be closer to phocines. Other phocines evolved in the vast inland Parathethys Sea from 14 to 10 My and differentiated mostly in the Pleistocene.

10.2.4. Unanswered Questions

Relationships between walruses and phocids

The position of walruses regarding other groups of pinnipeds has yet to be clarified. Many believe that walruses and phocids are linked because the following synapomorphies:

a) Middle ear bones enlarged
b) Abdominal testes

c) Primary hair non-medullated (they lack a pith or medulla)
d) Thick subcutaneous fat
e) External ear pinna lacking
f) Same specialized venous system related, in part, to their exceptional diving capabilities such as inflated hepatic sinus, well-developed caval sphincter, large invertebral sphincter, duplicate posterior vena cava, and gluteal route for hind limbs

But these shared characteristics could be the result of convergence.

Desmatophocids: Phocid Relatives or Otariods?

Desmatophoca and *Allodesmus* are examples of a group that has been identified as at the trunk of phocid pinnipeds called desmatophocids. This is a group known from the early middle Miocene (23-15 My) of the western U.S. and Japan. Newly reported fossils of *Desmatophoca* from Oregon confirm the presence of sexual dimorphism and large body size in these pinnipeds. Allodesmids are known from the middle to late Miocene of California and from Japan. They are a diverse group characterized, among other things, by pronounced sexual dimorphism, large eye orbits, bulbous cheek tooth crowns, and deep lower jaws.

A number of features are shared among phocids and their close fossil relatives *Allodesmus* and *Desmatophoca* (identified as the Phocoidea clade) and hence they support a close link between these taxa. These synapomorphies include, among others:

a) Posterior termination of nasals posterior to contact between the frontal and maxilla bones

b) Squamosal-jugal (cheekbones) contact mortised (interlocked).

10.2.5. Historical Biogeography

There are two different hypotheses on walrus dispersal: one is from the north Pacific through the Central America Seaway (between 5 and 8 My), and dispersed northward into the North Atlantic and than less than 1 My, the living genus *Odobenus* returned to the North Pacific through the Arctic Ocean. The alternative explanation is that it evolved in the North Pacific and then entered the North Atlantic through the Arctic Ocean during the late Pleistocene.

Dispersal of otariids south of the equator occurred presumably at times when a continuum cold-water habitat existed along the eastern Pacific Rim.

10.3. Sirenian Evolution

The monophyly of sirenians is well established. Sirenians are united by the possession of the following synapomorphies:

1. External nares retracted and enlarged, reaching to or beyond the level of the anterior margin of the orbit.

2. Premaxilla contacts frontal.

3. Sagittal crest absent.

4. Five premolars, or secondarily reduced from this condition by loss of anterior premolars.

5. Mastoid inflated and exposed through occipital fenestra.

6. Ectotympanic inflated and drop-like.

7. Pachyostosis and osteosclerosis present in skeleton.

10.3.1. Sirenian Affinities

Proboscideans (elephants) are usually considered the closest living relatives of sirenians. Sirenians, proboscideans, and the extinct desmostylians are recognized as a monophyletic clade, termed Tethytheria.

10.3.2. Fossil Record

Sirenians are members of the group known as subungulates, thought to be distantly related to hyraxes, elephants, and perhaps, artiodactyls and perissodactyls (horses, rhinos, and tapirs). Proboscideans (elephants) are usually considered the closest living relatives of sirenians. Characters that unite both groups include rostral displacement of the orbits with associated reorganization of the antorbital region, strongly laterally-flared zygomatic process of the squamosal, and incipiently bilophodot (double crested) teeth. Studies using biochemical analysis of proteins show that the closest modern relatives of sirenians are elephants, aardvarks, and small mammals known as hyraxes. Scientists once thought manatees were closely related to walruses based on facial similarities.

The fossil record of sirenians is incomplete, and the relationships between manatees and their ancestors are still poorly known. Their fossil record goes back to the early Eocene (50 My), but at that time both families were distinct and specialized for aquatic life, so their origin is likely to have been considerably earlier. The oldest known sirenian fossil, *Prorastomus sirenoirdes* is from early to middle Eocene (50 My) of Jamaica. It occupies a basal position close to the ancestry of all other sirenians. The dense and swollen ribs of prorastomids point to at least a partially aquatic lifestyle, as does its occurrence in marine deposits. The hip joint and pelvic bones of these animals indicate that the most primitive known sirenians possessed a functional hind limb. Other early fossils such as *Protosiren smithae*, from the middle Eocene of Fayum, Egypt, indicate that this animal was capable of terrestrial locomotion. CAT scans of *Protosiren fraasi*, indicates small olfactory bulbs, small optic tracts, and large maxillary nerves, consistent with the diminished importance of olfaction and vision in the aquatic environment and consistent with enhanced tactile sensitivity of the enlarged downturned snout of most Sirenia. The peculiar forceps-like snouts of Prorastomus and other early sea cows, suggests selective browsing.

Additional anatomical, ecologic, and taphonomic data support consideration of the prorastomids as fluviatile or estuarine semiaquatic herbivore.

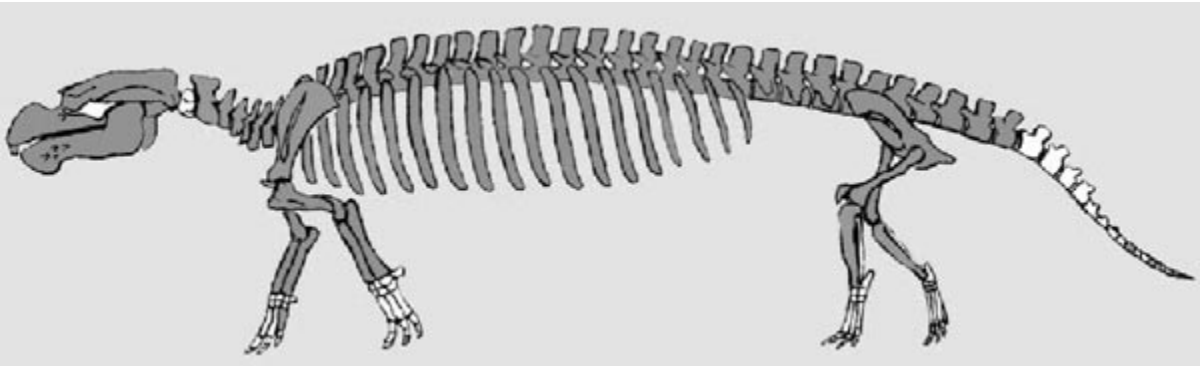


Figure 10.1. An intermediate sirenian fossil: a seacow with legs. Reconstructed skeleton of *Pezosiren portelli*. Length is approximately 7 feet. Gray coloring represents extant fossils; white elements are partly conjectural. (Domning 2001; Image © 2001 Macmillan Magazines Ltd.)

Trichechidae: Manatees are known from early Miocene (15 My) to the Recent in the New World Tropics.

Dugongidae: Dugongs were more diverse in the past with 13 genera and a fossil record that extends back to the Eocene. Dugongs have a good fossil record going back to Eocene terrestrial ancestors. Genera with fossil representatives, in addition to Dugong itself, are: *Bharatisiren*, *Corystosiren*, *Crenatosiren*, *Dioplotherium*, *Rytiodus*, and *Xenosiren*. These fossils have been found from 15 My in the Mediterranean, western Europe, southeastern U.S., Caribbean, Indian Ocean, South America, and the North Pacific. The most elaborate development of tusks in the Sirenia are found in the latter diverging dugongines, such as *Rytiodus*, *Corystosiren*, *Xenosiren*, and *Dioplotherium*. These species possessed enlarged, blade-like, self-sharpening tusks that may have been used to dig up sea grasses. The modern dugong may have evolved large tusks for a similar reason, but now appears to use them chiefly for social interactions.

Ancestry of the Steller's Sea Cow: The ancestry of this species involves *Metaxytherium* and *Dusisiren jordani* from the Miocene of California. *Dusisiren dewana*, describe from 9 My rocks of Japan, makes a good structural intermediate between *Dusisiren jordani* and the Steller's sea cow in showing a reduction of teeth and finger bones. A penultimate stage in the evolution of the Steller's sea cow is represented by *Hydrodamalis cuestae* from 3-8 My deposits in California. It lacked teeth and, probably, even finger bones, and was very large.

10.3.3. Subfamily: Halitheriinae

It includes the paraphyletic genera *Halitherium*, *Eotheroides*, *Prototherium*, *Eosiren*, *Caribosiren*, and *Metaxytherium*. The later is the best known. It was widely distributed in both the Old and the New World during the Miocene. *Metaxytherium* had a strongly downturned snout and small upper incisor tusks and members of this lineage were most likely generalized bottom-feeders, probably consuming rhizomes of small to moderate size sea-grasses and sea grass leaves. A New World origin has been suggested, specifically in the Caribbean and West Atlantic, with subsequent dispersal to the North Pacific via de Central America Seaway and later dispersal to coastal Peru.

This extinct subfamily included the paraphyletic genus *Dusisiren* and the lineage that led to the recently extinct Steller's sea cow. *Dusisiren* evolved a very large body size, decreased snout deflection, and the loss of tusks, suggesting that these animals may have fed on kelp which grows higher in the water column that do sea grasses.

10.3.4. Decodonts

Based on an extraordinarily well-preserved fossil, scientists from the Nanjing University, the Chinese Academy of Geological Sciences, and the Carnegie Museum of Natural History in Pittsburgh, Pennsylvania, were able to reconstruct an animal that has many characteristics of many aquatic mammals: a broad scaly tail like a beaver, fur, webbing in their limbs and collar bones typical of many other swimming creatures such as the river otter, and seal-like teeth for eating small fish and other creatures. The fossil was found in China and is 164 MYA.

They gave it the scientific name of *Castorcauda lustrasimilis*.

This animal was the size of a small platypus: a bit less than 2 feet in length. The fur is extremely well preserved. The rocks of this area in China have properties that have yielded excellent fossils of birds and their feathers. Other fossils found in the same region include pterosaurs (flying reptiles like the ones seen in the movie *King Kong*), dinosaurs, fishes, insects, and gigantic amphibians.

10.3.5. Other Extinct Sirenian Relatives

The **Desmostyla** bear a name derived from the bundled columnar shape of the cusps of the molar teeth in some taxa. These bizarre animals constitute the only extinct order of marine mammals. They were confined to the North Pacific (Japan, Kamchatka, and North America) during the late Oligocene and Middle Miocene epochs (33-10 My). At least six genera and 10 species have been described so far. They were hippopotamus-like, amphibious quadrupeds that probably fed on marine algae and sea grasses in subtropical to cool-template waters.

Locomotion in the water probably resembled that of polar bears, with the forelimbs providing the principal means of propulsion and the hindlimbs used for steering.

Kolponomos: Two species from Washington state and Oregon. They had a massive skull. It is an ursoid found in costal areas. The crushing teeth would have been suited to a diet of hard-shelled marine invertebrates, prying them off with the incisors and canines, crushing their shells, and consuming the soft parts as sea otters often do. Only the sea otter today occupies the same niche.

Thalassocnus: An aquatic sloth composed of known five species from the early Pliocene of the coasts of Peru. They had aquatic or semiaquatic habits and grazed on sea grasses or seaweeds. The tail was probably used for swimming and a ventrally down-turned premaxilla expanded at the apex suggests the presence of a well-developed lip for grazing.

10.4. Sea and Marine Otter

The modern sea otter arose in the North Pacific at the beginning of the Pleistocene, about 1 to 4 My, and has not dispersed since that time. There are records of *Enhydra* from the early Pleistocene of Oregon and California. One extinct species, *Enhydra macrodonta*, has been described from the late Pleistocene of California and Oregon. According to both, morphological and molecular data, the closest living relative to the sea otter is the freshwater otter *Lutra.*

10.5. Polar Bear

The oldest known polar bear fossil is less than 100,000 years old. Morphological and molecular data support the contention that polar bears developed during the middle Pleistocene (300,000 - 400,000 y) from an ancestral brown bear from the islands of southwestern Alaska. Polar bears and brown bears are still closely related; when crossbred in captivity, they produce fertile offspring. No hybridization has been confirmed in the wild.

Chapter 11

Skin and Thermoregulation

11.1. The Skin

This section deals with the study of the marine mammals' skin, hair, glands, vibrissae and claws. This is what is called the **integument**. The integument is a multifunctional organ system that defines the animal's boundary with its aquatic environment. It forms a protective and dynamic insulative layer, adds buoyancy, and comprises propulsive structures, such as the flukes of cetaceans and sirenians.

11.1.1. Structure

As in all mammals, the skin consists of an outer layer (the epidermis), a middle layer (the dermis), and a deep blubber layer (the hypodermis). The dermis contains hair follicles, sebaceous and sweat glands, and claws (only present in pinnipeds, sea otters, and polar bears). The skin of cetaceans and sirenians is distinguished by the absence of hair, except for bristle-like hairs especially dense around the mouth.

The structure of the **epidermis** of marine mammals is made of multiple strata of squamous epithelium consisting of a least three of the five layers typical in most mammals (particular terrestrial species): stratum basale, stratum spinosum, and stratum corneum. The outmost layer of the epidermis, the **stratum corneum**, consists of a layer of flattened, solid, keratinized cells that make the skin waterproof. In pinnipeds, lipids from sebaceous glands, which form a pliable waterproof layer, lubricate these keratinized cells. The thickness of the epidermis varies among pinnipeds, but is thickest in the walrus and thinnest in fur seals. The epidermis of phocids is heavily pigmented. The epidermis of the walrus is characterized by the presence of transverse projections on the underside, similar to those seen in sirenians.

Cetacean skin is smooth with a rubbery feel. **Cutaneous ridges** have been described on the surface of the skin in many cetaceans. While the function of these structures is unknown, it has been suggested that they may play a role in tactile sensing or in the hydrodynamic characteristics of the animal or both. Another distinguishing feature of the cetacean integument is the development of cutaneous ridges of germinal cells on the underside of the epidermis that are oriented parallel to the body axis. These ridges form slender flap-like projections between which dermal papillae are located. The epidermis of odontocetes is 1-20 times thicker than that of terrestrial mammals. Thickness of the epidermis varies over the surface of the animal and changes with age.

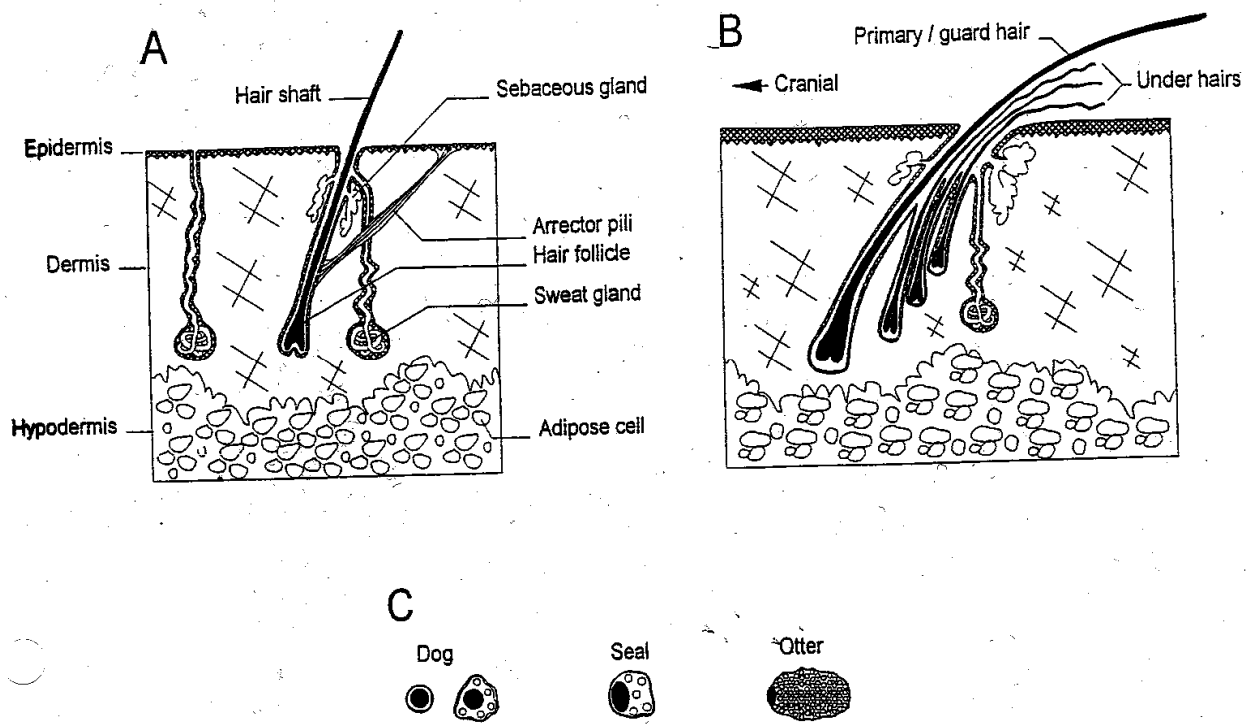
The outmost layer of the epidermis is renewed every two hours (12 times a day), which is nine times faster than the sloughing rate in humans. This high turnover is not due to increased rates of epidermal cell proliferation, but rather as a result of the relatively large and convoluted surface area of the germinal cells that lie on the tall and densely packed dermal papillae of cetaceans. Thus, underlying and replacing a relatively small surface area of superficial skin is a very large surface area of germinal cells. This high turnover rate helps maintain a smooth, self-cleaning surface that in addition to reduce drag, may serve to reduce opportunities for fouling organisms to settle and attached to skin surface. It is not known whether all cetaceans have such high turnover rates of epidermal cells.

Seasonal epidermal molt has been reported for beluga but not for other cetaceans. This molt takes place when they move from cold, open waters into warmer estuaries, which allows them to save energy by molting more rapidly than they would be able to if they remained in the open ocean.

Hair, vibrissae, nails, claws, and sebaceous glands are all specialized epidermal structures. They will be described later in this chapter.

The **dermis** is composed of dense irregular connective tissue. It is well vascularized and contains fat cells which increase in number with depth as it becomes continuous with the hypodermis. Hair follicles are located in the dermis of pinnipeds, sea otters, and polar bears. The unusual thickness, strength, and durability of walrus skin can be attributed mainly to the reticular layer of the dermis, in which thick bundles of collagen fibrils form a particularly dense network. In the walrus the skin is thickest on the neck and shoulders of adult males, where it is supplanted by rounded “bosses,” or lumps, about one centimeter thicker than the surrounding skin. These bosses have generally been regarded as a secondary sexual characteristic that males develop as they approach maturity.

The most notable features of the cetacean dermis are the absence of hair follicles and sebaceous and sweat glands, its thinness relative to the epidermis, and the elaborate of finger-like projections or dermal papillae, which extend into epidermal ridges. In sirenians, dermal papillae and a subpapillary layer form a very thick dermis. Dermal papillae often penetrate the epidermis and may even extend into the horny layer, so that they lay only a few cell rows below the surface. They may therefore have tactile function.



The **hypodermis** or **blubber** is loose connective tissue beneath the skin composed of fat cells interlayered with bundles of collagen. It is loosely connected to the underlying muscle layer. Blubber is found in all marine mammals with the exception of polar bears and sea and marine otters, *sensu stricto*. The fatty hypodermis of walruses, phocids, cetaceans, and sirenians is a substitute for the absence of hair and functions as an insulator. Blubber's thickness and lipid content varies depending on the age and sex of the animal, as well as individual and seasonal variations. Blubber thickness varies among pinnipeds and its pattern of distribution optimizes streamlining, insulation, and buoyancy. In some species, during certain stages of their lives, blubber may be up to 50% of the body mass of a marine mammal. In the Atlantic harp seal, blubber was thickest and most variable dorsally along the posterior region of the body, becoming gradually thinner through the neck region and around the flippers. A similar distribution of blubber can be found in any marine mammal, with an average depth of 23 cm, but reaching a depth of 50 cm in some parts of the body. Blubber is thinner in sirenians than in most other marine mammals, with the exception of the polar bear and the sea otter and the marine otter.

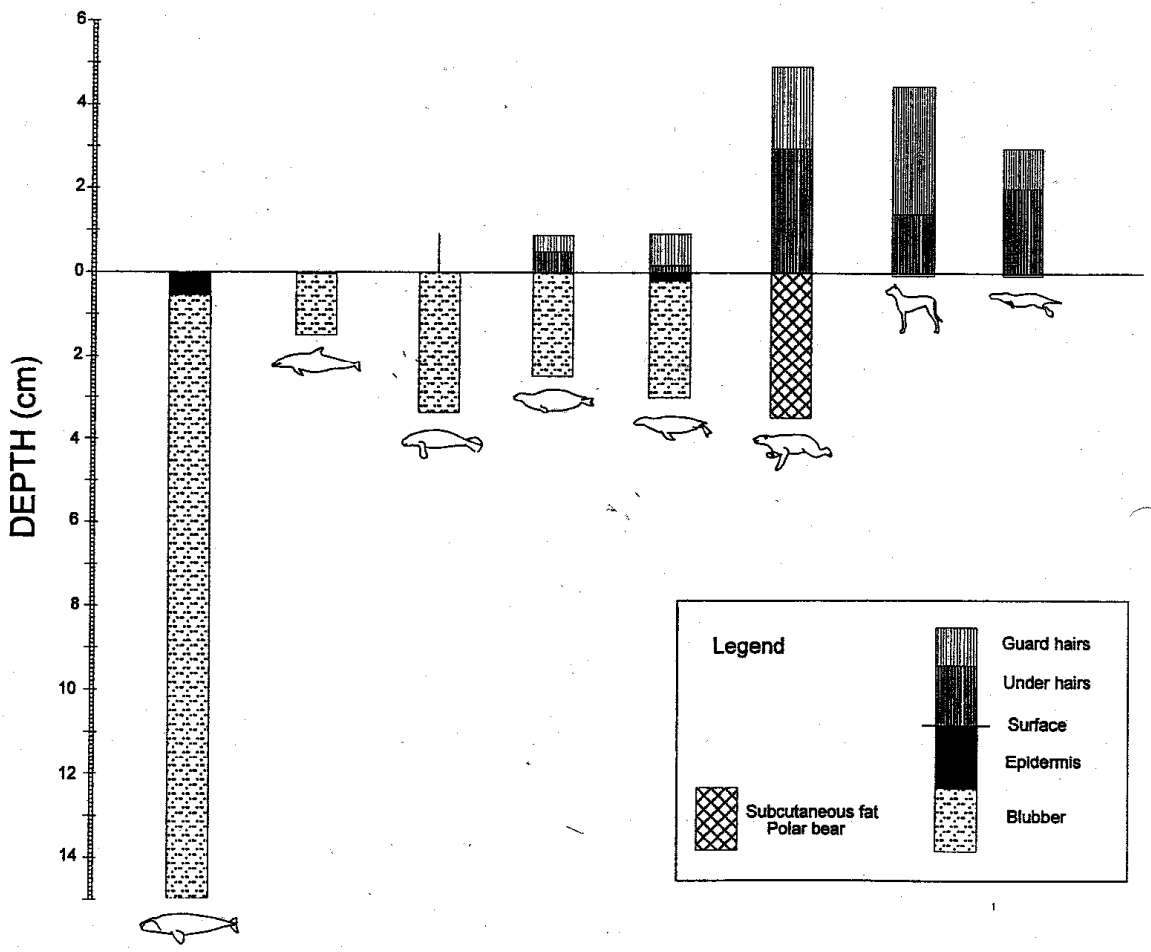


Figure 2-4. Integumentary structures used for insulation in marine mammals. Marine mammals use either blubber (a specialized hypodermal tissue) or fur as their primary insulation. The polar bear may also use subcutaneous fat deposits for insulation although this hypothesis is controversial (Pond et al. 1992). (The insulation values for polar bear hair shown in Figure 2-3 are for hair only; in this study, the subcutaneous fat layers were removed.) Compare thicknesses of each structure used by mammals of diverse sizes. (Thickness measurements from Omura 1958, Sokolov 1960, Oritsland 1970, Bonde et al. 1983, Williams et al. 1992, and authors' unpublished data.)

11.1.2. Color

The outer epithelial portion of the skin and/or pelage of marine mammals may be pigmented. Color patterns in the pelage of pinnipeds occur almost exclusively among phocids. Pagophilic, or ice breeding, phocids (e.g., ribbon seal, harp seal, hooded seal, ringed seal, crabeater seal, Weddell seal, and leopard seal) show contrasting dark and light or disruptive patterns. The unique, striking markings of the ribbon seal and harp seal contain information about the age and gender of the animal because they develop with age and are most strongly expressed in males. Other more uniformly colored pinnipeds (e.g., harp seal pups, which are white) allow them to blend more readily into their arctic environment.

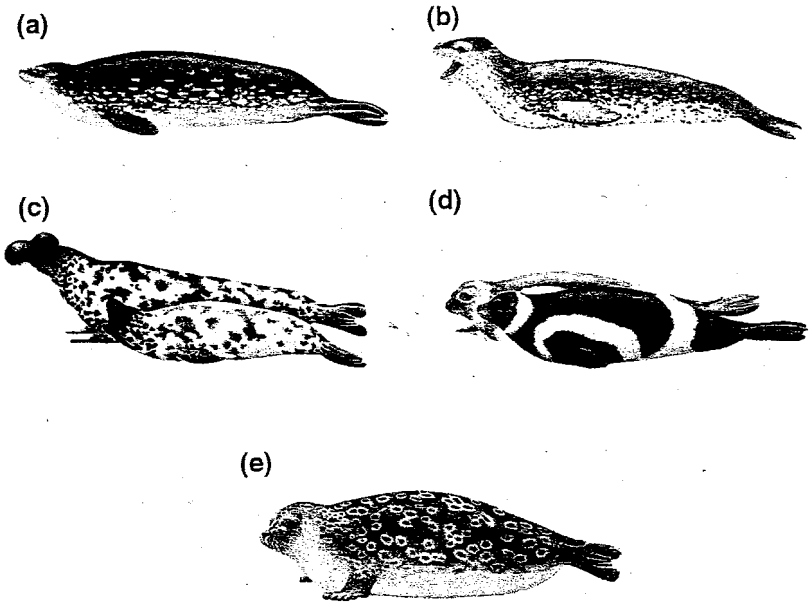


Figure 7.2. Examples of phocid pelage patterns (a) Weddell seal, *Leptonychotes Weddellii,* (b) leopard seal, *Hydrurga leptonyx,* (c) hooded seal, *Cystophora cristata,* (d) ribbon seal, *Phoca fasciata,* and (e) ringed seal, *Phoca hispida.* (Illustrated by P. Folkens from Reeves *et al.,* 1992).

Coloration patterns are determined by regional differences in the concentration of melanocytes in the epidermis. Numerous melanocytes are present throughout the epidermis of phocids, especially in the basal layers of dark regions. Otariid skin possesses only minor amounts of melanin. Walrus skin is darkest in young individuals, becoming lighter with age.

Three basic color patterns are recognized: (1) A uniform pattern (e.g., the completely white coloration of the beluga), (2) A spotted or striped pattern with sharp colored areas on the head, side, belly, and flukes (e.g., the killer whale), and (3) A saddled or countershading pattern, in which the animal is dark above and light below. The most common saddled and striped patterns function primarily as camouflage. Different coloration patterns are probably related to the search for food, protection from enemies, and intraspecific communication. For example, signaling between individual Hawaiian spinner dolphins and white-sided dolphins may be accomplished through their body patterns, which consist of a dark gray cape, a lighter ray lateral field, and a white belly. These patterns may allow the animal to determine the degree of rotation of an adjacent neighbor. If rotation of the back is toward a neighbor, the dark cape increases in area and the belly exposure decreases. The white belly covers a larger area if the animal rotates the other way. Such pattern relationship cues may be used as part of the overall system that allows synchrony of animals during dives and turns, especially while schooling.

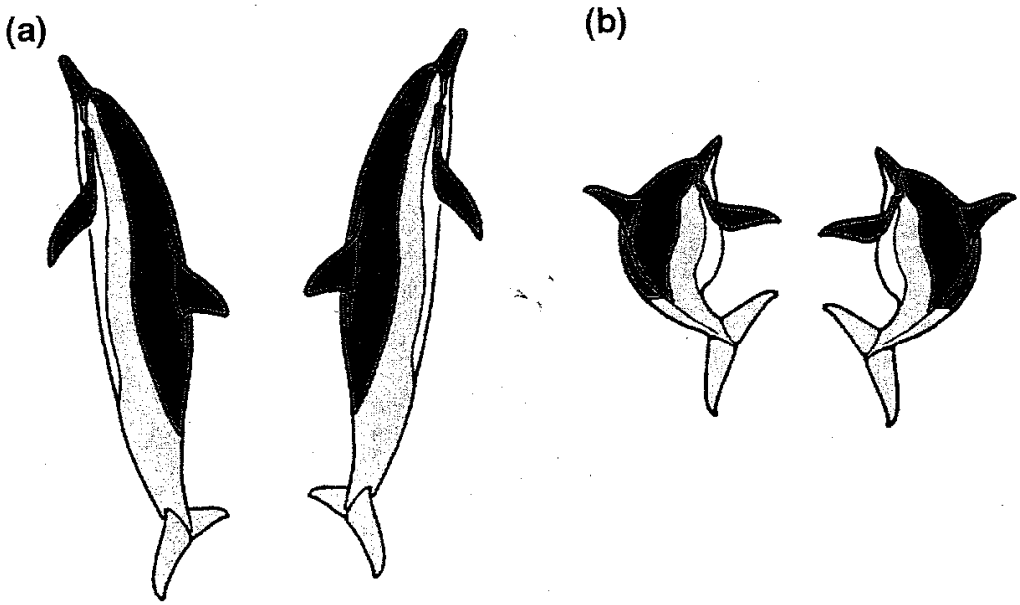


Figure 7.5. Rotating pairs of Hawaiian spinner dolphins illustrating the use of pigment patterns in signaling (a) tilt away and (b) tilt-toward (from Norris *et al.*, 1994).

Pigment granules and dendritic (branching) melanocytes of epidermal origin are present in sirenians. Numerous fibers occur in and between the cells of the spinosum stratum and probably account for a considerable amount of elasticity in the epidermis. There are no major differences between the skin structure of manatees and dugongs, except that the dugong skin may be less pigmented in the adult.

11.1.3. Hair

Pinnipeds, sea otters, and polar bears: These animals have two layers of hair: the outer **protective guard or primary hairs** and the **inner soft underfur hairs**. The longer, thicker guard hairs lie on top of the shorter, finer underfur hairs. Growth of the pelage is influenced by thyroid, adrenal, and gonadal hormones and by nutrition. It is also influenced indirectly by day length, thermal condition, and reproduction. In most mammals there are one to ten underfur hairs per guard hair. Sea otters and fur seals have between 50 and 1000. Pinnipeds, monk seals, elephant seals, and walruses lack underfur. The guard hairs have a pith or medulla (central cavity) in otariids, which is lacking in walruses and phocids. Since medullated hair has been documented among other carnivores, the non-medullated condition has been interpreted as being phylogenetically informative. In otariids, the hairs are arranged in clusters of two to four or in rows. As with sea otters, the hairs of pinnipeds lack arrector pili muscles that serve to erect the hair. This may enhance the ability of the hairs to lie flat during submersion, further contributing to streamlining of the body.

The natal or first coat of a pinniped differs from the adult pelage. Monk seals and elephant seals are born with black pelage whereas phocines and the walrus have white or gray natal coats. Natal coats in otariids are dark brown to black. Based on these patterns, the light-colored pelage of phocids has been interpreted as a share derived feature uniting phocines and lobodontines.

In *Enhydra lutra*, the guard hairs are medullated and underfur hairs are often medullated at the base. The sea otter has the densest pelage of any animal, an adaptation against heat loss. The mean hair density in the midback region of the sea otter is approximately 130,000 hairs/cm^2. This is more than twice that of the northern fur seal. The guard hairs are sparse compared to underfur hairs and probably have little direct insulative value. The main function may be to protect the integrity of the underfur hairs when the animal is immersed in water. Also, the guard hairs' relatively short length and springiness may assist in elevating the underfur hairs to renew trapped air when the animal emerges from the water. The wavy underfur hairs are shorter and more uniform in diameter than the guard hairs. Their waviness helps to reduce the size of the air spaces in the longitudinal plane. Thus, when the animal is immersed, the underhairs overlap and interlock to help retain trapped air. The sea otter has an extra feature that adds to its waterproofing: the fur is richly covered with a hydrophobic lipid, squalene.

Polar bear: The guard hairs are medullated. The pelage is not always creamy white, as is commonly assumed. It varies according to the season and lighting condition between white, yellow, gray, or even brownish. Immediately after molting, the fur is nearly pure white, matching the Arctic landscape. In summer, it often takes on a yellowish cast, probably due to oxidation by the sun. The green coloration of the pelage is due to algal growth within the shafts of the hairs. The claim that polar bear hair reveals very small optical fibers, which direct the sun's UV radiation to the skin where it warms the animal, has been refuted. Direct measurement of the transmission of light through polar bear hairs reveals a very small optic loss that is of little consequence to the heat conservation of polar bears. What is more likely is that the polar bear guard hairs are long enough to effectively trap a "dead layer" of water that acts to help insulate their body, much like a wet suit on humans. Unlike guard hairs on most marine mammals, which lie flat against the body, polar bear hairs stand erect, exposing underfur hairs. The underfur hairs trap a layer of relatively undisturbed water, which maintains an insulative shell around the bear's body.

11.1.4. Molt

All phocid seals, the sea otter, and one cetacean, the beluga, are known to undergo an annual molt. Although molting is a process related to an acclimation process to accommodate for seasonal changes among terrestrial vertebrates, for phocids, which spend most of their time as pelagic organisms, such a process probably has a different function.

Pinnipeds: The molt pattern varies among pinnipeds. The natal coat is molted in the uterus of some species such as the hooded seal and the harbor seal before the pups are born. This may be an adaptation for breeding on ice. In all other pinnipeds the natal coat is molted at varying periods of up to a few months of age. After this molt, the adult pelage is shed and replaced

annually. Molting takes place during the summer and autumn (December-May) in the southern hemisphere. In the northern hemisphere the molting time is more variable, usually occurring during spring (April-June). Molting begins in the area around the face and is followed the face, abdomen, and finally the back. The molt then spreads over the body surface, eventually replacing the entire pelage.

The molting period varies from 25 days among elephant seals to up to 170 days in the harbor seal. In Elephant and Hawaiian monk seals, the shed hairs are attached by their roots to larger sheets of molted epidermis. In other pinnipeds hairs are shed individually.

Fur seals and sea lions renew their pelts continuously all year long.

Sea Otter: Molting takes place gradually throughout the year with a peak period in spring among captive Alaskan otters.

11.1.5. Glands

Cetaceans and Sirenians: No sweat glands and no sebaceous glands in cetaceans, although there is a rudimentary sebaceous gland associated with snout hairs of sirenians.

Pinnipeds: Sebaceous glands are associated with each hair canal and their thick secretions function primarily to keep the epidermis flexible. The sweat glands of pinnipeds occur singly in association with guard hair follicles and their ducts open into the follicle. The sweat glands vary from large coiled structures in fur seals (related to their need for a large cooling surface, especially on land) to simple coiled tubules in phocids. The largest sweat glands of the walrus are located around the mouth and it has been suggested and their odiferous secretions may function in mother and pulp recognition.

Sea Otter: Sebaceous glands are associated with hair follicles and characteristically have a long, thin shape, but are often dilated at the base. Sebaceous secretions in the sea otter are predominantly composed of lipids. Removal of lipids from these sebaceous secretions, especially in the sea otter, greatly lessens the water repellency of the fur, reducing its thermoregulatory capability. Apocrine sweat glands are more prominent than the other sebaceous glands.

11.1.6 Vibrissae (whiskers)

Cetaceans: Whiskers exist only on the head and are distributed along the margins of the upper and lower jaws. The structure and especially the innervations of vibrissae indicate a sensory role and suggest a role in feeding. Baleen whales possess a larger number of vibrissae than odontocetes, and some odontocetes have only vestigial follicles. The Ganges and Indus River dolphins and the boto are notable exceptions in possessing a large number of well-developed vibrissae that have been related to the murky waters in which they live.

Pinnipeds: Vibrissae are only on the face. They are larger, more deeply rooted, stiffer, and have follicles surrounded by three rather than two blood sinuses when compared with terrestrial

mammals. There are three kinds of vibrissae: rhinal, superciliary, and mystacial (the most prominent). They appear early during the embryonic development, long before pelage hairs appear. Vibrissae follicles are similar to hair follicles except that they are controlled by voluntary muscles. They are heavily enervated, with blood vessels in the connective tissue sheath surrounding the follicle and prominent circular (ring) sinuses around the vibrissae. Walruses possess on average 600-700 vibrissae, more than other pinnipeds and most terrestrial carnivores.

Mystacial whiskers are arranged in rows along the sides of the snout and have either a smooth or beaded outline. Beaded mystacial whiskers are unique to phocids (excluding monk seals). The primitive smooth condition is seen in bearded, Ross, and leopard seals, as well as otariids and walruses. The functional significance of these differences is not known. Mystacial whiskers range in size from the short stiff bristles of the walrus to the very long whiskers of fur seals. Walruses have the toughest mystacial vibrissae. The upper lip, in which the follicles are implanted, is characterized by small compartments with fibrous septa filled with adipose tissue. This gives the upper lip both rigidity and flexibility. The walrus uses its mystacial vibrissae for sensory purposes both as a group and individually.

Superciliary (supraorbital) whiskers, located above the eyes, are usually better developed in phocids than otariids. Rhinal whiskers, one or two on each side just posterior to each nostril are found only in phocids.

Vibrissae function as tactile receptors and most research on them has been conducted using phocids. Vibrissae's sensitivity to sound improves with increasing frequency stimulation. The best sensitivity is at 100 HZ with a range up to 2500 Hz. The Baltic ringed seal has extraordinarily well developed vibrissae, which seem to help it find its way in the dark waters beneath the ice. A single vibrissa of a Baltic ringed seal contains 10 times the number of nerve fibers typically found in that of a land mammal.

A number of functions have been proposed for the vibrissae: to sense compressional waves, as a speedometer for navigation in the darkness, for prey detection, even for discrimination of size and shape of objects and surfaces in the cases of walruses and California sea lions.

Sirenians: Vibrissae are of the sinus type, intermediate in form between pelage hairs and true vibrissae. The hairs are loosely scattered over the body but become denser and very robust on the muzzle and around the mouth. Unlike the body hairs, the facial hair surrounding the mouth contains prominent bristles with medulla, and the follicles are of the true sinus type. Blood vessels and nerves penetrate the follicle. A well-developed dermal papilla extends deep into the hair shaft where it protrudes into the medulla.

Sea Otter: It has all three types of vibrissae, but mystacial whiskers are most numerous.

Polar bear: Their vibrissae are few in number but very stiff.

11.1.7. Claws/Nails

Cetaceans: No trace of claws/nails.

Pinnipeds: The fore- and hindflippers of phocine seals are characterized by the presence of well-developed claws. In contrast, monachine seals' claws tend to be poorly developed. The claws of the hand are reduced to small modules in otariids and walruses. The fore- and hindflippers of otariids have cartilaginous extensions that project from the distal edge of the flipper border. Short cartilaginous extensions are present in the claws of the walrus.

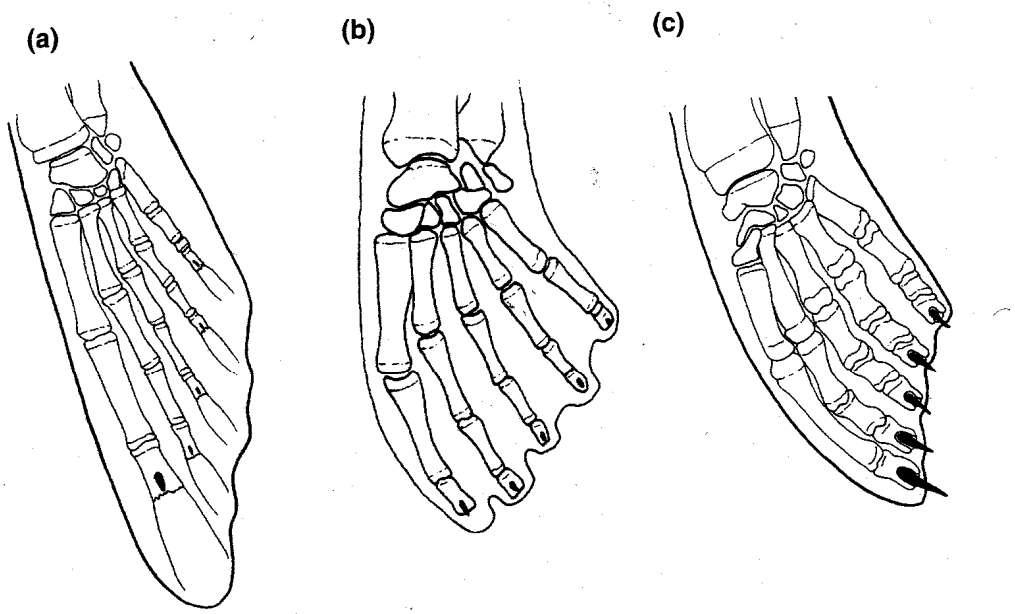


Figure 7.14. Claws and cartilaginous extensions on the fore flippers of pinnipeds. (a) Sea lion, (b) Walrus illustrating the otariid and walrus condition in which there are cartilagenous extensions to the digits and the nails are reduced to small nodules, and (c) Harbor seal illustrating the phocine condition with well-developed claws. (Illustrated by P. Adam; modified from Howell, 1930).

Sirenians: Rudimentary nails are present on the second, third, and fourth digits in manatees, except for the Amazon manatee, which lacks nails.

Polar bear and sea otter: Possess claws on both fore- and hind digits. The claws are not retractable in the polar bear, and the sea otter can only retract those of the forefeet.

11.2. Thermoregulation

Marine mammals spend most, if not all of their lives surrounded by water that is colder than their maintained body temperature. Water has 25 times the heat capacity of air. Many marine animals have to withstand environmental temperatures of 25 times lower or even colder than inside their bodies (these two "25" numbers are coincidental, they are not directly related to each other). Seawater temperature can be as low as 2° C and some species spend a considerable amount of

time resting on ice and exposed to even lower temperatures, as is the case for some pinnipeds and polar bears. The type of ice also affects the distribution of marine mammals. There are two types of ice that can be found in polar regions: **fast ice** (attached to land) and **pack ice** (floating

or moving ice). On the former, we will find Weddell, ringed, elephant, Caspian, Baikal, and gray seals, while the harp, hooded, bearded, ribbon, Ross, crabeater, leopard, largha, gray, and harbor seals as well as the Steller sea lion and the walrus are found on pack ice.

Mammals are homeothermic endotherms, which mean that they maintain a high (36 to 38°C) and relatively stable body temperature. To maintain a constant body temperature, a mammal must produce metabolic heat at the same rate at which is removed from the body. This process is called **thermoregulation**, meaning the maintenance of a constant S and warm S body temperature.

To understand how and why heat is lost from the body, we must take a look of the physics involved in the process. It can be explained through the following formula:

$$H' = (SA)\ C\ (T_b - T_a)$$

where H' is the rate of conductive loss, SA is surface area, C is thermal conductance, T_b is the body temperature, and T_a is ambient water temperature.

Let us examine the meaning of this formula. First, a marine mammal can reduce heat loss by reducing the surface area of its body. We will examine this option in section 13.2.1. Another way to reduce heat loss would be to reduce the thermal conductance of a body in contact with the water, which is achieved through insulation (the inverse of conductance). We will discuss that in section 12.2.2. Reducing the (T_b - T_a) differential by lowering body temperature is another strategy for minimizing heat loss. Since marine mammals are homeotherms, however, that is not an option for them. Not apparent in the formula is the possibility that an animal can make physiologic adjustments in their circulatory system in order to control heat loss. We will analyze that alternative in section 12.2.3.

As a result of the above-mentioned strategies, marine mammals do not need to have a metabolic rate 25 times higher than a terrestrial mammal to survive in cold conditions. They can avoid the potentially immense heat loss threatened by their cold environment in three ways: (1) Decreased surface-to-volume ratios; (2) Increased insulation; and, (3) Adaptations in the circulatory system (known as Heat Exchanged Systems). There is no empirical evidence that marine mammals either increase their metabolic rate (very expensive from the energetic viewpoint) or decrease their body temperature to adjust to cold conditions.

Let us analyze those approaches in detail.

11.2.1. Surface-to-Volume Ratio

The surface area of a body increases as a function of the square of its linear dimension while its volume increases as a function of the cube. It follows that for bodies of the same general shape, the larger ones will have a relatively low surface area: volume ratio (SA:V). Marine mammals are not spherical, which would give them the lowest SA:V ratio, they are torpedo shaped with reduced appendages, a compromise between thermoregulatory and locomotive needs. The surface areas of marine mammals (including pinnipeds, cetaceans, and the sea otter) are, on

average, about 23% smaller than those of terrestrial mammals of similar size. The generalization that animals that live in cold conditions tend to reduce their SA:V ratio is known as **Bergman's Rule**.

Marine mammals are large and are thus capable of producing considerable heat with relatively little loss at the surface. The sea otter, although small in comparison to most marine mammals, is more than twice as large as the largest terrestrial mustelid, the European badger. The polar bear is the largest of the living species of ursids. Most cetaceans, pinnipeds, and sirenians are relatively large mammals. The blue whale is the largest mammal ever to have existed.

Overheating is a side effect of adaptations against heat loss, and most adaptations with which it is addressed are behavioral. Marine mammals in warm environments cool off by entering the water or resting in tide pools. Others, such as northern elephant seals, New Zealand sea lions, and Southern sea lions, cool of by flipping sand on their backs. The northern fur seal pants like a dog to dissipate heat. The monk seal, a tropical species, cools of by resting near the water in damp sand, often digging holes to expose cooler layers. When on land, Galapagos fur seal pups too young to cool off in the sea resort to seeking shelter in the shade of boulders and minimizing their activity during the heat of the day.

11.2.2. Insulation

The dense fur or blubber covering marine mammals minimizes heat loss in water. Blubber not only insulates the animals from cold but also improves their hydrodynamic shape, stores elastic energy, and serves as an energy reservoir, providing nourishment during long periods between feeding. Studies show that blubber can also provide information about the nutritional state and diet of marine mammals. In contrast to the fat reservoirs of adult seals and whales, most pinniped pups are born with little blubber and must quickly develop a covering of fatty insulation to survive. In place of blubber, newborn Weddell seals' hair, or **lanugo**, is several times longer than the fur of the adult, which helps to conserve heat. Harp seal pups born on Arctic ice use the sunlight, which is reflected by the white hairs onto the surface of the skin, where the heat is absorbed. The pup's coat traps this warmth between the hair and the skin, producing a "greenhouse effect" that prevents heat loss. In addition, although the newborns lack a layer of blubber and have fur of poor insulative quality, they do possess a subcutaneous layer of **brown fat** along the back, around the neck and heart, kidneys, and abdominal walls, and at several internal sites. This specialized brown fat, also found in human babies and many hibernating mammals, helps keep the pups warm by means of **non-shivering thermogenesis**. Instead of shivering, seals metabolize this high energy fat to produce considerable heat. A few days after birth, the thermogenic fat stores remain to provide heat at the time pups are weaned and enter water for the first time.

In fetal life, phocids develop a coat of woolly lanugo hair. Hooded seals, most harbor seals and some bearded seals shed the lanugo in the uterus, while other species shed theirs a few days to several weeks after birth. Hair has little insulating value for adult phocids; they depend on a thick layer of blubber to retain body heat. Otariids are less tolerant of cold and rely more on their dense pelage. Fur seals must remain active to prevent hypothermia when in cold water.

Whales and seals rely on controlled peripheral blood flow from the body core to the skin and appendages for heat conservation or loss. Unlike terrestrial mammals, whose insulation

typically overlies vascular circulation to the skin, vascular beds to the base of the epidermis penetrate the insulating blanket of whale and seal blubber. Consequently, minimum heat flux is

achieved when peripheral vasoconstriction is greatest and is independent of maximum heat flux achieved during periods of heat stress.

The **thermal conductivity** (**conductance**) of blubber is the inverse of its insulative value and is a function of both its thickness and its peripheral blood flow. For cetaceans, the thermal conductivity of blubber is mostly a function of its lipid content. There is both higher lipid content and greater thickness in the blubber of temperate-water harbor porpoises than in that of tropical spotted dolphins, giving the former four times the overall insulative value. In bottlenose dolphins, the thickness of the blubber layer adapts to water temperature by changing as quickly as two millimeters a month. Seal blubber seems to be a better insulator than whale blubber, probably because there is a very fibrous tissue present in seal blubber, which whale blubber lacks. In addition to blubber conductivity, another important variable with respect to heat loss models is the asymmetrical distribution of blubber around the body core.

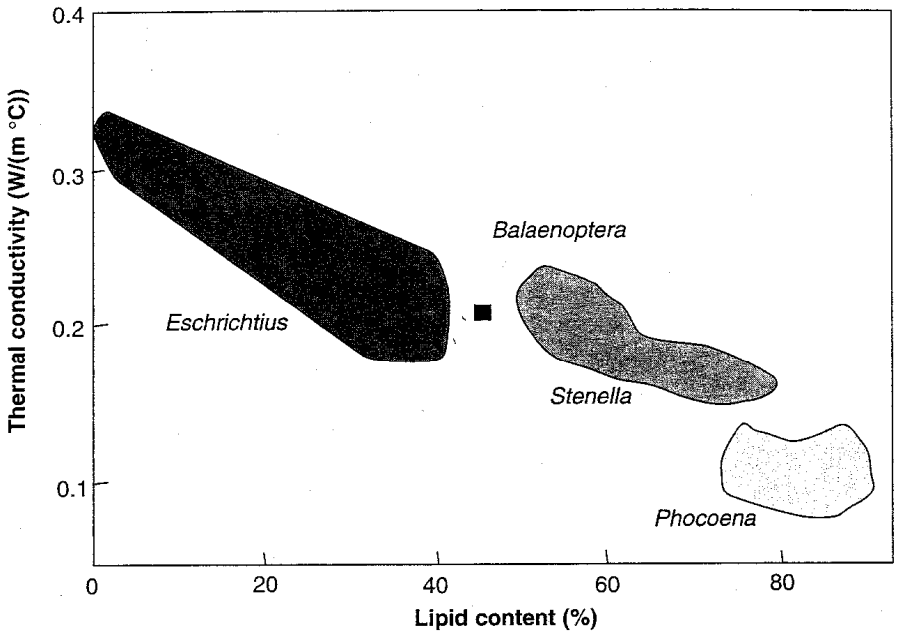
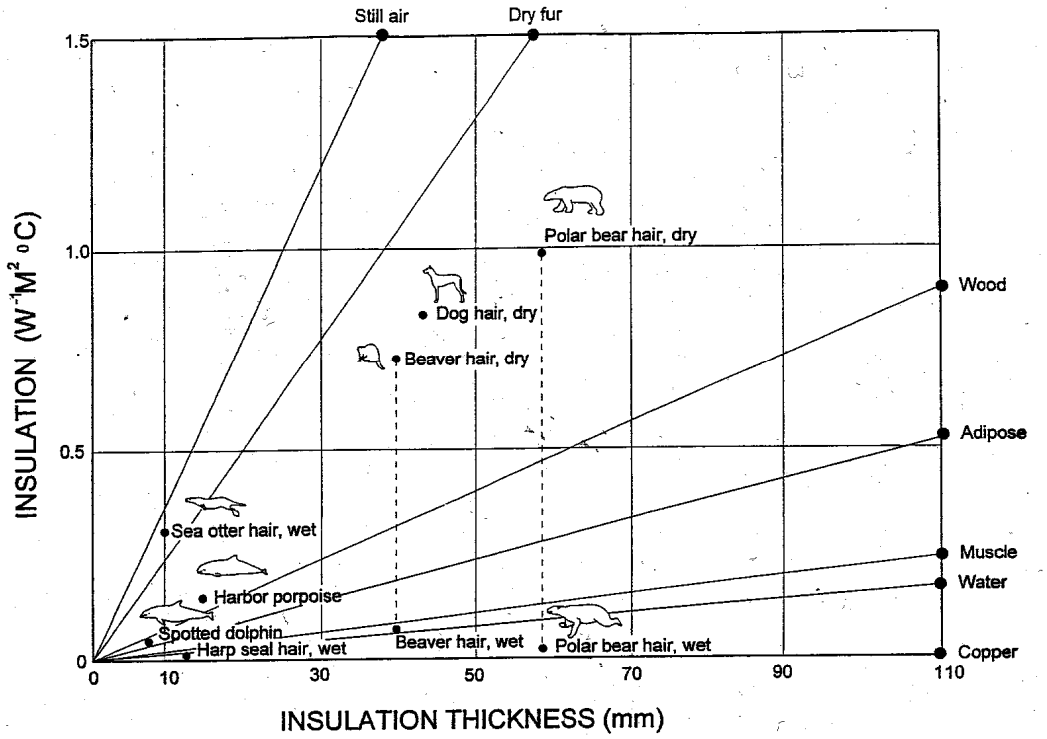


Figure 7.15. The relationship between lipid content and thermal conductivity of the blubber of four genera of cetaceans (adapted from Worthy and Edwards, 1990).



Ambient air temperature plays an important role in limiting the distribution of seals. Cold temperatures seem to affect the distribution of gray seals throughout the breeding season. The cold air has thermoregulatory effects on small, fasting pups during the period before they enter the water. Fasting seals are especially vulnerable because they have a thinner insulative layer than when they are eating, and their metabolic rates are reduced. Temperatures at the opposite extreme could also be limiting factors to seal populations, and could explain why there are so few seal species around the equator: they may have trouble regulating for high temperatures.

11.2.3. Heat Exchange Systems

A striking feature in the vascular system of all marine mammals is the **rete mirabilia** (miraculous network) or **periarterial venous rete**. It is a massive system of contorted spirals of blood vessels, mainly arteries but with thin-walled veins among them, that usually forms blocks of tissue on the inner dorsal wall of the thoracic cavity, the extremities, and the periphery of the body. Among cetaceans, the sperm whale has the most extensive rete mirabilia.
Retia function as **countercurrent heat exchangers (CCHE)** which work by maintaining a heat differential between oppositely directed flows, which increases the amount of heat transferred. Countercurrent heat exchangers in the flippers, fins, and flukes function to conserve body temperature. So that these tissues may stay alive and functional, and not freeze solid, it is necessary to maintain some blood circulation though them. Each artery at the surface (particularly evident in the flukes, flippers and dorsal fin) is surrounded by a network of veins, all encased in a rigid channel of connective tissue underlying the dermis. When there is a need

to retain body heat, arterial blood flows to the surface under low pressure and returns along the surrounding venous rete, which absorbs heat from the central artery. To cool, blood flows under high pressure, thereby collapsing the surrounding veins against the rigid tunnel walls, and returns instead by superficial veins that lie closer to the surface of the skin. The vessels in the flukes are the usual sites for blood sampling.

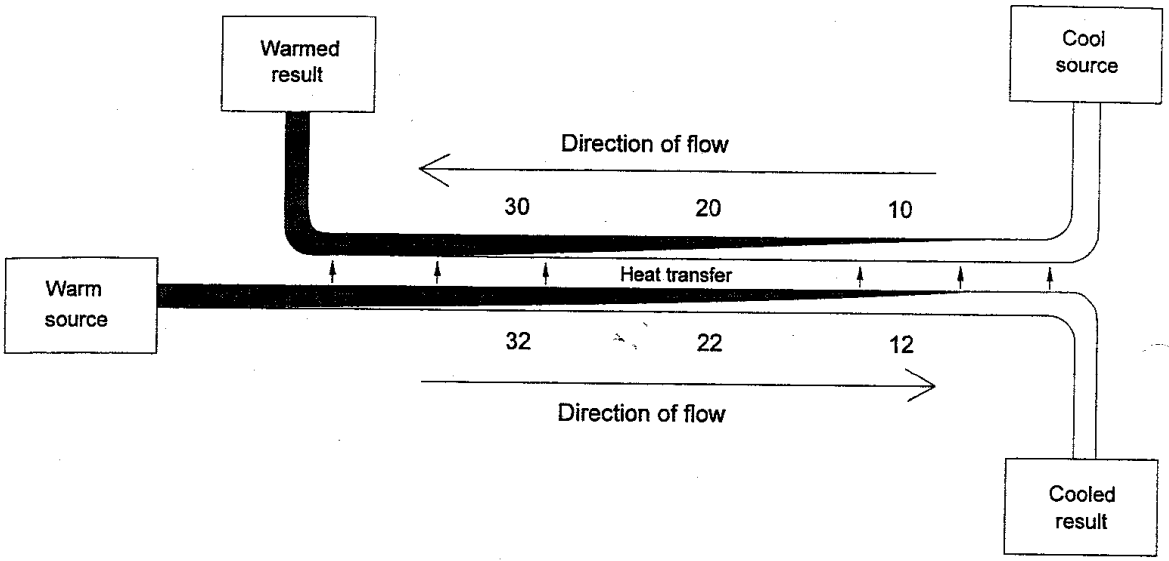


Figure 2-5. Countercurrent heat exchange—a maximally efficient design. How does a countercurrent heat exchanger work? Consider the two pipes in this figure, juxtaposed to each other. The lower pipe is carrying warm fluid that flows in one direction (from left to right in this example). The upper pipe carries cool fluid that is flowing in the opposite direction. Because these pipes are juxtaposed and have opposite (antiparallel) flows, heat is maximally transferred from the fluid in the lower pipe to the fluid in the upper pipe. Almost 100% heat exchange can be achieved with a countercurrent heat exchanger. The result is that by the time the fluid in the lower pipe reaches the point marked "result," it has been significantly cooled. Countercurrent heat exchange is common in animals, and the "pipes" are arteries and veins.

Countercurrent heat exchangers are also associated with reproductive tracts, where they prevent overheating in these heat-sensitive organs. Phocid seals and dolphins possess a vascular countercurrent exchanger that cools their testes. In phocids, venous plexuses located between the veins of the distal hind limbs and the pelvis, suggest that the testes are cooled directly. Cooled blood from the hind flipper flowing through the inguinal plexus located in the groin would introduce a thermal gradient which could allow local and direct heat transfer from the testes and adjacent muscles. Testicular temperature can be lower than core body temperature by as much as 6-7°C in elephant seals.

In dolphins, spermatic arteries in the posterior abdomen are juxtaposed over veins returning cooled blood from the surfaces of the dorsal fin and tail flukes. Immediately after vigorous swimming, temperatures at the CCHE decrease relative to resting and pre-swim values; post-swim temperatures at the CCHE are at most 0.5^{o}C cooler than pre-swim temperatures. These data suggest that the CCHE has an increased ability to cool the arterial blood supply to the testes while the dolphin is swimming. Deep body temperature measurements in male dolphins have supported this thermoregulatory hypothesis; low temperatures were present in their pelvic

CCHE's. Female dolphins and phocid seals use a similar countercurrent exchange system. In dolphins, cool blood flows directly to the fetus from the tail and fin, and it flows from the hind flipper for seals. This keeps the fetus (which has a metabolic rate of about twice that of the mother) from overheating and experiencing fetal distress, developmental disorders, or death.

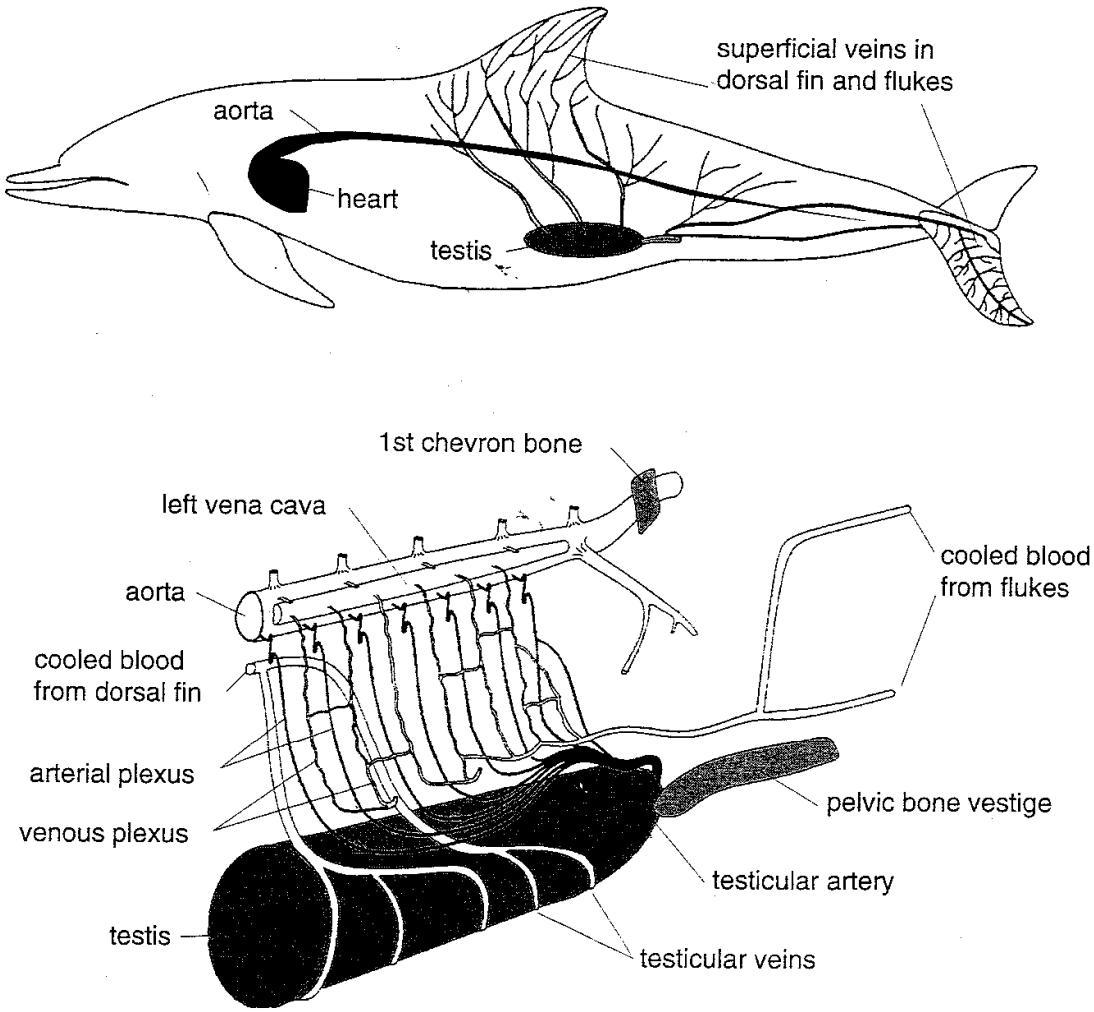


Figure 7.18. Dolphin testes as countercurrent exchange system (modified from Pabst *et al.*, 1995).

Baleen whales have a CCHE in their mouths, enabling them to reduce heat loss when feeding in cold waters. The same can be found in the nasal structure of elephant seals, which enables them to reduce their heat loss.

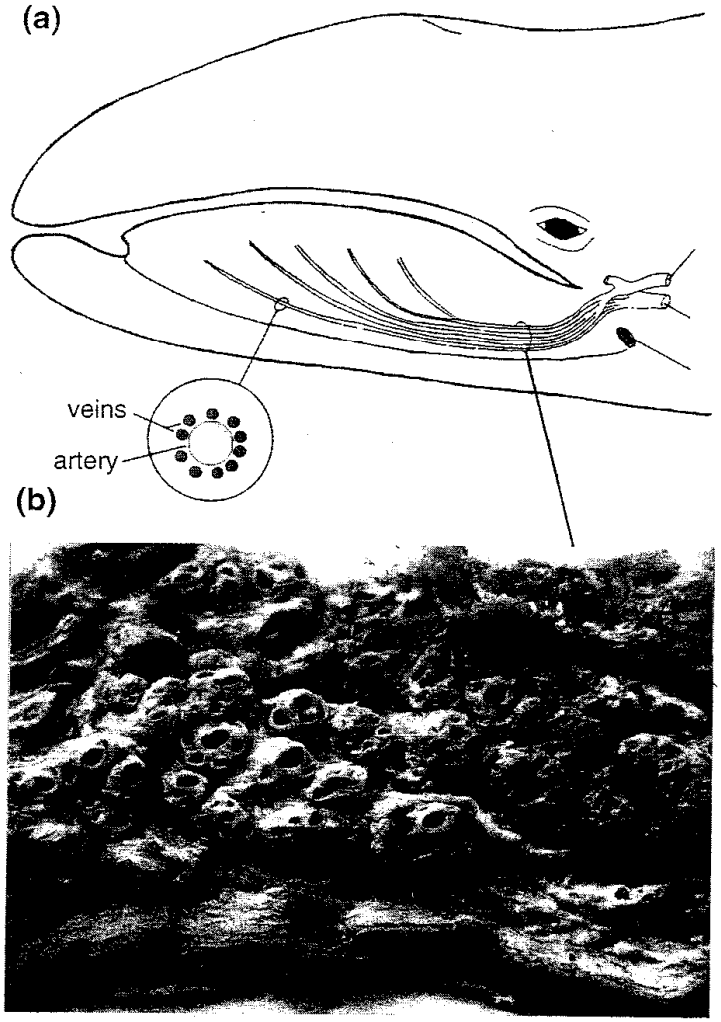


Figure 7.19. Countercurrent exchange system in gray whale mouth (a) schematic diagram and (b) cross section through lingual rete. From Heyning and Mead, 1997; courtesy of John Heyning.

The retia in sirenians are in the form of vascular bundles rather than networks and are scattered throughout the body, including the body walls, face and jaw, tail, and spinal cord, but they are best developed in the flippers.

11.3. Locomotion

The musculoskeletal (bones and muscles) system acts to define the body shape and provide support and protection of internal organs. This system of muscles, bones, tendons, ligaments, and joints also produces and transmits the mechanical forces required for movement trough the aquatic environment.

In this section we will review the major features of the musculoskeletal system used by marine mammals that have to do with locomotion both for swimming (all marine mammals) and walking on land (pinnipeds, otters, polar bear). We will also see how those structures provide support for soft tissues and their role in controlling buoyancy.

Aquatic mammals in general, and marine mammals in particular, have developed a number of adaptations to move efficiently in that medium. Propulsion for swimming by marine mammals is derived from paired flipper movements (pinnipeds and sea otters) or vertical movements of caudal flukes (cetaceans and sirenians). Paired flipper propulsion is more efficient at low speeds where maneuverability is critical.

However, they have to contend with the fact that they need to move in much more dense medium.

11.3.1. Viscosity

A major challenge to any swimming marine organism is to reduce its drag

Water is a difficult medium in which to move. This is due to the fact that water is about 60 times more viscous than air.

Drag forces are much higher in the marine environment than in air, because of the increased **viscosity** and density of seawater. The **rate of energy use** (power output - P'), required of an aquatic mammal to move through such a medium is proportional to its **drag** (D), multiplied by the **speed** (*u*), at which it swims.

$$P' \square Du$$

Thus, a marine mammal could reduce its power output to save energy (not very efficient if you want to move around), or alternatively, swim at a higher speed (very expensive energetically) in order to reduce the drag it experiences.

There are two types of drag forces that act on a body, **viscous or frictional drag** (D_v) and **pressure or inertial drag** (D_p). Viscous drag results from the viscosity in the water (60 times greater in seawater than in air). It is a measure of the stickiness between thin layers of fluid that slide, or are sheared, past it other. Viscous drag results from fluid being sheared across the surface of the body. The fluid in contact with the body surface is not moving relative to that surface, and the fluid close to the bossy surface is moving more slowly than fluid that is farther away. Thus, the more body surface, the higher the viscous drag. A smooth body surface reduces surface area, and thus, acts to decrease the viscous drag.

Pressure drag, which is influenced by both the viscosity and density of the fluid, results from the distribution of pressure around a body and its effect on fluid flow. In general, for a body moving through a fluid, pressures are highest at the cranial end and lowest at the widest part. Fluids flow from areas of high to low pressure, therefore the fluid flowing along the front of the body stays lose to the surface. As fluid flows past the widest part of the body and toward the caudal end, pressure begins to increase again. Because fluid does not begin voluntarily flow from areas of low to high pressure, the fluid separates from the surface and heads downstream, leaving a wake behind the body. The larger the wake, the higher the pressure drag. The most effective way to reduce pressure drag is to postpone the separation point until it is further toward the rear of the body and thus, reduce the wake. This is best accomplished by gradually tapering the tail-end of the body, rather than having it terminate abruptly. The resulting fusiform (spindle) shape is referred to as **streamlined**. For the flow regimes experienced by marine mammals, pressure drag will be a much larger percentage of the total drag on the body than viscous drag.

Based on this, we can understand some of the adaptations in functional morphology in order to become more efficient swimmers. To reduce viscous drag, they have: (a) reduced the surface area relative to their volume (SA:V) (which also has some energy saving advantages as we saw in detail in Chapter 13) and (b) smoothed their surfaces. To reduce pressure drag, they postpone flow separation around their bodies by streamlining. This is, in fact, the single most effective way to decrease total drag.

Fineness ratio, f.r., is a hydrodynamic parameter that reflects streamline shape. It can be defined as the ratio of maximum body length to maximum body diameter. It is equal to total body length divided by maximum body diameter. An optimally streamlined body has maximum volume and minimum surface area at a fineness ratio of 4.5. Cetaceans, pinnipeds, sirenians, and the sea otter have fineness ratios between 3.3 and 8, with most species having body shapes incurring drag only 10% above theoretical optimum. The killer whale, probably the best swimmer among marine mammals, has the one closest to the ideal one with 4.0 to 4.5 f.r. No data is available for polar bears, although their external body shape is not obviously streamlined, except when compared with other ursids.

Other adaptations to reduce drag by decreasing body surface are eyes at the same level than the skin. Behavioral adaptation such as wave riding, help them to decrease water resistance. They also have a strong caudal fin for trust that they achieve by flapping. Some marine mammals attain high speeds such as the killer whale or orca (55 km/h or 40 mph) and some species of dolphins in the genus *Stenella* (40 km/h or 25 mph). Because this common adaptations and their ecological role, free-swimming animals such as marine mammals, fish, and squid, are generically called **nekton**.

Now, regardless of how many external morphological adaptations are developed by marine mammals, there are other, less noticeable ones, under their skin. Remember that the rate of energy expended, or the power output required to swim is a function of the drag force on a body multiplied by its velocity. A marine mammal swimming at a constant velocity produces **thrust forces**, T, that are equal to its drag forces, D. Thus, the power output is equal to

$$P' \eta = Du = Tu$$

where η is the propulsive efficiency.

In order to achieve this propulsive efficiency, the musculoskeletal system must have certain design features. Thrust forces are dependent on muscle morphology and the mechanical design of the skeletal system. The propulsive efficiency of the animal is dependent on the site, shape, position, and behavior of the appendage used to produce thrust.

To swim, terrestrial mammals use the system we usually see among dogs knows as "dog paddle." That very system is used by the polar bear, the least swim-adapted marine mammal. The polar bear's hind limbs trail behind the body, which may help to streamline the overall body shape. The pinnipeds and sea otters also use their limbs to swim. The fully aquatic cetaceans and sirenians have a totally different approach: they swim using their vertebral or axial musculoskeletal system.

Muscles produced contractile force, which is transmitted by tendons to skeletal elements. If the muscular force produced is large enough, the skeletal element changes its position, usually by pivoting at a low friction joint. Thus, the musculoskeletal system is a machine that transmits force from one place in the body to another, and the mechanical design underlying its function is **leverage**. A lever is simply a rigid structure that transmits force by rotating at a pivot point or fulcrum.

A lever system can be design to optimize either its force output or the velocity at which it moves. Force output (force-out) is increased by increasing either (1) the force-in, or (2) the mechanical advantage of the lever system, which is defined as the ratio of the length of the lever arm-in to length of lever arm-out.

Thus, for marine mammals to produce large thrust forces they have to either develop locomotor muscles with high force-generating potential (increased force-in measurable by its cross-sectional area) or the skeletal elements should have the appropriate proportions to increase the mechanical advantages of the lever system. As we will see, marine mammals combine both approaches.

Finally, we must consider **propulsive efficiency**. The paddle stroke can be divided in two phases: the **power phase** that produces the useful thrust forces, and the **recovery phase** that produces no thrust but just repositioning for the next power phase. In order to maximize propulsive efficiency, thrust should be produced during both phases and, if possible, with equal efficiency.

The solution to that problem is the **hydrofoil** design. When hydrofoils are oriented appropriately to flow, they can produce lift-based thrust throughout the locomotor stroke. Rather than stick a broad, flat "paddle" out in the water, marine mammals could use an oscillating "wing" capable of generating lift and thrust continuously. A good hydrofoil design is one that has a long **span** (the length of the wing from base to tip) and short **chord** (the width of the hydrofoil in the direction of the flow). The ratio of span to chord is called the **aspect ratio**. A high aspect ratio hydrofoil will produce large lift and thrust forces with low drag, but may compromise maneuverability.

11.3.2. Cetaceans

To reduce drag, cetaceans have developed the following adaptations:

a) Head is elongated with no obvious neck or shoulders
b) The skull has become **telescoped** so that there is a cranial elongation of the bones that form the rostrum including the maxilla) with an overlapping of skull bones that tend to produce a shortened braincase
c) The one/two blowhole(s) has/have migrated to the top of the head where they can exchange air while the animal is still moving
d) Reduction, by fusion, in the number of cervical vertebrates
e) Forelimbs transformed into flippers (for steering and stability)
f) Hindlimbs lost externally
g) No external ears
h) The penis is completely hidden within muscular folds
i) The tits are concealed within slits on either side of the genital area
j) A tail fluke powered by two muscle masses (one in the upper and the other in the lower part of the tail stock) to drive the animal forward
k) An upright fin (in most species) made of fatty material that functions as a keel
l) The outer layer of the epidermis secretes tiny droplets of a high polymer of ethylene oxide to reduce drag

Other anatomical adaptations:

Skull: Marine mammals in general and cetaceans in particular, have undergone a massive reorganization of their skulls in order to:
(a) Provide support for the soft tissues of the respiratory and digestive system
(b) Form the bony capsules of sensory structures such as eyes, ears, and olfactory senses
(c) Protect the brain and its associated structures
Because of this, we can use the characteristics of the 20 bones or so of the skull to study of evolution of marine mammals. These skulls are strongly bilaterally asymmetric.

Mandibles: The lower jaws, or mandibles, appear straight when viewed dorsally in odontocetes. The posterior non-tooth bearing part has thin walls that form the fat filled **pan bone** that has been linked to sound reception. In mysticetes, the mandibles curve laterally and there is no pan bone. The mandibular symphysis, a fibrocartilage articulation, connects the tapered distal ends of the paired dentary bones.

Hyoid Apparatus: the hyoid bone is well developed in all cetaceans.

Vertebral Column: The vertebral column does no contain a sacral region because the pelvic girdle is lacking. The boundaries between cervical, thoracic, and lumbar regions are established according to the presence of ribs, and the boundary between the lumbar and caudal segments is determined by the presence of chevron bones. The typical cetacean vertebral formula is C7,

T11-12, L usually 9-24 (range 2-30), C usually 15-45 (range 15-49). At least in the bottlenose dolphin the vertebral column has the capacity to store elastic energy and to dampen oscillations as well as to control the pattern of body deformation observed during swimming.

Sternum and ribs: In odontocetes, usually 5-7 pairs of ribs are attached to the sternum (sternal ribs) while in mysticetes there is only one pair attached to the sternum and the sternum is shorter and broader than in odontocetes.

Flippers: They vary in size and shape, with the humpback whale having the longest (25-33% of the body length). It provides them with high maneuverability associated with the whale's unique "bubble-cloud" feeding behavior. Flippers are filled with subdermal connective tissue sheath that provides an enlarged surface to anchor flexor and extensor muscles. The elbow joint of modern cetaceans is uniquely immobile. The foreflippers are used primarily for steering rather than for propulsion. Cetaceans' flippers are unique in exhibiting **hyperphalangy** (they have more than the standard number of phalanges). **Polydactyly** has been observed in some occasions.

Tails or Flukes: Shapes differ among cetaceans. They are made of our basic components: (1) a cutaneous layer, (2) a thin blubber layer, (3) a ligamentous layer, and (4) a core of extremely tough, dense, fibrous tissue that forms the bulk of the fluke. Flukes are used to produce thrust forces. The lunate flukes of cetaceans are considered highly derived and efficient hydrofoils that decrease the energetic costs of swimming.

Dorsal fin: Extremely variable among cetaceans, with some species lacking it altogether. It has no bone structure associate to it and is made of tough fibrous tissue. It serves to assist in the maintenance of balance and thermoregulation as well as a sexual character (in killer whales) functions have been suggested as well.

Locomotion Efficiency: All thrust is provided by the up and down movements of the tail. The axial muscles move the tail. The action of the axial muscles is to bend a variable flexible beam: the vertebral column. Epaxial mules bend the vertebral the vertebral column dorsally in an upstroke; hypaxial muscles, and probably abdominal muscles as well, bend the vertebral column ventrally in a downstroke. In so doing, the muscles generate thrust forces that are delivered to the water by the flukes.

Axial muscles are long muscles bodies (they can run virtually the entire length of the vertebral column) composed of many other shorter muscles fibers. Unlike appendicular muscles that have discrete tendons of insertions, axial muscles have individual tendons, that is, individual tendons insert sequently on vertebrae along the length of the muscle.

The functional cross-sectional areas and thus, the force generated by the axial locomotor muscles are large in cetaceans. The elongated neural spines and transverse processes of cetacean vertebrae also increase the mechanical advantage of the axial muscles relative to terrestrial mammals. By inserting far from the point of vertebral column rotation, the lever arm-in is increased, and thus, force output is increased. A unique interaction between the tendons of the epaxial muscles and a subdermal connective tissue sheath that envelops those muscles also increases the work output. Instead of inserting on neural spines, some tendons travel through the

subdermal sheath at oblique angles to insert on transverse processes of the vertebrae located further caudally. The oblique tendon geometry increases the distance through which these tendons can be pulled by their muscles.

The best examples of these functional adaptations are found in short-finned pilot whales, short-beaked common dolphins, and the bottlenose dolphins.

Swimming Speeds: Speeds reached by cetaceans are variable but some are impressive. When migrating for almost 4,000 km, dolphins may attain a cruising sped of 17 km/h. Fast-moving rorquals get up 30 km/h. Oceanic spinner dolphins can attain 40 km/h (or 11 m/s) and killer whales can peak between 40 and 55 km/h. The higher the speed, the lower the maneuverability.

Swimming and diving represent major energetic expenditures in marine mammals. In wild bottlenose dolphins, locomotor activities can represent more than 82% of the animal's daytime activity budget. This is measured by the cost of transport (COT).

$$COT = P/MV$$

where P = power required to move a given body mass (M) at some velocity (V).

Experimental studies have shown that the COT for bottlenose dolphins is minimum at 2.1 m/s doubling at 2.9 m/s. However, when speeds were increased above approximately 3 m/s, dolphins switch to wave riding, i.e., surfing the stern wake of the boat from which the studies were conducted. At 3.8 m/s, for example, the COT was only 13% higher than swimming at 2.1 m/s when COT is optimum. This explains this common practice among many delphinids.

When submerged swimming mammals approach the sea surface to breathe, they encounter additional drag due to gravitational forces associated with creating waves at the air-sea interface. At depths below three times an animal's greatest body diameter, these gravitational forces are negligible, but as a swimming mammal ascends, its total drag increases to a maximum of fivefold at the sea surface due to energy lost in the formation of surface waves. Any animal can reduce its COT by swimming at depths below 2.5 body diameters for a period approaching the duration of its aerobic breathhold capacity, then surfacing to breathe only as frequently as O_2 demands dictate. This explains the typical surfacing behavior of many marine mammals of extended submerged breathhold swims punctuated by surface bouts of several closely-spaced ventilatory cycles.

Smaller marine mammals must surface to breathe more frequently at higher swimming velocities. At high speeds, the high drag associated with surfacing can be partly avoided by leaping above the water-air interface and gliding airborne for a few body lengths. The aerial phase of this type of **porpoising** or leaping locomotion removes the animal from the high drag environment of the water surface, while simultaneously providing an opportunity the breath. The velocity at which it becomes more efficient to leap rather than to remain submerged is known as the **crossover speed** (about 5 m/s for spotted dolphins) and increases with body size, becoming prohibitively expensive for cetaceans larger than 10 m in length.

11.3.3. Pinnipeds

All four limbs are modified for swimming. Otariids have developed the forelimbs into a pair of broad paddles with which the animal "rows" synchronously. Their primary locomotor muscles are those acting in the brachium (the upper arm). Not only their muscles acting on the brachium have large force-generating capacity (enhanced force-in), but the humerus, the proximal bone of the forelimb, is greatly shortened, which reduces the length of the lever arm-out which, in turn, increases the mechanical advantage of the primary locomotor muscles. Phocids, on the other hand, rely on the alternate strokes of their hindlimbs, supplemented by movements of the hind part of the body, to propel themselves through the water, much as a human diver wearing rubber fin does. Muscles on the femur are relatively large, and the femur is also a shortened bone. In consequence, true seals' locomotory musculature is concentrated at the back end of their body. The walrus swim by alternating the action of their hind limbs. They have larger cross-sectional areas (enhanced force-in) and their femur (their proximal hindlimb bone) is also shortened.

Certain obvious features distinguish phocids from otariids. Most notable are their contrasting methods of locomotion. Phocids move awkwardly on land. Unable to turn the hind flippers forward to support themselves, they must hump along on their bellies, using their short foreflippers for an occasional boost ahead (**sagittal undulation**). They are more graceful in the water, propelling themselves by sculling with their hind flippers and using the foreflippers for steering (**pelvic oscillation**). Otariids depend on paddle-like movements of the forelimbs for swimming, and on the hind flippers and a long neck for steering (**pectoral oscillation**). Using both the fore- and hind flippers, they move on land with a speed and agility that allow them to utilize high rocky habitats inaccessible to phocids (**ambulatory locomotion**). The walrus, somewhere in the middle, although closer to phocids than otariids, uses the hind flippers for swimming, foreflippers for steering, and both sets of limbs for moving on land.

Other pinniped adaptations include:

Skull and Mandible: Large eye orbits and relatively short snout. The skull of otariids has shelf-like supraorbital processes on the frontal bones, while the walrus has a large maxilla to accommodate the upper canine tusks, while the phocid skull is characterized by an inflated tympanic bulla.

Hyoid Apparatus: The hyoid bone serves for attachment of the tongue muscles.

Vertebral Column: The typical vertebral formula is C7, T15, L5, S3, and C10-12. The cervical vertebrae are m ore developed among otariids, which help them to maintain balance while swimming better than phocids do. In the walrus and phocids, the enlarged processes of the lumbar vertebrae provide attachment surfaces for hypaxial muscles associated with horizontal movements of the posterior end of the body.

Sternum and Ribs: Sternums are elongated (particularly the manubria bone). Ribs are firmly articulated.

Flippers: Bones of the fore- and hindlimbs are short, flattened and modified as flippers.

Distal limbs: They are shaped like a high aspect ratio hydrofoil. In fur seals and sea lions, the bones of the forearm (radius and ulna) are dorsoventrally flattened, and bones of the manus have lengthened to form then wing-like flipper used for propulsion. Cartilaginous rods at the distal tips of the phalanges increase the effective span of the otariid flipper. Similarly, the pes of walruses and phocid seals are expanded, predominantly owing to increases in length of the phalanges and distally placed cartilaginous rods. These appendages form hydrofoils that increase efficiency by creating lift and thrust throughout the locomotor stroke.

Swimming Speeds: California sea lions achieve in tanks speeds between 2.7 and 3.5 m/s. Most other otariids and seals reach speeds between 0.9 and 1.9 m/s (about 25 km/h).

11.3.4. Sirenians

Although the vertical swimming movements of sirenians resemble those of cetaceans, there are many differences between these two groups. Although sirenians locomotor system is based on their axial musculature as in cetaceans, these muscles are less developed in sirenians, increasing only near the fluke. The sirenian axial skeleton does not display the elongated neural spines of cetaceans, which would increase the lever arm-in for dorsoventral flexion; the lumbar and the cranial-most caudal vertebrae, tough, have elongated transverse processes.

All this indicates that virtually all the thrust is generated at the flukes, and that is precisely what happens. Movement is initiated from a stationary position by an upswing of the tail followed by a downswing, repeated until undulatory movement is established. The tail also serves as a ruder. Cruising animals can bank, steer, and roll by means of the tail alone.

The use of flippers in locomotion also differs of that in cetaceans. While cruising, the flippers of adult manatees are held motionless at the sides and juveniles have been reported swimming exclusively with their flippers. Flippers in manatees are used in adult only for precise maneuvering and for corrective movements to stabilize and orient the animal while feeding. The primary use of flippers is to turn the animal right or left. Flukes in the marine dugong are lunate-shape hydrofoil (like in cetaceans); while in manatees is less streamline and oval in shape. The dugong, which tends to be more marine in its distribution and is a more accomplished swimmer than the manatee, has a smoother skin. Cetaceans often use the flippers as planning surfaces to assist diving and surfacing.

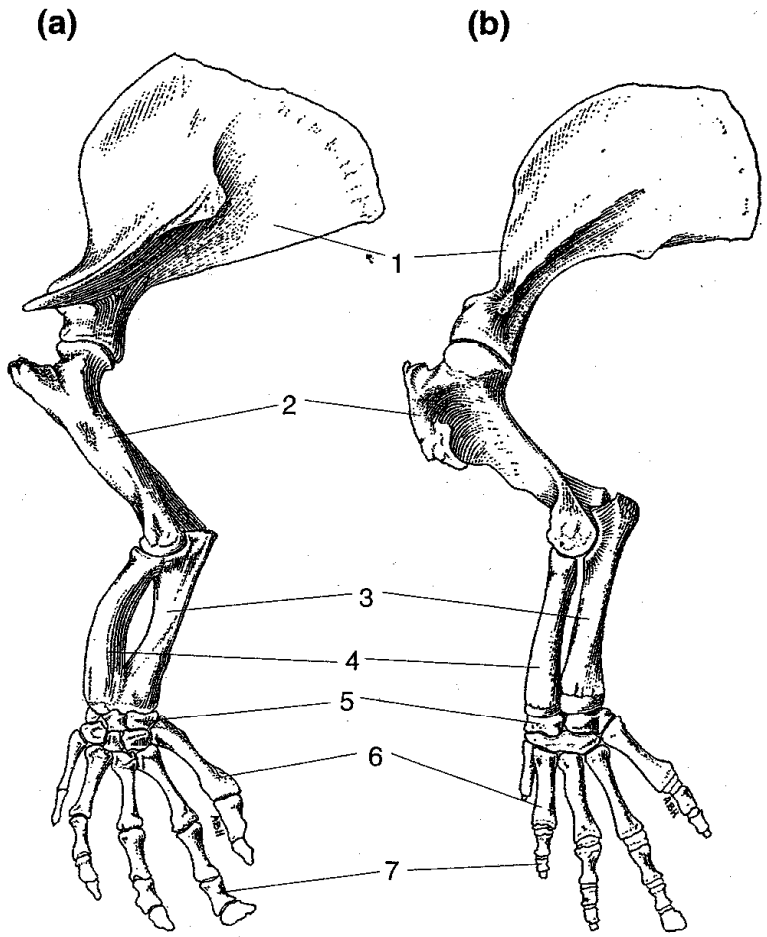


Figure 8.33. Forelimb of manatee (a) and dugong (b). Numbers: 1=scapula, 2=humerus, 3=ulna, 4=radius, 5=carpals, 6=metacarpals, 7=phalanges (from Howell, 1930a).

. The sirenian skull is different from al other marine mammals by its down-turned premaxilla. It is more sharply inclined in the dugong than in manatees. The shoulder girdle is composed only of scapula since, like all other marine mammals, they lack a clavicle. The pelvic girdle is vestigial in dugongs and absent in the West African manatee.

A major feature unique to sirenians has to do with hydrostatic adaptations. The skeleton of sirenians is both **pachyostotic** (thick dense bone) and **osteosclerotic** (containing cancellous bone). These two features, together with the patterns of growth in weight of the skeletons, the position of gravity and buoyancy centers, and the lung morphology all are involved in hydrostatic regulation which may free locomotor efforts from the additional requirement of providing lift.

. Sirenians are poor swimmers and unable to reach and sustain high speeds. Average leisurely speed for manatees and dugongs has been recorded at 0.6-0.8 m/s. When fleeing speeds of 6 m/s (22 km/h) have been recorded.

11.3.5. Sea Otter

The sea otter skull is short and robust and is characterized by a blunt rostrum, prominent cheeks, and well-developed bony crests for the attachment of powerful jaw-closing muscles. They possess 50-51 vertebrae distributed as follows: C7, T14, L6, C20-21. Because the hind limbs are larger than the forelimbs, locomotion on land is slow and clumsy. Swimming involves undulations of the vertebral column, tail, and hindfoot. Their hind limbs have been described as relatively short. Correlated with this is an increased development of vertebral processes in the lumbosacral region for attachment of the epaxial musculature involved in swimming. The sea otter has expanded feet due to the lengthening of the phalanges (like in walruses). The individual is not shape like a hydrofoil, but like a square-shaped oar, which sea otters use for slow paddling. When swimming at higher velocities otters undelete their hind limbs dorsoventrally and synchronously, from a propulsive surface that approximates a hydrofoil with a lunate caudal border. Steady swimming by submerged sea otters ranged from 0.6 to 1.4 m/s. Based on these results, crossover speeds between surface and submerged swimming ranged from 0.6 to 0.9 m/s.

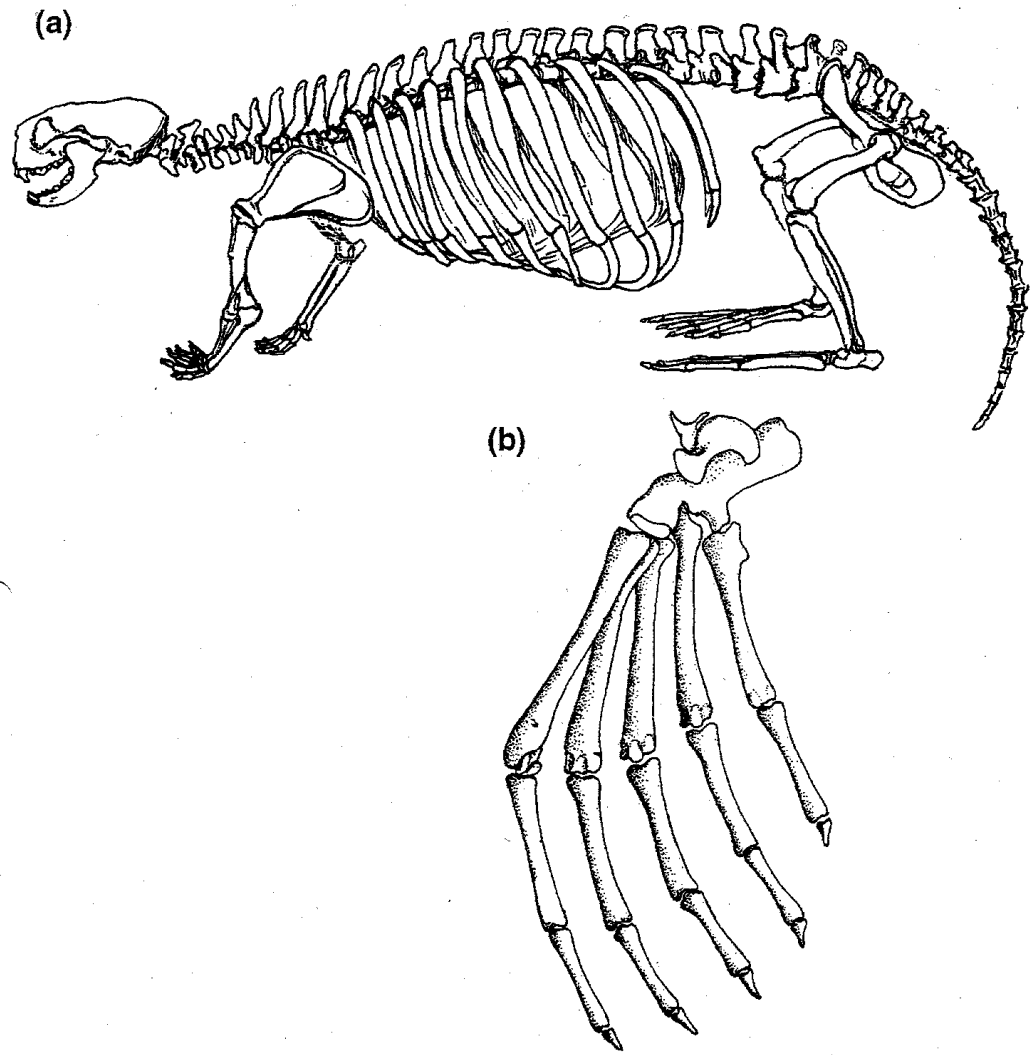


Figure 8.36. Sea otter, *Enhydra lutris* (a) Skeleton (from Chanin, 1985), (b) hindfoot (from Taylor, 1989).

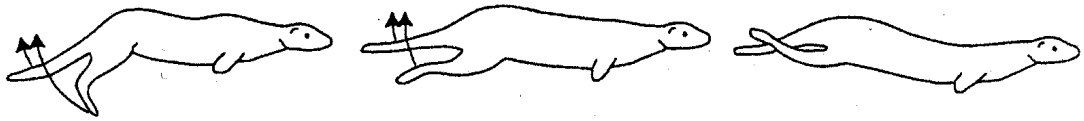
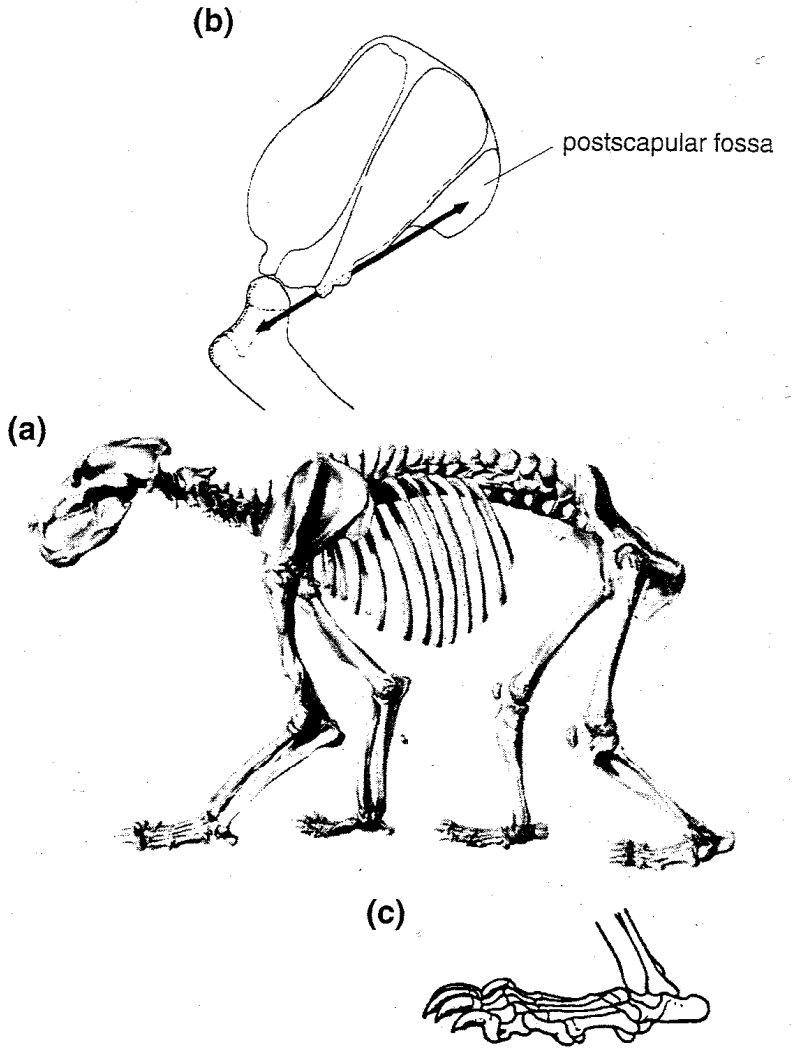


Figure 8.37. Aquatic locomotion in the sea otter, tracings of body, limb, and tail movements (from Tarasoff *et al.*, 1972).

11.3.6. Polar Bear

Modern polar bears are the largest bear species, although they are smaller than their Pleistocene ancestors. Males are larger than females. They possess 39-45 vertebrae as C7, T14-15, L5-6, S4-6, and C9-11. The neck muscles are especially well developed.

Polar bears have large plantigrade feet that aid in propulsion during swimming. They swim with a stroke like a crawl, pulling itself through the water with its forelimbs (which are large) while its hind legs trail behind. This is reflected in the development of a wide flange on the posterior margin of the scapula called the **postscapular fossa**. When raveling on land, huge paws help distribute their body weight while their footpads, covered with small soft papillae, increase friction between the feet and the ice. Terrestrial locomotion has been measured at 40 km/h.



Polar bear, *Ursus maritimus* (a) Skeleton, (b) Scapula with arrow showing line of action of subscapularis muscle, and (c) Plantigrade foot (from Ewer, 1973).

11.4. Buoyancy

Animals are denser than water, therefore tend to sink

Between 80 and 90% of the body volume of most marine organisms is made of water. If the weight of the body is less than the weight of the water it displaces, it experiences a net upward force. On the other hand, if the body weighs more than the volume of water it displaces, it will experience a net downward force. This force is **buoyancy**, and it can be expressed as:

$$B = Mg = (\rho_{body} - \rho_{water}) Vg$$

where B is buoyancy, M is body mass, g is the acceleration due to gravity (9.8 m sec^{-2}), ρ_{body} is the density of the body, ρ_{water} is the density of the water (seawater = 1024 kg m^{-3}), and V is the volume of the body.

Marine mammals are made of materials that, in general, are denser than water (e.g., bones, muscles). However, there are two major exceptions to this rule: their accumulated fat and their air-filled lungs. Since their need for breathing, marine mammals have to surface to breathe and rest there without effort.

To avoid sinking, marine mammals may try two strategies: (1) to reduce the amount of heavy material in their bodies (particularly bones); and, (2) increase the material that is less dense that water (fat, air-filled lungs).

Of these, marine mammals seem to rely mostly on accumulation of fat and their lungs to attain buoyancy. Fat has a density of 900 to 920 kg m^{-3}; incredibly enough, we lack hard data to substantiate this generalization.

Regarding lungs, we know that changing the air volume we can control buoyancy. The volume of some marine mammals is relatively large in comparison with those of terrestrial mammals. The sea otter, and animal that lacks a buoyant blubber layer, has the largest lung volume-to-body weight ratio of any marine mammal. It is twice than predicted for a terrestrial mammal of its body mass. This is particularly important for an animal that feeds while floating on the surface. Another strategy of the sea otter is to have air trapped in the dense, water-repellent fur.

This is an area in which we have not a clear picture of the adaptations achieved by different groups in relation to buoyancy. For example, sirenians and cetaceans diverge in bone density; yet, they both are the best adapted to the aquatic environment: while sirenians increase their bone density, cetaceans (and also some pinnipeds) have reduced it. Manatee lungs are also quite unique. Each is supplied with a single bronchus that runs virtually the entire length of each lung. Their very elongated and horizontally oriented lungs may serve as a buoyancy apparatus.

Regardless of the differences, it seems that increased lung volumes relative to terrestrial mammals, may function to decrease the energetic cost of floating at the surface.

Chapter 12

Respiration, Diving Physiology, and Breath Holding

12.1. Introduction

The respiratory system provides for the uptake of oxygen, and the disposal of carbon dioxide. Oxygen is drawn into the lungs by the process of respiration, and is carried via the blood to the tissues where it is used in the combustion reactions that transform food into energy within the cells. This process produces CO_2 and water that are released back into the blood. The CO_2 is delivered to the lungs and exhaled. Because oxygen requirements increase with increasing body size and because most marine mammals spend extended periods of time diving, marine mammals have extraordinary anatomical and physiological adaptations to increase oxygen storage. Experienced humans are able to hold their breath for up to six minutes without any adaptations other than training. Marine mammals, however, are able to do so for much longer periods of times at greater depths. Figures 1 and 2 summarize current knowledge of maximal depths and maximal duration of breath hold for marine mammals. This chapter describes the major adaptations among marine mammals to achieve these physiological feats.

Fig. 12.1. Known Maximal Depths Among Marine Mammals

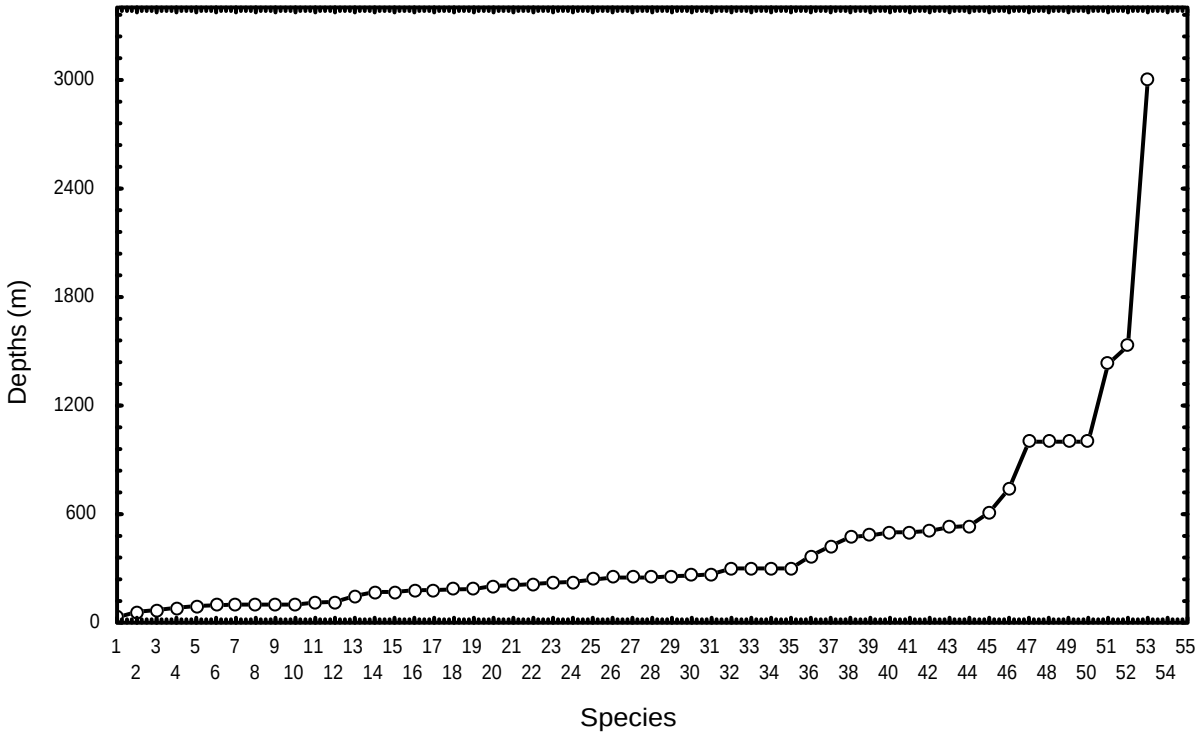


Fig. 12.2. Known Diving Times Among Marine Mammals

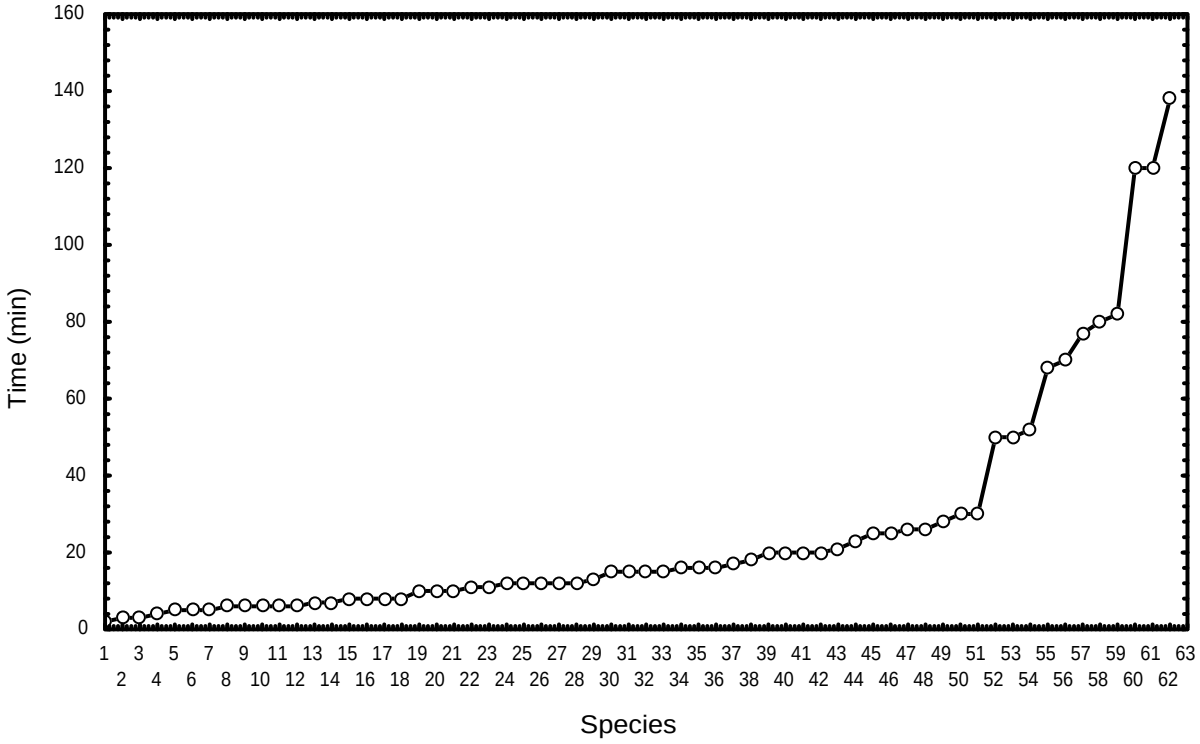


Figure 1. Known depths that can be reached by marine mammals (based on Slip et al. 1994, Schreer and Kovacs 1997, Hochachka and Mottishaw 1998). First number corresponds to the axis of the figure, followed by the common name, and scientific name (sometimes only the genus is known) followed by the depths (in m). 1. Vaquita (*Phocoena sinus*) 30; 2. Atlantic spotted dolphin (*Stenella frontalis*) 60; 3. Rough-toothed dolphin (*Steno bredanensis*) 70; 4. Guadalupe fur seal (*Arctocephalus townsendi*) 82; 5. Australian sea lion (*Neophoca cinerea*) 92; 6. Sea otter (*Enhydra lutris*) 97; 7. Blue whale (*Balaenoptera musculus*) 100; 8. Pantropical spotted dolphin (*Stenella attenuata*) 100; 9. Larga seal (*Phoca largha*) 100; 10. Walrus (*Odobenus rosmarus*) 100; 11. South American sea lion (*Otaria byronia*) 112; 12. Galapagos fur seal (*Arctocephalus galapagoensis*) 115; 13. Humpback whale (*Megaptera novaeangliae*) 148; 14. Gray whale (*Eschrichtius robustus*) 170; 15. South American fur seal (*Arctocephalus australis*) 170; 16. Dall's porpoise (*Phocoenoides dalli*) 180; 17. Antarctic fur seal (*Arctocephalus gazella*) 181; 18. Right whale (*Eubalaena* sp.) 184; 19. Galapagos sea lion (*Zalophus californianus wollebaeki*) 186; 20. South African fur seal (*Arctocephalus pusillus*) 204; 21. Northern fur seal (*Callorhinus ursinus*) 207; 22. Pacific white-sided dolphin (*Lagenorhynchus obliquidens*) 214; 23. Ringed seal (*Phoca hispida*) 222; 24. Harbor porpoise (*Phocoena phocoena*) 226; 25. New Zealand fur seal *(Arctocephalus forsteri*) 238; 26. Northern right whale dolphin (*Lissodelphis borealis*) 250; 27. Spinner dolphin (*Stenella longirostris*) 250; 28. Bearded seal (*Erignathus barbatus*) 250; 29. Common dolphin (*Delphinus delphis*) 258; 30. Killer whale (*Orcinus orca*) 260; 31. Gray seal (*Halichoerus grypus*) 268; 32. Dwarf sperm whale (*Kogia simus*) 300; 33. Southern right whale dolphin (*Lissodelphis peronii*) 300; 34. Bowhead whale (*Balaena mysticetus*) 300; 35. False killer whale (*Pseudorca crassidens*) 300; 36. Harp seal (*Phoca groenlandica*) 370; 37. Steller sea lion (*Eumetopias jubatus*) 424; 38. Hooker's sea lion (*Phocarctos hookeri*) 474; 39. California sea lion (*Zalophus californianus californianus*) 482; 40. Fraser's dolphin (*Lagenodelphis hosei*) 500; 41. Fin whale (*Balaenoptera physalus*) 500; 42. Harbor seal (*Phoca vitulina*) 508; 43. Crabeater seal (*Lobodon carcinopohagus*) 528; 44. Bottlenose dolphin (*Tursiops truncatus*) 535; 45. Pilot whale (*Globicephala* sp.) 610; 46. Weddell seal (*Leptonychotes weddellii*) 741; 47. Beluga (*Delphinapterus leucas*) 1000; 48. Hooded seal male and female (*Cystophora cristata*) 1000; 49. Bottlenose whale (*Hyperoodon* sp.) 1000; 50. Narwhal (*Monodon monoceros*) 1000; 51. Southern elephant seal (*Mirounga leonina*) 1430; 52. Northern elephant seal (*Mirounga angustirostris*) 1530; 53. Sperm whale (*Physeter macrocephalus*) 3000.

Figure 2. Known maximum duration of breath holding by marine mammals (based on Slip et al. 1994, Schreer and Kovacs 1997, Hochachka and Mottishaw 1998). First number corresponds to the axis of the figure, followed by the common name, and scientific name (sometimes only the genus is known) followed by the time of breath holding (in min). 1. Baiji (*Lipotes vexillifer*) 2; 2. Ganges River dolphin (*Platanista gangetica*) 3; 3. Spinner dolphin (*Stenella longirostris*) 3; 4. Sea Otter (*Enhydra lutris*) 4; 5. Atlantic spotted dolphin (*Stenella frontalis*) 5; 6. Common dolphin (*Delphinus delphis*) 5; 7. Pantropical spotted dolphin (*Stenella attenuata*) 5; 8. Pacific white-sided dolphin (*Lagenorhynchus obliquidens*) 6; 9. Northern right whale dolphin (*Lissodelphis borealis*) 6; 10. South American sea lion (*Otaria byronia*) 6; 11. Australian sea lion (*Neophoca cinerea*) 6; 12. Galapagos sea lion (*Zalophus californianus wollebaeki*) 6; 13. Southern right whale dolphin (*Lissodelphis peronii*) 7; 14. South American fur seal (*Arctocephalus australis*) 7; 15. South African fur seal (*Arctocephalus pusillus*) 8; 16. Northern fur seal _ (*Callorhinus ursinus*) 8; 17.Galapagos fur seal (*Arctocephalus galapagoensis*) 8; 18. Dugong (*Dugong dugon*) 8; 19. Larga seal (*Phoca largha*) 10; 20. Antarctic fur seal (*Arctocephalus gazella*) 10; 21. Ross seal (*Omimatophoca rossii*) 10; 22. New Zealand fur seal *(Arctocephalus forsteri*) 11; 23. Crabeater seal (*Lobodon carcinopohagus*) 11; 24. Irrawaddy dolphin (*Orcaella brevirostris*). 12; 25. Pygmy sperm whale (*Kogia breviceps*) 12; 26. Bottlenose dolphin (*Tursiops truncatus*) 12; 27. Hooker's sea lion (*Phocarctos hookeri*) 12; 28. Hawaiian monk seal (*Monachus schauinslandi*) 12; 29. Harbor porpoise (*Phocoena phocoena*) 12; 30. Walrus _ (*Odobenus rosmarus*) 13; 31. Killer whale (*Orcinus orca*) 15; 32. Sei whale (*Balaenoptera borealis*) 15; 33. Rough-toothed dolphin (*Steno bredanensis*) 15; 34. California sea lion (*Zalophus californianus californianus*) 15; 35. Harp seal (*Phoca groenlandica*) 16; 36. Steller sea lion (*Eumetopias jubatus*) 16; 37. West Indian manatee (*Trichechus manatus*) 16; 38. Minke whale (*Balaenoptera acutorostrata*) 17; 39. Guadalupe fur seal (*Arctocephalus townsendi*) 18; 40. Bryde's whale (*Balaenoptera edeni*) 20; 41. Pilot whale (*Globicephala* sp.) 20; 42. Narwhal (*Monodon monoceros*) 20; 43. Bearded seal (*Erignathus barbatus*) 20; 44. Humpback whale (*Megaptera novaeangliae*) 21; 45. Gray seal (*Halichoerus grypus*) 23; 46. Beluga (*Delphinapterus leucas*) 25; 47. Gray whale (*Eschrichtius robustus*) 26; 48. Ringed seal (*Phoca hispida*) 26; 49. Harbor seal (*Phoca vitulina*) 28; 50. Fin whale (*Balaenoptera physalus*) 30; 51. Cuvier's beaked whale (*Ziphius cavirostris*) 30; 52. Right whale (*Eubalaena* sp.) 50; 53. Blue whale (*Balaenoptera musculus*) 50; 54. Hooded seal (*Cystophora cristata*) 52; 55. Baikal seal (*Phoca sabrica*) 68; 56. Arnoux's beaked whale (*Berardius arnuxii*) 70; 57. Northern elephant seal (*Mirounga angustirostris*) 77; 58. Bowhead whale (*Balaena mysticetus*) 80; 59. Weddell seal (*Leptonychotes weddellii*) 82; 60. Southern elephant seal (*Mirounga leonina*) 120; 61. Bottlenose whale (*Hyperoodon* sp.) 120; 62. Sperm whale (*Physeter macrocephalus*) 138.

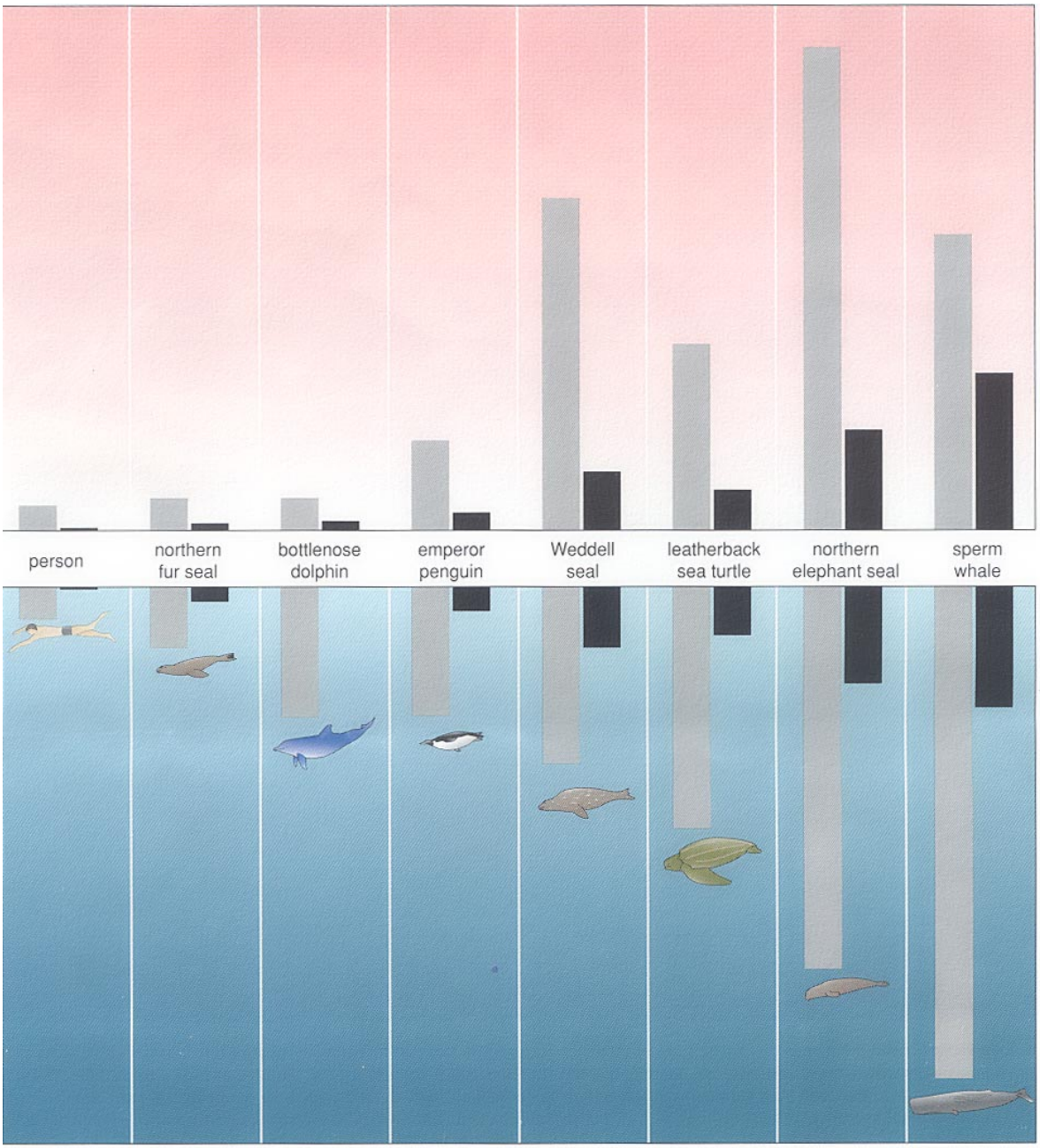


Figure 3. Marine divers are found in every ocean from the North Pole to the Antarctic and include mammals, birds and reptiles. Initial research into these divers focused on the length and depth of the dives. Such studies helped establish that the premier divers were the sperm whale and the northern elephant seal. The world record for a very exceptional human diver is included for comparison (from Kooyman and Ponganis 1997).

12.2. Anatomical Adaptations

12.2.1. The Respiratory System

The respiratory system serves two purposes: 1) to deliver air to a location in the body where gas exchange can occur, and 2) to produce vocalizations. The latter is true for most, but not all, mammals. The generalized mammalian respiratory system begins with the nostrils, or external nares, and the mouth. From these openings air travels into the pharynx, a short muscular tube that is partially shared by both the respiratory and digestive systems through which food preferentially travels to the esophagus and air to the larynx. The larynx is made up of a complex set of cartilaginous rings and muscles that protect the respiratory system from food and fluids and that house the vocal cords used for sound production.

From the larynx, air enters the trachea, which is reinforced with cartilaginous rings, and which terminates by bifurcating into the primary bronchi. From there, the airway continues to branch into cartilage-reinforced conducting tubes of decreasing diameter known as secondary bronchi. The smallest of these conducting tubes, the bronchioles, lack cartilaginous reinforcement, being reinforced instead by a few obliquely oriented muscle fibers. The bronchioles, in turn, lead to the sites of gas exchange, the thin-walled, membranous respiratory bronchioles, alveolar sacs, and alveoli. The conducting and respiratory tubes from the primary bronchi to the alveoli comprise the **bronchial tree**.

The alveoli expand and contract thousands of times per day during the process of respiration that is driven by the **diaphragm**. The alveoli also secrete **surfactant,** a mixture of lipoproteins that reduce the surface tension inside the alveoli. In terrestrial mammals the surfactant helps prevent the collapse of the alveoli. In marine mammals it may facilitate the reinflation of the lungs when the animal surfaces and resumes respiration.

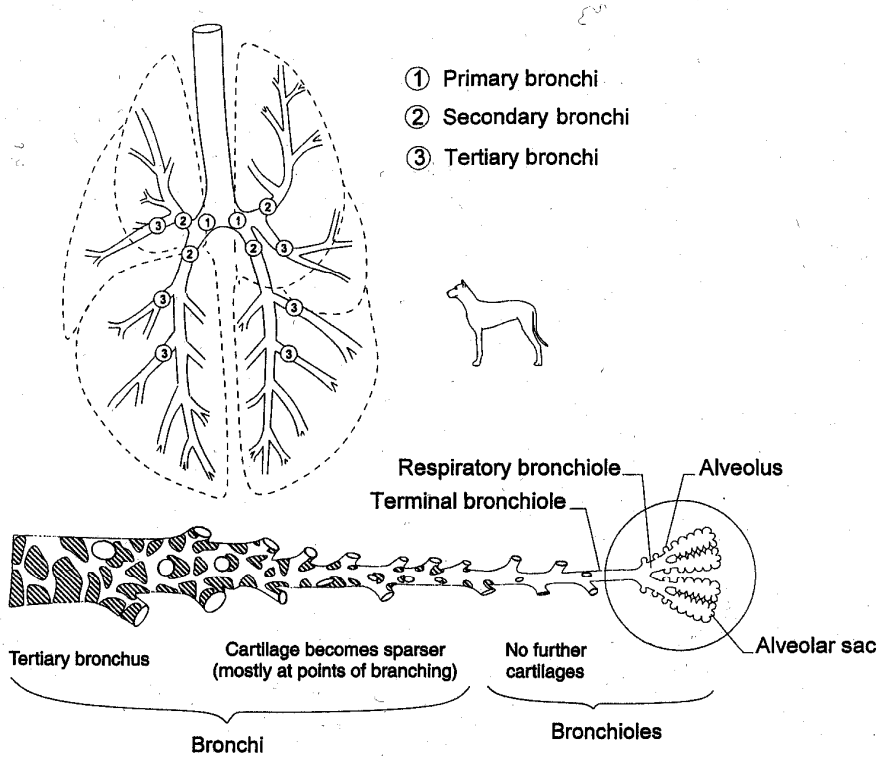


Figure 2-11. Lower respiratory tract of the dog. Air traveling from the larynx enters the cartilage-reinforced trachea. The trachea bifurcates into primary bronchi that enter the lungs. The bronchi continue to branch into the small bronchioles, which lack cartilaginous reinforcement. Bronchioles lead to sites of gas exchange, the respiratory bronchioles and alveoli. (Illustrations adapted from Schummer et al. 1979, Evans 1993.)

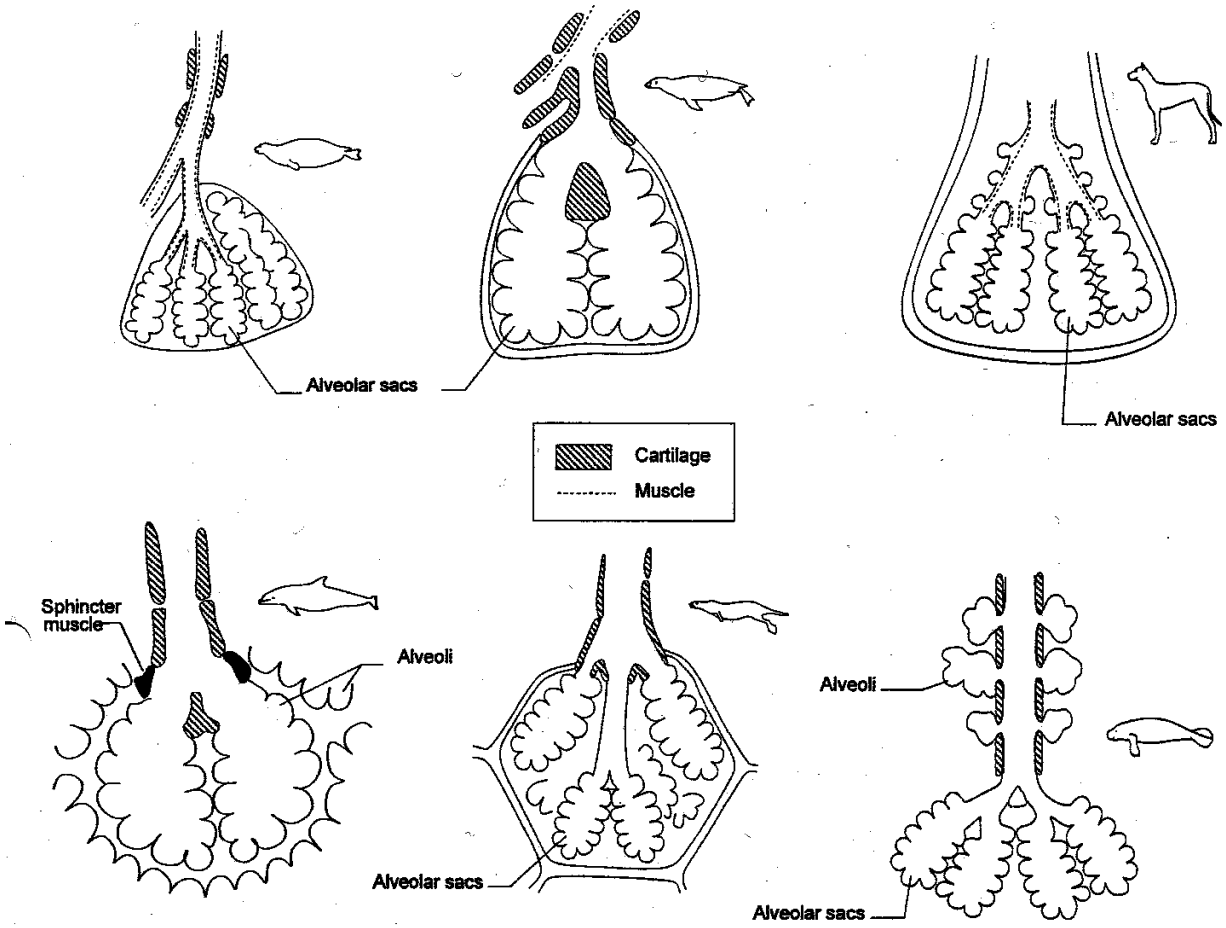


Figure 2-15. Morphology of the terminal airways and alveoli in the lungs of different mammals. The terminal airway of the "typical" mammal is not reinforced with cartilage and can collapse under pressure, trapping air in the alveoli during a dive. The terminal airways of all marine mammals investigated thus far are reinforced with cartilage or thickened muscle (stippled line). When alveoli in the marine mammal lung collapse, air is forced into the reinforced upper airways of the bronchial tree; nitrogen is isolated from the site of gas exchange, and the danger of the bends is avoided. (Illustrations adapted from Belanger 1940, Engel 1962, Denison and Kooyman 1973, Schummer et al. 1979, Drabek and Kooyman 1983, Bergey 1986, Evans 1993.)

Cetaceans

With the exception of sperm whales and bottlenose whales, the diving capabilities of cetaceans are generally not as advanced as those of the phocids[25]. Most cetaceans obtain their food from the photic zone (within 50-100 m of the surface), and thus have less need for deep diving.

[25]Most beaked whales have not been investigated in this regard.

A major respiratory feature among cetaceans is the presence of one or two **blowholes**. The blowhole is situated on top of the head. Odontocetes have one visible blowhole while mysticetes have two. Among odontocetes, the blowhole is somewhat to the left of the dorsal midline. All mysticetes have two nasal passages that correspond to the blowholes. In odontocetes (with the exception of the physeterids), the single nasal passage (vestibule) extends vertically to the bony nares. Occluding the bony nares of cetaceans is a pair of large fleshy masses of tissue, the **nasal plugs**, which consist of connective tissue, muscle, and fat. The nasal plugs of mysticetes contain less fatty tissue but are otherwise similar in general morphology to those of the odontocetes. Paired muscles that originate from the premaxillae retract the nasal plugs. Contraction of the muscles pulls the nasal plugs anterolaterally. When the nasal plugs are retracted during inhalation and exhalation, the nasal passage remains fully open. The neutral posture of the nasal plug is closed and that happens when the nasal plug muscles are relaxed. In addition to this respiratory function, it also has been suggested that nasal plugs function in sound production. The skull of odontocetes is bilaterally asymmetrical near the nares, and it supports a round, fatty organ called the **melon** (see Chapter 17).

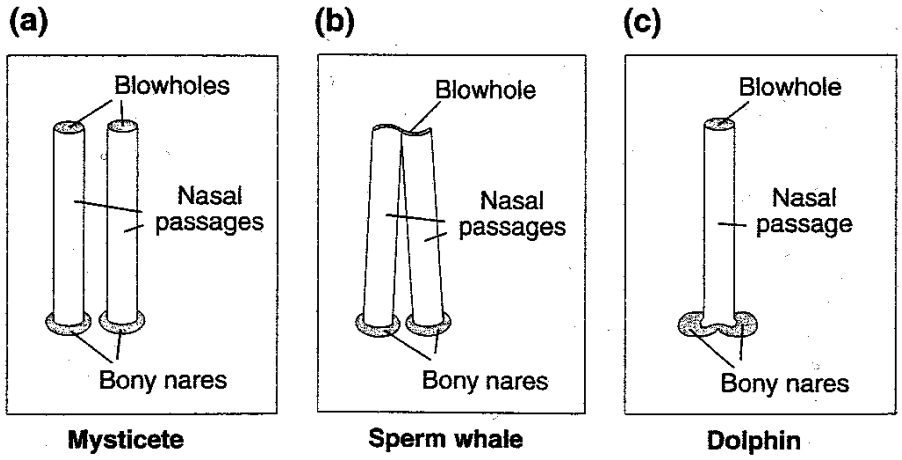
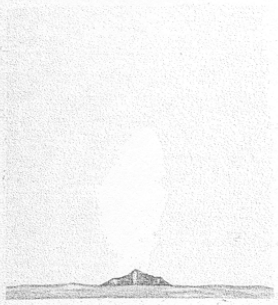


Figure 4.18. Alternate interpretation for homology of the blowholes in whales (modified from Milinkovitch, 1995). According to Milinkovitch's interpretation: Ancestral condition (two nasal passages) (a) present in mysticetes and sperm whales (b) with derived state (single nasal passage) seen in other toothed whales (c). Alternate interpretation: Ancestral condition (a) with two derived conditions (b) and (c).

A series of blind-ended sacs (**air sacs**) branch off from the nasal passages. The nasal air spaces are variable, both within a single species and between species. The musculature associated with the nasal passages is extremely complex. Sperm whales are unique among odontocetes in the retention of two nasal passages. The left nasal passage extends posteroventrally in nearly a straight line to the enlarged left bony naris and lacks air sacs. The right nasal passage extends ventrally from the blowhole and expands into the air sac (vestibular air sac). On the posterior wall of this sac is a muscular ridge with a narrow slit-like orifice that

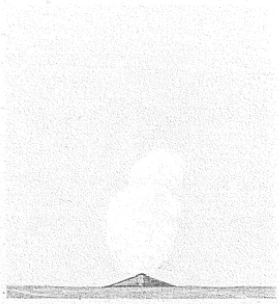
opens to the right nasal passage. The gross appearance of this valve-like structure gives it the name **museau de singe**, or **monkey's lips (or muscle)**. Just superficial to the bony naris, there is another air sac off the right nasal passage.

Distinctive whale blows (head-on view)



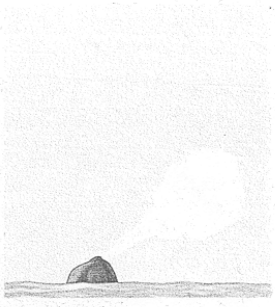
BRYDE'S WHALE

The thin, hazy blow produced by Bryde's whale is variable in height, although, typically, it rises to about 10–13 feet (3–4 m); it is rarely distinctive from a distance, especially if the whale begins to exhale before breaking the surface.



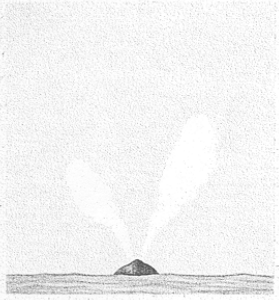
SEI WHALE

Sometimes described as shaped like an inverted cone, or a pear, the sei whale's blow appears as a single, narrow cloud; it resembles the blows of fin and blue whales, but reaches a height of only about 10 feet (3 m). It is also not as dense.



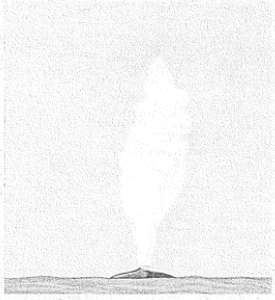
SPERM WHALE

The sperm whale's unique, angled blow is extremely distinctive, especially on windless days, and projects to a height of 6½ feet (2 m) or more. Since the blowhole is on the extreme left-hand side of the forehead, the blow is projected forward and to its left.



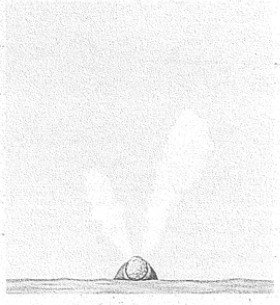
BOWHEAD WHALE

With two widely separated blowholes, the bowhead whale produces a rather bushy, V-shaped blow; the two diverging clouds of spray rise directly upward to a height of about 23 feet (7 m).



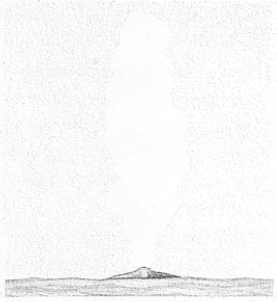
FIN WHALE

The fin whale's strong, straight blow appears as a tall, narrow column of spray; it is usually 13–20 feet (4–6 m) high, and can be seen from a considerable distance.



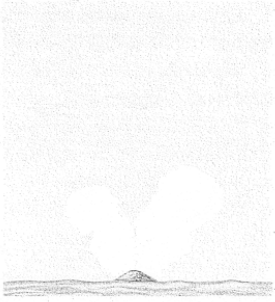
RIGHT WHALES

The right whale produces a distinctive V-shaped blow, having widely separated blowholes like the bowhead. The plumes rise to a maximum height of about 16½ feet (5 m).



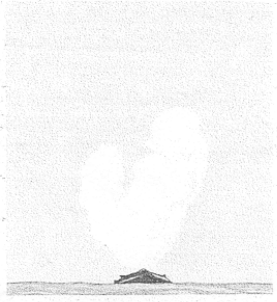
BLUE WHALE

Blowing as soon as its head begins to break the surface, the blue whale produces a spectacular column of spray rising to 29½ feet (9 m) or more. The tallest and strongest blow of all whales, it is noticeably slender and upright.



GRAY WHALE

The gray whale's bushy blow is normally described as V-shaped, but sometimes the two plumes meet in the middle and produce a distinctive heart shape; they normally rise to a height of 10–15 feet (3–4.5 m).



HUMPBACK WHALE

Rising to a height of about 8–10 feet (2.5–3 m), the single bushy blow of the humpback whale is surprisingly visible and distinctive; it is usually wide relative to its height, and can occasionally be clearly V-shaped from a distance.

In most terrestrial mammals, the larynx is located cranially and dorsally in the neck. The epiglottis in the breathing position contacts the soft palate and effectively separates the digestive and respiratory passages. This intranarial position of the epiglottis changes during swallowing: the larynx is raised and the epiglottis folds over the entrance to the trachea to protect the respiratory system from food or fluids being swallowed. Thus, terrestrial mammals can swallow fluids that enter their oral cavities without choking.

A unique arrangement of the larynx allows odontocetes to swallow, breathe, and echolocate at the same time. The odontocete larynx is the most specialized of all marine mammals. The epiglottis and corniculate cartilages form an elongated structure that resembles a goose-beak. These cartilages fit rigidly into the elongate nasal passage. The palatopharyngeal sphincter muscle keeps the goose beak firmly sealed in an intranarial position. Wide lateral channels in the esophagus allow food to pass around the larynx during swallowing, and the sphincter muscles ensure that no food or fluids enter the respiratory system. The structure and internal position of the larynx effectively separates the respiratory tract from the digestive tract to a greater extent than that found among other mammals.

The lungs of cetaceans are not lobulated, as in terrestrial mammals, and they are asymmetrical, with the right side larger. This asymmetry is related to the asymmetrical position of the heart. The lungs are also turgidly elastic and the pleura are unusually thick and well vascularized. There is a well-defined lung-associated lymph node.

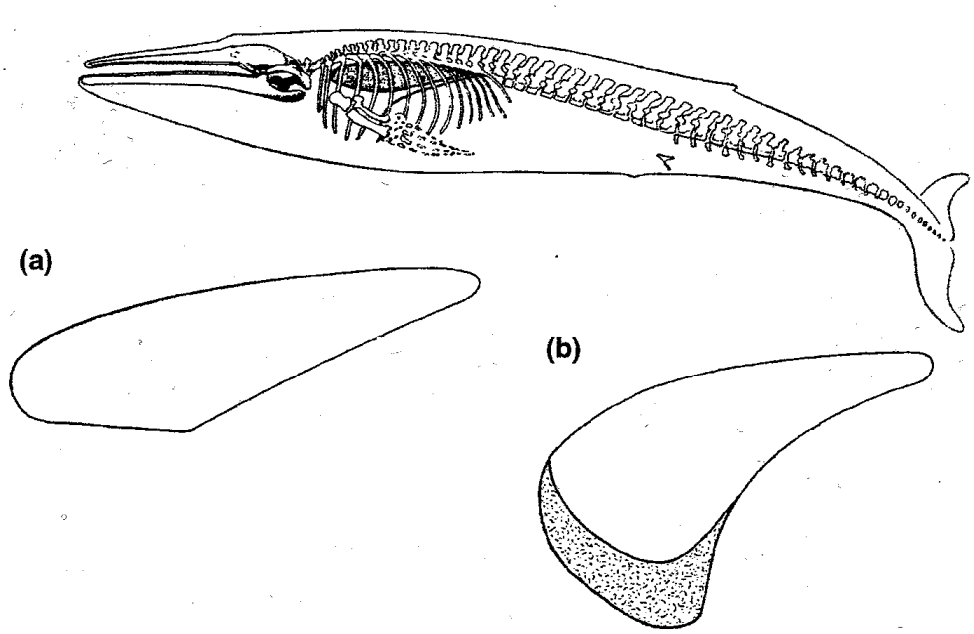


Figure 9.7. Diagram showing position of the cetacean lung and comparison of (a) mysticete (fin whale) and (b) odontocete (bottlenose dolphin) lung on right. Stippled area indicates particularly thin section of lung (from Slijper, 1979).

Upon surfacing, cetaceans exhale and then inhale in one single rapid cycle. They can exchange 90% of the air in their lungs in a single breath. This is the **vital capacity**. Lung

capacity of cetaceans is lower than for terrestrial mammals, when expressed as a proportion of total body size. This means that it is the oxygen storage capability rather than lung volume that enables whales to remain submerged for extended periods of time. When a whale comes to the surface to breathe, air is expelled from the blowhole. The water contained within the exhaled air condenses, and mixes with water on the back of the whale, creating a cloud of mist above the ocean surface. It was this cloud that enabled whalers to spot whales and led to the famous "Thar she blows!" The double blowhole of the baleen whale creates a characteristic v-shaped spout, and that of the toothed whale a single spout pointed diagonally forward. The shape, direction, and height of this condensation, known as the spout, varies among the baleen and toothed whales, and can be used to identify some species of whales from a distance. The vapor formed by contact between air heated in the lungs and the cold external air contains an emulsion of fine oil droplets arising from cells lining the air sinuses, mucus from the tracheal glands, and surfactant from the lungs. The blow leaves a greasy film on the water after a whale has surfaced.

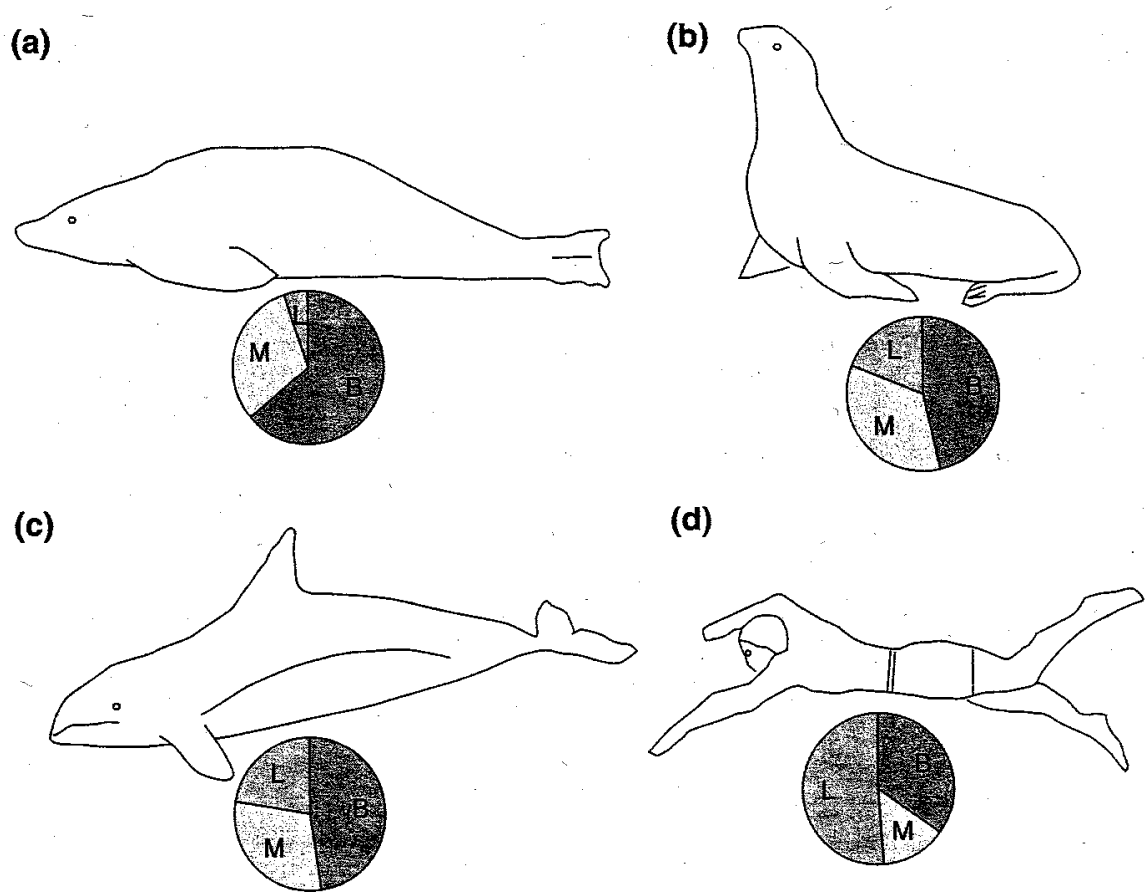


Figure 9.3. Generalized comparison of relative blood (B), muscle (M), and lung (L) oxygen stores for (a) phocids, (b) otariids, (c) odontocetes, and (d) humans (after Kooyman, 1985).

It has been debated whether whales dive at full or partial lung capacity (Ridgeway, 1986). Lung volume may have to do more with buoyancy than with oxygen supply. Seals and odontocetes have flexible rib cages that are easily deformed. Lungs can collapse during the first 10-100 m for most marine mammals, thus eliminating the problem of buoyancy created by lungs. Most of the air is squeezed into alveoli, bronchi, and trachea (whose cartilages are very flexible and may even collapse during very deep dives). This also helps them to avoid decompression sickness since very little gas is forced into the tissues by the high pressure.

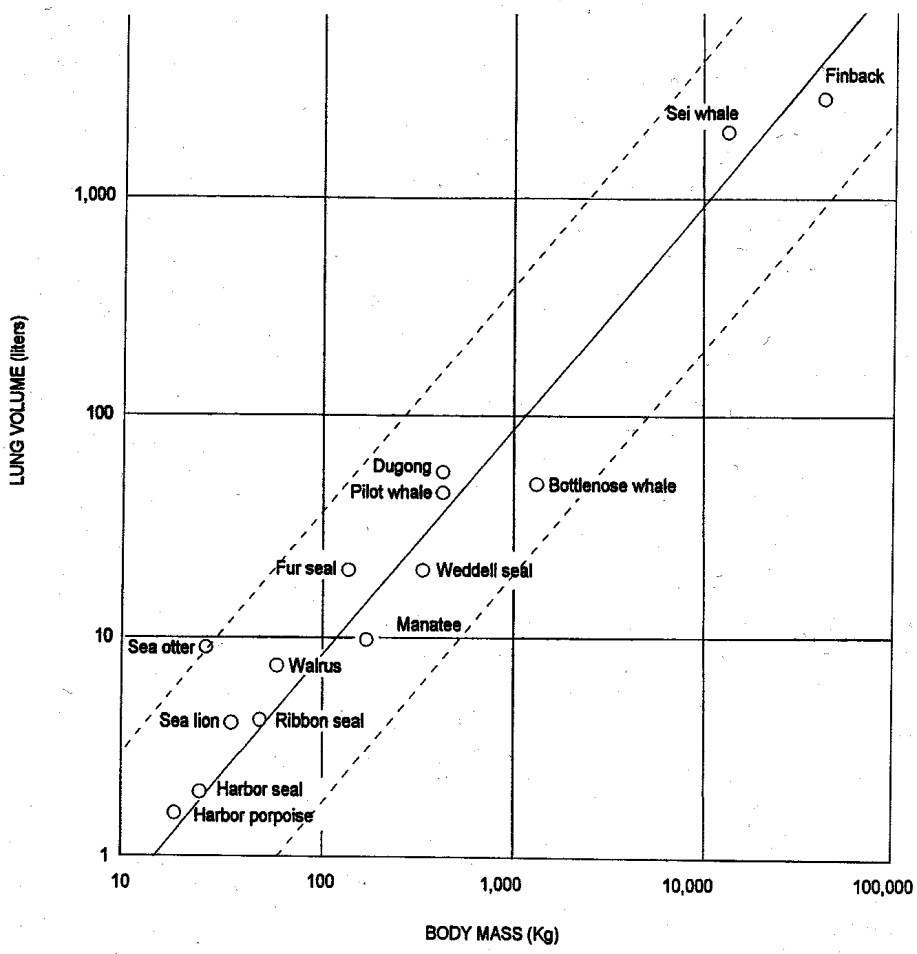


Figure 2-12. Graph of lung volume (in liters) to body mass (in kilograms) for a variety of marine mammals. The solid line is a best-fit regression for a variety of mammals (Tenney and Remmers 1963). The slope of this line is very close to 1, illustrating that most mammals tend to maintain similar relative lung volumes (approximately 5% of their total body volume) no matter their body size (Schmidt-Nielsen 1990). A number of marine mammals fall off the line (data from Kooyman 1973). Most notably, the sea otter, a shallow-diving mammal that spends much of its time floating at the sea surface, has a lung volume twice that predicted for a mammal of its size. The upper dotted line represents twice the values on the solid line; the lower dotted line represents half of the values on the solid line. Contrarily, the lung volumes of the Weddell seal and bottlenose whales, both deep and prolonged divers, are less than would be predicted.

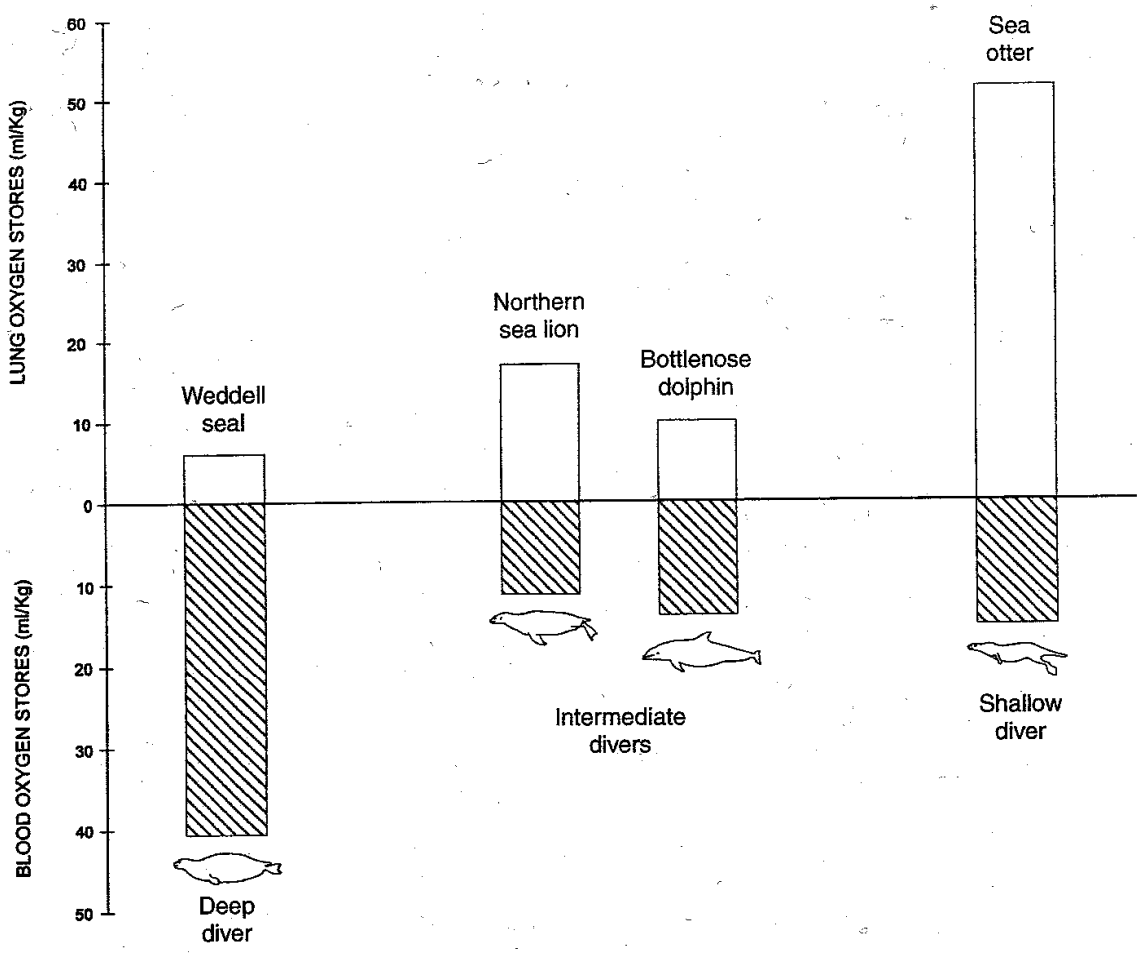


Figure 2-14. Lung versus blood oxygen stores in shallow- and deep-diving mammals. In deeper and longer divers, the lung is a less important oxygen reserve. (Illustration adapted from Kooyman 1973.)

Pinnipeds

The nares of pinnipeds are relatively simple in most species, but they are enlarged, forming an inflatable hood on top of the head, in adult male hooded seals. The hood reaches its maximum size in sexually mature bulls that use it for courtship display. Likewise, the nose of the elephant seal is highly developed among adult males for dominance displays. The most specialized feature of the pinniped nostrils is that their neutral position appears to be closed. For example, northern elephant seals undergo sleep apnea on land with their nostrils closed.

The elongated thorax of pinnipeds stretches the diaphragm into a decidedly oblique orientation. The lungs of pinnipeds show reduction in lobulation. The lungs of some species

(e.g., ribbon seal) are made firm by microscopic cartilaginous coils that surround the airways, resulting in a lumpy texture. The cardiovascular system is specialized for diving; one obvious adaptation is the immense hepatic sinus, an enlargement of the vena cava that, when constricted by a sphincter at the diaphragm, acts as a reservoir of oxygenated blood during a dive. Pinnipeds breathe vigorously and frequently during the recovery phase after diving and exhale to about 50% of total lung capacity prior to diving.

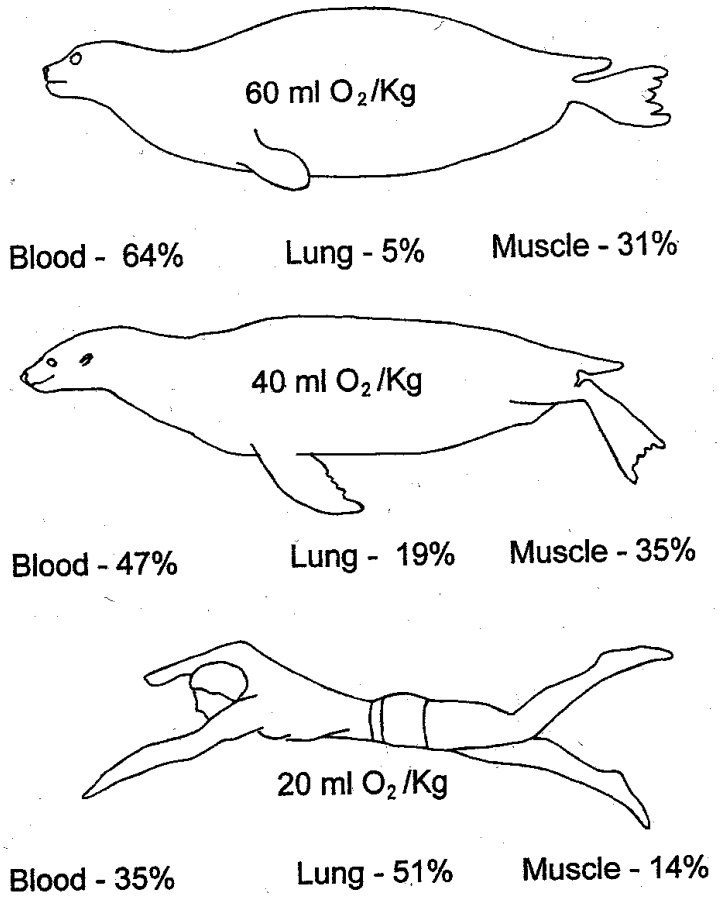


Figure 2-13. Relative oxygen stores in mammals. The deep-diving Weddell seal (top) carries more than 95% of its oxygen reserves in blood and muscle. A fur seal (middle), a shorter duration diver, also carries the majority of its oxygen reserves in blood and muscle, but relies more on the lungs stores than does the seal. The human relies most heavily on the lung as an important oxygen reserve. Note the differences in total oxygen stored per kilogram of body mass between these mammals. (Illustration adapted from Kooyman 1985.)

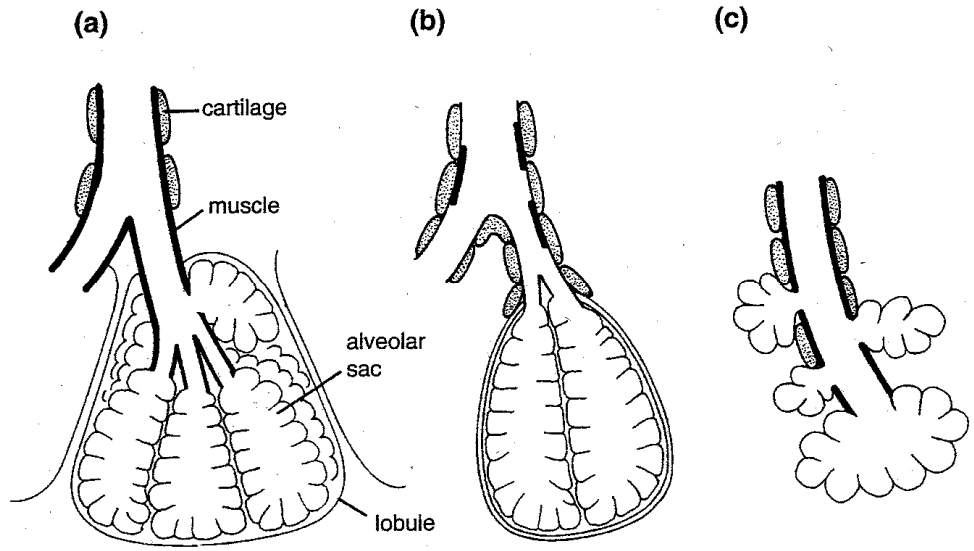


Figure 9.6. Diagram of the structure of alveoli and associated cartilage and muscle in pinnipeds (a) phocid, (b) otariid, and (c) odobenid (from King, 1983).

Sirenians

The sirenians breathe through a pair of two-valve semicircular nostrils situated at the tip of the rostrum. The pharynx and larynx conduct the air to a relatively short trachea. The trachea of the dugong is shorter and less well supported by cartilaginous rings than the trachea of the manatee. The lungs of the sirenians are dorsally located in the thoracic cavity, which extends posteriorly due to an oblique diaphragm. This dorsal location makes the sirenians susceptible to pneumothorax if boats hit them. The bronchial tree of sirenians is similar to that of other mammals, with the exception that the respiratory vesicles originate along the length of the bronchioles, and not just from their ends. The bronchioles are very muscular, and possess cartilaginous rings. Manatees exhale after surfacing and like cetaceans they have a vital capacity of about 90%, while humans have a vital capacity of only 10% and other terrestrial mammals about 10-20%).

12.2.2. Physiological Adaptations

12.2.2.1. Oxygen Storage

During a breath-hold dive, the oxygen stored in the blood and other tissues is depleted, resulting in an oxygen deficiency, or **hypoxia**, in the animal's tissues. The higher the intensity of muscular activity during a dive, the faster the oxygen will be depleted. Once the oxygen is depleted, skeletal muscle continues to operate under **anaerobic conditions**, producing CO_2 and

lactic acid. Both CO_2 and lactic acid accumulate in the blood and muscle tissue, resulting in a condition called **acidosis**. Continued anaerobic muscle activity causes the accumulation of even more lactic acid. The brain and heart cannot tolerate hypoxia, and blood circulation continues into these organs, although much reduced, during a dive.

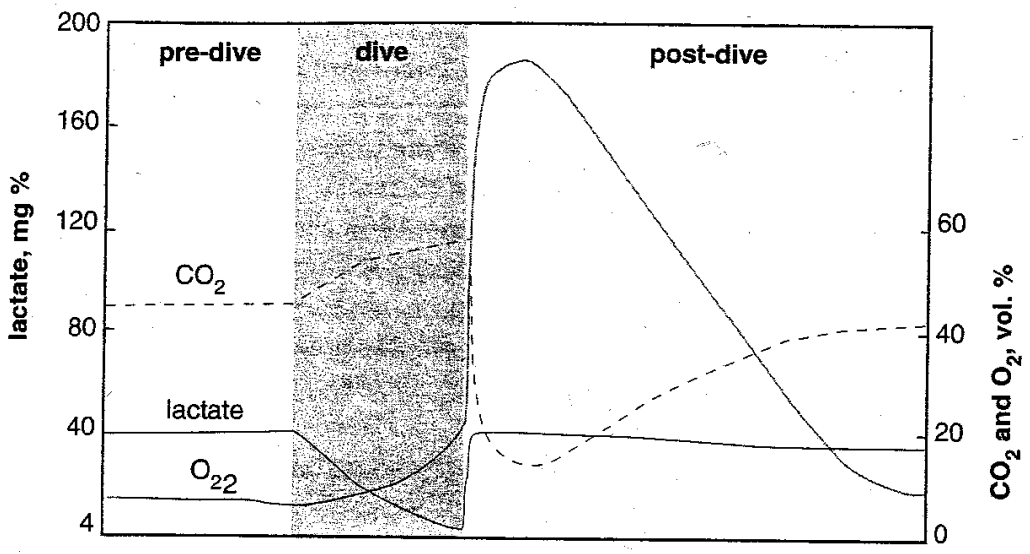


Figure 9.11. Monitored changes in arterial blood lactate, O_2 and CO_2 before, during, and immediately following an 18 min. forced immersion by a 42 kg gray seal (redrawn from Scholander, 1940).

Vertebrates store oxygen in the respiratory system, blood, and muscles. Therefore, diving lung volume, blood volume, hemoglobin concentration, myoglobin concentration, and muscle mass are factors involved in the adaptations for diving among marine mammals. The storage of oxygen in the lungs seems to be of secondary importance for deep divers. Seals, for example, exhale before diving. Oxygen storage in the lungs among seals and the deep diving sperm whale is small. Among deep divers 80 to 90% of the oxygen is stored in blood and muscles (Table 12.2).

	total oxygen (milliliters per kilogram of body weight)	percent of total		
		lungs	blood	muscle
people	20	24	57	15
California sea lion	40	21	45	34
bottlenose dolphin	36	34	27	39
emperor penguin	55	19	34	47
Weddell seal	87	5	66	29
leatherback sea turtle	18	26	63	11

Figure 7. Magnitude and distribution of oxygen in the various stores varies among species. For each species shown here, the total oxygen store is given, as well as the concentration typically held in each of the three stores—lungs, blood and muscle. People maintain a lower supply of total-body oxygen than do most of the diving animals. In addition, the largest oxygen stores for people are the lungs and blood, whereas the blood and muscle are the primary stores in most diving animals.

The total blood volume of some marine mammals can be up to 2-3 times greater than in non-diving mammals. Large blood volumes are especially typical of deep-diving phocids. Such large blood volumes are achieved by expanding the circulatory system with specialized reservoirs such as the thoracic rete in cetaceans and the hepatic venous sinus in pinnipeds (Pfeiffer and Kinkead, 1990). These structures can be used for storing blood until it is needed, or for rerouting it elsewhere. Pumping this large volume of blood necessitates increasing the size of the heart and its reservoir of glycogen (a carbohydrate used for energy production). Deep, pelagic divers, such as the Dall's porpoise, tend to have a larger heart when compared with inshore species such as the bottlenose dolphin (Ridgeway and Johnston, 1966). Greater amounts of stored glycogen have been reported for the bowhead whale heart (Pfeiffer, 1990) and the phocids (Pfeiffer and Viers, 1995).

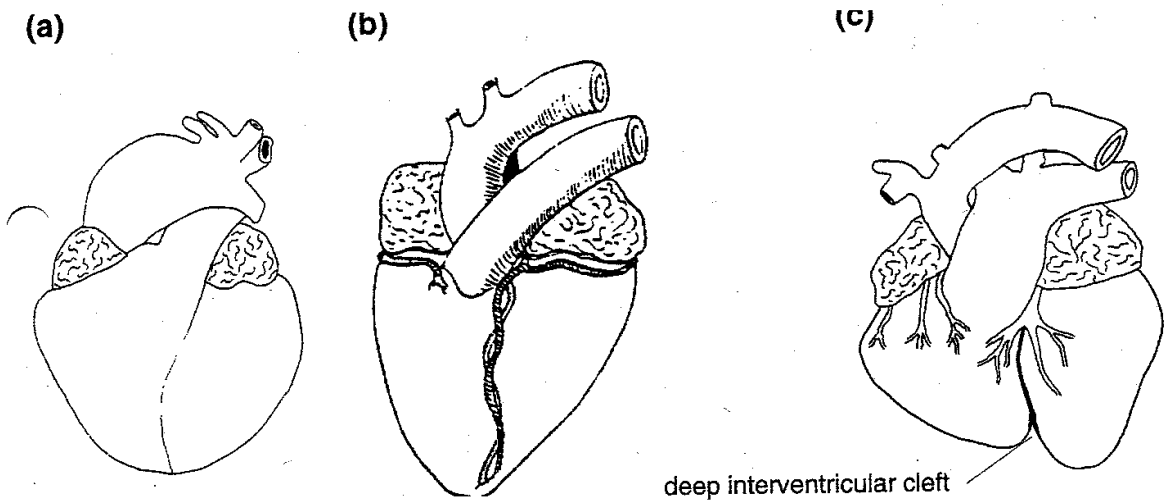


Figure 9.1. Ventral view of heart of (a) pinniped (Weddell seal) (modified from Drabek, 1977), (b) cetacean (porpoise) (modified from Slijper, 1979), and (c) sirenian (dugong) (modified from Rowlatt and Marsh, 1985).

Increasing the diameter and number of branches of the blood vessels enhances oxygen delivery to the tissues. For example, the ascending aorta in pinnipeds and whales increases in diameter immediately after leaving the heart to form an expanded elastic aortic bulb (King, 1977; Melnikov, 1997). This feature is common among pinnipeds and is correlated with the diving habits of the species (the deeper they dive, the larger the aortic bulb). The spleen acts as a blood reservoir, storing oxygen-rich red blood cells until needed during a dive. It tends to be larger among pinnipeds, up to 4.5% of the body weight (Hochachka and Mottishaw, 1998). However, when compared with terrestrial mammals, cetaceans have a rather small spleen.

The oxygen content of the blood itself is increased by an increase in the hematocrit, or percentage of the blood volume occupied by red blood cells. This is accomplished either by increasing the number of cells, or by increasing the size of the cells. This has the consequence of increasing the concentration of **hemoglobin**, the oxygen-carrying protein in the blood. The blood of marine mammals is dark red in color due to the high levels of iron associated with this protein. Hemoglobin also acts as a protein buffer, helping to increase the tolerance to lactic acidosis.

Oxygen is stored in the skeletal muscles, bound to **Myoglobin.** The concentration of this oxygen binding protein is very high in the skeletal muscles used for swimming. Myoglobin has a higher affinity for oxygen than hemoglobin and thus oxygen leaves the circulation and enters the muscle cells. The amount of myoglobin in the muscles of marine mammals can be from 3 to 10 times higher than that for terrestrial mammals (Kooyman and Ponganis, 1997). Because myoglobin also contains iron, the muscles of marine mammals also look very dark red (Butler and Jones, 1997).

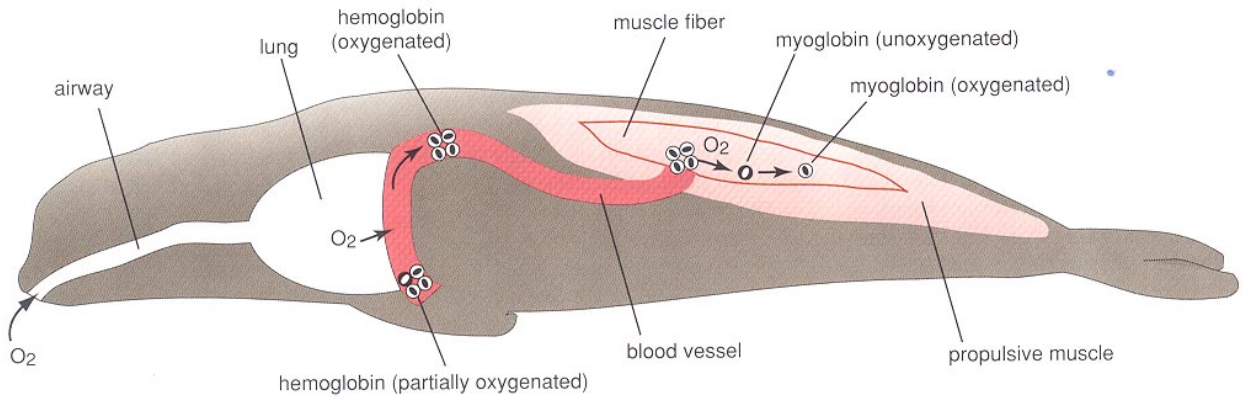


Figure 4. It is crucial that each organ and cell receive sufficient quantities of oxygen. With each breath, an animal takes in oxygen along with nitrogen and other gases in the air. In the seal shown here, as in other animals, oxygen travels down the airway into the lungs and there diffuses into the blood. Once in the blood, it binds to the protein hemoglobin, which carries the oxygen to all of the tissues and organs in the body. In muscle cells, the oxygen is transferred from hemoglobin to a related oxygen-carrying protein called myoglobin. The three largest reservoirs for oxygen are the lungs, blood and muscles, and the distribution of oxygen among these stores is important for diving animals. Diving animals have 3 to 10 times more myoglobin in their muscles than do their terrestrial counterparts, enabling divers to store more oxygen in their muscles than do other animals. A potential consequence of this is that the oxygen in the blood can be used by organs that do not store oxygen, most notably the brain. Still other organs may practically cease operation, so as not to use up oxygen. The abdomens of diving penguins have been found to drop in temperature during a dive, suggesting a slowdown in metabolic activity.

Table 12.2. Magnitude and distribution of oxygen among some cetaceans and pinnipeds and compared to humans (from Kooyman, 2002).

Species	Body mass (kg)	Total body oxygen stores (ml O_2 kg $^{-1}$)	Respiratory (%)	Blood (%)	Muscle (%)
H. sapiens	70	20	24	57	15
P. macrocephalus	10000	77	10	58	34
T. truncatus	200	36	34	27	39
L. weddellii	400	87	5	66	29
Z. californianus	100	40	21	45	

The proportion of myoglobin increases with age and is larger among pelagic species (Dolar et al., 1999). An added advantage of having high levels of myoglobin is that this protein has a high buffering capacity, i.e. the ability to hold tissue pH constant in the face of an increasing amount of acidic byproducts created by anaerobic metabolism. This reflects the capacity of marine mammals to tolerate both hypoxia and metabolic acidosis.

12.3 Dealing with Pressure

While diving, marine mammals have to deal not only with lack of oxygen but also with increased pressure. Pressure increases rapidly in the water column. At sea level it is 1 Kg/cm^2 (1 atmosphere or atm) on average. With every 10 m in water depth, that pressure increases 1 Kg/cm^2. Thus, a sperm whale diving at 3000 m experiences 301 atm of pressure. There are three major consequences of deep diving: a) external water pressure can compress air-filled tissue spaces inside the animal, causing these to distort or collapse as the air they contain is compressed; b) increased gas absorption into the blood due to higher gas tensions in the compressed lungs. Oxygen can be toxic at high concentrations and nitrogen can have a narcotic effect on the central nervous system (CNS); c) dissolved gas tensions that may be higher than ambient pressure during ascent, resulting in the potential for gas bubble formation in blood and tissues during and immediately after ascent (**embolism**). Marine mammals deal with each one of these situations in different ways.

One way to avoid the compression of air-filled organs is by reducing the air content in those organs. Some seals, for example, exhale before diving. Another strategy is to have flexible rib cages that are easily deformed. Lungs collapse during the first 10-100 m of a dive for most marine mammals, thus eliminating the problem of lung buoyancy. However, makes these organs useless for oxygen storage purposes. Most of the air in the lungs is squeezed into the alveoli, bronchi, and trachea (whose cartilages are very flexible and may even collapse during very deep dives, see above). This has been confirmed for seals and odontocetes (Falke et al., 1985). The mechanism by which lungs are reinflated after extended periods of collapse remains a mystery, but is likely facilitated by the presence of surfactant (see above).

One mechanism that reduces the noxious effects of oxygen and nitrogen at pressure is **alveolar collapse**, during which air (consisting mostly of nitrogen and oxygen) is forced into the reinforced upper airways of the bronchial tree. In this way both gases are isolated from the site of gas exchange. The fact that this system of airway reinforcement is found only among diverse taxa of deep diving marine mammals is an interesting case of functional convergent evolution. The reinforcement of the airways does vary from species to species however. In seals, for example, the penultimate airways are reinforced with cartilage, whereas the terminal airways emptying into the alveoli are reinforced only with muscle. On the other hand, the terminal airways of sea lions and cetaceans are reinforced with cartilage all the way to the entrance to the alveoli. That extra reinforcement may represent an additional protection during the explosive expiratory phase of respiration in these fast-breathing mammals.

Another interesting and enigmatic feature of the cetacean bronchial tree is the presence of circular muscular and elastic sphincters at the entrance of the alveoli together with the loss of respiratory bronchioles and the reinforcement of peripheral airways. It has been hypothesized that the sphincters function to trap air in the alveoli and to regulate airflow from the alveoli during a dive. If air were trapped within the alveoli during a dive, the body may be exposed to nitrogen under pressure (Belanger, 1940). This interesting morphological feature is apparently unique to cetaceans and is not well understood.

Some extreme divers may use nitrogen to facilitate their diving capabilities. Adult female northern elephant seals dive for approximately 20 min to depths between 500 and 800 m,

with less than 3.5 min at the surface between dives, and repeat this pattern continuously for more than 2.5 months while at sea. Some have suggested that the elephant seals may use nitrogen as a narcotic during the dive to counteract the effects of high pressure on the nervous system. These extreme divers must have some mechanism for coping with nitrogen saturation, but to date, this is not understood.

Inhaled air increases its contact with the blood when the lungs and the thoracic cavity compress during a dive. The amount of gas that goes into solution in the fluid increases following Henry's gas law:

$$V_{gas} \propto p_{gas} V_{fluid}$$

where V_{gas} is the volume of gas dissolved in the fluid, p_{gas} is the pressure of the gas, and V_{fluid} is the volume of the fluid into which the gas is dissolving. Contrarily, decreasing the gas pressure over the solution allows the dissolved gases to come out of solution. A carbonated beverage provides a familiar example of Henry's law. While sealed under pressure the carbon dioxide remains in solution, but once the container is opened the carbon dioxide escapes as effervescent bubbles.

In diving mammals, the increased pressure of air within the lungs causes more nitrogen to dissolve into the blood across the alveolar membrane. Mammalian tissues can become saturated with nitrogen at pressures above 2 atm, 10 m below the surface, particularly after prolonged and repeated dives. If tissues become saturated and subsequently the diver surfaces too quickly, the nitrogen can come out of solution and form bubbles in the tissues and blood. This condition is known as **the bends** (**Caisson disease** or **aeroembolism**), and can be extremely painful and even fatal. This happens among divers breathing compressed air who dive too deep or too frequently without taking the appropriate precautions of decompression. Marine mammals do not suffer the bends for several reasons. First of all, unlike humans using SCUBA, these animals only take at most one inhalation before diving. Thus, they are not exposed to continuous influx of pressurized gases while diving. Also, as mentioned earlier, some seals exhale before diving. Third the alveolar collapse, described earlier, isolates nitrogen from the site of gas exchange.

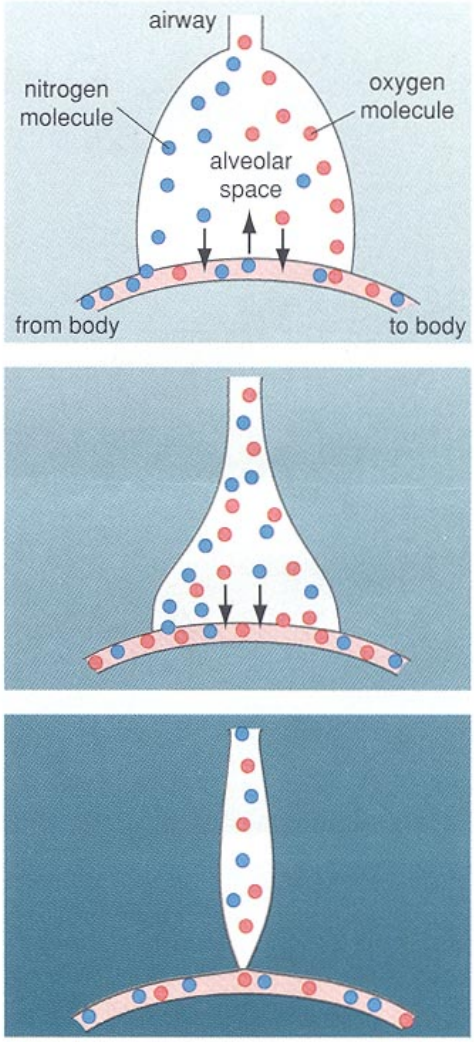


Figure 10. Dynamics of the lung help explain how seals avoid the bends. At the surface *(top)*, the lungs are fully inflated, and gases pass freely between the lungs and the blood. As the seal descends, the lungs start to collapse *(middle)*. Alveolar gas pressures rise because of the impinging ambient pressure. At that point, nitrogen diffusion is unidirectional into the blood, and the blood-nitrogen concentration reaches a maximum. As the seal continues to descend, the lung collapses completely, entirely curtailing any gas exchange between the lungs and the blood *(bottom)*. This limits the amount of nitrogen in the blood and helps the seal avoid the risks of elevation of nitrogen pressure.

12.4. Physiological Responses to Breath Holding (Mammalian Dive Response)

During a dive, marine mammals constrict the arteries leading to the organs and the skeletal muscles, shunting most of the circulating blood to the brain and heart. This is known as **peripheral vasoconstriction**. The other response that occurs in parallel is **bradycardia**, or the marked slowing of the heart rate. These two phenomena initiate the **mammalian dive response (MDR)**, which is a 7-step process:

1. Cessation of breathing (**apnea**).
2. Extreme bradycardia (5-20% of the normal hearty beat) regardless of the dive duration.
3. Strong peripheral and some central vasoconstriction.
4. Reduced aerobic metabolism in most organs.
5. Rapid depletion of muscle O_2.
6. Lactic acid accumulation in muscles.
7. Muscle buffering reactions.

However, it has been demonstrated that Weddell seals may dive up to 20 minutes without undergoing the typical mammalian dive response because they are able to store enough oxygen at the beginning of the dive to remain aerobic during the dive. The period of time that an animal's on-board oxygen stores can last is known as the **aerobic diving limit** (**ADL**) and is defined as the diving duration during which blood lactate accumulation does not occur, until the muscle O_2 store is depleted (Kooyman and Ponganis, 1998). This has been reported for other species of marine mammals as well. After exceeding their ADL, Weddell seals sleep for hours, something unusual among most marine mammals. However, it seems that a large proportion of the dives by most marine mammals are aerobic.

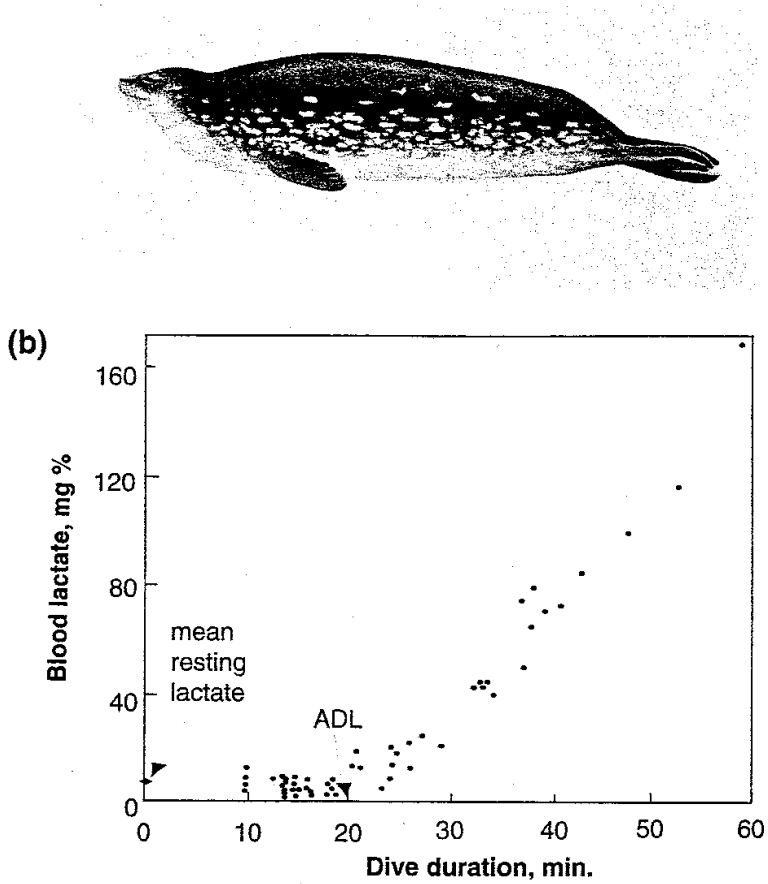


Figure 9.13. (a) Weddell seal (illustrated by P. Folkens), (b) Peak arterial lactate concentrations obtained following dives of varying durations for three Weddell seals. Commencement of post-dive increases in arterial lactate define ADL (redrawn from Kooyman *et al.*, 1981).

Diving could actually be an adaptive behavior even when the diving animal does not feed. It has been shown that during **apnea** (cessation of breathing) many marine mammals reduce their metabolic rate between 20 and 50%. This could represent an energy conservation strategy. Apnea also occurs while pinnipeds are sleeping on land, which may help them conserve water by reducing expiratory water losses. Another adaptive advantage of diving is predator avoidance.

Otariids and phocids present divergent diving strategies. While otariids usually only dive for a few minutes they execute the **energy dissipative strategy** while phocids, diving much longer, execute the **energy conserving strategy**. These strategies can be summarized as follows (Table 12.3).

12.5. Behavioral Responses

One of the most interesting discoveries of how marine mammals cope with the lack of oxygen while diving was reported by Williams and collaborators (2000). Analyzing video sequences of freely diving seals and whales wearing submersible cameras, they found that marine mammals

use prolonged gliding (both while descending and ascending) during dives exceeding 80 m in depth which result in up to 60% reduction of oxygen consumption. This discovery is very interesting because for many years researchers could not develop precise calculations of oxygen consumption that could account for all the effort involved in deep diving. This type of behavioral adaptation helps to explain how these diving mammals can be so efficient in terms of oxygen consumption.

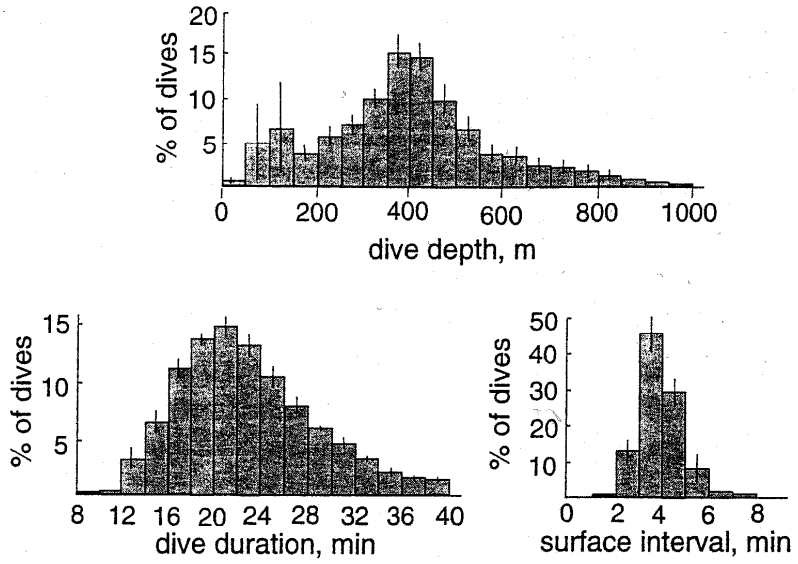


Figure 9.14. Summaries of depths, durations, and post-dive intervals of over 36,000 dives made by six adult male northern elephant seals (error bars = ±1 s.e.) (redrawn from DeLong and Stewart, 1991; Fig. 1).

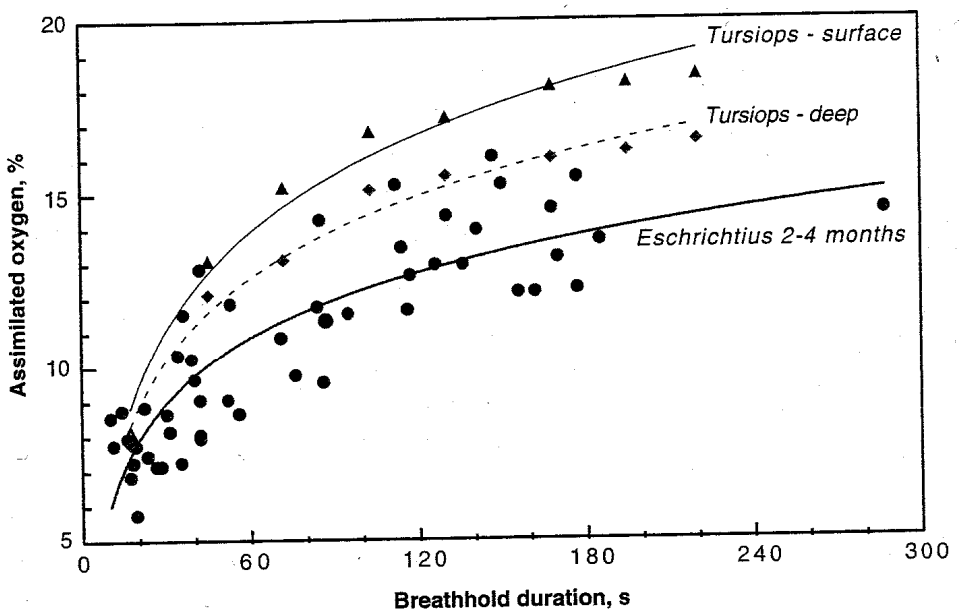


Figure 9.17. Influence of breathhold duration on % oxygen uptake for a bottlenose dolphin at the surface and 30 m deep, and for a young captive gray whale (from Ridgway, 1972 and Sumich, unpublished data).

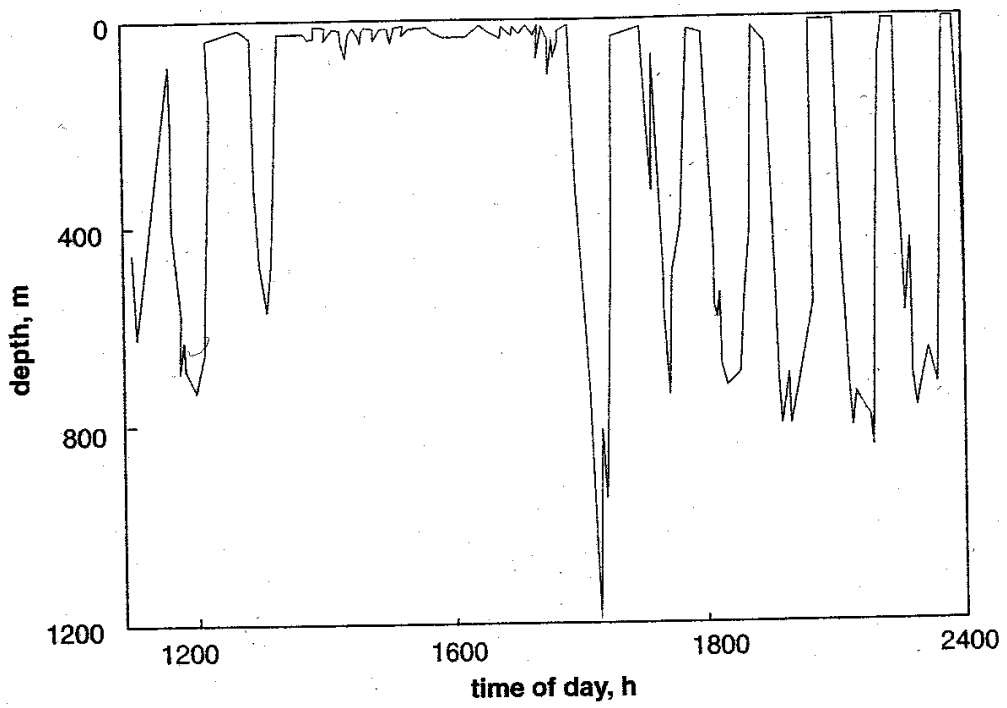


Figure 9.18. Continuous dive profile of a single sperm whale, generated by connecting depth points recorded by a digital depth monitor tag (redrawn from Watkins *et al.*, 1993).

12.6. Unanswered Questions

With the development of microprocessor-based monitoring of diving animals in their natural environment, great strides have been made in our understanding of the diving response since the late 1970's. Yet, despite our recently gained knowledge in this area, a number of questions remain answered. For example, we do not know the exact mechanism responsible for the reinflation of lungs after a deep dive. Do marine mammals produce more surfactant than terrestrial mammals? What is the morphology and physiology of the polar bear respiratory system? Do polar bears share any morphological features with other marine mammals? How can we explain, from a phylogenetic viewpoint, the convergences and divergences that lead to similar adaptations to deep diving? Why, in some cases, are phocids more similar to cetaceans than to their closer relatives, the otariids?

Future progress will depend on both new technologies and new approaches. For example, the use of magnetic resonance imaging (MRI) and spectroscopy (MRS) together with more synthetic/evolutionary approaches should give us a better understanding of diving physiology among diving mammals (Hochachka, 2000). Also, more studies of cetaceans and the polar bear are needed because most of the data and understanding in this area has come from studies of pinnipeds.

Table 12.3. Comparative otariid and phocid diving strategies (after Hochachka et al., 1999).

Otariids	Phocids
(energy dissipative strategy)	**(energy conserving strategy)**
Apnea limited to inhalation	Apnea with exhalation
Bradycardia	Bradycardia
Peripheral vasoconstriction except for propulsive muscles, CNS, and heart	Peripheral vasoconstriction except for CNS and heart
Hypometabolism	Hypometabolism
O_2 carrying capacity intermediate between large phocids and terrestrial mammals	Enlarged O_2 carrying capacity (enlarged blood volume, increased red blood cells mass/volume, higher myoglobin is muscles and heart)
Spleen of normal volume relative to terrestrial mammals	Enlarged spleen

Summary

Marine mammals possess a number of adaptations enabling them to dive efficiently while dealing with the lack of oxygen and great pressure. Those adaptations include:

Lungs: Have small coils of cartilage that encircle the airways throughout, permitting the lungs to virtually snap open after a dive.

Circulatory system:
General architecture. Expansive with specialized reservoirs, the thoracic rete in cetaceans, and the hepatic venous sinus in pinnipeds. These store blood until it is needed, or for rerouting it elsewhere.
Heart. Generally increased in size, larger in pelagic species. Has enhanced glycogen storage capabilities.
Blood vessels. Increased diameter and number of branches (particularly among deep diving species).
Blood volume and composition. Larger (2-3x) than in non-diving mammals (particularly high among phocids). A rich supply of oxygen-carrying hemoglobin (which makes the blood quite dark because high levels of iron associated with the hemoglobin).

Skeletal muscles: Muscles (particularly swimming ones) with high content of myoglobin, a protein with a greater affinity for oxygen than hemoglobin. Myoglobin can store extra oxygen for release during long dives (because the myoglobin also contains iron, marine mammal muscles also look darker). The proportion of myoglobin increases with age and is larger among pelagic species.

Spleen: Acts as a blood reservoir and tends to be large in pinnipeds.

Diving Biochemistry and Metabolism: Myoglobin, and consequently the muscles, has high levels of buffering capacity, i.e., the ability to hold tissue pH constant in the face of an increasing amount of acidic byproducts created by anaerobic metabolism. This reflects the capacity of marine mammals to tolerate hypoxia and metabolic acidosis.

Behavior: Use of prolonged gliding during dives exceeding 80 m in depth (both while descending and ascending) resulting in up to a 60% reduction in oxygen consumption.

Literature Cited

Belanger, L.F. 1940. A study of the histological structure of the respiratory portion of the lungs of aquatic mammals. Amer. J. Ant. 67:437-461.

Berta, A. and J.L. Sumich. 1999. Marine mammals: evolutionary biology. San Diego: Academic Press. 494 pp.

Bryden, M.M. and G.H.K. Lim. 1969. Blood parameters of the southern elephant seal (*Mirounga leonina*) in relation to diving. Comp. Biochem. Physiol. 28:139-148.

Butler, P.W. and D.R. Jones. 1997. The physiology of diving birds and mammals. Physiol. Rev. 77:837-899.

Dolar, M.L.L.; P. Suarez, P.J. Ponganis and G.L. Kooyman. 1999. Myoglobin in pelagic small cetaceans. J. Exper. Biol. 202:227-236.

Falke, K.J.; R.D. Hill, J. Qvist, R.C. Schneider and M. Guppy. 1985. Seal lung collapse during free diving: evidence from arterial nitrogen tensions. Science 229:556-558.

Hochachka, P.W. 2000. Pinniped diving response mechanism and evolution: a window on the paradigm of comparative biochemistry and physiology. Comp. Biochem. Physiol. A 126:435-458.

Hochachka, P.W. and P.D. Mottishaw. 1998. Evolution and adaptation of the diving response: phocids and otariids. pp. 391-431, *In:* H.O. Portner and R.D. Playle (eds.) Cold ocean physiology. Cambridge, UK: Cambridge University Press, 498 pp.

Hochachka, P.W., S.J. Thornton and P.D. Mottishaw. 1999. The diving response mechanism and its surprising evolutionary path in seal and sea lions. Amer. Zool. 39:434-450.

King, J.E. 1977. Comparative anatomy of the blood vessels of the sea lions *Neophoca* and *Phocarctos*; with comments on the differences between the otariid and phocid vascular systems. J. Zool. 181:69-94.

Kooyman, G.L. and P.J. Ponganis. 1997. The challenges of diving to depth. Amer. Sci. 85:530-539.

Kooyman, G.L. and P.J. Ponganis. 1998. The physiological basis of diving to depth: birds and mammals. Annu. Rev. Physiol. 60:19-32.

Kooyman, G.L. 2002. Diving Physiology. pp. 339-344, *In* W. F. Perrin, B. Wursig, and J. G. M. Thewissen (eds.) *Encyclopedia of marine mammals*. New York, NY, USA. Academic Press, 1414 pp.

Melnikov, V.V. The arterial system of the sperm whale (*Physeter macrocephalus*). J. Morphol.234:37-50.

Panigada, S.; M. Zanardelli, S. Canese and M. Jahoda. 1999. How deep can baleen whales dive? Mar. Ecol. Prog. Series 187:309-311.

Pfeiffer, C.J. 1990. Observations on the ultrastructural morphology of the bowhead whale (*Balaena mysticetus*) heart. J. Zool. Wild. Med. 21:48-55.

Pfeiffer, C.J. and T.P. Kinkhead. 1990. Microanatomy of retia mirabilia of bowhead whale foramen magnum and mandibular foramen. Acta Anat. 139:141-150.

Pfeiffer, C.J. and V.S. Viers. 1995. Cardiac ultrastructure in the ringed seal, *Phoca hispida* and harp seal, *Phoca groenlandica*. Aquat. Mamm. 21:109-119.

Ponganis, P.J.; G.L. Kooyman, D. Sartoris and P.F. Jobsis. 1992. Pinniped splenic volumes. Amer. J. Physiol. 262:R322-325.

Ridgeway, S.H. 1986. Diving by cetaceans. pp. 33-62. *In:* Diving in animals and man: An international symposium, Kongsvoll, 3-7 June 1985. A.O. Brubakk, J.W. Kanwishes and G. Sunders (eds.) Trondheim, Norway : the Royal Norwegian Society of Sciences and Letters, the Foundation. 308 pp.

Ridgeway, S.H. and D.G. Johnston. 1966. Blood oxygen and ecology or porpoises of three genera. Science 151:456-458.

Schreer, J. F. and K. M. Kovacs. 1997. Allometry of diving capacity in air-breathing vertebrates. Can. J. Zool. 75:339-358.

Williams, T.M.; R.W. Davis, L.A. Fuiman, J. Francis, B.J. Le Boeuf, M. Horning, J. Calambokidis and D.A. Croll. 2000. Sink or swim: strategies for cost-efficient diving by marine mammals. Science 288:133-136.

Chapter 13

Sound Production, Hearing, Echolocation, and Communication

13.1. Introduction

Communication is defined as the emission of a signal by a sender and the receiving of that signal by a receiver producing a response by the latter. Only if there is response (in any form) we can conclude that communication has taken place.

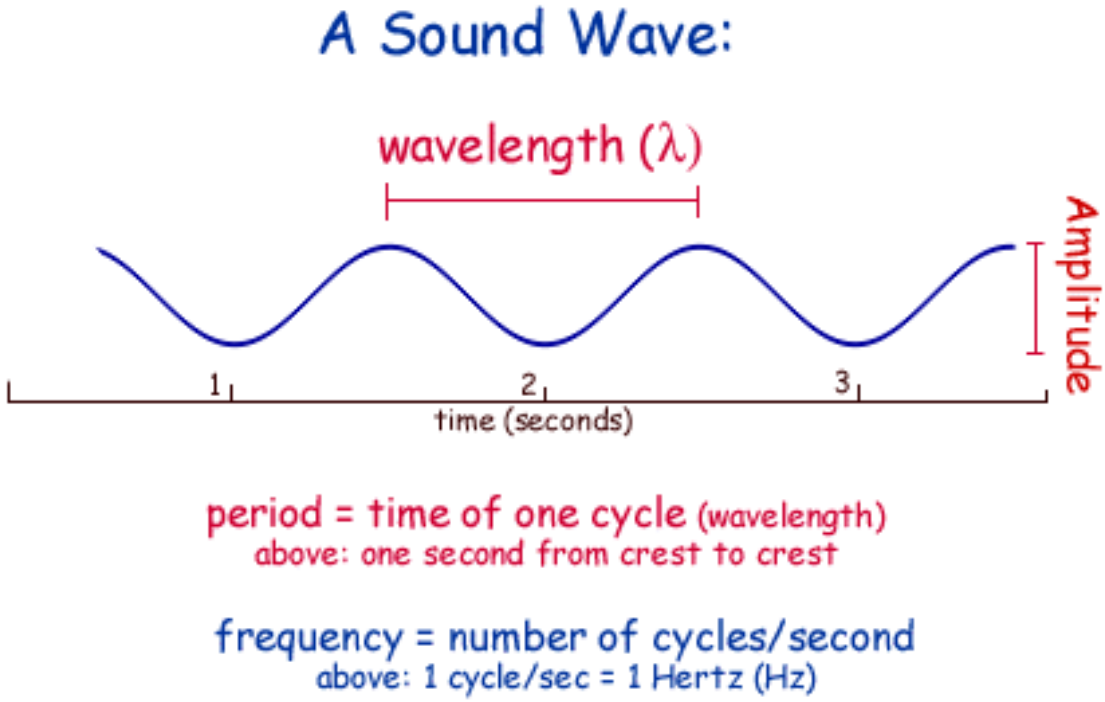
There is no question that communication is one of the most attractive aspects in the study of marine mammals. Fueled in part by fantasy, in part by scientific research, and in part by a mixture of the two, a whole set of myths have been created around this issue. We will try in this chapter to separate both, to study the functional adaptations of hearing and sound emission, the true differentiation between communication and echolocation and, finally, some aspects of one of the most recent controversies on human impacts on marine mammals: noise pollution.

13.2. Sound Production

Most mammals produce sounds by vibrating elastic ligaments (vocal cords or folds) in the larynx. Vibrations are generated by passing air across these ligaments. These sounds can be modulated by actions of the tongue or the teeth, or both. Resonating chambers, such as bony sinuses and pharyngeal air sacs, also influence sound production.

13.2.1. Underwater Sound Propagation

The units used are **Hertz** (Hz) for frequency and meters (m) for wavelength. Thus, velocity is measured in meters per second (m/s).



The frequency, its durations, and energy level are conventionally portrayed graphically as a **sonogram** or **frequency (power) spectrum**. The sound energy in water is measured as **sound pressure level** (**SPL**) in units called **decibels**.

13.2.2. Cetaceans

With exception of sounds producing by slapping the sea surface with their flukes, flippers, and body flanks, which are thought to have signal function, all sounds produced by cetaceans are underwater.

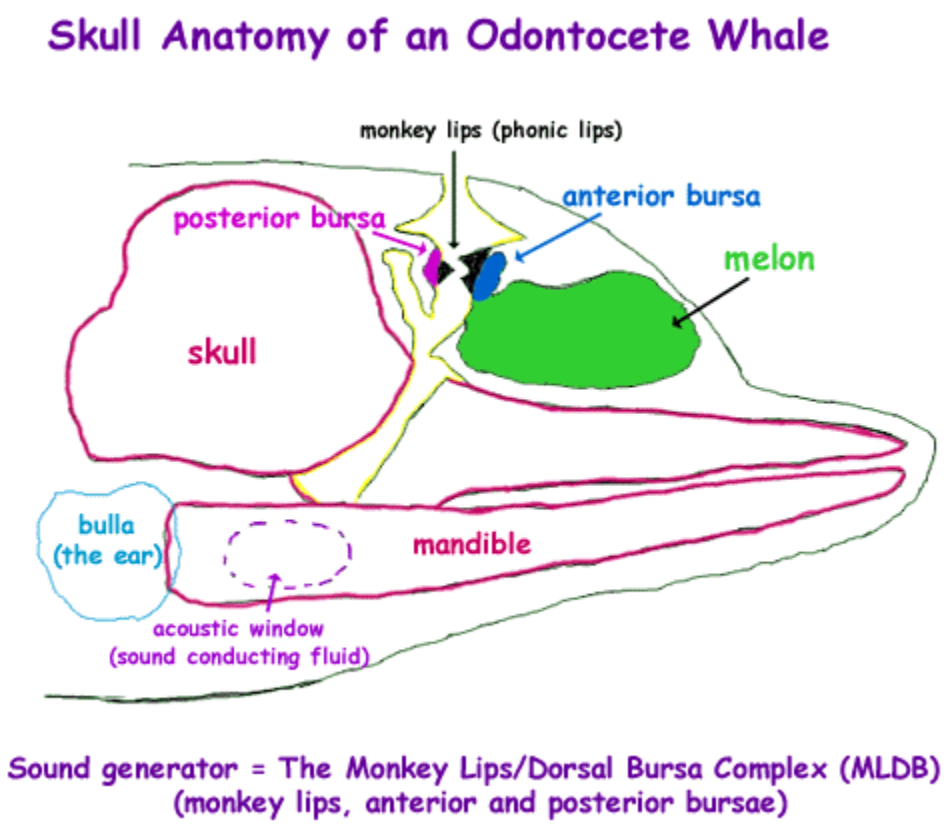
13.2.2.1. Mysticetes

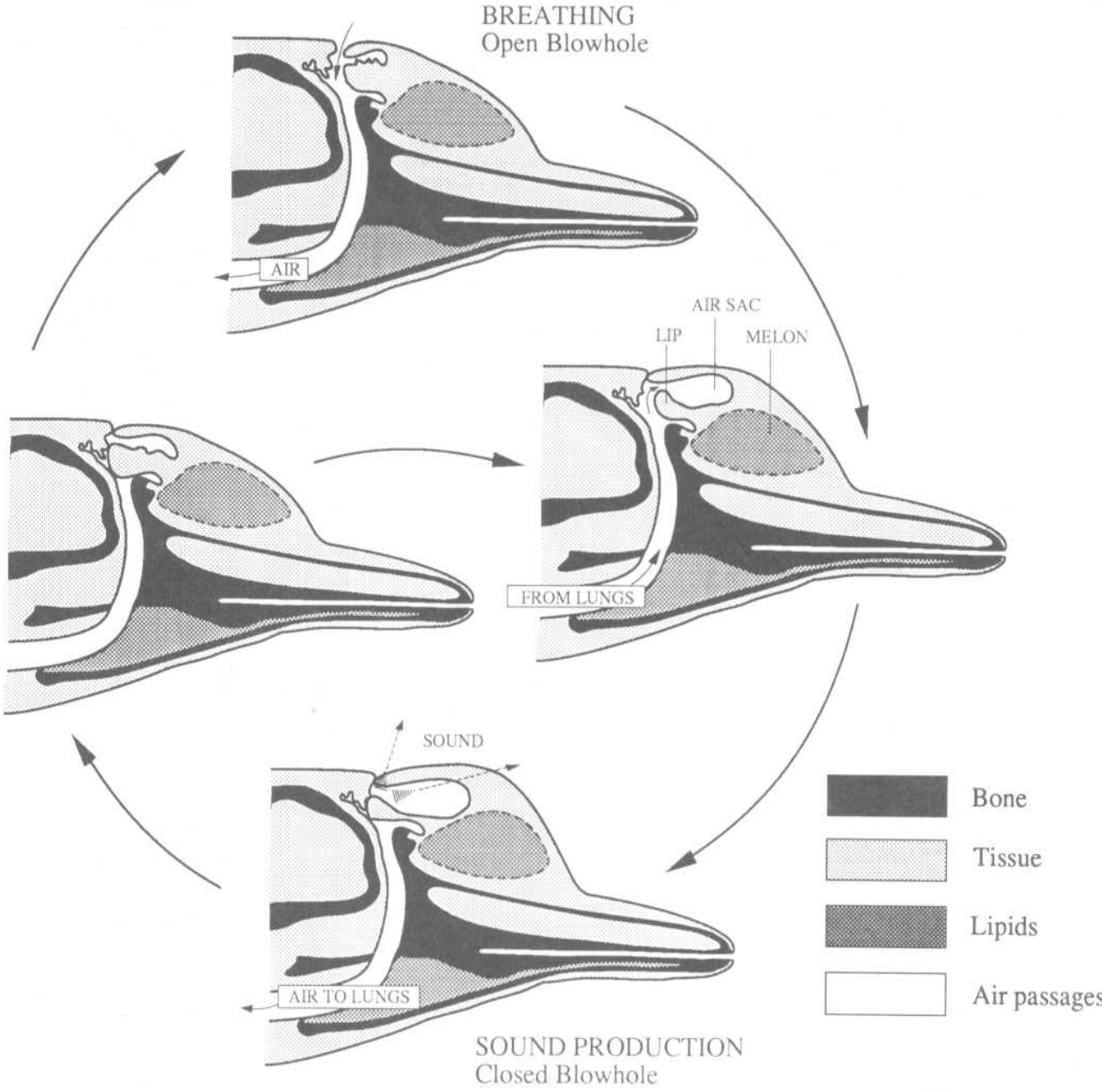
Baleen whale sounds may be the loudest produced by any animal and may travel for tens or hundreds of kilometers underwater. These sounds may be for long-range contact, assembly calls, advertisement for mates, greeting, location, threat, or individual identification. Baleen whales have a larynx but no vocal cords. Baleen whales produce primarily low-frequency sounds, below 5,000 Hz. The repertoire of baleen whales sounds includes low-frequency (20-200 Hz) moans, grunts, thumps, and knocks; and higher-frequency (above 1000 Hz) chirps, cries, and whistles. The specific vocalizations vary by species. Bowhead and humpback whales also produce a series of repeating units of sounds up to 5,000 Hz that are classified as songs. These are produced primarily by males on the breeding grounds. The songs, which can last up to 36 minutes each for humpbacks, probably communicate species, sex, location, mate status, and readiness to compete with other males for mates. More analysis of the behavior and song is needed before the true function of whale songs is known.

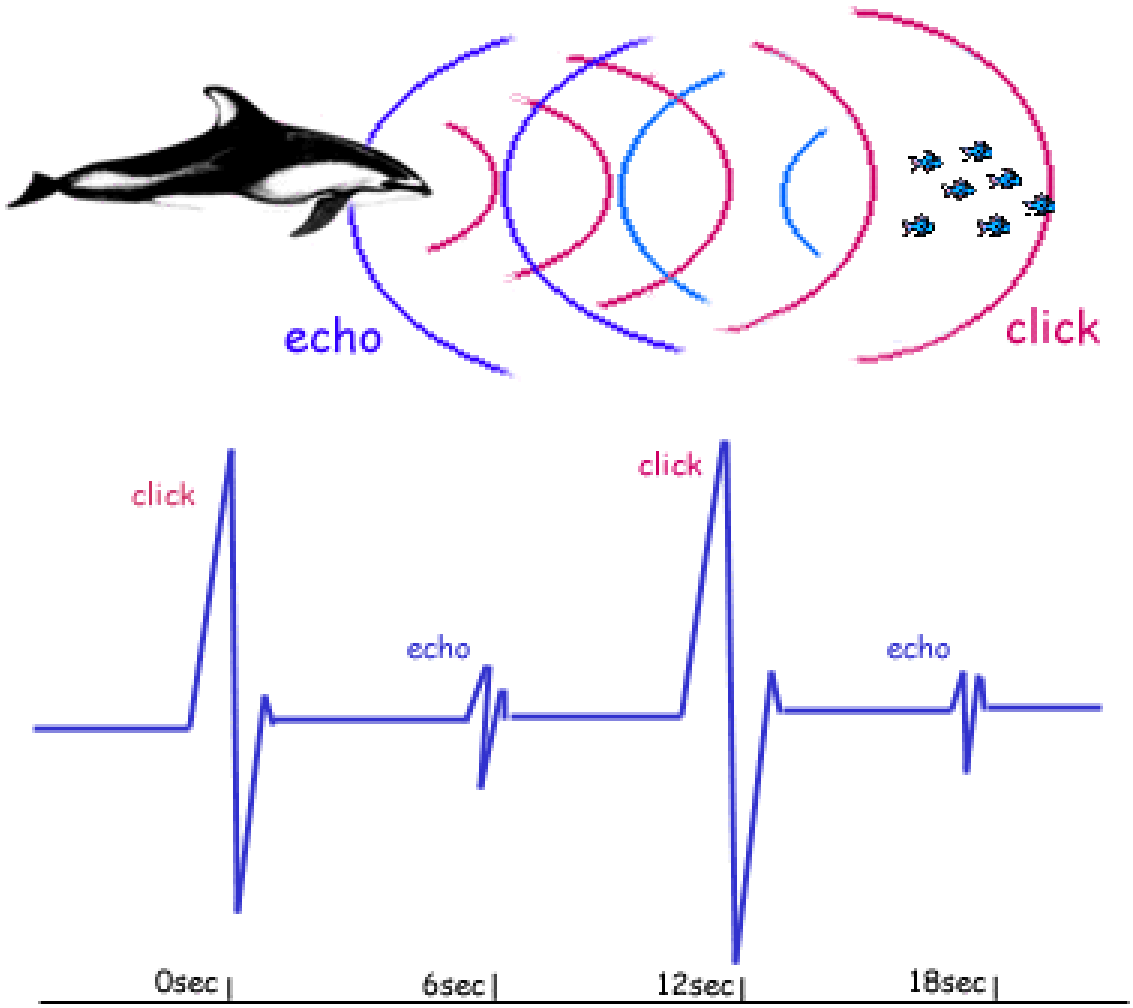
Some sounds produced by the body may be involved with communication. Noises such as forceful spouts may signal aggravation. Slapping pectoral flippers or flukes may indicate arousal, excitement, or aggression.

13.2.2.2. Odontocetes

Odontocetes can produce extremely high-frequency sounds (> 100,000 Hz) known to function as echolocation signals. The larynx of toothed whales does not possess vocal cords. The location of sound production is the region of the nasal sac system just inside the blowhole, as the click generating structures in odontocetes. The exact site of the sound generator is still controversial. It is believed that the basic sound-production system consists of a sound generator, the structural complex associated with the upper nasal passages termed the "**monkey's lips"/dorsal bursa (MLDB) Complex**. All odontocetes except sperm whales, possess two bilaterally place MLDB complexes. Each MLDB complex is located just below the ventral floor of the vestibular air sac and is composed of a pair of fatty-filled anterior and posterior dorsal bursae embedded in a pair of "monkey's lips," a resilient cartilaginous blade (bursal cartilages), and a stout blowhole ligament, all suspended within a complex array of muscles and air spaces.




BREATHING
Open Blowhole
AIR
AIR SAC
LIP
MELON
FROM LUNGS
SOUND
AIR TO LUNGS
SOUND PRODUCTION
Closed Blowhole
Bone
Tissue
Lipids
Air passages



The sounds are transmitted to the environment through the fatty melon. Nasal air sacs, the steeply sloping maxillary bones, and the rostrum reflect sounds and help focus the sound beam forward through the melon. Lipids found in various regions of the melon affect the speed off sound transmission.

Another useful distinction of odontocetes is a difference in telescoping the skull in which the maxilla "telescopes," or extends posteriorly, over the orbit to form an expanded bony supraorbital process of the frontal. In living odontocetes, this supraorbital process forms an origin for a facial (maxillonasolabialis) muscle, which inserts around the single blowhole and associated nasal passages. Typically, the odontocete skull displays cranial and facial asymmetry in which those bones and soft anatomical structures on the right side are larger than those on the left side. It has been suggested that asymmetry is involved in sound production perhaps with the right side being more specialized for producing sound and the left side primarily adapted for respiration.

Odontocetes can produce sounds for two overlapping functions: communicating and navigating. Orcas can communicate and navigate at the same time.

During some vocalizations, bottlenose dolphins actually release air from the blowhole. These bubbles trail and clouds may be a visual display and not necessary related to sound production. Bottlenose dolphins produce clicks and sounds that resemble moans, trills, grunts, squeaks, and creaking doors. They also produce whistles. They make these sounds at any time and at considerable depths. The sounds vary in volume, wavelength, frequency, and pattern.

The frequency of the sounds produced by a bottlenose dolphin ranges from 0.25 to 150 kHz. The lower frequency vocalizations (about 0.25 to 50 kHz) probably function mainly in social communication. Social signals have their most energy at frequencies less than 40 kHz. Higher frequency clicks (40 to 150 kHz) probably are used primarily in echolocation. Peak frequency of typical echolocation clicks is about 100 kHz, but frequency varies considerably with specific echolocation tasks.

Orcas produce clicks and sounds that resemble moans, trills, grunts, squeaks and creaking doors. They also produce "whistles." They make these sounds at any time and at all depths. The sounds vary in volume, wavelength, frequency and pattern. Each individual sound that an orca makes is termed a call. Calls that sound the same way time after time are stereotyped calls. All the stereotyped calls in an orca's repertoire make up a vocalization system called a dialect. Orcas that are separated by great geographical distances have completely different dialects. During some vocalizations, orcas actually release air from the blowhole. The frequency of the sounds produced by an orca ranges from about 0.1 kHz to about 40 kHz. Most sounds produced as a part of social behavior range in frequency to about 16 kHz. Higher frequency clicks probably function primarily in echolocation.

Belugas are extremely vocal. The frequency and large repertoire of their vocalizations earned them the nickname "sea canaries." At least 11 different beluga sounds have been documented, including high-pitched, resonant whistles and squeals; clucks; mews; chirps; trills; and bell-like tones. Beluga sounds can be heard above water and through the hulls of ships. During sound production, the beluga's melon changes shape.

Although there is some type of ordering or structure to the calls, a dialect is not the same thing as a language. The individuals of any particular pod share the same repertoire of calls. Pods that associate with one another share certain calls, but the vocal repertoires of each pod remain distinct enough that scientists can identify pods by the sounds they make.

13.2.3. Pinnipeds

13.2.3.1. Air-Borne Sounds

Pinnipeds can produce a wide variety of sounds in air, including barking, crying, growling, roaring, and snorting, and it is believed that these sounds are produced by the vocal cords.

Seals are often very vocal in air. Some of the sounds are similar to those produced underwater, like the thrills and throbs of Weddell and Ross seals, but some are used only on land. Elephant seals produce a wide range of grunts, roars, and belches. Some of these are simple coughs, barks, and snorts but the roars of adult bulls play an

important role in establishing dominance on the breeding beaches. Those sounds are usually within the range of human hearing and their presumed functions are social on nature: "threat calls" by breeding males or "pup-attraction calls" by mothers.

Here is a survey of air-borne sounds by pinnipeds:

1. Female harbor seals: Except for while attending pups they rarely vocalize.
2. Male California and northern sea lions: constant barking for threatening other males.
3. Male fur seals: "Trumpeted roars" to assert their claim over a territory.
4. Male elephant seals: Vocalizations to communicate their breeding status.
5. Walruses: Most pinniped vocalizations are produced in the larynx, although male walruses also make clacking noises with their teeth and produce distinctive gong-like sounds in air
   and underwater by striking inflated pharyngeal (throat) pouches with their front flippers. These pouches are present only in males, and the gong-like sounds are produced almost exclusively by adult males during the breeding season as part of their courting display. Another pinniped that produces similar sounds both in air and underwater is the hooded seal.
6. Elephant seals, sea lions, harp seal, and fur seal mothers: Produce mother-pup calls to attract their pups when returning from foraging at sea. This, together with olfactory clues, helps to identify each other.

Pinniped ear is very similar than that of terrestrial mammals.

13.2.3.2. Underwater Sounds

Some pinnipeds can produce higher frequency sounds including bell-like ringing, clicks, rains of pulses, whistles, and warblers. These sounds may be produced by structures other than vocal cords. Otariids circulate a relatively small volume of air through the larynx and over the vocal cords or by movement of air between the larynx and trachea causing the tracheal membrane to vibrate. Interestingly, phocid seals do not possess extra-pharyngeal structures and is not yet known how these underwater sounds are produced. Pinnipeds do not take down large quantities of air when they dive, though many seals may make communication calls near the surface where air supplies would be easily replenished.

Bearded seals produce a distinctive song. The long, musical underwater sounds are well known to Inuit (Eskimo) hunters who, in the days when kayaks were extensively used for spring hunting, tried to locate animals by listening for them. Although parts of the song are audible at close range in air, it is easily heard by placing a paddle in the water and pressing an ear against the butt of the handle. These songs are associated with mating. There is definitely a marked peak in "singing" during the breeding season, from April to May.

Analysis of these songs shows them to be complex, long, oscillating frequency-modulated warbles that may be longer than a minute in duration, followed by a short unmodulated low-frequency moan. These sounds are stereotype and repetitive. Once located, the singing animals are easy to approach. They dive slowly, apparently in a loose spiral, release bubbles, and surface in the center of their activity. This behavior is

repeated many times. So far only male bearded seals have been identified producing these songs, which may indicate territoriality, breeding state, or both.

13.2.4. Sirenians

Manatees and dugongs produce "squeaky and rather ragged" sounds. They apparently possess vocal cords and we assume that this is their sound-producing organ. They do not release bubbles when producing sounds.

13.2.5. Sea Otters

Above water they produce low frequency, low intensity signals that are similar in complexity to those of the California sea lion and the northern elephant seal. One known moderately long distance (<1 km) signal is likely important for mother-pup recognition. Of particular interest is the presence of graded signals (i.e., those that vary over a continuum of frequencies rather than forming discrete units) that are most appropriate for short-range communication between familiar individuals.

13.2.6. Polar Bears

Polar bears lack most of the distinctive vocalizations that characterize other carnivores. Females may produce mother-cub recognition calls and males snort and huff. The latter is a low intensity repetitive call during interactions with one another.

13.3. Hearing

Hearing operates differently under water than in air. While water is less favorable for the transmission of light than air is, the opposite applies to sound. Sound not only travels four and a half times faster in water than in air, but also sound is less attenuated in water so sound travels further.

In a terrestrial mammal in air there is a great difference in **acoustic impedance** between the air and the tissues of the head. This results in 90% of the sound being reflected away from the head. However, at the external ears sound is reflected down the trumpet-shaped pinna to the tympanic membrane or ear drum where it transmits the vibrations on a series of tiny bones, the ossicle (the malleus, incus, and stapes). These bones conduct sound vibrations to the oval window of the inner ear, amplifying them considerably and whose final result is the stimulation of sense cells in the inner ear. The organ of sound reception is the cochlea, located in the inner ear. The ossicle and the cochlea are enclosed in the Arbon, or auditory bulla. The cochlea is a coiled organ that is divided lengthwise into three parallel tubular canals, which become progressively narrower toward the apex. The base of the vestibular canal is formed by the oval window contacting the stapes. The tympanic canal is continuous with the vestibular canal and is closed by the round window. Between these two parallel canals lies the cochlear duct containing the actual sensory structure, the organ of Corti. Within the organ of Corti there are rows of thousands of sensory hairs cells, each of which is connected to a neuron to the auditory nerve. These hairs cells are supported on the basilar membrane with the

Tectaria membrane directly over them. The entire organ of Corti is bathed in the endolymph of the cochlear duct. The mammalian inner ear houses two organs of equilibrium: the vestibule and the semicircular canal. As an animal's head changes of position, moving fluid in the semicircular canals and vestibule puts shearing force on the hair cells. Changes in shearing forces are transmitted into neuronal impulses.

The range of frequency detectable by humans is between 18 and 15,000 Hz (or 15 kHz). Sounds below that range are called **infrasonic** and above 20 kHz are called **ultrasonic**.

A terrestrial mammal can determine the direction of the origin of a sound by computing the difference in time for the sound to arrive at each ear. The "sound shadow" cast by the skull and tissues between it and the opposite ear gives additional clues as to the direction of the sound. Neither of these methods works well in the water. Because of the increased speed of sound in water small differences are more difficult to detect and method using sound shadows will only be efficient if the ears can operate independently. This is difficult if the head is immersed in water; a human diver, for example, has great difficulty localizing sound. The reason for this is that because there is little difference in acoustic impedance between water and the tissues of the skull sound waves arrive at the inner ear by bone conduction from all directions and localization is lost.

13.3.1. Cetaceans

An obvious physical characteristic of cetaceans is the absence of external ears. These have been sacrificed for the sake of a streamlined body shape for efficient swimming. Cetaceans do still have ears but they are barely noticeable, being marked only by a small hole just behind the eye.

There is still considerable argument among scientists as how cetaceans use their ears. Baleen whales have the external ears filled with a horny, wax plug, which is thought to transmit underwater sounds to the inner ear. Because the impedance of the wax plug matches that of seawater, baleen whales are probably deaf in air.

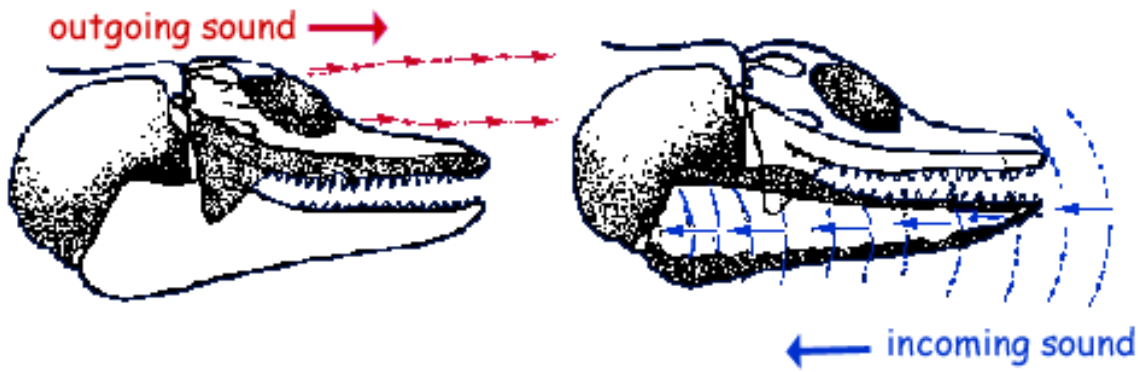
13.3.1.1. Mysticetes

Baleen whales have well developed hearing, which is valuable in the poorly lit ocean environment where vision is less dependable. Portions of the baleen whale brain dedicated to hearing suggest this sense is excellent. Baleen whales probably hear very well in the low frequency ranges but may lack the ability to hear high frequency sounds. Baleen whales react to noises such as boat engines and cameras clicking underwater. Baleen whales have a small external ear opening on each side of the head. Each opening leads to a narrow auditory canal that is completely closed by a waxy substance and reduced to a strand of fibrous connective tissue. The effectiveness of sound reception and hearing through the ear canal is unknown. The middle and inner ear follow the basic mammalian ear structure. More research is needed to determine the exact mechanism for sound reception in baleen whales. Foam surrounds the ear bones. This foam contains air. Air stops sound waves traveling through water and living tissues. Many scientists believe that this foam acoustically isolates the ears, enabling a whale to tell from which direction a sound comes.

13.3.1.2. Odontocetes

Dolphins have a well-developed, acute sense of hearing. The auditory cortex of the brain is highly developed. The auditory nerve may have 67,900 or more cochlear fibers. This is twice as many as in the human auditory nerve. Bottlenose dolphins respond to tones within the frequency range of 0.15 to 150 kHz. They are most sensitive to sounds in the range of 40 to 100 kHz (the average hearing range for humans is about .02 to 17 kHz.).

Most sound reception, or hearing, probably takes place through the lower jaw (**bone conduction**). Dolphins may also receive sound through soft tissue and bone surrounding the ear (**tissue conduction**). A fat-filled cavity in the lower jawbone appears to conduct sound waves through the jaw to bones in the middle ears. The lower jawbone of toothed whales broadens and is hollow at the base, where it hinges with the skull. Within this very thin, hollow bone is a fat deposit that extends back toward the **auditory bulla** (Arbon complex). Sounds are received and conducted through the lower jaw to the middle ear, inner ear, and then to hearing centers in the brain via the auditory nerve. This method of conducting sound waves is important in echolocation.



Dolphins do have small external ear openings, 5-6 cm behind the eye and is only 2-3 mm in diameter. Each opening leads to a reduced ear canal and an eardrum. Some believe that dolphins receive sound through these openings while others believe that a dolphin's external ear openings are nonfunctional. Foam also surrounds the ear bones of dolphins on all sides. Many believe that this foam acoustically isolates the ears enabling a dolphin to tell which direction a sound comes from.

Odontocetes do not have earplugs. There is also considerable controversy on whether dolphins' ear canal is filled with seawater or air, since many dolphins seem to be able to hear in the air.

Orcas also have a well-developed, acute sense of hearing. The auditory cortex of the brain is highly developed. Orcas have responded to tones within the frequency range of about 0.5 to 100 kHz. Peak sensitivity is about 15 kHz. Our knowledge on their bone reception, tissue conduction, and functionality of their ears, is similar to that of dolphins. As for other odontocetes, the auditory cortex of the brain is highly developed. Belugas can hear sounds in the range of 1.2 to 120 kHz, with a peak sensitivity of about 10 to 75 kHz.

Cetaceans are exceptional in having semicircular canals that are significantly smaller than the cochlear canal. If the semicircular canals are vestigial, these animals may not have any rotational or three-dimensional positional sense, which may permit the flying turns of spinner dolphins without the side effects of motion sickness.

13.3.2. Pinnipeds

Pinnipeds have modified the bones of their skulls so that they can localize sounds. One bone that is associated with the ear, the squamosal, is enlarged and has a large flat surface facing upwards and to the front. Sound waves arriving normal to this surface are transmitted into the squamosal and through it to the inner ear. Waves, which arrive obliquely to the squamosal, are reflected. By making scanning movements of its head the pinniped can localize the source of the sound. A Harbor seal can separate two sound sources only 3° apart. The ear oscicles of phocids are much more massive than those found in other terrestrial mammals. In the harp seal they may weight 227 mg. It is believed that this character is used in the general reception of sound. Because in water sound will act on the whole head the entire skull will vibrate, but the inertia of the loosely attached oscicles set up the impulses that activate the sense cells. All phocids are more sensitive to the sounds in water than in air.

13.3.3. Manatees

External pinnae are absent and the external meatus is reduced. The structure of their inner ear implies that the manatees lack sensitivity and directionality compared with other marine mammals.

13.4. Echolocation

The term echolocation refers to an ability that odontocetes (and some other marine mammals and most bats, as well as some shrews, golden hamsters, and flying lemurs) possess that enables them to locate and discriminate objects by listening for echoes. Echolocation involves an active process of emitting in the form of short broad-spectrum burst-pulses (clicks) and gaining information on the surrounding environment (nearby objects, obstructions) by analysis of the returning echoes.

The only marine mammals known to have evolved echolocation are the odontocetes.

13.4.1. Cetaceans

Echolocation is highly developed among odontocetes. Actually this system is very powerful given that sound waves can carry more information than light since sound can gives us a three-dimensional perspective, including internal organs. That is the principle of sonography employed today in medicine and industry that toothed whales developed millions of years ago. By this complex system of echolocation, odontocetes can

determine size, shape, speed, distance, direction, and even some of the internal structure of objects in the water.

Although there are some interspecific differences, the basic principles for all odontocetes are the same. All these species contain a large ovoid deposit of fat anterior on the facial region in their heads and lower jaws called **melon**. The melon typically is asymmetrically positioned, slightly off to the right side. It rests on a pad of dense connective tissue on top of the bony rostrum of the skull. The core region of fatty tissue has a higher lipid content and as different lipid composition than the surrounding outer melon and blubber and is an important component of the echolocation system. Lipid composition of the melon varies between major groups of odontocetes. Such deposits are unique among animals and for a number of reasons. First, they are large in relation to the size of the animal and represent an immense potential deposit of metabolic energy. Second, the chemical composition of these deposits is markedly different from that of the normal body fat and from that of the animal's normal dietary fat intake. Third, the shape and positioning of the deposits has apparently been so important that major changes in the shape and structure of the skull have been necessary in order to accommodate them.

A widely accepted theory regarding their function is that they aid in echolocation. The process is believed to work like this:

1. Sound is produced internally by the animal
2. The head fat organ focuses this sound into a directional beam
3. Reflected echoes carrying information about targets are received at the "acoustic window" are in the lower jaw.
4. This sound is transmitted by the fat organ in the lower jaw to the middle ear and subsequently to the brain for processing and interpretation.

In the forehead of sperm whales there is a large structure, the **spermaceti organ** that may occupy more than 30% of the whale's total length and 20% of its weight. The fatty tissue in the facial region of physeterids is highly modified and very different in structure than the melon of all other odontocetes. Because it is situated posterodorsal to the nasal passages, some think that the spermaceti organ is not homologous with the melon. In adults there is an elongate connective tissue sac, or case, that is filled with a viscous waxy fluid called **spermaceti**. This is the sperm whale oil that was most sought after by whalers for candlemaking and for burning in lanterns. The spermaceti organ is contained within a thick case of muscles and ligaments. Below the spermaceti organ is a region of connective tissue alternating with spaces filled with spermaceti oil. This region was called the **junk** by whalers because it has a lesser quantity of oil in it. The spermaceti "junk" is probably homologous with the melon of other odontocetes. It has been proposed that the function of the spermaceti organ is the control of buoyancy. The hypothesis is that as sperm whales dive into cooler, deeper water, the flow of water in the head passages lowers the temperature of the wax, which solidifies, shrinks, and in doing so, increases buoyancy and allows the animal to rise with the minimum effort. However, because the head is not a closed circuit with respect to blood circulation, when sperm whales dive into cooler, deeper water the entire body temperature would be reduced, not just the head temperature. The small size and low density of blood vessels penetrating the spermaceti organ make this hypothesis of "rapid warming" untenable. In addition,

the small size of the spermaceti organ in the pygmy sperm whale would result in an insignificant decrease in density of the head and thus precludes its role as a hydrostatic organ.

The other large fat deposit in sperm whales is in the lower jaw and is strategically placed behind an area of the jaw where the bone is very thin. This deposit is similar in composition to the melon and extends up to the middle ear region.

A vestigial melon has been described in baleen whales. Two hypotheses have been proposed to explain this: (1) the original function of the melon in cetaceans is to allow the free movement of the nasal plugs as they are drawn posteriorly over the premaxillae during contraction of the nasal plug muscles; (2) the presence of the melon is mysticetes indicates that the ancestor of al whales may have possesses a well-developed melon and correspondingly well-developed echolocation abilities.

Unlike lower-frequency, narrow band whistles, the dolphins' echolocation clicks, which they use for navigation and for exploring features of its environment, are broad band pulses, ranging up to 150 kHz. Individual clicks last on the order of 70 (range 10-100) milliseconds and may be repeated as many as 600 times each second. These beams are like flashlights of sound. Dolphins produce directional clicks in trains. Each click lasts about 50 to 128 microseconds. Bottlenose dolphins are able to learn and later recognize the echo signatures returned by preferred prey species. Despite the effectiveness of echolocation, studies show that a visually-deprived dolphin takes more time to echolocate on an object than a dolphin using vision in tandem with echolocation.

Major prey of odontocetes, cupleid fish, can detect ultrasound clicks up to 180 kHz. They respond to echolocating sounds by dolphins is escape behavior. This is similar to moths that are also able to detect and escape from echolocating bats.

Dolphins are much more flexible with echolocation that bats are, whereas bats' echolocation clicks tend to be frequency specific. Dolphins can shift the peak frequency of the echolocation clicks all over the place. They voluntarily control click amplitude as well. Dolphins seem to utilize low-frequency scans to get a coarse overall picture of the environment, and shifts to higher frequencies to examine things in more detail. Experiments have revealed that dolphins wearing soft latex eyecups can distinguish between two cylinders based on a wall thickness difference of just two tenths of a millimeter.

It has even been observed that dolphins' echolocation clicks can penetrate solids in much the same way as our ultrasound devices, stunning fish and allowing the animals to peer inside one another. In addition, dolphins can determine direction stereophonically and distance and relative motion from the beat frequency caused by interference between the current and previous clicks.

Echolocation is extremely sensitive and may provide cetaceans with a three dimensional view of their world. A recent hypothesis suggests that very high intensity focused bursts may be used to stun or disorient prey. This **big bang theory** suggests that, even if dolphins cannot kill their prey outright with bursts of sound, they can impair their prey's equilibrium or sensory system, making them easier to capture. The big bang theory may explain, for example, how dolphins can catch prey that can easily out-distance and out-maneuver them; or why dolphins have lost a large number of their functional teeth and their once-powerful jaws; or the high degree of cooperation between dolphins, necessary because they are carrying around the equivalent of a "loaded gun".

These so-called “loud impulse sounds” have been recorded during predation in the wild by bottlenose dolphins and orcas, made when the animals were hunting mullet and salmon respectively. Further evidence supporting this hypothesis was presented in 1989, based on experiments where the exposed anchovies to pneumatically-generated “loud impulse sounds” similar to those recorded in the wild. They discovered that these sounds killed and injured the anchovies.

Many researchers believe that dolphins can interpret some information from echolocation clicks of other dolphins. This idea has even been taken a step further, to a hypothesis where dolphins may communicate directly using their echolocation clicks. The dolphin constructs its image of the environment from the pair of acoustical waveforms arriving at its two acoustic receptors. The dolphin also has two separate sound producing organs, which it can use together as well as independently. In humans the principal mode of communication is acoustic, different from the principal mode of perception, visual. Dolphins communicate using the same acoustic sense with which they perceive, and could possibly even be capable of transmitting imagery to another dolphin.

Orcas also produce directional clicks in trains. Each click lasts from less than one to about five milliseconds. Clicks include a wide range of frequencies. A 25-kHz peak is common. Individuals can probably vary the peak frequency to suit the circumstances.

Belugas also produce directional clicks in rapid sequences. In one echolocation study, a single beluga produced signals with peak frequencies of 40 to 60 kHz in San Diego Bay, California, and 100 to 120 kHz when moved to Kaneohe Bay, Hawaii. The different frequencies were thought to be a response to the amount of ambient noise in the area. For belugas, echolocation is especially important for navigating under ice fields and locating breathing holes in the ice. Studies show that belugas have a higher capability of echolocating in the presence of ambient noise than bottlenose dolphins. Belugas are also able to receive and use surface-reflected echoes, which may aid them in navigating under an extensive ice pack.

The echolocation sounds produced by sperm whales consist of reverberant pulses that are repeated more slowly and at lower frequencies than those of bottlenose dolphins. Each click pulse lasts about 24 ms and consists of a series of up to nine individuals rapidly reverberating clicks. The repetition rate of the pulses is adjusted so that the echo of one-click pulse returns from the target before the next pulse is emitted. The click pulses of sperm whales are intense and many travel for several kilometers.

Acoustic signals produced by harbor porpoises cover a very broad frequency range (40 Hz - 150 kHz), with low, middle and high frequency components. The Commerson’s dolphin produces a narrow band frequency with nearly all the energy above 100 kHz and in a narrow region around 4 kHz.

The boto produces whistles that are very different than those from the oceanic delphinids. They are represented b y low and narrow frequency signals that have better refractive capabilities, which is important for species that live in rivers which have higher noise levels than pelagic environments and carry more suspended materials.

It is still unclear whether or not mysticetes have echolocating abilities. Mysticetes produce only very low frequency sounds in a manner that suggests that they are used only for communication. Some have suggested that they may still be useful to locate large objects or the general features of the sea bottom. Even if that were the case, its use seems to be much more reduced since the production of “clicks” are rare among

baleen whales and they do not have the anatomical adaptation described above for odontocetes. Studies have shown that bowhead whales produce low-frequency sounds that may give the whales information about the ocean floor and locations of ice.

13.4.2. Pinnipeds

Some sound may function as echolocation signals, which may be particularly useful when these animals are navigating and feeding and feeding in deep, poorly lit or turbid water. For example, diving Weddell seals produce eerie sounds hypothesized as echolocation signals, but no experimental confirmation that those clicks are used for echolocation has been presented.

13.5. Communication

Since virtually all the available information on communication among marine mammals is on the acoustic version of it that is where we are going to concentrate our efforts. We recognize that these animals may communicate visually and by touch or even by chemicals, but the information in these areas is so poor and scant that is of little use at this point.

13.5.1. Acoustic Communication

13.5.1.1. Cetaceans

Despite the numerous studies on this area, there is little that we know. The major reason for that is the tremendous difficulty of studying cetaceans in their natural environment so we can correlate sounds with behavior.

Bottlenose dolphins identify themselves with a **signature whistle**, which is unique for each individual. It is within a narrow band of frequency modulated (FM) sound often with a harmonic structure. Typically the frequency of these pure-tone emissions rises and falls between 7 and 15 kHz and averages less than a second. It is distinguished from the whistles of the other dolphins by its distinctive contour, or frequency variation over time, as revealed in sonograms. Calves appear to develop their own signature whistles between about two months and one year of age. These whistles remain unchanged for at least 12 years and quite likely through the animal's lifetime. Dolphins often whistle when separated from other group members or in response to the whistlers of group members. A mother dolphin may whistle to her calf almost continuously for several days after giving birth. This acoustic imprinting helps the calf learn to identify its mother. Dolphins also respond to “playbacks” from the whistles of other group members using recording. Additionally, the more social the delphinid species, the more whistles they seem to produce.

Scientific evidence suggests a general association between behavioral activity and the various types of vocals belugas. For example, researchers have observed that belugas tend to emit more squawk-type calls during periods of social interaction than during alarm situations. There is no evidence that belugas use anything resembling human language.

Louis Herman is perhaps today's foremost researcher studying communication and cognitive abilities in dolphins through using artificial languages (i.e. simple languages created for the research). He has focused on language comprehension rather than production, because comprehension is the first sign of linguistic competency in young children, and because comprehension can be tested in a more controlled manner than production.

In Herman's work, two dolphins, Akeakamai (Ake), and Phoenix, were taught artificial languages. Phoenix was taught an acoustical language made of computer generated sounds. Ake was taught a gestural, or visual, language. The signals of the artificial languages represent objects, object modifiers, or actions. Neither the gestures nor the sounds resemble the objects or relational terms to which they refer. The languages also use syntax or simple grammar rules, meaning that the word order affects the meaning of the sentence. Phoenix was taught a straightforward left-to-right grammar. Ake's gestural language grammar is inverse, requiring her to view an entire gestured sequence before it can be interpreted correctly. For example, in Ake's gestural language, the sequence of signals PIPE SURFBOARD FETCH means bring the surfboard to the pipe, and SURFBOARD PIPE FETCH means bring the pipe to the surfboard. Phoenix and Ake have each learned approx. 50 words, these 50 words allow more than 1000 different "sentences", each eliciting an unlearned, unrehearsed response. To minimize any possible effects of orientation to space or person on dolphin learning, stations and trainers are changed from session to session. Blind observers, people who do not know and cannot see the commands given, are used to label the actions they observe the dolphins perform as a means of comparing objectively the response to the command.

Trainers wear dark goggles, maintain expressionless faces, and hold their bodies steady during formal training sessions. Dolphins can understand gestural signals given by televised images of signers about as well as they can from live signers. Even just showing white hands in black space, or white spots of light tracing out the dynamics of the gesture, were understood. Because of these experiments, it seems that the dolphins are responding to the abstract symbols of the language rather than to any non-language communication or cues.

In addition to following the language instructions, Herman's dolphins can now correctly answer whether a specified item is present or absent by pressing the appropriate paddle (the white one for yes, or present, and the black one for no, or absent). This demonstrates the skill of displacement, the conjuring of images that are not around. It has been similarly demonstrated by Sue Savage-Rumbaugh, of Yerkes Primate Research Center, that apes are able to understand a reference to something that is not in their presence.

Things Herman has been unable to successfully teach the dolphins include the concept "not" as a logical modifier, so that jump over "NOT BALL" would indicate jump over anything but a ball. Also large and small do not seem to have been understood by the dolphins.

Data acquired from whale vocalization studies was practically applied to save a young whale when Herman provided a recorded whale feeding sound that was used to successfully lure Humphrey, the humpback whale who had swam more than fifty miles up the Sacramento River, back to the open ocean.

In addition to making their own signature whistles, some of the other whistles dolphins make are precise imitations of the signature whistles of companions, which appear to be for calling one another “by name”.

Psychologist James Ralston and computer specialist Humphrey Williams have found that the signature whistle can convey more than just a dolphin's identity. By comparing sonograms of the dolphin's signature whistles during normal social activities and stressful situations, they found that although keeping its general configuration, a signature whistle may change in pitch and duration, conveying information about the emotional state of the animal. The variation due to emotional states on intonations of the signature whistles varies with the individual.

The dolphins appear to use whistles to maintain contact, when socializing and meeting other dolphin groups, and perhaps to coordinate school activities. For example, whistles are often heard when groups change direction or activity.

Orcas have been found to produce repetitious calls that are now considered to be group dialects. Repertoires consisting of a small number of discrete calls (averaging about 10) are shared by individuals within a pod and appear to persist unchanged for several decades. These pod-specific repertoires seem to serve as vocal indicators of pod affiliation and help to make vocal communication within a pod more efficient.

There is some evidence that suggests that sperm whales clicks used for echolocation are also used for communication. Rhythmic pattern of clicks, known as **codas**, last up to 1-2 s and consist of 3-30 click pulses. Repeated production of these codas suggests that they are used as recognition codes for individual whales. These identity codas may allow pod members to keep track of each other when they disperse over large areas during foraging dives. Other sperm whale codas are shared by several whales in local groups, suggesting that they serve some communication function other than individual identity. Coda repertoires distinctive to groups seem to persist over several years and show significant, but weaker, geographical differences. The group-specific coda repertoires in sperm whales have, in fact, been likened to group dialects in killer whales.

By far the most vocal of all mysticetes are the humpback whales. While on their breeding grounds, they sing long and acoustically complex songs, which are shared by all singing whales occupying the same breeding ground. Each song, although often repeated for hours last between 10 and 15 minutes (with a maximum of 35) and is composed of repeated themes, phrases, and subphrases. Individual units that make up subphrases are typically a few seconds in duration with frequencies generally below 1.5 kHz.

The structure of these songs changes progressively over time. Most of the changes occur during the winter months on breeding grounds and typically include changes in the frequency and duration of individual units as well as deletion of old and insertion of new phrases or themes. The composition and sequence of themes within a song also change with time so that the song structure at the beginning of a winter breeding season is modified substantially by the end of that season a few months later, although all whales sing the same song at any point in time. Individual whales express same changes at the same rate as the rest of the group of singing whales. Thus, singing whales seem to actively learn songs from each other.

Only adult males sing, suggesting that these songs play a reproductive role similar to that of birds by communicating a singer’s sex, location, readiness to mate with females

and to engage in competitive behavior with other males. Some have also suggested that simultaneous singing by many males may serve as a communal display to synchronize the ovulation of females. Another possible use is to define territories.

13.5.1.2. Pinnipeds

Weddell seal vocalizations underwater are very loud and can be detected nearly 30 km away. They consist of trills, each composed of a series of pulses of decreasing frequency, which probably function as dominance signals; chirps, which sweep through a range of frequencies; and growls, usually below 0.2 kHz, which function as threats. The trills have the same character as the pulses used in echolocation by dolphins and it is likely that they are used for the same purpose, but this has not been proven. Tests on a harbor seal locating a ring in the dark in a small (7.5 m diameter) tank seemed to indicate echolocating ability.

Complex musical underwater songs, consisting of oscillating warbles that change frequencies and are punctuated by brief unmodulated low frequency moans, are produce by breaded seal males and possibly also females. Leopard seal vocalizations have been described as soft, lyrical calls. They showed a geographic variation ("dialects") from opposite sides of the Antarctic.

The most distinctive, however, are those of the male walrus. They produce a series of knocking sounds (including bells, bells-knocks, and double-knock bell phonations) often described a ringing bells that are produced both above and underwater. Similar sounds have been recorded in hooded seals.

13.5.2. Non-acoustical Communication

13.5.2.1. Chemical Communication

Water imposes limited ranges of diffusion of chemical communication, especially when compared with the mobility of marine mammals. That explains why chemical communication is very limited among these animals. Pinnipeds do use odor cues, for example, for mother-infant recognition, but these are primarily used in air. The olfactory bulbs and nerves used by terrestrial mammals are reduced in mysticetes and absent in odontocetes. There are some suggestions of the use of pheromones.

13.5.2.2. Tactile Communication

The vibrissae of seals are very sensitive to movement or vibrations, and the walrus can even discriminate the shapes of objects using mustache-like Vibrissae. Among many species mothers and calf keep in physical touch and manatees tend to embrace their young. Muzzle-to-muzzle contact is also common among pinnipeds when they greet one another. Dolphins and whales may rub or caress one another with their flippers and other appendages. Gentle rubbing seems to play an important role in maintaining affiliative relationships in some species of dolphins, perhaps analogous to social grooming in primates. Gentle touching by humans can provide positive reinforcement to captive bottlenose dolphins.

Sexual contact among males and between a male calf and its mother is not unusual and may serve the same reinforcement function seen among large primates. Suckling between a mother and its calf may continue for more than ten years.

13.5.2.3. Visual Communication

Many aggressive visual signals in marine mammals follow patterns that are common among other mammals, including vigorous moving of the head toward another animal, prolonged staring at another animal, jerking the head, opening the mouth, or even making threats that resemble biting actions. Some behaviors appear to increase the apparent size of a male and many function as visual display. For example, male humpbacks competing for access to females may lunge with their jaws open, expanding the pleated area under the lower jaw with water. Visual signals that have been identified in submissive interactions among dolphins include flinching, looking away, and orienting the body away from another animal. Thrusting or presenting the genital region toward another animal may function as sexual visual signals. Direction of gaze is an important visual clue among primates, and human observers can often tell immediately when a dolphin or seal is making eye contact. Although the behavioral consequences have not been well studied, gaze cues may be important for marine mammals in clear water as well as in air.

Besides vocalizations, belugas may communicate through facial expressions and physical contact. Visual behaviors such as breaches, pectoral slaps (slapping a pectoral flipper on the water's surface), and lobtails are not as common in belugas as in some other whale species.

13.6. Noise Pollution

In 1991, oceanographers from the U.S. and other countries conducted an experiment to determine if measuring the transmission time of low-frequency sounds across ocean basins could be used to detect changes in ocean temperature to monitor global warming. This experiment, referred to as the Heard Island Feasibility Test, was successful and a follow-up study was authorized. This study, the **Acoustic Thermometry of Ocean Climate** (**ATOC**) Program, called for installing 260-watt, low frequency sound generators in deep water off the coast of Hawaii and central California. Since then, oceanographers who routinely use sound waves to measure things in the water have faced scrutiny over whether their work harassed marine mammals.

After delaying the project for more than a year and finally agreeing to move the sound emitter away from a marine sanctuary off San Francisco, scientists in the California study began, in 1995, to broadcast low-frequency sounds that can be detected as far away as Alaska. Mammals did not appear to be bothered and certainly have not fled the area, but it is too soon to tell whether the noise is having any subtle effects on swimming patterns or other behaviors.

The U.S. Navy has been conducting broadcasting of loud, high-pitched sounds from underwater speakers, in part to test whether noise harms or disorients orcas and other sea mammals.

The scientists say the pulses of noise, the loudest of which would have the same sound intensity as a jet taking off, likely would not seriously hurt the roughly 100 killer

whales, or orcas that inhabit north Puget Sound waters in June or July. But critics contend the scientists actually have no idea whether the noise will cause temporary or permanent hearing loss in whales, and that the scientists' own proposal concedes the month long study may alter behavior patterns of whales swimming up to 4 miles away. The scientists proposing the study are from Woods Hole Oceanographic Institution and the Massachusetts Institute of Technology. They plan the sound pulses primarily to study the chemical and physical properties of a marine "front," where salt water and fresh water meet and first begin to mix.

Patrick Miller, a researcher from Woods Hole, says that most of the noise is not any louder than that emitted by a fish-finding sonar device. In total, the experiments should be less disruptive - and maybe even less noisy - than the 50 or more whale-watching boats that follow the whale pods every day, the researchers say.

But broadcasting sounds into prime orca habitat to see if the whales are bothered is "a bit like pouring poison into a river to see if it's toxic to fish," said Paul Spong, a scientist at OrcaLab, a research group that studies orcas whales at Vancouver Island.

This research also uses two 6-foot-long underwater robots to analyze water characteristics. The testing area is in Haro Strait, a key waterway for orcas as well as for porpoises, seals and other mammals, which rely on hearing to feed and navigate.

Though it is extremely unlikely the noises will severely injure or kill a marine mammal, the research could force some mammals, particularly whales, temporarily away from their preferred habitat, according to a review by the National Marine Fisheries Service.

The loudest underwater pulsed "ping" will be about 195 decibels, equivalent to about 135 decibels on land, or the approximate sound intensity of a nearby jet engine as heard by the human ear. An outboard motor issues a sound intensity of about 170 decibels underwater.

The sounds will be broadcast at high frequencies, in some cases out of the range of human hearing but certainly detectable by many marine mammals, the scientists say. The fisheries agency has announced it intends to grant the researchers a permit to do the experiments because the area in question is only a small fraction of orca habitat in Puget Sound. Further, the researchers have agreed to let an independent panel of four Northwest scientists monitor the work and shut it down if it appears the noise is directly harming sea life.

Sound to a marine mammal is like vision to humans, said Dan Costa, a professor of biology at the University of California-Santa Cruz, but the scientific community doesn't understand much more than that about it. "If somebody's shining a spotlight, is it going to be a problem for you to see? It depends on how bright it is and whether it's shining in your face and the same is probably true for a whale confronted by a loud sound," he said.

A whale or porpoise traveling close enough to a loud, directed sound may experience sensations ranging from pain to annoyance to nothing at all, Costa said. If it hears the sound and doesn't like it, the mammal typically will respond by swimming somewhere else, said Costa, who has been studying the effect of low-frequency noise blasts on sea mammals in California. "But the answer is, we don't really know what it does to them," he said. 'We do know there is so much more noise in the ocean from

boats than there is from researchers that if these animals is really that sensitive, and then we have an incredible problem on our hands."

Chapter 14

Diet, Food Finding, and Feeding Apparatus

14.1. Introduction

Marine mammals widely diverge in their feeding habits. Some are top predators eating large preys (e.g., orcas, sperm whales), while others specialize in consuming large quantities of very small organisms (e.g., baleen whales, crabeater seals). Many pinnipeds have a much diversified diet while manatees are grazers.

This diversity of feeding preferences is also reflected in their feeding apparatus and foraging structures. Also, feeding is, for many species, highly seasonal since the abundance of most of their food sources also show strong seasonality related to ecological conditions.

In this and next chapter we will examine the food, feeding apparatus, and foraging strategies of marine mammals.

14.2. Ecological Constraints and Feeding

Marine mammal diets and foraging behaviors are direct consequences of both the spatial and temporal patterns of marine primary productivity. This productivity is highest over continental shelves and other shallow banks, in regions of upwelling, and in areas that cool appreciably during the winter months. At high latitudes, phytoplankton essentially disappears during the cool ('night') months of the year that, in turn, diminishes the abundance of any other type of organisms in the food chain. That is why baleen whales feed in those waters only during the warm or summer months. Most tropical and subtropical pelagic areas are characterized by very low rates of primary productivity with very little seasonal variability.

14.2.1. Cetaceans

Cetaceans tend to be clumped in their distribution that is primarily determined by food sources. We find the largest concentrations of baleen whales in those areas with high productivity, particularly during their feeding season. In the southern hemisphere that is true for areas of high concentrations of krill while in the northern hemisphere that is the case for large concentrations of other crustaceans. Odontocetes, on the other hand, can be found where there are discontinuities in the sea topography such as along the continental shelf edge where a larger proportion of fish shoals and plankton can be found.

14.2.2. Pinnipeds

There are both geographic and seasonal variations in the diet of many pinnipeds. This is especially true for otariids living in temperate and tropical areas where there is considerable inter-annual variability related to the ENSO events.

14.3. Diet

An efficient diet is a compromise between the energy consumed in food and the energy spent while pursuing that food. For most pinnipeds and odontocetes, food items are large and relatively sparse and are located and captured one at a time. For mysticetes, food items are much smaller and taken in great quantities at the same time.

There are some generalizations that we need to remember in order to understand food preferences among marine mammals.

(1) In general, more energy per unit body weight could be obtained by feeding on fish or plankton than on squid
(2) Fish proteins are more digestible, while the chitin present in euphasiids is hard to digest
(3) Different fish have different caloric content due to differences in their relative amount of fat
(4) Number and size of individuals eaten will influence the energy intake

14.3.1. Mysticetes

Mysticetes feed primarily on planktonic or micronectonic crustaceans (e.g., krill) and/or small pelagic fish found at relatively shallow depths, usually between 100 and 500 m.

In Antarctic waters the Antarctic krill, *Euphasia superba*, represents one half of the total zooplankton mass. All the southern great whales feed primarily upon this krill species. Blue whales feed almost exclusively upon krill while the sei whale does not penetrate so far south and has a more varied diet hat includes other crustaceans such as copepods and amphipods. The more tropical Bryde's whale takes only a relatively small amount of plankton, feeding instead upon anchovy and other schooling fish.

In the northern hemisphere where krill is not so dominant, the diet of great whales is more varied also. They include not only other species of crustaceans but also fish and squid. Because the lack of uniformity in the Arctic when compared with the more homogeneous environment created by the circumpolar current of the Antarctic, there are not only geographic but also seasonal variations in diet. Sei and fin whales depend much more upon squid and fish. Other species, such as the southern right whales and the northern right whales feed mostly copepod crustaceans of the genus *Calanus* regardless of where they may be. The blue whale although feeds upon euphausiids no matter where they are, shift among genera of this krill: in the Southern Oceans they prey on *Euphasia* while in the North Pacific and North Atlantic they do it on *Meganyctiphanes* or *Thysanoessa*.

14.3.2. Odontocetes

They are all carnivores, feeding on fish, squid, and large crustaceans, birds and, some species, on other marine mammals. Prey is usually captured individually unlike the massive sieve feeding behavior of the mysticetes. The daily consumption of odontocetes ranges between 5 and 20 per cent of their body weight. Toothed whales feed all year round and do not typically migrate.

These teeth are suitable for grasping quick-moving prey. Most odontocetes feed on either fish or squid (or a combination of both) although orcas feed on other marine mammals as well. Some of the squid eaters have the tendency of having a reduced number of teeth; such is the case of the sperm whale, which has no functional teeth in the upper jaw, and the beaked whales. These species employ the tongue as a piston-sucking squid into the mouth.

The sperm whale eats almost exclusively on squid. They concentrate in the largest of the species of squids of the family Architeuthidae of 12 meters in length or more. However when inshore they may shifty toward fish. Pygmy sperm whales and dwarf sperm whales also feed on squids, but are more open to eat other species such as octopuses and crabs. The beluga eats not only fish but also squids, crustaceans, nereids (marine worms) and even gastropod mollusks showing, thus, a great variety in diet.

The orca is the only species that regularly feeds upon other marine mammals besides fish (salmon and cod) and squids. They include California's and southern sea lions, elephant seals, Dall's and harbor porpoises, and large baleen whales. Occasionally they may feed upon penguins. They have been described as both, generalist and opportunistic feeders. In 1999 it was reported that they switched from eating pinnipeds to consuming sea otters. This seems to be due to the fact that pinniped populations have been reduced by the diminishing population of fish in the northwester waters of the U.S.

River dolphins such as the boto of the Amazon and Orinoco basins feeds on armored or heavily scale fish which it sizes with the front part of the beak and then moves backwards to the rear of the mouth where they are crushed with the help of its large somewhat molar shaped rear teeth.

Bottlenose dolphins feed on a variety of prey. In offshore regions these include pelagic fish and squid. In coastal waters, they feed upon various shallow water benthic fish as well as upon shrimps and other crustaceans.

Other delphinids such as *Stenella* spp. and *Delphinus* spp. are opportunistic feeders as well. Their diet varies seasonally and from one year to the next. The pincer-like action of the jaws of these long-snouted forms allows fish to be trapped by the interlocking tips of thee teeth when jaw closes and water is forced out.

14.3.3. Pinnipeds

Most pinnipeds are generalist feeders. While generally favoring schooling fish (mostly herring, anchovy, and capelin) and squid (most commonly squid), pinnipeds have a varied diet that may range from planktonic crustaceans and bivalve mollusks to mammals, and birds. They tend to switch from one prey to another depending upon availability. Some species, and certainly individuals, show distinct preferences in their choice of prey, often determined by seasonal or regional abundance.

Prey preferences usually changes with age. For example, adult harp seals typically feed on fish and some crustaceans whereas pups eat mainly zooplankton. They may be due to the fact that juveniles require prey that is easier to capture. A difference in foraging strategies by young and adult female Steller sea lions has been implicated as a factor in the recent decline in their Alaskan populations. It has been suggested that because the young have a more limited diving ability they are more affected by changes in prey distribution.

Pinnipeds forage both individually and cooperatively in groups. These resources most efficiently captured by an individual animal include non-schooling fish, slow moving or sessile invertebrates, or relatively small warm-blooded prey. Many phocids, including elephant and harbor seals, are solitary foragers. Cooperative foraging occurs most frequently among pinnipeds that exploit large, patchily distributed schools of fish or squid. Many fur seals and sea lions cooperate and forage in groups. Foraging strategies exhibit considerable plasticity depending on the type and distribution of the food resource. For example, Steller sea lion forage together in large groups when feeding on schooling fish or squid, but feed singly or in small groups otherwise

Some species, such as the harbor seal and California sea lion, feed in coastal waters and often enter rivers. Others, such as the northern fur seal, northern elephant seal and gray seal, forage in deep water, well offshore. Walruses and Steller sea lions occasionally prey upon other species of pinnipeds.

The Steller's sea lion seems to be less particular when choosing prey than the California sea lion, and regularly eats mollusks, bivalves, crustaceans, krill, and more diverse types of fish than the California species. Steller's sea lions have even been known to prey on marine mammals, including two local species, the harbor seal (*Phoca vitulina*) and the sea otter (*Enhydra lutris*). However, this behavior tends to be limited to the large adult or subadult Steller's males. Leopard seals are known to prey on birds.

Walruses prefer mollusks, mainly bivalves such as clams. They can eat up to 6,000 off them per day, at a rate of six clams per minute, which means that they send between 16 and 17 hours foraging. They obtain them by swimming along the sea bottom in a head-down position, stirring up sediments with their snout and sensitive vibrissae. When the clam is located they either suck it directly in their mouth or is first excavated with jets of water squirted from then mouth. The soft tissue in then sucked from the shell by the tongue, which acts as a piston creating very low pressure in the mouth cavity. Pressure changes are caused by retraction of the tongue by the large styloglossus muscle and its depression by the large genoglossus muscles.

Walruses also eat many other kinds of benthic invertebrates including worms, gastropods, cephalopods, crustaceans, sea cucumbers, and other soft-bodied animals. Walruses may occasionally prey on fishes such as polar cod. Walruses may eat the remains of young seals when food is scarce. There are some rare but habitual seal-eating walruses. Their diet consists mainly of ringed and bearded seals. These are usually male walruses, recognizable because they are usually larger than other males with powerful shoulder and chest muscles. Their skin may become grease-stained from the blubber of the seals. They use their tongue vacuum pump to suck away the skin, blubber, and intestines.

14.3.4. Sirenians

Sea grasses they consume include species of the genera *Enhalus*, *Halophila*, *Halodule*, *Cymodocea*, *Thalassia*, *Thalasodendron*, *Syringodium*, and *Zostera*. Algae are also taken but only in very small amounts if the sea grasses are very abundant. Manatees may also graze on floating freshwater plants such as *Hydrilla* and water hyacinths). Dugongs in Australia may consume sessile benthic invertebrates such as ascidians (sea squirts) and polychaetes (marine annelids).

14.3.5. Sea Otters

Sea otters preferentially forage on benthic invertebrates, particularly sea urchins, gastropod and bivalve mollusks, and crustaceans.

14.3.6. Polar Bears

Polar bears use their powerful jaws to capture large prey items, such as other marine mammals and large fish, although they also scavenge on carcasses. They prey preferentially on ice seals (ringed, bearded, and ribbon), and sometimes harbor and sharp seals. They would occasionally take walruses (especially pups in the Canadian Arctic), belugas, and birds.

14.4. Food Finding

The process of finding, localizing, and approaching prey requires specialized sensory systems.

Whales and dolphins prey mostly upon schooling prey. Since most **cetaceans** are very social, most of the food search is also conducted in groups, which help them to cover a wider area. Most dolphins and fish- or squid-feeding small whales travel in schools that are broader than they are long. In this way they are able acoustically to scan a greater area than would otherwise be possible. The number of individuals that can be sustained by the prey concentration probably determines the size of the school. This could explain why the great whales tend to feed singly or in twos. Their food intake is such that plankton concentrations may rarely be sufficiently large to support a number of animals at any one time. Squid eating whales such as sperm whales, pilot whales and beaked whales are usually found in concentrations of less than 100 individuals. Dolphins such as the common, spinner and spotted are occasionally found in the hundreds, sometimes even in groups of over a thousand individuals. River dolphins usually are found solitary or in groups of no more than three individuals. Concentrations of dolphins are used by other animals as well as by fishers, to locate fish schools. That is the case with dolphins and tuna in the Eastern Pacific Ocean.

Mysticetes possess vibrissae on the dorsal and lateral surfaces of the rostrum, which might function in determining maximum prey density in the water column and orienting the whale during feeding bouts. Odontocetes use a highly developed echolocation system important to prey location.

Pinnipeds and sea otters have extremely sensitive tactile vibrissae located on the lips and cheek that are used to locate prey. Walruses locate benthic invertebrates by probing the ocean sediment with their vibrissae.

Sea cows also possess abundant and sensitive vibrissae that are probably important to integrating feeding behavior.

Polar bears possess highly developed nasal turbinates with large surface areas covered with olfactory sensory epithelium that allow them to smell seals even through meters of snow.

14.5. Variations in the Feeding Apparatus

The function of the digestive system can be described in three steps: (1) capture and manipulation of food/prey (**feeding**), (2) mechanical and chemical **digestion**, and (3) **nutrition**.

Food enters the oral cavity (**ingestion**), is processed (**mastication**), and swallowed (**deglutition**), through the coordinated action of the lips, muscular tongue, and teeth. Carnivores tend to move their jaws up and down, with little lateral and no rotary movements at the jaw joint. Contrarily, herbivores spend considerable time chewing, grinding, and processing their food to break down the tough cell walls of plants. In both carnivores and herbivores the process of mechanical and chemical digestion (with salivary enzymes) begins in the oral cavity.

Swallowed food passes through the muscular pharynx to the esophagus, then is carried by peristalsis to the stomach, where mechanical and chemical digestion continue. The stomach of mammals can be simple sacs (e.g., humans, carnivores) or complex, compartmentalized structures (e.g., ruminants). The slurry of food and digestive enzymes (now called **chyme**) passes out of the stomach and enters the small intestine where bile and digestive enzymes from the liver gallbladder, and pancreas are added, and where nutrients and water are absorbed. Food then passes into the large intestine where more absorption takes place. Generally, if the diet of mammals is easy to digest, as in carnivores, the intestine length will be relatively short. Contrarily, herbivores, which feed on low-nutrition plants, tend to have very long or voluminous gut tubes. Because mammals lack enzymes to digest cellulose, commensal bacteria in the gut must help to digest plant matter. The undigested material passes through the gut and is eliminated from the body as feces.

Marine mammals present a wide range of variations in their feeding methods:
Total herbivory: manatees
Quasitotal herbivory: dugongs
Hunting and capture of individual prey: most odontocetes and pinnipeds
Suction feeding: walruses, sperm whales, beaked whales
Engulfing whole schools of fish and/or invertebrates: baleen whales

These variations in feeding methods are accompanied by variations in their feeding apparatus.

Finally, we must take into consideration that because of the aquatic environment, most marine mammals have developed unique system for locating their prey as well as locomotory strategies in order to capture that prey.

14.5.1. Cetaceans

The evolutionary history of cetaceans and, hence, their classification, is linked to their feeding strategies. Mysticetes feed by straining large quantities of water containing plankton and other larger organisms through a series of horny plates or baleens that grow down from the sides of the upper jaw. Odontocetes capture prey with their conical teeth.

14.5.1.1. Mysticetes

14.5.1.1.1. Baleen Plates

Mysticetes only have visible teeth in their fetal stage. From birth, instead of teeth, they have a series of **baleen plates** suspended from each side of the upper jaw. They are projected ventrally from the outer edges of the roof of the mouth. The base of each plate is deeply embedded into the epidermal pad of the palate. The baleen, also known as 'whalebone' is not really bone, but is made of keratin, the same protein substance as our own hair and nails, and the horns of cattle. This chemical nature was the bases of its multiple uses in human society comparable to the uses we give today to plastics.

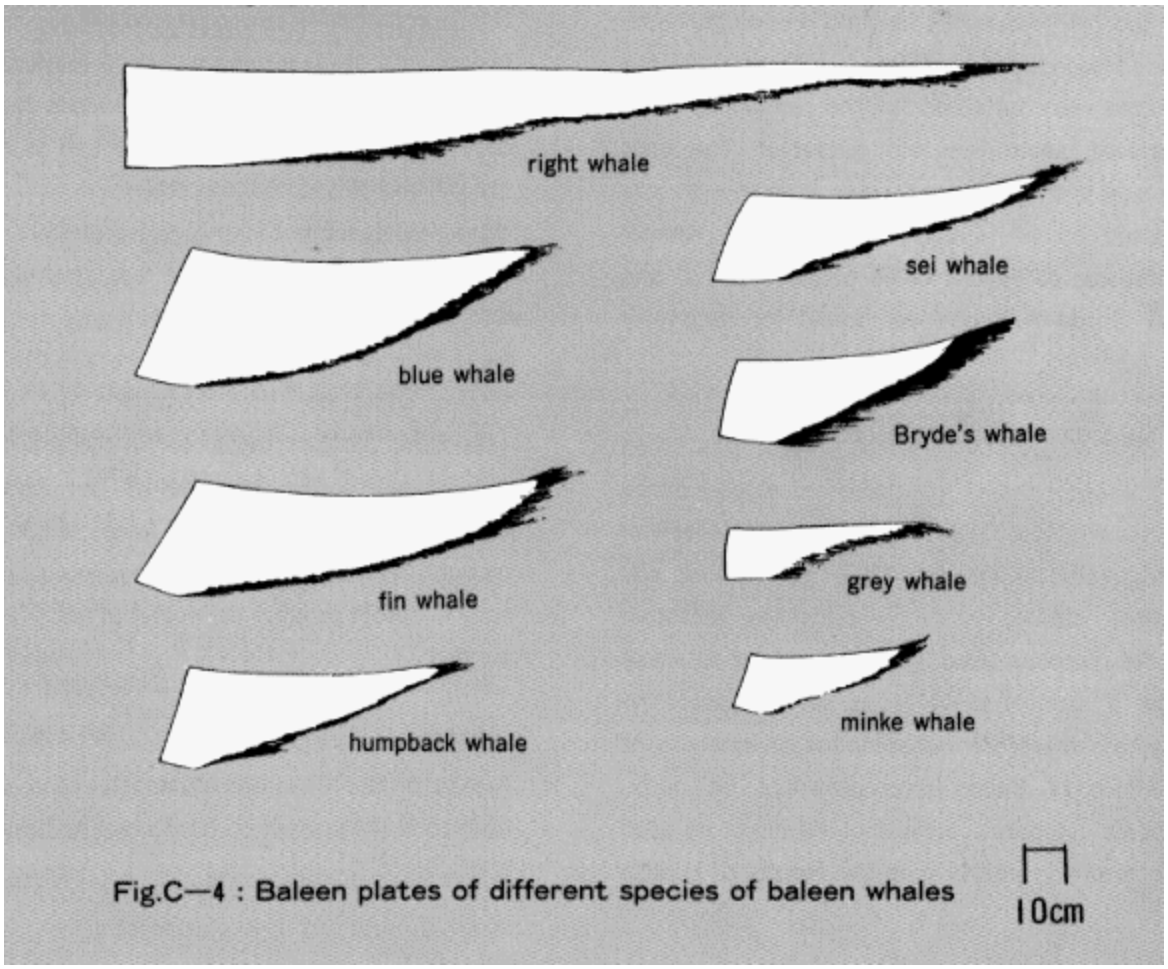


Fig.C—4 : Baleen plates of different species of baleen whales

Each baleen plate is formed as a sandwich -two outer sheets of keratin surrounding a tubular-keratin 'marrow' layer. The action of the tongue passing back and forth across the baleen abrades the adjacent keratin sheets and exposes the tubular marrow layer. These exposed tubules overlap creating a mat that functions as a sieve to rap engulfed prey. The baleen plates grow continuously from the maxilla throughout the life of the individual.

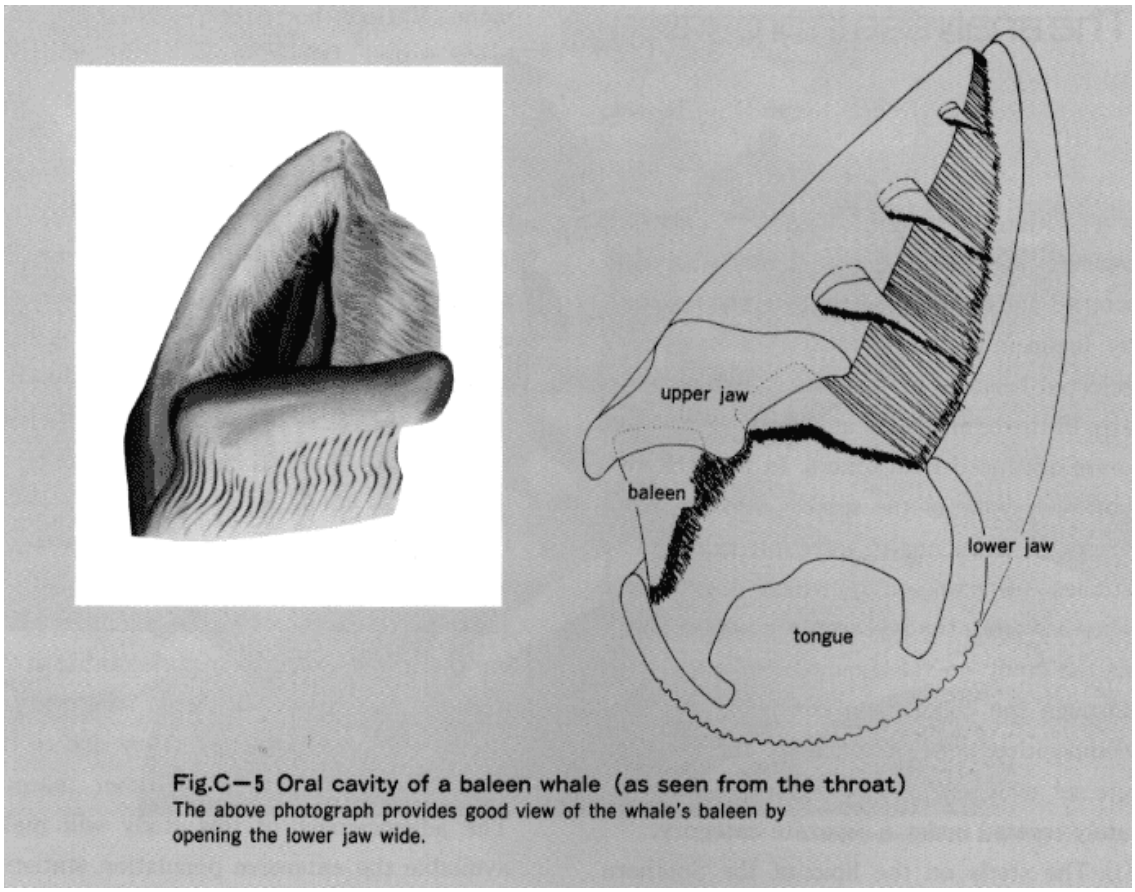


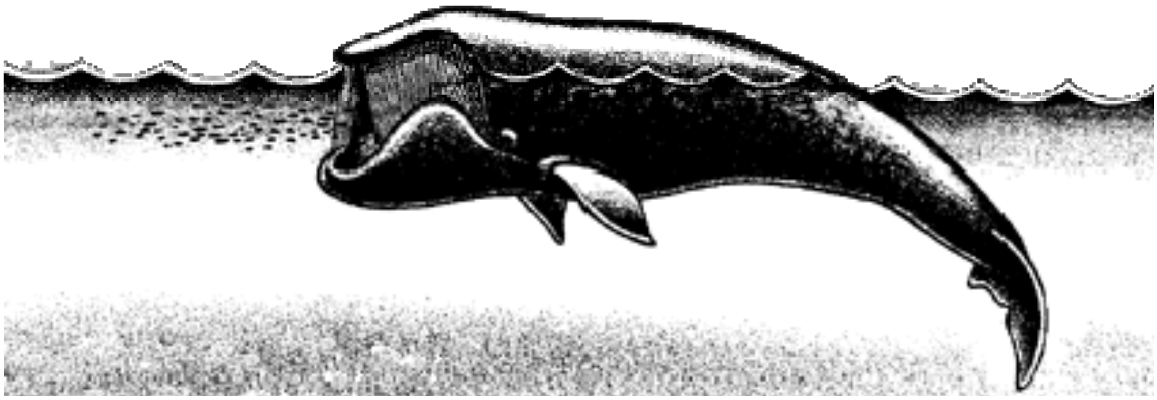
Fig.C—5 Oral cavity of a baleen whale (as seen from the throat)
The above photograph provides good view of the whale's baleen by opening the lower jaw wide.

The number and size of plates varies from species to species, from about 100 each of 1 m in length in gray whales to more than 350 and more than 3 m in length in right whales. Bowhead whales have 4 m long plates while blue whales have 75 cm long ones. The plates are fringed with hairs along their inner edges and descend like curtains in two rows from the upper jaw. Right whales have fine-fringed baleen plates that function to capture small euphasiids, whereas balaenopterid whales have a coarser fringe suitable for capturing fish and larger invertebrates.

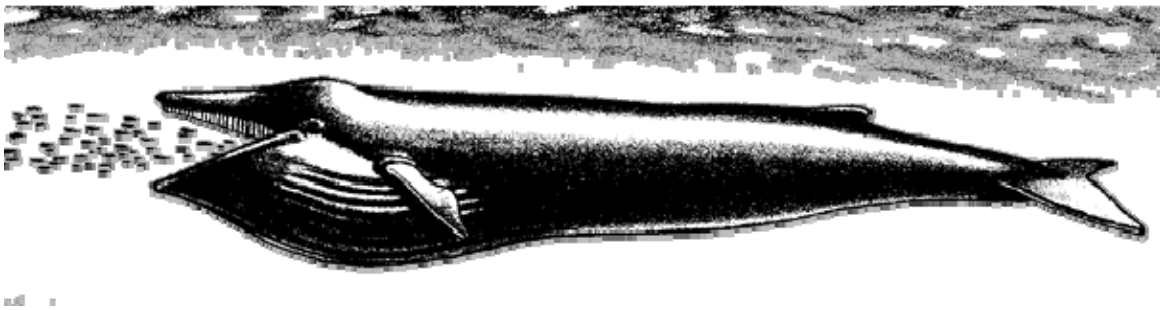
It may help to remember the two different types of cetaceans by knowing that the scientific name for baleen whales, mysticetes, comes from the Greek word *mystax* which means mustache. It refers to the hairy appearance of the baleen plates, which baleen whales have instead of teeth. The color, number and length of the plates can be used to help identify the species.

Mysticeti jaws are also adapted for wide opening. In the humpback whale, for example, it has been shown that the jaw will temporarily dislocate to increase its size during feeding.

The balaenids (bowhead and right whales) have a long narrow upper jaw or rostrum, which arches upwards to accommodate the long slender baleen plates (2-3 m long in the right whale, 4 m or greater on the bowhead). There may be 200-400 plates on each side of the jaw, lines with long fine bristles. They feed by skimming the surface with their mouths open, collecting food organisms and dislodging them into the mouth with the tongue.

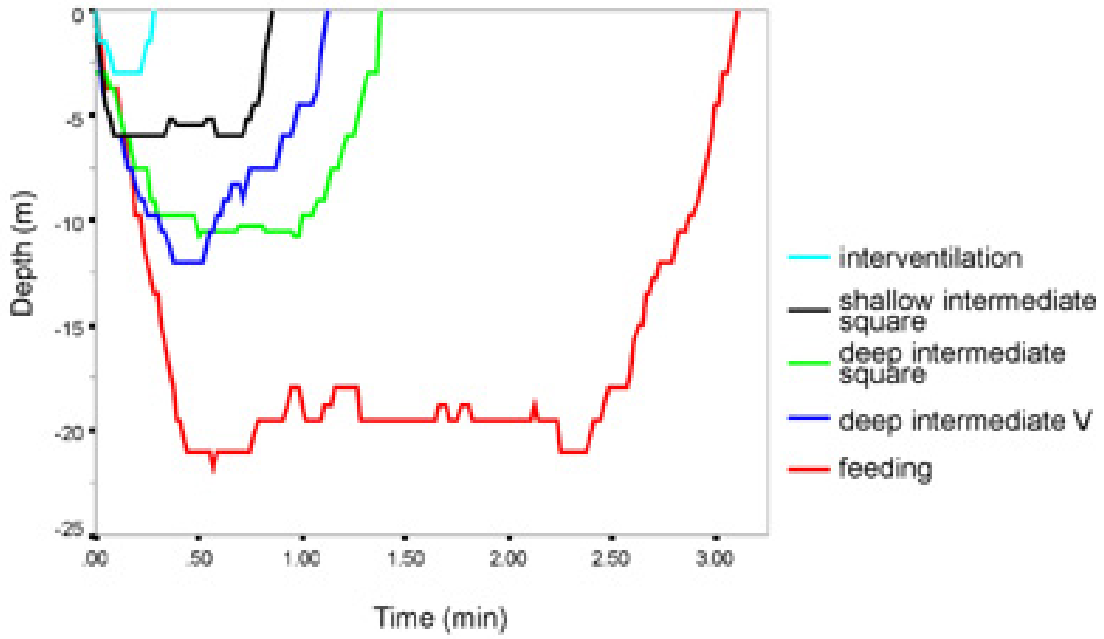


Balaenopteridae (rorqual whales): The rostrum is broader and only gently curved, and the baleen plates much shorter although they vary somewhat in size between species. Sei and blue whales have up to 400 relatively short baleen plates.



Eschrichtiidae (gray whales): They are bottom feeders. Have a shorter and thicker jaw with between 130 and 180 stiff plates.

Invertebrates eaten by marine mammals include mysids (*Holmesimysis sculpta*) (A), amphipods (*Ampelisca agassizi*) (B), and porcelain crab larvae (*Pachycheles rudis*) (C).



14.5.1.1.2. Digestive Tract

Most marine mammals (with the notable exception n of orcas) although not feeding on large single prey, nonetheless can swallow huge amounts of food at a time. They possess nonglandular forestomach that essentially acts as a holding sac for later stomach chambers. All cetaceans have a distensible forestomach that leads to a glandular main stomach. From there, food passes through connecting channels to the pyloric stomach. Despite the fact that cetaceans are carnivorous, they retain a complex stomach, superficially more similar to that of herbivorous artiodactyls. Cetaceans in general lack a gallbladder.

14.5.1.2. Odontocetes

14.5.1.2.1. Teeth

As their name implies, toothed cetaceans have teeth. The shape of the mouth and jaw, and the number, size, and shape of teeth vary considerable among odontocete families, yet most exhibit strong differences in tooth numbers and shapes from typical placental mammals. Unlike many mammals, toothed whales do not have 'baby' teeth, but develop a single set, none of which are ever replaced. Because only one set of teeth is produced in the lifetime of the animal they are called **monophyodont**. Odontocete teeth are usually disposed in a single row, closely spaced, and bear growth rings in cross section that are useful for estimating the age of the animal. Most of the tooth consists of dentin covered by a thin layer of cementum (on root) and a very thin layer of enamel (on crown). The teeth are usually unicuspid, conical (but phocoenids have spatulate), and with a long root, and because they are very similar among themselves, it is said that odontocetes have a **homodont** dentition.

The number of teeth varies from 1 on each side of the lower jaw to 260 in total. Even within a single species, the number of teeth may vary in up to 450%. On the other hand, certain species such as beaked whales tend to have a fairly constant number of teeth. Because it is not possible to distinguish teeth by type (incisors, canines, etc.), the number of teeth is indicated in 16 simple fractions. For example, 16/20 indicates that there are 16 teeth per side in the upper jaw and 20 per side in the mandible. Some species (e.g., in the Phocoenidae) have the same number of teeth in the upper and lower jaws (15/15 to 30/30). Members of the family Delphinidae range between 0/2 (Risso's dolphin) to 65/58 (long-snouted spotted dolphin). The count for sperm whales is 0/25 and 0/8 -0/16 for the pygmy sperm whale.

Two very unique types of dentitions are found among odontocetes. One is the case of the beaked whales and the other is the case of the narwhal.

Beaked whales have only one tooth in the lower jaw. Given that they have small mouth, the way they capture they prey is still a mystery. These animals erupt mandibular teeth curve medially above the rostrum, thereby limiting the extent to which they can open their mouths. Since females and immature males lack these teeth, it has been suggested that it is a sexual character that may play a role in intraspecific fighting. It has also been hypothesized that, because they lack teeth functional for feeding, they may practice suction feeding. Of all of these species, the strap-toothed whale (*Mesoplodon layardii*) may represent the most extreme case. Its paired teeth arise from the mandible and cross tightly above the dorsal surface of the rostrum. This configuration apparently keeps the oral cavity from opening more than a few centimeters.

The case of the narwhal is even more remarkable. Males have a tusk that may exceed 3 m in length. Generally it is an overgrown canine whose outer surface is marked by a series of prominent spiral ridges that may number five or six 360° turns on a large specimen. The spiral of the tusk is always sinistral (or counter-clock wise) when viewed from the root. Males occasionally may develop two tusks or none at all, and females may erupt a left tusk or both tusks. When present, the tusks of females are shorter and less robust than those of males.

Although it was thought initially that tusks were used for stirring food from the bottom, a film showing two males using their tusks as sort of 'swords' in ritualistic combats led to believe that such was its function, especially given the fact that they developed mostly among males at sexual maturity. Yet, a number of questions remain unanswered. Why some males never develop them while some females develop up to two tusks? How come scars show that they may be used in violent fights when even females may be killed?

In any case, the precise function tusk remains a mystery. We do not know, however, that it is likely responsible for the myth of the unicorn.

14.5.1.2.2. Digestive Tract

They have an extremely long alimentary canal. This may be related to the increased metabolic demands of a larger body size. The **gastrointestinal tract** has some unusual modifications. The long **esophagus** is penetrated dorso-ventrally by the laryngeal tube. In most species, food must pass to either side of this structure to reach the **three-chambered stomach**; in pygmy sperm whales, the left side is a blind pouch and food

must pass to the right of the laryngeal tube. Digestion begins in the first stomach (**forestomach**), actually an enlargement of the distal part of the esophagus, aided by enzymes and hydrochloric acid that reflux from the second (**fundic**) chamber also known as main stomach. Undiluted acid in excess can produce ulcers in all chambers (particularly the first), a condition often seen in starving strandings. The third (**pyloric**) stomach secretes mucus and prepares the food for intestinal digestion.

This pattern of stomach compartmentalization is found in all cetaceans, except for the beaked whales and river dolphins.

In odontocetes, the first and second chambers often contain **nematodes**, and it is not unusual for the second and third chambers to have a mucosal surface embedded with grape-like structures, each containing the **trematode** *Braunina cordiformis*. The intestinal tract of odontocetes is not visibly organized into small and large intestines, and in small animals it can measure 20 to 30 m in length. Mysticetes have a distinguishable colon. The basic difference between the intestine of baleen and toothed whales is that there is a caecum in baleen whales and none (with the exception of the Ganges River dolphin) in toothed whales. Cetaceans seem to lack an appendix, but anal tonsils are found in most, if not all species of cetaceans.

Other notable features include the absence of a gall bladder, a peculiarly small and firm spleen, which may be accompanied by one or more even smaller accessory spleens, and a long chain of large mesenteric lymph nodes. Their liver is bilobulated, and a third lobe may be present. The kidneys are elongated and lobulated, and the urinary bladder small.

14.5.2. Pinnipeds

14.5.2.1. Teeth

The dentition of most pinnipeds is rather simple. Pinniped teeth, following the typical mammalian convention, are named according to their type and position in the toothrow. Abbreviations used for each tooth type are as follows: I = incisors, C = canines, P = premolars, M = molars, PC = postcanines. The incisors and canines are always well developed. The molars are less developed among the general feeders. There is no obvious distinction between premolars and molars, reason by which all teeth behind the incisors and canines, which have a nearly uniform shape characteristic for each species, and are referred to simply as 'postcanines.' The canines have annular rings in cross section that can be used for determining the animal's age.

The number of teeth of each type (I, C, P, M) is called the **dental formula**. It is written as the number of each type of tooth on one side of the upper jaw over the corresponding number occurring in one side of the lower jaw. Humans, for example, have a dentition formula of incisors = 2/2, canines = 1/1, premolars = 3/3, molars = 2/2. Because the tooth types are always presented in the same order, this formula may be abbreviated as I2/2, C1/1, P3/3, M2/2 = 32 (total). Numbers affixed to the letters used to identify teeth can be of two types: superscript for teeth in the upper jaw and subscript in the lower jaw. The number itself refers to the position of the tooth counting from the front. Thus, I^2 , refers to the upper second incisor; PC_3 , refers to the second postcanine. Small letters indicate milk dentition.

There is a reduction in the number of teeth among pinnipeds when compared with most carnivores. Except for the double rooted condition of the postcanines, all teeth have a single root. The decrease in the number of roots is a derived character among these mammals.

Otariids have more teeth (34-38) than phocids (22-36), and more than the walrus (18-24). The typical otariid dental formula is I3/2, C1/1, PC 5-6/5. Among phocids, the phocines have I3/2 (except for the hooded seal which has 2/1) and the monachines have I2/2 (except for the elephant seal which has 2/1). The rest of the dental formula for phocids is C1/1, PC5/5.

Deciduous or milk teeth in phocids are reabsorbed before birth or shed shortly after, and those of otariids, within three to four months. Deciduous or milk teeth are very small and simple in shape and precede only incisors, canines, and P2-4.

The most prominent teeth among pinnipeds are the tusks of walruses. They are two in number, present in both sexes, but slightly slender in females. These tusks are modified upper canines, and their large size has resulted has resulted in changes to the shape of the anterior end of the skull. A single tusk may reach one meter in length and weigh as much as 5.4 kg. Male walruses use their tusks mostly mainly for dominance displays and females use to defend themselves and their young, and are occasionally use by both sexes to pull themselves onto ice floes.

Crabeaters have elaborately cusped teeth that interdigitate when the jaws are closed to produce a fine sieve. The dentition may function to strain small schooling krill from the engulfed water just as the baleens in mysticeti whales.

14.5.2.2. Digestive Tract

Pinniped internal anatomy is similar to that of most carnivores. They have a single, highly distensible stomach, which is essentially a dilation of the gut tube. They have a small intestine, caecum, a short large intestine, and a multi-lobed liver. Salivary glands are relatively small. The food is usually swallowed whole, without mastication and the saliva has no digestive enzymes.

14.5.3. Sirenians

Sirenians have highly mobile lips and vibrissae to gather aquatic vegetation.

14.5.3.1. Teeth

Manatees: Five to seven functional teeth in each upper and lower jaw and it has been estimated that from 20 to 20 teeth per jaw are possible within the lifetime of a given individual. The cheek teeth are **brachyodont**, i.e., short-crowned, and are enameled but lack cementum. Teeth are replaced from the rear. Frontal teeth wear from excessive sand and grit and then fall out.

Dugongs: They have a fixed dental formula of I1/0, C0/0, P0/0, M2-3/2-3, with vertical replacement. Their teeth are replaced vertically as in most mammals. Two mil incisors are present on juveniles. They are too small, do not erupt, and are reabsorbed. Among

males they are lost by the time of tusk eruption, while in females they persist until the animal is about 30 years old.

14.5.3.2. Digestive Tract

Sirenians have a glandular stomach of sirenians is generally similar in structure to that of other nonruminant herbivores. The most unusual feature of the sirenian stomach is an accessory digestive gland, called the cardiac gland, which apparently functions to isolate delicate glandular tissue from abrasive food entering the stomach.

The West Indian manatee has submaxillary salivary glands while large parotid glands are the only salivary glands in the dugong. The most characteristic feature of the sirenian tongue in the form of the taste buds: in the dugong they are contained in pits and in the manatee they occur in swellings. Tonsils are absent.

The digestive tracts of both the dugong and the manatee are extremely long. Their stomach is a simple sac with a unique cardiac gland whose function may have to do with the vegetarian diet of these animals. The caecum and large intestine are three main areas of absorption of the fiber portion of the diet. In the adult dugong the large intestine is up to 30 m long, twice than the long intestine while the large intestine of the manatee measures between 18 and 20 m in adults. The shape, length, and rich bacterial flora support the contention that sirenians are non-ruminant herbivores that digest cellulose and other fiber carbohydrates. In many ways, their gross anatomy is very similar than that of their close relatives, the elephants.

The liver of the dugong has three main lobes and is position against the almost horizontal diaphragm. The gall bladder is small in the dugong and large in the manatees.

14.5.4. Sea Otters

Their dentition and jaw structure does not differ much from that of other carnivores. The dental formula of sea otters is I3/2, C1/1, P3/3, M1/2, differing from that of most other carnivores in having a reduced number in the lower incisors. In addition, the carnassials and molars are modified from their slicing roles in terrestrial carnivores to blunt crushing teeth suitable for breaking up exoskeletons and shells of invertebrate preys.

14.5.5. Polar Bears

Like sea otters, polar bears have a dentition not really different of those of other carnivores. They have 38-42 teeth and a dental formula of I3/3, C1/1, P2-4/2-4, M2/3. The molars are broad, flat and multicusped with an emphasis on grinding and crushing rather than slicing using their powerful jaws.

Chapter 15

Foraging Strategies and Social Behavior

15.1. Mysticetes

Mysticetes have six different strategies for efficiently feeding on small prey: (1) skimming, (2) engulfment, (3) bubble-cloud feeding, (4) flick or lobtail feeding, (5) lunge feeding, and (6) mud scooping. Each one of these strategies is related to specific morphological features in the mouth, tongue, and the way by which the mouth is expanded.

Skimming: This is the strategy followed by members of the Balaenidae family (right and bowhead whales). They are slow swimmers, with highly arched rostrum and very long and finely textured baleen housed within a tall and blunt mouth. These whales feed by skimming the surface of the water collecting prey on the baleen, as the tongue expels water.

Engulfment Feeding: This is the preferred method employed by members of the balaenopterids family (rorquals). They are fast, streamlined swimmers with shorter and coarser baleens. Their mouths are very large, extending posteriorly nearly half the total length of the body. They have 70-80 external grooves (furrows) in the ventral wall of the mouth and throat, collectively referred as **throat grooves**. During feeding in blue and fin whales, this grooved mouth floor can open like pleats to lengths of up to four times its circumferential resting length as it inflates with a volume of water equivalent to 70% of the animal's body weight. It has been estimated that a mature blue whale may engulf as much as 70 tons of water at one time. Alternating longitudinal strips of muscle and blubber, both with large amounts of the protein elastin, facilitate this extension. During extension, capillary networks within the tissue give the throat a reddish color. The feature has conferred the name 'rorqual' or red throat to the balaenopterids.

Feeding bouts involve the intake of immense volume of seawater (in blue whales up to 60 cm^3). The whale begins feeding by lunging (usually on its side) and dropping the mandible to an angle of 90° from the body axis. Water pours into the rapidly expanding oral cavity. The tongue muscles and pleat blubber contain large amounts of elastin fibers that can be stretched t four times their resting length. As the oral cavity expands, the soft, flaccid tongue inverts and lines the floor of the oral cavity, something unique to balaenopterids.

Water and the small prey it contains (dense patches of krill [euphausiid and copepod crustaceans] and small schooling fishes such as capelin and menhaden), enters the open mouth by negative pressure produced by the backward movement of the tongue

and by the forward swimming motion of the swimming animal. After engulfing the prey, the muscular tongue acts in concert with contraction of the ventral walls muscles of the mouth (and sometimes with vertical surfacing behavior) to force the water out through the baleen and to assist in swallowing trapped prey. The baleen plates serve as a strainer. Baleen whales consume between 1000 and 5000 kilos (2000 and 9000 pounds) of fish and krill a day. It has also been proposed for fin whales that during the brief period of full gape during feeding, prey might be startled and retained within the ventral pouch by noise generated by the rapid opening of the jaw. The sound produced at full gape and their resonance along the mandibles might affect an escape reaction in prey contained within the mouth cavity. This may direct the movement of prey away from the jaws, resulting in their concentration and retention within the mouth.

They do not feed all year round, however, but only during half of the year when they are in the cold, nutrient-rich waters of their summer feeding grounds. Approximately 25% of what they eat during the summer is stored in the form of fat to provide extra energy and insulation during their winter fast when they migrate to warmer waters.

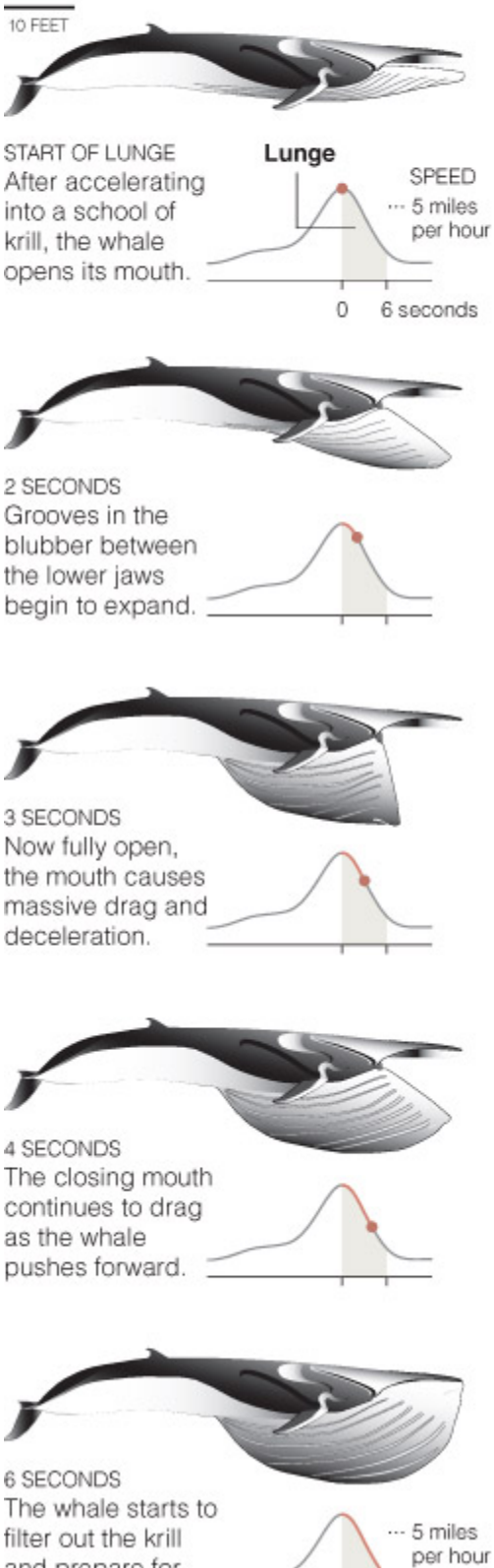
Bubble-Cloud Feeding: When feeding on herring, humpback whales often produce a large (about 10 m in diameter) cloud of ascending grapefruit-sized bubbles of expired air. One or two members of a group of several cooperating whales that form long-term foraging associations produce this net of bubbles. These bubble clouds are emitted from the blowhole. They seem to confuse prey or cause them to clump into tight food balls for more efficient feeding by the whales. As one whale produces the bubble curtain, other members of the group dive below the target herring school and force it into the curtain, then lunge through the confused school from below. Low-frequency calls are sometimes produced as the whales lunge through the school of prey and may aid in orienting whales during this complex maneuver. The release of the bubbles during foraging activities has also been reported for gray, fin, and Bryde's whales, orcas and spotted dolphins. Laboratory experiments have confirmed that bubble nets do contain prey such as herring.

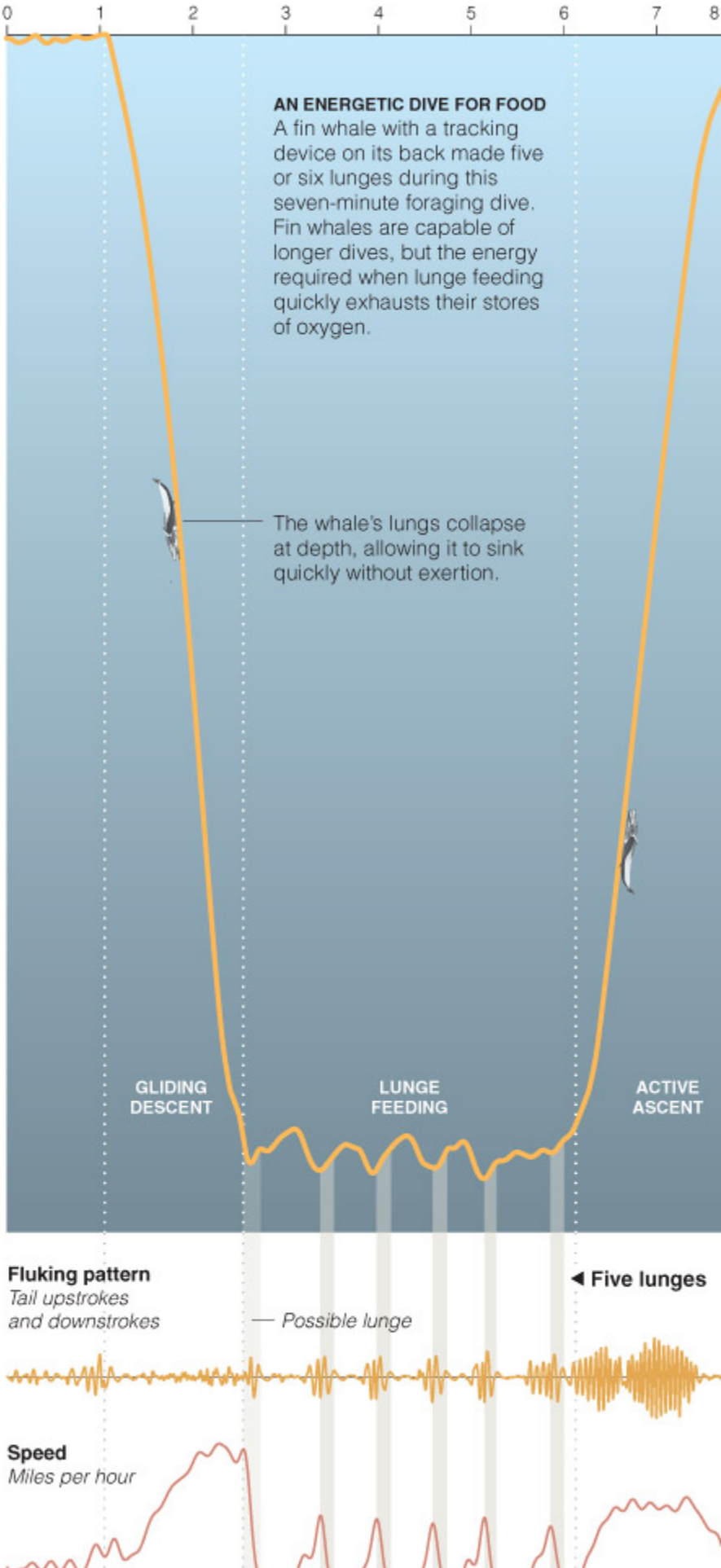
Flick or Lobtail Feeding: It has been observed among humpbacks feeding in New England waters. In it, the whale dives but as it does so, it flicks the massive tail forward generating a wave above it which it then passes through with mouth open. The production of this wave appears to concentrate the euphasiids. It has been hypothesized that this behavior is initiated as the whales switched from feeding on herring to smaller sand lance (copepods), which may react to a lobtail by clumping more densely, making the bubble cloud more effective.

Lunge Feeding: Also practiced by humpbacks. It takes place when feeding upon schooling fish two or more whales in unison, lunge towards and through the surface with greatly distended throats and open jaws, landing on their belly, sides or even their backs.

Lunge Feeding

Scientists tracking fin whales have created the first detailed model of how they feed. After gliding to depths of more than 600 feet in search of krill, a fin whale will repeatedly accelerate and open its mouth wide, engulfing about 20 pounds of krill and more than its own weight in water as it grinds to a halt.





Bottom Feeding: The gray whale feeds primarily upon the ocean floor, turns on its side (usually the right side) and swims forward with the head forced through the top layer of the sediment. Then, they suck their prey into the side of the mouth and expel water out the other side in mud scooping strategy in search for bottom invertebrates, particularly amphipod crustaceans. The whale then surfaces and, staining these sediments through its stiff baleen plates, it collects and swallows the gammarid amphipods upon which it feeds. The mud plumes that trail behind the feeding whales are often spotted by sea birds such as horned puffins, arctic terns and gulls and they feed upon those crustaceans that may have escaped the baleen during the straining process. Gray whales leave a record of their feeding activities, mouth-size depressions, in bottom sediments. Bottom feeding has also been observed among humpback whales.

Migrations for Feeding: Intensive, high latitude summer feeding is followed by long distance migrations to low latitudes in winter months for both hemispheres. When away from high latitude feeding grounds, these whales reduce their intake of food or completely cease feeding. The seasonal variations of feeding intensity impose annual cycles of fattening and fasting on these animals that can be as extreme as those of small hibernating terrestrial mammals. Although neither the migratory routes nor the patterns of energy apportionment for these migrations are known in detail for most mysticetes species, a few generalizations can be made.

Successful winter migrations to low latitudes while fasting require that sufficient energy be stored as lipids before summer feeding ceases. Additionally, fasting migratory animals must be large enough to have sufficient body volume to accommodate these lipid stores. The threshold body size for successful winter fasting migrations is unclear. Certainly small juvenile animals of all mysticetes species tend to feed throughout the year. The same occurs with the adults of the smallest species of mysticetes, the mike and the pygmy right whales, although only the former makes annual latitudinal migrations. Adult gray whales fast for most or all of the 5-6 moths that they are away from their summer feeding grounds, while the fin whale feeds, although at a reduced rate, during the winter months.

Gray whales have the longest migrations of any mammal, between 15,000 and 20,000 km. It spans 50° of latitude from summer feeding areas in the Bering, Chucki, and Okhotsk Seas to winter breeding, calving, and assembling grounds along subtropical Pacific coastlines in winter. Almost all the migrations occur within 10 km of the shore. The pregnant or lactating females incur the highest energy costs during migration. Small lactating female gray whales require about 3.2 metric tons of lipids, out of an estimated reserve of 4.4 metric tons, for feeding their young and for their own maintenance costs through the end of the winter lagoon season. Small adults must resume feeding during their northbound migration, whereas whales unburdened with the costs of lactations, as well as older, larger pregnant females, have the necessary lipid reserves to complete the north migration without feeding.

During the Last Glacial Maximum (LGM, 18,000 YBP) the sea level was about 150 m below to present stand. With the shift of polar and subpolar waters southward, all the shallow sea floor areas presently used by and accessible to gray whales were inaccessible during the LGM. The shallow portions of the Bering, Chukchi, and Okhotsk

Seas now used intensively for summer foraging were either drained of water during the LGM or were completely icebound. Thus, the extensive prey assemblages presently exploited by gray whales either did not exist or were unavailable in these areas to gray whales during then LGM. Most of then present continental shelves in both the North Pacific and North Atlantic oceans were also exposed above sea level, leaving much narrower continental shelves than exist at the present.

The strong contrast between present and LGM oceanographic conditions in both the North Pacific and North Atlantic oceans leads to the conjecture that gray whales may be thriving now because a particularly fortuitous set of environmental circumstances exists in polar seas during this (and possibly earlier) interglacial period, but which disappears during glacial maxima. The present foraging flexibility expressed by gray whales feeding in their migratory corridor suggests that they always have been food generalists, but have specialized temporarily into a narrow ecological niche to capitalize on benthic amphipods which are currently abundantly available. During glacial advances and consequent sea level lowering and polar sea exclusion by ice, this food resource disappears or at least becomes unavailable to gray whales.

Gray whales exhibit evolutionarily conservative feeding structures, especially the relatively small head with few extensible throat pleats, in addition to short, coarse baleen, which seem to make them poor competitors with other mysticetes whales for pelagic food resources in other latitudes. The present abundance of shallow water benthic prey, which are not exploited by any other whale species, permits gray whales to avoid such competition.

15.2. Odontocetes

Toothed whales tend to cooperate in large, concentrated groups, herding particularly schooling fish. While searching for food, many dolphin species move in tight schools that are distributed over a large area, possibly in acoustic or visual contact with one another, and using broad-band echolocation clicks to find fish schools. Once found, they spread out; some individuals dive down to the school and herd it to the surface by swimming around and under the fish in an ever-tightening formation.

Many delphinids show herding and crisscrossing behavior. Some species use sloping sandy shore to trap their prey. On Mauritanian coasts fishermen actually cooperate with bottlenose dolphins to capture mullet. The dolphins herd the fish into shallow waters. Fishermen then place gill nets among the fish, allowing the dolphins to feed at the same time. The dolphins even respond to the slapping of the water with sticks, as a clue for food. Similar cooperative feeding has been reported for the harbor porpoise and California sea lion in Monterrey Bay. Orcas also hunt cooperatively. Other species of toothed whales hunt either singly or in small groups such as species of the genus *Mesoplodon*. Coastal dolphins such as the bottle nosed also prey in small groups or sometimes even individually.

Probably the best studies species in terms of prey capturing strategies is the orca. Orcas are cooperative foragers that take advantage of the ability, probably unique among marine mammals, to capture preys larger than themselves. The degree of foraging cooperation is variable, depending on the type of prey; it can involve cooperative prey encirclement and capture, division of labor during an attack, and sharing prey after

capture. Individual orcas in Patagonia repeatedly swim up sloping beaches at high tide to capture hauled-out southern elephant seals and sea lions. This hunting strategy, known as intentional stranding, is also observed among juveniles female orcas in the capture of elephant seal pups. Evidence suggests that adult teach this behavior to juveniles and that apprenticeship likely plays an important part in the transfer of hunting techniques from one generation to the next.

Different populations of orcas may use different prey capturing strategies, even when in close proximity. In the Pacific Northwest, for example, transient and resident population forage using different strategies. While the resident populations are found in large groups, feeding in deep waters preying on salmon and other fish, transient populations go in small groups, swimming in shallow waters and preying on marine mammals.

How the different cetacean feeding behavior evolves? When looking at the fossil record we can see that from heterodont teeth in early archaeocetes (which probably shear and grind its prey as well as snap the jaw shut during capture). Echolocation seems to have appear early in cetacean evolution. Simplification of teeth is seen as a case of convergent evolution for animals like odontocetes and crocodiles, with similar type of prey preferences. A strange feeding adaptation found among fossil cetaceans is that of a fossil from the early Pliocene found in Peru. *Odobenocetops peruvianus* was a coastal odontocete whose skull has a large, downturned, asymmetrical tusk and a blunt snout very similar to that of the walrus. Strong muscle scars on the anterior edge of the premaxillae suggest the presence of a powerful upper lip. This feature together with the deeply vaulted palate and absence of teeth suggest a convergent feeding adaptation with the walrus for eating benthic mollusks using suction.

The case of the evolution of baleen plates is also a remarkable transformation from using food for capturing preys to filter feeding (mostly common among lower invertebrates, with the exception of few shark species). Early mysticetes (aetiocetids) already show the basic structure for filter feeding, which suggests that this character evolved quite rapidly. It has been suggested that filter feeding evolved as a response to the availability of new food and in turn to new oceanic circulation patterns associated with the development of the Southern Ocean and the final breakup of Gondwana. Migration perhaps evolved at the same time, allowing seasonal high altitude feeding alternating with breeding in warmer altitudes. Baleen bearing mysticetes evolved by the late Oligocene (4-5 MYA) after toothed mysticetes appeared in the fossil record. They were probably skimmers because their mouth resembled that of the balaenids.

15.3. Pinnipeds

Species of otariids express different foraging strategies that depend on variations in the type of prey, environmental conditions like season, location, and time of day. They will often feed alone or in small groups (2-5 animals), but also will shift to larger cooperative efforts (50 and more animals) when there are schools of squid or fish present.

These gregarious animals can often be seen milling around or vocalizing at certain times when hauled out on shore, which is behavior speculated to aid in the coordination of group foraging. Often, an observer of a group of resting pinnipeds will notice increasing agitation at certain times of day, resulting in the whole group eventually diving

into the water and heading out to sea to forage. Whether these feeding outings result in the gathering breaking up into small groups, animals venturing off on their own, or a coordinated group effort will depend on the type of prey the animals seek/encounter. Sometimes otariids are also seen feeding in the company of cetaceans and seabirds but it is difficult to tell whether these interactions are cooperative or parasitic. It is speculated that these different groups of animals watch for other groups aggregating and use this as a signal that a food source has been located.

It is interesting to note that the juveniles and adults of the harbor seal tend to prey on different animals (this is also a characteristic of some other phocids, for example the Largha seal, *Phoca largha*). Research has demonstrated that weaned pups and juvenile animals tend to eat more benthic crustaceans and shrimp than adult harbor seals, whose diet consists mostly of fish, along with cephalopods and some other invertebrates. There are various theories as to why this occurs, for example, juveniles may not yet have the skills necessary to chase fish or dive deep enough to obtain the prey items that adult animals prefer.

Observations of wild harbor seals show that these animals tend to forage alone. However, these relatively shy creatures can be difficult to observe, and it is currently not known whether these phocids ever forage in groups out in the open ocean or when diving.

The northern elephant seal also tends to forage alone, which is probably in part due to the fact that animals leaving at the end of the breeding season tend to depart independently of each other. Adults of both species of elephant seals stay at sea between eight and nine months. During this time they make two round-trip migrations between nearshore island-breeding rookeries and offshore foraging regions. With the development of the microprocessor-based Geographic Location Dive Time and Depth Recorders (GLTDRs) we have learned a number of things about the patterns of foraging behavior of these deep-diving seals.

For example, we have learned that elephant seals make a double migration every year. Their individual annual movements of 18,000-21,000 km rival that of gray whales en terms of distance traveled. When ashore for breeding of for molting, adult elephant seals fast. Each fasting is followed by prolonged periods of foraging. While at sea, both males and females dive almost continuously, remaining submerged for about 90% of the total time. Dives average 23 min, with males with slightly longer dives. They spend about 35% of their dive time near maximum depth, between 200 and 800 m. In general, daytime dives are 100-200 m deeper than nighttime dives. They mostly on mesopelagic squid and fish that spend daylight time below 400 m and ascend nearer the surface at night. This is consistent with the pattern of vertical movements of the Seep Scattering Layer (DSL).

Males and females show differences in geographic location of foraging areas. Males tend to go to higher latitudes. This may be due to the males' preferences for the larger and more oil-rich species of squid found in higher latitudes. Although they obtain less calories per unit of food, females also have to travel less to obtain it. Similar geographic segregation has been found among sperm whales, which also feed on mesopelagic squids.

Adult walruses eat about 4.2% to 6.2% of their total body weight per day. They eat less on their northward migration. Observations of feedings indicate that walruses fill their stomachs twice daily. Adults may eat as many as 3,000 to 6,000 clams at a single

feeding. Walruses usually forage within 80 m (262 ft.) of the surface. Most feeding probably takes place between 10 and 50 m (33-164 ft.). Because visibility is poor in deep and murky waters, walruses rely on their vibrissae to locate food. A walrus moves its snout along the bottom, rooting through the sediment. Abrasion patterns of the tusks show that they are dragged through the sediment, but are not used to dig up prey. Evidence shows that walruses may also take in mouthfuls of water and squirt powerful jets at the sea floor, excavating burrowing invertebrates such as clams. Walruses do not chew their food, but they do sometimes crush clamshells. Soft-bodied invertebrates are usually not crushed or torn. A walrus sucks off the foot and the fleshy siphon of a clam and swallows it whole. The cheek teeth do get worn, but this is probably from abrasion by minute particles of sand that walruses inadvertently take into their mouths and not from crushing clamshells. Researchers have found numerous pebbles and small stones in the stomachs of walruses which some think are ingested while feeding.

15.4. Sirenians

Sirenians and sea turtles are the only sirenians to commonly graze on sea grass meadows. The degree of snout deflection is manatees and dugongs appear to be correlated with the degree of specialization for bottom feeding. The strongly downturned snout of the dugong causes its mouth to open almost straight downward and it is virtually an obligate bottom feeder subsisting on sea grasses less than 20 cm high. Manatees, in contrast, have only relatively slightly deflection, and are generalists feeding at any level in the water column from bottom to surface and are able to easily take floating vegetation.

The manatee appears to be the only marine mammal that uses the snout in a prehensile manner through modified vibrissae. During feeding, dugongs gouge tracks into the bottom sediments. It is apparent that the tracts represent the action of the snout while grubbing sea grasses from the bottom.

It has been suggested that he ‘conveyor belt’ tooth replacement pattern in manatees is an adaptation to an abrasive diet and increased tooth wear that results from their exploitation of a new silica-containing resource, sea grasses, during the late Miocene. In the Indo-Pacific, dugongids responded slightly differently by evolving ever-growing teeth as an adaptation to increased tooth wear.

Among sirenians, the Steller’s sea cow shows a number of unique cold-water adaptations, including reaching a body length double that of other sea cows, and extraordinarily thick epidermis, inability to dive, and loss of teeth and phalanges. It has been suggested that these adaptations reflect a change in diet away from bottom feeding to feeding on plants growing at the surface (and mainly on algae growing exposed to rocky shallows). The loss of phalanges could be correlated to a specialization for surface and rough-water feeding and suggest that stout claw-like forelimbs are adapted to grasp or fend against rocks and pull the animal forward while grazing in the shallows during bottom feeding. The relative ease of chewing algae compared to stringer sea-grasses probably led to loss of teeth.

Although the ‘overkill’ by humans is usually blamed for the ultimate demise of the Steller’s sea cow, they may have already had small, restricted populations that interactively compete with kelp-sea urchin-sea otter relation. According to this hypothesis, the shallow-water kelp communities are prolific only when sea otters are

sufficiently abundant to limit sea urchin populations. If the sea cow food supply was otter dependent, then the niche into which Steller's sea cow evolved was precariously balanced on sea otter carnivory. The aboriginal hunting of sea otters, urchin grazing, and replacement of shallow-water kelps by deep-water species could have destroyed sea cow foraging areas, thereby limiting their populations prior to their discovery in the mid-1700's.

15.5. Sea Otters

Captured preys are manipulated with the forepaws or are held temporarily in loose skin pouches in the armpits. For larger, heavier-shelled prey, otters will sometimes carry rocks to the surface to crack open their hard shells as they float on their backs. Otters have exceptionally high metabolic and food consumption rates: typical adult otters in Alaskan waters daily consume prey equal to 23-37% of their body weight.

These animals show a an extensive variation in their patterns of dive duration and success rate, surface interval length, size and species of prey consumed, foraging bout length, and the degree of difference between diurnal and nocturnal foraging patterns. That is particularly true between juveniles and adults. Juvenile males often forage further offshore over deeper waters than otters in other age and sex classes and, in consequence, they also tend to make longer dives. Juvenile females forage closer to the shore and do shorter dives.

Sea otters are completely restricted to shallow (generally <35 m depth) coastal waters of the North Pacific Ocean, where substantial populations of invertebrates inhabit rocky or sandy substrates. Sea otters are most commonly affiliated with near shore canopy-forming kelps (principally the phaeophyta or brown algae *Macrocystis* or *Nereocystis*), although large numbers of otters have been observed as much as 30 km offshore.

In portions where sea otters have recovered their original range or where they have been reintroduced, they are considered a keystone predator, playing a pivotal role in kelp bed communities by keeping populations of herbivorous invertebrates, mostly grazing sea urchins, low in number and allowing kelp plants to reestablish and thrive. In the southern part of their historical California and northern Baja California range however, healthy kelp forests persist even though sea otters have been absent for more than a century. There, water temperature variations, storm surges, or other disturbances also may play important roles in the dynamics of these otter-free near-shore kelp communities.

In the Australasian region, where there is not a comparable predator of herbivores, brown algae have develop a number of chemical defenses against their predators, something that is missing in their northern hemisphere relatives.

15.6. Polar Bears

Predation of bears on ice seals occurs primarily in unstable ice conditions where the bears can stalk seals resting out of water. Seal pups are especially vulnerable to bear predation. In the Canadian Arctic, ring seals give birth to pups in snow caves above breathing holes in the ice. At weaning, these pups are 50% fat, and it is from these pups that bears secure

most of their annual energy supply during the short period just after the ring seal pups are weaned. It is not known whether bears commonly prey on seals underwater.

Polar bears (as well as their more terrestrial relatives), undergo prolonged seasonal fasting as result of declined in food availability or when reproductive activities prevent foraging. They have the ability to conserve proteins for long periods of time.

Chapter 16

Cardiovascular and Urinary System

16.1. The Cardiovascular System

16.1.1. Introduction

The mammalian cardiovascular system can be thought of as a pluming system that uses a pump (heart) to transport a fluid (blood) through a series of pipes (arteries and veins). The blood is transported to and from exchange sites (capillaries) where dissolved gases, nutrients, waste products, and heat are transferred across the capillary membrane.

The four-chambered heart is a double pump with separate pulmonary and systemic circulatory routes. The right half of the heart pumps blood returning from the body to the lungs; here, carbon dioxide diffuses out and oxygen diffuses into the blood across the alveolar and capillary membranes. The oxygenated blood enters the left half of the heart, where it is pumped, through the aorta, throughout the body.

Because the amount of oxygen that can be stored in any tissue is limited in most terrestrial mammals, the cardiovascular system must provide a constant supply of oxygenated blood. Oxygen-sensitive tissues, such as the heart and brain, can generally only survive brief hypoxic/anoxic periods without experiencing irreversible damage or death. Likewise, some mammalian tissues, such as delicate neural and reproductive tissues, are temperature sensitive. Thus, another important function of the cardiovascular system is to regulate the temperature of body tissues.

The cardiovascular systems of marine mammals perform the same function as that of out 'typical' mammal. How is oxygen delivered to sensitive neural tissues during extended breath-hold episodes? How do marine mammals regulate the temperature of their reproductive system structures?

16.1.2. Arterial Supply to the Brain

The 'typical' mammalian brain receives its blood supply by way of the internal carotid and vertebral arteries, with some contribution from the external carotid arteries. These vessels enter the cranial cavity and anastomose (from a junction, or join together) at the base of the brain. This circular-shaped anastomosis (sometimes called the Circle of Willis) gives rise to all arteries that supply the brain. Hypothesized functions for the

arterial circle include (1) pressure damping so that the delicate neural tissues do not experience potentially damaging pressure pulses, and (2) establishing collateral flow so that damage/occlusion of one vessel does not necessarily stop blood flow to those areas of the brain supplied by the vessels.

Given that most marine mammals undergo extended breath-hold periods, when blood oxygen stores are not continuously replenished, we might expect some specialized arterial supply to the brain to assure an uninterrupted supply of oxygen. Perhaps surprisingly, those species of seals and sea lions investigated thus far possess a 'typical' arterial supply to the brain. The major arterial path to the brain of these animals is through well-developed internal carotid and vertebral arteries, with some contribution from the external carotid arteries. Although detailed accounts of the arterial supply to the brain of the sea otter are unknown, the pattern in the river otter (*Lutra lutra*) is similar to that of a terrestrial mammal. Bears possess a unique arterial supply to the brain that the polar bear appears to share. Therefore, pinnipeds, polar bears, and sea otters display 'typical' terrestrial arterial blood supplies to the brain.

Unlike these marine mammals, cetaceans possess a highly derived arterial blood supply to the brain. Cetaceans lack vertebral arteries, and their internal carotid arteries are degenerate, often not reaching the cranial cavity. Thus, the two major paths of arterial blood to the brains of many mammals do not exist in cetaceans. Rather, arterial blood travels to the brain through a series of arterial retia. Retia are networks of vessels formed when a single vessel splits into multiple smaller channels. Retial vessels can either be organized into multiple, parallel pipes or tortuous, twisting networks.

Arterial blood destined to feed the cetacean brain travels through the thoracic aorta to segmentally arranged inter-vertebral arteries. The intervertebral arteries become convoluted, anastomotic bundles that are collectively termed the thoracic rete. The thoracic rete lies between ribs in the dorsal thoracic cavity. Vessels extending from the thoracic rete enter the neural canal of the vertebral column and form yet another tortuous, anastomotic plexus called the epidural (spinal or vertebral) rete. The epidural rete runs the length of the spinal cord and enters the cranial cavity through the foramen magnum. Within the cranial cavity, these arteries form other retia that give rise to arteries that feed the brain.

The serial arrangement of extracranial arterial retia, apparently unique to cetaceans, has been identified as an adaptation to diving. Some data support the hypothesis that the thoracic rete acts to dampen pressure fluctuations resulting from the pulsed flows produced by the heart. For example, we know that blood pressure measured at the aorta of anesthetized bottlenose dolphins are higher and more pulsatile in nature than those measured in arteries within the cranium. Interestingly, this is the same function ascribed to the arterial circle at the base of the brain of many terrestrial mammals. Such an elaborate structure is also clearly not required for deep diving or extended breath-hold periods, as it is not found in seals or sea lions. Thus, we do not yet fully understand the functions of the thoracic rete in cetaceans.

Sirenians have not been as extensively investigated as seals and dolphins, and indeed we do not yet completely understand the arterial blood supply to the brain. Manatees do possess internal carotid and vertebral arteries. Sirenians also have an extravagantly elaborate thoracic rete. Unlike the convoluted and anastomosing rete in cetaceans, the sirenian thoracic rete is formed by multiple parallel arranged arteries that

tend to fan out like brooms from each intercostal artery. These vascular bundles appear to run peripherally and nourish the thoracic wall, rather than enter the neural canal as they do in cetaceans. Thus, although sirenians do possess a thoracic retial system, there is little evidence that it plays a role in supplying the brain with blood.

Marine mammals do not display a consistent pattern of blood supply to the brain, and many possess arterial systems undifferentiated from terrestrial mammals. Thus, perfusion of the brain with oxygenated, arterial blood during a dive does not necessarily require novel arterial structures. Rather, dynamic changes in blood flow patterns through vascular structures occur during diving. Arterial blood can be shunted from its normal systemic circulatory routes during a dive; perfusion of peripheral tissues is decreased, while blood flow to the brain remains constant. One mechanism to redistribute blood during a dive is large-scale reduction in the diameter of the aorta and muscular distributing arteries. Educing the diameter of the aorta or arteries near the aorta limits the blood supply to peripheral tissues and thus conserves oxygen for vital organs. Another mechanism that can redistribute blood flow and provide a short circuit to the normal systemic circulation is the arteriovenous anastomosis.

16.1.3. Arteriovenous Anastomoses

Arteriovenous anastomoses (AVA) are vascular channels that connect an artery to a vein proximal to the level of the capillary bed. Arterial blood routed through AVA thus bypasses the site of gas and nutrient exchange at the capillaries. The AVA are most commonly observed at the entrance to the microcirculation, that is, the vessels leading directly to and from capillaries. The AVA are also found in more proximal vessels, and can shunt arterial blood into veins higher in the circulatory system. The AVA in the flukes of bottlenose dolphins, for example, can be as large as 2 mm in diameter, are found connecting major arteries and veins. These large shunts, also apparently found in the deep-diving Weddell seal, may be important in redistributing blood flow from peripheral tissues to vital organs during a dive.

The AVA also perform a critical thermoregulatory function by adjusting blood flow to the surface of the body. The skins of many mammals are supplied by AVA. Increased blood flow through AVA and capillary beds in the skin increase connective heat loss to the environment. The skins of phocid seals are particularly well supplied with AVA, which lie superficial to the insulatory blubber layer and hence are in a position to dump heat to the environment. The AVA are also found superficial to the blubber layer in bottlenose dolphins. Unlike seals and dolphins, fur seals have their insulatory fur layer superficial to the skin surface. Interestingly, the skin of their bare flippers is richly invested with AVA. Thus, AVA are found in regions of the marine mammal body where they can, if dilated, effectively transfer heat to the environment. Dugongs appear to lack AVA. AVA has yet to be described in polar bears and sea otters.

16.2. Urinary System

16.2.1. Introduction

The mammalian urinary system functions to maintain the body's water balance and to excrete metabolic waste products (and soluble foreign substances) in the form of urine. Urine is produced as an ultrafiltrate of the blood by the kidney.

16.2.2. Kidneys

The functional unit of the kidney is the nephron. Urine is produced in a two-step process. The blood is first filtered across the capillary membrane and the membrane of the Malpighian body (also called Bowman's capsule) into the nephron. The filtration step filters metabolic waste products, water, glucose, and important electrolytes out of the blood. Thus, the second step in urine formation is to reabsorb water and nutrients so that they are not lost from the body. Reabsorption occurs along the remainder of the length of the nephron tubule system. This reabsorption step can create more concentrated urine in some salts and metabolic waste products (predominantly the nitrogenous waste urea) than the blood; urine with a higher osmotic pressure than blood is termed hyperosmotic. From the kidneys, the urine flows through a ureter to the urinary bladder, and exits the body through the urethra.

The cortex of the kidney contains Bowman's capsule and convoluted tubules, and the loops of Henle are found in the medulla. Mammals with longer Loops of Henle, and hence, thicker medullae, tend to be able to create more highly concentrated urine. It has been hypothesized that marine mammals must be able to create more concentrated urine than terrestrial mammals, as most have no access to freshwater. Is there any morphological evidence to support this hypothesis? Let's take a look of kidney shape and relative thickness of the cortex and medulla.

16.2.2.1. Kidneys Shape and Size

The kidney of a typical mammal is a smooth bean-shaped organ but mammalian kidneys can be lobulated in their appearance. With the exception of sirenians, marine mammals possess a multiunit kidney -the whole organ is formed by a number of smaller, independently functioning units called reniculi ('little kidneys'). Each reniculus is like a small single kidney with its own cortex, medulla, and calyx, and the duct from it joins with others to form the ureter. These kidneys are called reticulate kidney. The kidneys of otters, bears, pinnipeds, and cetaceans are 'discretely multireniculated,' that is, each subunit is a fully functional reniculus.

The number of reniculi varies among species. Elephant seal and harbor porpoise kidneys are formed by approximately 300 reniculi, whereas the fin whale kidney possesses more than 6000 reniculi. Among cetaceans the number ranges from hundreds to thousands per kidney. One structure in the kidneys of cetaceans and certain pinnipeds that appear to be unique is the **sporta perimedullaris musculosa**, an extension of muscle and cartilaginous tissue from the calyx, which penetrates the reniculus and surrounds the medullary pyramid. This feature together with other features of cetacean reniculus, such

as large reservoirs of glycogen and unique medullary blood vessels, are considered specialized adaptations in the kidney, which may facilitate diving.

Manatees possess a compound multireniculated kidney where each lobe of the kidney is formed by a fusion of a number of reniculi. Thus, it can be said that the kidneys of the manatee are only superficially lobulate. They lie on the surface of the diaphragm. Dugong kidneys are elongated and quite unique since they are unlobulated, unlike the lobulate kidneys of other marine mammals and rather look like the one of ungulates. Unlike the manatee, the dugong appears to be physiologically independent of fresh water. Its salt metabolism has yet to be studied. The Steller's sea cow kidneys were multireniculate and similar in form to those of seals and sea otters. Kidney shapes vary among sirenians.

Kidneys size also varies among marine mammals. The kidneys of sea otters are large relative to body size and consist of oval clusters divided into reniculi. The lobulation of the kidneys allows the sea otter to produce large volumes of moderately concentrated urine. The polar bear has the largest number of lobules (65) recorded for a carnivore.

The multiunit kidney possesses more surface area than a similarly sized single-lobed kidney. The relatively increased surface area of this type of kidney may increase both the volume of blood that can be filtered per unit time and the volume of urine that can be produced. Similarly, the relatively large size of size of sea otter and harbor porpoise kidneys may also influence urine production in these species. Yet, large kidney size is not a feature shared by all marine mammals. Although the size and shape of multiunit kidneys increase the amount of urine produced, do these features suggest that marine mammals produce concentrated urine? To date, there is no definitive evidence that the shape of the marine mammal kidney is specifically adapted to osmoregulation in the marine environment. These kidneys may also be artifacts of large body size. The multiunit shape may increase kidney blood filtration capacity and has been suggested as an adaptation for diving.

16.2.2.2. Kidney Cortex and Medulla

Since the length of the Loop of Henle influences urine concentration, it is valid to ask then question of how long they are among marine mammals. Sirenians and harbor porpoises possess relatively thick medullae, suggesting that they have long loops of Henle and can concentrate urine. The extent to which these animals do produce concentrated urine is unknown. Sea otters can produce moderately concentrated urine. The functional significance of medullary thickness in pinnipeds is controversial.

The somewhat confusing data on urine concentration in marine mammals is perhaps understandable. The urinary system functions to regulate precisely the body's water and electrolyte requirements, which is, by its very nature, a highly dynamic process. The variably concentrated urine sampled from mammals in the field probably reflects its extreme dependence on diet, activity, time between feeding or imbibing water, and age of the animals.

16.2.3. Water Balance

Most marine mammals are hyposmotic, i.e., their body fluids have a lower salt content than the surrounding environment and they are in constant danger of losing water to the more concentrated or salty ocean water. Among the ways that seals reduce their water loss is through countercurrent heat exchangers located in the nasal passages and through ventilatory patterns discussed previously. It has been shown experimentally that seals can obtain all the water they need from the food they eat. If, however, seawater is given to seals, the stomach becomes upset and the excess salts have to be eliminated using body water.

Despite this, seals from warm climates have been seen drinking seawater, a practice called **mariposia**. It has been suggested that seals consume small amounts of seawater at intervals that would not be enough to cause digestive problems but would be sufficient for facilitating nitrogen excretion. Mariposia is especially common among adult male otariids.

A study of renal function in the Baikal seal, an inhabitant of freshwater, and in the ringed seal, its marine counterpart, reveals no major differences in renal function. It was concluded that the Baikal seal, isolated from seawater and living in freshwater for .5 MY, remarkably retained the renal function they possessed at their time of isolation.

Although odontocetes drink small amounts of salt water that is not essential for their survival. The concentration range of urea produced by cetaceans is comparable to that of most terrestrial mammals.

The isotopic concentration of mammalian tooth phosphate reflects the type of water ingested. And it is possible to ascertain when cetaceans adapted to the excess salt load associated with ingesting salt water. The earliest cetaceans (pakicetids), for example, consumed freshwater and terrestrial food; thus, they were not really marine in their physiology. By the middle Eocene, *Indocetus* showed adaptations to increased salt loads.

Sea otters drink seawater. They consume primarily invertebrates (which possess higher electrolyte concentrations than bony fish or mammals), they must process large amounts of electrolytes, nitrogen, and water. Ingestion of seawater promotes urea elimination by increasing the urinary osmotic space without increasing the electrolyte concentration in the urine.

16.2.3.1. High Salinity

Because of the salinity of the seawater, marine mammals have developed a number of physiological adaptations to survive in a type of water that is essentially unsafe to living cells. Because most of the water retained in living tissues is freshwater in nature this creates an unbalance between the body's water and the salty water of their environment. In other words, the seawater is **hyperosmotic**.

Marine mammals obtain freshwater directly from their prey. During fasting, or when prey is scarce, fat from the blubber is released for energy, and, like that in a camel's hump, produces crucial fresh water as a by-product. To endow her newborn with precious blubber, a mother hooded seal will transfer enough fat-rich milk to the pup for it to double its body weight within four days of birth (an average gain of 6.5 kg/day), while

losing about 30 kg of blubber herself. Also, their skin is impervious to seawater. To achieve this impenetrable state, the epidermis of cetaceans employs extraordinary cells tightly woven into an architecture that is unique among mammals. The adrenal glands' response to stress both in cetaceans and pinnipeds also serves to protect the animals from surrounding seawater. Aldosterone released from the adrenal cortex causes the animal to retain its own salt and water, freeing it from the need to drink any quantity of seawater. By this mechanism, an animal in stress becomes physiologically isolated from the external environment. These adaptations enable an otter, for example, to keep warm in icy waters, a baleen whale to migrate thousands of kilometers over several months while fasting, a sperm whale to breath-hold for hour-long dives to 2,000 meters or more, and a seal pup to begin life with energy reserves in place. On the other hand, failure of a system can jeopardize the tenuous shield protecting the animal from its environment. An animal that cannot eat for whatever reason becomes thin. With less blubber, it must work harder simply to stay afloat and keep warm, thereby burning more energy that depletes more fat -its only remaining source of nourishment and water. The life-draining spiral tightens rapidly, and its effect can be seen in animals that come ashore to strand. Many are emaciated, dehydrated, and exhausted.

Chapter 17

Nervous System and Sensory Mechanisms. Brain and Intelligence

For this class I will review briefly the most outstanding features of the nervous system, sensory mechanisms (with the exception of hearing that was discussed in depth in the class on echolocation), and endocrine glands in marine mammals. I will also discuss the issue of 'intelligence' among these animals.

17.1. Nervous System-General

The mammalian nervous system detects and responds changes in both the internal and external environment of the animal. The nervous system is subdivided into the **central nervous system** (**CNS**) and the **peripheral nervous system** (**PNS**). The CNS is formed by the brain and spinal cord; the PNS includes all other nervous tissues. In the PNS, specialized neurons called **receptors** transduce mechanical, thermal, and electromagnetic signals into nervous signals that are transmitted to the CNS through **sensory** (**afferent**) **nerves**. **Interneurons** (neurons that lie between sensory and motor neurons) in the CNS integrate incoming sensory information and coordinate rapid and appropriate responses by transmitting signals through **motor** (**efferent**) **nerves** to effector organs such as muscles.

Pairs of spinal nerves, which arise at each intervertebral level, connect the PNS with the spinal cord. Spinal nerves are mixed nerves that carry both sensory and motor neurons. Twelve pairs of **cranial nerves** connect the PNS with the brain; three are sensory (I, II, and VIII), four are motor (III, IV, VI, and XII), and five are mixed (V, VII, IX, X, XI). A thirteenth cranial nerve was discovered after the standard numbering system was established. The terminal nerve, numbered 0, is closely associated with the olfactory nerve (I) and is sensory in function.

17.1.1. The Brain

17.1.1.1. Brain Size

Historically, humans have been interested in knowing which animals have a high level of 'intelligence.' A common perception is that the larger the brain, the more 'intelligent' an animal will be. For example, the sperm whale has the largest brain of any animal in

absolute terms (see Table 19.1). This is misleading on several counts. First, brain size is not the same thing than brain development and complexity; second, we are still arguing how to measure human intelligence. Thus, it is unscientific to use brain size to determine intelligence when we cannot even agree how to define among humans.

There are measurable differences in brain size and shape across different mammalian groups, though that may offer insights into the mammal's ecology, life history, energetics, and so forth. To elucidate such relationships, one must have a comparable measure of the brain size. Researchers use the allometric relationship between brain mass and total body length. The approach is theoretically simple: weigh a wide variety of mammal brains and whole bodies and calculate the exponential relationship between two measured values:

$$M_{BR} = a\,(M)^b$$

where M_{BR} is brain mass and M is body mass. A log-log plot of this equation will yield a straight line with slope b and y-intercept a.

Allometric relationships are used to predict the expected brain mass of any mammal based on its total body mass. A value used to compare relative brain size is the **encephalization quotient** (**EQ**), calculated as the ratio of brain mass observed-to-brain mass predicted from the allometric equation for mammals as a group. A mammal with an EQ equal to 1 would have exactly the brain mass that would be predicted for its body mass. The allometric relationship can be used to identify any systematic deviations from the one predicted for its body mass. If your mammal of choice instead had an EQ equal of 0.5, it would have one-half the brain mass that would be predicted for its body mass. The allometric relationships can be used to identify any systematic deviations from predicted brain mass values within a specific group (i.e., small odontocetes tend to lie above the line and sirenians below). These differences, in turn, may be related to other measurable features of the animal.

Be aware that sometimes the values obtained employing this method can be influenced by factors as simple as sample size. It is well known, for example, that there is intraspecific brain size variation; thus, a single value for an entire species may not represent the average brain size. Given that it is so difficult to obtain brains from so many species of marine mammals that is a factor to be taken into consideration. Also, contrary to earlier assertions, there is no correlation between brain size and metabolic rate has been found.

The only generalization that we can make at this point regarding EQ, is that small odontocetes tend to have large relative brain size; pinnipeds within the expected range, and mysticetes, sirenians and, get this, sperm whales, rather small brains (Table 19.1). How can we explain this? Archaeoceti brains were comparatively smaller than those of extant cetaceans. It has been hypothesize that brain size increased with the enhancement of echolocation capabilities. To support this hypothesis, it has been stated that some auditory structures are reportedly larger in small odontocetes than in either mysticetes or sirenians. There are several problems with this hypothesis. First, the data supporting the contention of larger auditory areas among small odontocetes is not strong. Second, other mammals such as bats that have highly developed echolocation capabilities actually have a rather small EQ. Further, the sperm whales, well known for their echolocating

capabilities, have also a small EQ. In other words, we still do not know how to explain these brain size differences.

Table 17.1
Brain and body weights of some marine mammals and humans

Species	Brain weight (g)	Body weight (tones)	(Brain weight/Body weight) X 100
Humans	1500	64	2.344
Bottlenose dolphins	1600	154	1.038
Common dolphins	840	100	.840
Killer whale	5620	5448	.103
Pilot whale	2670	3187	.074
Sperm whale	7820	33596	.023
Fin whale	6930	81720	.008
California sea lion	363	101	.359
Southern sea lion	550	260	.211
Northern fur seal	355	250 (male)	.142
Leopard seal	542	222	.244
Gray seal	320	163	.196
Bearded seal	460	281	.163
Weddell seal	550	400	.138
Walrus	1020	600	.170
Florida manatee	360	756	.047

17.1.1.2. Brian Shape and Surface Features

Most mammalian brains are longer than they are wide, reflecting the elongated shape of the brain case. Again, among marine mammals we find a wide variety of shapes whose functional significance has yet to be satisfactorily explained. For example, most mysticete brains are approximately as wide as they are long, while odontocete and sirenian brains tend to be wider than they are long. Pinniped brains tend to be more spherical than those of terrestrial mammals, while the brains of sea otters and polar bears are similar in shape to those of their close, non-marine relatives.

Brain complexity, although more difficult to assess, seems to have some correlation with specific functions. For example, folding of the cerebral cortex (**convolutedness**) has been used to infer brain function. Surface folding increases the area available for cerebral cortex, the area of the brain where higher neural processing occurs. Odontocetes exceed humans and all other animals, in terms of convolutedness. Pinniped brains are more convoluted than those of terrestrial carnivores. Sirenians possess an exceptionally smooth cerebral surface, a condition referred to as **lissencephaly**.

The degree of cortical folding is often reported as the **gyration index** (**GI**), i.e., the ratio of total perimeter to exposed perimeter of cerebral cortex. Sirenians GI is close to 1, human and ungulate GIs lie between 2 and 3, and odontocete cetacean GIs can exceed 4. Differences in cortical folding can dramatically influence cerebral surface area. Another way to contrast convolutedness is to compute the ratio of surface area of cerebral cortex (cm^2) to brain mass (grams). Based on that, bottlenose dolphins have 2.4 cm^2/g, whereas manatees have 0.4 cm^2/g. That is, per unit weight, there is a six-fold difference in cortical surface area between the dolphin and the manatee. Odontocetes possess considerably more (both relatively and absolutely) cerebral cortex than manatees. These numbers allow us to quantify differences between brain structures, but not to explain them. In a way, cetaceans and sirenians represent the two extremes of mammalian cortex organization.

17.1.2. The Brain of Some Marine Mammals

17.1.2.1. Cetaceans

Bottlenose dolphin brain cells are more uniform and less specialized than human brain cells. Dolphins are born with about 40 percent of their brain mass, and reach full brain development in about 10 years, while humans are born with about 25 percent of their brain mass, and reach full brain development in about 18 years.

Their brains appear to be double-brains, that is, composed of two similar sub-brains, whereas human brains appear to be composed of two mirror-symmetric dissimilar hemispheres. Each of the two sub-brains of bottlenose dolphin has an independent blood supply. They never sleep with both brains at once. One brain sleeps while the other brain stays awake (perhaps for breathing or predator defense). Dolphin sleep appears to be different from human sleep in another way: The brain waves of sleeping dolphins have no state that corresponds to the **rapid-eye-movement** (**REM**) sleep of dreaming humans.

The two eyes of the dolphin are each connected to one of the two sub-brains. The dolphin brain area for visual imaging is only about one-tenth that of the human brain, while the dolphin brain area for acoustical imaging is about 10 times that of the human brain. Dolphins not only have two sub-brains, but they also have two sets of sound-producing organs, including two ‘tongues’ on each side of their blowhole. Therefore, dolphins can produce two independent sounds, from their right and left sides. They can use interference to focus sounds and to produce harmonic interference effects. Two dolphins speaking can sound like four.

Mysticetes have a large cerebellum (more than 20% of the total brain weight) while in bottlenose dolphins it corresponds to about 15% of the brain and in humans is about 11%.

17.1.2.2. Pinnipeds

Their brain weight ranges from 320 g for the gray seal to 550 g for the Weddell seal, and 1020 g for the walrus. It is more spherical and is more highly convoluted, especially in phocids, than that of terrestrial carnivores. The auditory area is also large. The olfactory area is reduced (more so in phocids than in odobenids or otariids) than that of terrestrial carnivores. In pinnipeds we find a highly developed cerebellum that in some cases is encased very markedly into the skull. The reason behind the size of the cerebellum is unknown, but may be related to the extraordinary ability of many pinnipeds to move very rapidly in different directions while diving. The encephalization quotient among pinnipeds reveals figures similar to those of terrestrial carnivores.

17.1.2.3. Sirenians

They have a small brain. Dugongs' brain is between 250 and 282 g and 364 for the Florida manatee. Their EQ is among the lowest among mammals. It is also much less complex. They have few and shallow sulci and convolutions on the surface cortex are almost absent. The hemispheres of the manatee brains are divided by a deep, wide, longitudinal fissure and there is a deep Sylvian fissure. However, their cerebral cortex is comparatively similar to those of other mammals including primates. The cerebrum architecture is also well defined, suggesting a great deal of ability for processing large amount of information, probably related to their sensory organs.

17.1.2.4. Sea otters

The brain size in these mammals is not significantly different than those of other mustelid species.

17.1.2.5. Polar Bear

We have very little information about the anatomy of the polar bear brain and how it compares to its terrestrial relatives.

17.2. Cranial Nerves

There is, again, a great deal of variation for these nervous features among marine mammals. Nerve size is an important source of information because the larger the nerve, the more neurons carrying information from an specific part of the body to the brain and vice versa.

17.2.1. Sensory Nerves

Olfactory Nerve (I): odontocetes do not have olfactory nerves as adults, and it is greatly reduced among mysticetes. At the same time, the terminal nerve (associated with olfaction) is present in odontocetes. Pinnipeds have a reduced olfactory nerve, particularly among phocids. Sea otters have a reduced olfactory lobe. On the other hand, polar bears (which use their sense of olfaction above the water), have an impressively developed olfactory nerve. All this seems to indicate, that the sense of olfaction in greatly reduced among marine mammals that spend most (if not all) of their time in the water.

Optic (II): Unremarkable among sirenians.

Vestibulocochlear (VIII): Odontocetes have massive vestibulocochlear nerves. Further, odontocetes possess not only more neurons in their vestibulocochlear nerves, but the axons are much larger in diameter than in any other terrestrial mammal. We can generalize that the larger the diameter, the faster the transmission of information. Thus, odontocetes not only seem to transmit massive amount of acoustic information to the brain, but also do it is a much greater speed.

17.2.2. Mixed Nerves

Trigeminal (V): Sirenians have large trigeminal nerves, which they constantly use for food finding and feeding. Mysticetes also have large trigeminal nerves that control the movement of their mouth. This is the second largest nerve in odontocetes and may reflect the high tactile sensitivity of the skin on the head. They are also large in pinnipeds where they carry sensory information from their vibrissae, functioning as tactile structures and in some species, may respond to sound.

Facial (VII): It is a motor nerve that innervates the facial muscles. In odontocetes it is large, apparently reflecting the extensive facial musculature involved with echolocation. It is also large among sirenians, where it may have to do with the masticatory apparatus in these mammals.

17.3. Spinal Cord

17.3.1. Cetaceans

The length varies considerably depending upon the animal size and the species, but on average, is similar to that of humans, with a body length/spinal cord length ratio of 4:1. Among cetaceans is almost entirely cylindrical, enlarged in the cervical area (associated with flippers) and less developed in the lumbar area (probably as result of having lost the hindlimbs). There are 40-44 pairs of spinal nerves. Dorsal (sensory) structures appear relatively small in comparison to ventral (motor) structures. While this is not unique to cetaceans, the sensory component (dorsal roots and horns) is relatively more reduced in cetaceans than in other mammals. This disparity has been attributed to a relative lack of

peripheral sensory innervation and, especially, in the lumbosacral region, the innervation of the powerful tail musculature.

17.3.2. Pinnipeds

It is short, terminating between the eighth and twelfth thoracic vertebrae. A functional relationship between neural canal size and locomotor type has been found among marine carnivores. This relationship has been interpreted to be the result of differential innervation and areas of musculature involved in generating movement of the limbs. Among otariids, lumbosacral (lower back to pelvis) enlargement of the neural canal is less than brachial (arm) enlargement. This pattern is correlated to their forelimb-dominated pattern of locomotion. The phocid neural canal is unique among marine carnivores. The forelimb enlargement is similar to that in otters or otariids, but the lumbosacral enlargement is always higher than the forelimb peak. This is related to their mode of locomotion in which the hind limbs are principally employed. The walrus neural canal displays a hind limb enlargement, a pattern that is very similar to that of phocids. This is reflected in their locomotor pattern in which both the fore- and hind limb are used.

17.3.3. Sirenians

The spinal cord ends at the last lumbar or first caudal vertebrae.

17.3.4. Sea otters

The neural canal cross section increases in size posteriorly in the thoracic and lumbar region suggesting extensive neural supply to the posterior torso and hind limb muscles.

17.3.5. Polar bears

They show enlargements of the neural canal at both the forelimb and hindlimb levels.

17.4. Senses

17.4.1. Vision

The mammalian eye evolved to function in air. Air has low reflectivity index and it is a particularly transparent substance, i.e., absorbs very little light and it does so quite unselectively. Water has a higher refractive index than air and it absorbs light much more readily. This means that light penetrates much less far through the water. In the sea at 10 m depth some 90% of the light has been absorbed or reflected at the air-water interface and this rises to 99% at 40 m. At 600 m virtually all the light has been absorbed. Furthermore the different wavelengths of light are absorbed at different rates, the longer wavelengths (corresponding to the red colors) being absorbed first and the short (blue) wavelengths last.

17.4.1.1. Light Conditions

Because, on average, there is virtually no light beyond 100 m in depth, marine mammals that adventure themselves into the deep have developed not only structural changes in their eyes that allow them to see better under darkness, but also other sense such as sound production and reception, that permits them the location of objects and mapping of the ocean floor.

Another adaptation to light conditions is known as **countershading**. Many marine mammals (and other aquatic animals such as fish for that matter) have silver bottom, gray/dark coloration on top of their bodies. This is a way for their potential prey not to see them coming from the top and for their potential predators to confound them with the darker bottom portion of the ocean when seen from above, particularly at open sea.

17.4.1.2. Cetaceans

The eyes of cetaceans are relatively small (the size of a grapefruit in right and sperm whales) and located on the sides of the head but directed forward. They are located directly above the corners of the lips, near the shoulders. The cetacean eye is markedly flattened anteriorly rather than being spherical as in most mammals. The sclera is very thick and may serve to hold the inner globe of the eye in an elliptical shape

The eyelids, though present, are so swollen with fatty matter known as **conjunctiva** that they are practically immobile. Associated with the conjunctiva they have a number of glands such as **Harderian glands** that regularly bathe the cornea in a viscous solution, as a protection against seawater. The composition of this solution seems to be especially important two achieve two other functions: (a) to increase the hydrodynamics of the eye, and (b) to remain fixed to the eye, so it is not washed out while swimming. We must emphasize that the glands that produce this solution are not homologous to the tear glands and that cetaceans lack that type of glands. Cetaceans also lack eyelashes.

The type of eye adaptations needed for see in through air are different from those needed for seeing through water. That is why we humans need masks when skin/scuba diving. Given that cetaceans were originally terrestrial mammals and that (at least many) see outside the water (gray whales use coastal topography to ascertain where they are), cetaceans have developed the ability to see in both environments. That has been achieved by developing strong eye muscles that can change the actual shape of the lens in the eye to suit either air or underwater vision.

The other major difference between air and water conditions is light intensity, which even in clear waters tends to be very low. This time the adaptation among cetaceans has been to develop a large pupil that collects large amounts of light for low light intensity situations. For high levels of light the pupil can be closed right down to a very narrow slit so it can be used for vision at the surface. A curtain-like extension of the upper iris margin, the operculum, comes down over the pupil proper in bright light leaving only two tiny openings in each of the two lower lateral quadrants of the eye. This is why some have said that cetaceans have a ‘double pupil.’ In addition to control light

intensity, this ‘double pupil’ may help some species of dolphins to focus on two points at the same time and, hence, being able to increase a sense of depth for objects (3-D vision).

They can swim sideways and use only one eye; they can also focus objects in front of them and see with binocular vision. This is particularly true among beaked whales and porpoises, while may not be the case for the sperm whale. Anatomical studies of the brain (large ganglion cells in the temporal area) support this contention.

It has been suggested that because they live in an environment that absorbs red and yellow quickly, they have a poor color vision. This has been contradicted by the fact that they possess both cone-like and rod-like cells in their eyes, which are a necessary, but no sufficient condition for color vision. Experimental evidence on their ability to differentiate colors has been contradictory. It is unknown whether or not they use vision at great depths, that is, in pursue of bioluminescent animals. Furthermore, the different patterns of coloration among all species of cetaceans strongly suggest that they must use eyesight to identify other individuals.

The baleen whale eye is flattened from front to back, and the cornea is less curved. This lowers the refractive index and allows better vision in low-light conditions. A **tapetum lucidum**, a reflective layer behind the retina, reflects light back to the retina a second time. This takes advantage of what light exists at depth. Baleen whales' eyes are constantly bathed in water. There are no tear ducts, but glands at the outer cornea and eyelids secrete an oily substance that lubricates and cleans the eyes. Baleen whales are nearsighted in air. Retinas of baleen whales' eyes contain mostly rods, cells that gather more low intensity light. Cone cells, which are responsible for color vision, are much less abundant. Rod cells respond to lower light levels than cone cells do.

Dolphins have acute vision both in and out of the water. A dolphin's eye is particularly adapted for seeing in water. In air, certain features of the pupil correct for shortsightedness. A light-reflecting layer of the eye sends light through the retina a second time. A dolphin's retinas contain both rod cells and cone cells indicating that they may have the ability to see in both dim and bright light. The presence of cone cells suggests that dolphins may be able to see colors, although studies on bottlenose dolphins have yet to fully document color vision. Eyes are on each side of the head, just behind and above the mouth. Glands at the inner corners of the eye sockets secrete oily, jellylike mucus that lubricates the eyes, washes away debris, and probably helps streamline a dolphin's eye as it swims. This tear-like film may also protect the eyes from infective organisms.

Killer whales have acute vision both in and out of the water. The eyes, about the same size as the eyes of a cow, are on each side of the head, just behind and above the mouth. As in dolphins, glands at the inner corners of the eye sockets secrete oily, jellylike mucus that lubricates the eyes, washes away debris, and probably helps streamline the eyes as a killer whale swims.

Belugas have acute vision both in and out of the water. A beluga's eye is particularly adapted for seeing in water. In air, certain features of the lens and cornea correct for nearsightedness. Belugas’ retinas contain both rod and cone cells, indicating that they may have the ability to see in both dim and bright light. The presence of cone cells suggests that belugas may be able to differentiate among colors, although this ability has not been documented. And, as for other odontocetes, glands at the inner corners of

the eye sockets secrete oily, jellylike mucus that lubricates the eyes and washes away debris.

A special case is the one of river dolphins. Since they live mostly in murky waters, their eyes have been greatly reduced. *Platanista gangetica*, for example, has no lenses at all and is in effect blind since it cannot see images, although they may still detect light intensities.

17.4.1.3. Pinnipeds

Pinnipeds have large, well-developed eyes. Walruses are an exception. The exposed part of their eye is protected by a highly keratinized corneal epithelium and a thick sclera. The sclera prevents the deformation of the eye as a result of pressure variations while diving and protection while swimming. The observation that the sclera is thinner in the equatorial region of the pinniped eyes suggests that it may function to flatten the eye when exposed to air outside of the water, thereby reducing myopia.

The lens is nearly spherical, which helps to focus images on the retina when underwater. The retina has only rods, which implies that they live in a monochromatic world. Although color discrimination has been reported, it is believed that it is related to brightness rather than hue (like bulls for which bullfighters use a red cap to attract their attention). Apparently two different photopigments are related to this function. The elephant seal, which is a deep diver, has been shown to possess a modified photopigment, resembling that of deep-sea fishes. The Weddell seal, another deep diver, does not have this modification and it has been suggested that the elephant seal uses its modified photopigment to respond to the illumination of the bioluminescent squids on which it feeds. Its absence in the Weddell seal perhaps indicates that they may have another means of finding their prey at depth.

Another eye modification among seals (as we saw for cetaceans) is the presence of **tapetum lucidum**. The *tapetum* is found in many nocturnal mammals: the reflection of a car's headlamps in the eyes of a cat at night is the most familiar example. In the seal, which is basically a diurnal mammal, it functions when submerged rather than at night.

Under terrestrial conditions when the light intensity is much higher, pinnipeds can protect their eyes by closing the pupil, the deeply pigmented brown iris contracting first to a vertical slit and then to a tiny pinhole. But excess light is not the only problem. The refractive apparatus of the pinniped's eye is developed to operate while submerged in water. In air the cornea will have its usual effect and this added to the refraction from the spherical lens will result in the light being brought to a focus short of the retina, in other words, the pinniped will tend to be short sighted. This is not the only problem arising from the refraction from the cornea. The surface of the pinniped's cornea is not spherical but has different curvatures in the horizontal and vertical planes. This difference in curvature may be a result of adaptation to reduce the pressure on the eye when the seal is swimming fast under water. In air, however, it results in the seal being not only shortsighted, but astigmatic as well. However, the vertical slit pupil parallel to the astigmatic axis has the effect in bright light of focusing to a point on the retina. Contraction of the pupil by well-developed ciliary muscles will also minimize myopia. The result is that a pinniped will see clearly in air only when the light is reasonable bright.

This does not mean, however, that seals do not rely to a considerable extent on vision on land. Even if their eyes do not allow them to define detail, they are very responsive to movement and a person stalking a seal ashore needs to move cautiously, though he/she needs take no special care to conceal his/her outline.

Pinnipeds have also the Harderian glands located in the outer corners of the eye. They produce oily mucus that protects the eye and prevents the cornea from drying out. Lacrimal glands, are small, and there is no nasolacrimal duct, which may imply hat they are no functional.

17.4.1.4. Sirenians

Manatees' eyes are small when compared with the size of the optical cavity and the eye nerve is slender. The shape of the lens is nearly spherical and the sclera appears thicker posteriorly than elsewhere. The dugongs' eyes are small, round, and black with a well-developed nictiating membrane. As is true for cetaceans, secretions from glands under the eyelids create a copious flow of viscous tears. Absence of a well-developed ciliary muscle has been reported for both the dugong and the manatee and is consistent with the poor visibility of their natural environment.

Behavioral studies in manatees in the wild suggest that they can see for considerable distances in clear water, but that they may be farsighted inasmuch as they tend to bump into objects within close range. They do have a well-developed *tapetum lucidum* and binocular vision has been supported by behavioral studies. West Indies manatees may have, at least, a dichromatic vision. This contention has been supported not only by the presence of both, cone-like and rod-like cells in their retina, but also by behavioral studies.

17.4.1.5. Sea Otters

The eyes are characterized by extensively developed ciliary musculature associated with a unique and well-developed accommodative mechanism that is able to change the refractive power of the lens; their accommodative range is at least three times greater than that reported for any terrestrial mammal. In addition, the well-developed anterior epithelium may be an adaptation that helps the sea otter to cope with salinity in its environment. They also have a well-developed *tapetum lucidum*.

Visual acuity in the sea otter seems to be good both above and under water. Sea otters depend on accommodation of the eyeball to compensate for the loss of the eye's corneal refractive power when underwater.

17.4.2. Touch

17.4.2.1. Cetaceans

Cetaceans have a very elaborated and specialized system of nerve endings whose concentration throughout the skin is irregular. It seems that this sensitive system is used as a pressure sensor to help them to sense whether or not turbulence is produced while swimming in order for them to improve swimming efficiency, which is only achieved

when water flows in a laminar form on their skin. Thus, the body shape is constantly adjusting while swimming. Also, around the blowhole, there seems to be a specialized sensitive area that helps them ascertain whether or not the blowhole is above water, so the can open it and breath. There are some reports of dolphins using their penis to investigate objects. Whether this is the case of just an act of masturbation (which has been observed in captivity) has yet to be determined.

Baleen whales have sensitive skin, especially on the head and flukes. Features of the brain indicate that both, bottlenose dolphin and killer whale's sense of touch are well developed. Bottlenose dolphins' and killer whale's skin is sensitive to touch. Studies on belugas in zoological environments indicate that they seek out physical contact with other belugas.

17.4.2.2. Pinnipeds

Unlike cetaceans, pinnipeds have their body fully covered by hair, so the type of skin sensitivity that has been attributed to whales and dolphins cannot be the same for seals and sea lions. However, pinnipeds have something that whales do not have: whiskers. All pinnipeds have well-developed whiskers or vibrissae. The bearded seal have whiskers so prominent that such is the reason for its name. The whiskers are arranged in definite groups. There are mystacial vibrissae, arrange on the upper lip, the superciliary vibrissae, above the eyes, and the nasal vibrissae, usually only a single pair of hairs on top of the nose. It has been demonstrated that harbor seals in murky waters whose whiskers have been clipped, took longer to capture live fish. A seal pushes its whiskers forward when chasing fish, usually to a considerable extent, and they could detect water displacements created by the swimming movements of fish, allowing the seal to position its head correctly so as to seize the fish in its jaws. Furthermore, there are reported cases in the literature of blinded seals in apparent perfect conditions, which would suggest that these animals are able to locate and capture fish without visual clues.

17.5.3. Taste and Smell

It is difficult to evaluate cetaceans and pinnipeds' sense of smell. Scents are detected in mammals by the olfactory epithelium that covers the scroll-like turbinal bone of the in the nostrils/nose. The sensory epithelium is irritated by contact with water, so odors can only be detected in air.

17.5.3.1. Cetaceans

Unlike terrestrial environment, the distinction between smell and taste is less obvious in the aquatic environment still 'smell' is used for distance information gathering while 'taste' for objects that are within the reach of the animal.

Although it seems that *Basilosaurus* and other archaeocetes still had well-developed olfactory peduncles, modern cetaceans seem to have largely lost the sense of airborne smell that exists in most mammals, as they have very limited olfactory receptors and by the fact that their olfactory lobes of the brain and olfactory nerves are absent in all toothed whales. Olfactory nerves and bulbs are present in baleen whales during the fetal

stage, but they are greatly reduced in the adult brain. Scientists have yet to discover whether such nerves and bulbs are functional. They may have lost this sense with the repositioning of the nostrils from the front to the top of the head when a number of important changes to the function and operation of organs associated with the nostrils must have occurred. The nostrils (blowhole) are usually closed except when the animal breathes at the surface and the breathing is so rapid that 'air smelling' must be of limited use. Baleen whales seem to have rather more olfactory receptors that the toothed whales and they may still be able to use these receptors to 'sniff the winds' in search of plankton-rich waters.

The sense of taste appears to be still present in at least some cetacean species. Dolphins can detect arrange of chemicals dissolved in water, distinguishing between what we would describe as sweet, sour, bitter and salty tastes. In addition, what appear to be taste buds are present on the tongues of several species of toothed whale. Little is known about a dolphin's sense of taste. Features of the brain and cranial nerves suggest they may have some sort of a taste sensation. They do have taste buds, although they have not been well studied. Sensory areas in beluga whale mouths suggest that they may function in taste. To date, no information is available on the sense of taste in any baleen whale. Nerves and the area of the brain concerned with taste are present. There are taste buds on the base of the tongue, but their importance is unknown.

Sense of taste among cetaceans might be used to investigate likely food items for signs of decomposition. Also they may use urine and fecal material from other cetaceans for social clues (e.g., for sexual pheromones).

17.5.3.2. Pinnipeds

Pinnipeds have very well developed turbinal bones in the nose but their nervous connections to the olfactory-sensible areas of the brain are very poorly developed. Nevertheless, it is clear that scent plays an important role in the life of pinnipeds. Many pinnipeds have very strong and characteristic scents: the ringed seal as once known as *Phoca foetida* (the stinking seal). The bond between mother and pup seems to be established by scent. A mother gray seal, returning to her pup on a crowded beach will first call and listen for her pup's answering call, but will always finally identify it by sniffing at its muzzle.

17.5.3.3. Sirenians

Manatees have a large olfactory organ and behaviorally they are often very selective in their food choice, but whether the selection is through smell, taste, or touch, or a combination of these is not known. In comparison with cetaceans, taste buds are more numerous among sirenians. In the dugong they are located in a row of pits along the lateral margins of the tongue. The West Indian manatee possesses a pair of swelling corresponding to the pits of the dugong tongue. Serous glands open into the pits and swellings and neighboring mucous glands open directly onto the surface of the tongue. The product of the glands may be used to rinse the taste buds, particularly in the case of the dugong, which feds on sea grasses. It is also possible that some enzymes contained in the fluid convert the polysaccharides of sea grasses and algae into smaller molecules,

which in turn stimulate the taste buds. Another characteristic feature of the dugong tongue is the presence of patches, fungiform papillae, on the lateral surface, which may serve as a tactile organ.

17.5.3.4. Sea Otter

They have well-developed turbinates and acute olfactory sensitivity, typical of terrestrial carnivores. Their social behavior also suggests that scent production and acute olfactory sensitivity are important. Males possibly locate and identify estrous females by olfactory cues.

17.6. Endocrine Glands

Pinnipeds differ from cetaceans in possessing a pituitary gland characterized by thick pars intermedia in the anterior lobe of the gland. It may be actively secreting growth hormone during the rapid early postnatal growth of pups. In manatees and dugong, the pituitary gland is divided into anterior and posterior lobes by a thick layer of dense connective tissue.

The pineal gland is particularly large at birth in elephant seals and Weddell seals. It may be involved in thermoregulation in early postnatal life. Pineal activity could also be correlated to light and reproductive cycle.

The pineal gland is absent among odontocetes and there is a report for a small one in the humpback whale. The organ has also been reported in embryonic stages of the blue whale.

The thyroid gland is two-lobed, with one lobe lying on each side of the larynx. The pinniped thyroid gland is probably very active within a few hours after birth, based on morphologic and physiologic evidence. Among cetaceans the thyroid is rather large, which has been linked to its role in the regulation of metabolism. Among sirenians, the thyroid has a relatively large abundance and density of its interfollicular connective tissue, which may be linked to the pachyostotic bone, sluggish behavior, and relatively low rate of oxygen consumption.

The adrenal gland in pinnipeds displays a marked lobulation and folding. It differs from most other mammals in having more cortical than medullary tissue. Among delphinids, the adrenal gland has been described as smooth ovoid organ but distinctly lobulated on the outside in mysticetes. Among West Indian manatees, the adrenal gland has been described as atypical because it has no cortical zones.

Chapter 18

Reproductive System and Cycles. Reproductive Patterns and Strategies

18.1. Introduction

The mammalian reproductive system consists of structures that produce and transport gametes, and provide development and support of offspring (Table 17.1.). Although all eutherian mammals share the function of each reproductive structure, there is great diversity in specific morphologies across the group.

Table 18.1. Reproductive Structures and Functions

Function	Male	Female
Production of gametes	Testis produce sperm	Ovary produces eggs
Transport of gametes from gonads to external environment	Epididymis	Uterine tube
Site of maintenance of pregnancy		Uterus
Supportive and erectile tissues	Scrotum, penis	Vulva, clitoris

Marine mammals, too, display a tremendous diversity in reproductive morphologies and behavior. Cetaceans, sirenians, and some sea otters give birth to and suckle their young in the aquatic environment, whereas the remaining marine mammals travel to land (or ice) during these times.

18.1.1. Male Reproductive Structures

The testis performs similar functions in all mammals, and varies little in its general morphology. Sperm is produced in seminiferous tubules and is stored in a highly convoluted epididymis. The ratio of testis-to-body size does vary across species. Testis size seems to be related to mating systems; males that compete for females and have high copulatory rates tend to have larger testis. That is particularly true among odontocete

species that engaged in sperm competition. Odontocetes have 7 to 25 times higher testis-to-body mass ratios than most mammals of their size. The most extreme case is that of the dusky dolphins whose testis mass is 8% of that of the body (male humans is 0.08%). Among mysticetes which engage in sperm competition, right whales possess testis 6 times lager than what would be predicted for their body size. They also have the absolute larger testis, a combined weight of more than 900 kg.

The penis of all marine mammals can be retracted into the body wall. Their structure is similar to that of terrestrial mammals. Pinnipeds have a vascular penis reinforced with a bone, the baculum, typical of carnivores. The vascular penis becomes rigid and increases in length and diameter when blood fills venous sinuses. We assume that the penis morphology of the sea otter and polar bear are similar. The cetacean penis is fibroelastic like that of most artiodactyls. The non-erect position of the cetacean penis is curved into a sigmoid flexure within the body wall, as is seen in ruminants. Upon erection, the cetacean penis straightens and becomes turgid, but does not dramatically change its length or diameter as does the vascular type. The penis of the sirenians is of the vascular type, is straight and lacks a baculum.

18.1.2. Female Reproductive Structure and Calving

The uterus of pinnipeds, cetaceans, and sirenians is bicornuate as in most mammals. The ovaries are paired, oval organs that lie at the distal portion of the uterine tubes, and are held in place by the broad ligament. The placenta type of each group tends to be similar to that of its terrestrial relatives. Thus, cetaceans possess a diffuse type, as do artiodactyls; sirenians possess a zonal type, similar to elephants; and pinnipeds, polar bears, and sea otters possess a zonal type as do carnivores. The female genital system of pinnipeds is similar to that of terrestrial carnivores. The testes in the Phocidae and the walrus are in the inguinal region, concealed between the blubber and the abdominal muscles. Otariids, in contrast, have a scrotum into which the adult testes descend during the mating season.

Most marine mammals have a pair of mammary glands. The walrus and the polar bear have four. They are located in abdominal position. Of the polar bear's four mammaries, the cranial pair lie just behind the axilla. In sirenians, the pair mammary glands lie in an axillary position.

Cetaceans and sirenians give birth to their young in the aquatic environment. Cetacean and manatee calves tend to be large, and must be precocial, at least in their locomotory skills. Pinniped neonates are also large, and their development at birth varies among species. All species spend some amount of time on land (or ice) before learning to swim and hunt. There is evidence that sea otters give birth both on land and at sea. These animals are unique in carrying out their maternal activities on the sea surface. The sea otter pup is said to be precocial relative to other otter pups. Polar bears, like other bears, give birth to altricial young while fasting in winter dens. Marine mammals tend to give birth to one offspring. Twinning can occur in all groups, and triplets have been reported in polar bears.

18.2. Reproductive Cycles

Reproductive cycle is the normal minimum time period for all stages of reproduction in the female from ovulation through conception and pregnancy to birth and lactation followed by a short rest period. The reproductive interval between one cycle and another may vary in time depending upon environmental, nutritional, and social circumstances.

18.2.1. Cetaceans

Life histories vary widely among species and even among geographic stocks. Some factors, including age at sexual maturity, lactation period and calving interval, are also influenced by external conditions such as population density and food availability, and are therefore subject to change. Despite the fact that female cetaceans have a pair of mammary glands, all species of whales and dolphins, without exception, typically produce a single young. Twin fetuses are extremely rare and when that happens one of both usually die. Season of births for cetaceans that at least spend some time in cold waters is usually very restricted while for those are basically tropical, that season is more flexible. While small toothed whales appear to give birth during periods of food abundance, the larger baleen whales also feed during this time but then migrate long distances to give birth in warm waters during the winter. An exception is the Bryde's whale, which makes only local seasonal movements in the tropics to warm temperate regions. In most species the sex ratio is 1:1 with preponderance toward males early on, just like in humans. Humpbacks and blue whales show the most preponderance toward males.

Mysticetes: There is sexual dimorphism in terms of body size with females about 5% lager than males, apparently related to their need to carry the fetus. Most baleen whales show a 2-year reproductive cycle comprising of a gestation period of about 11 months and a lactation period between 6 and 7 months, followed by a period of anestrous. Baleen whales evolved reproductive cycles that are synchronized with annual migrations between low latitude winter calving grounds and high latitude summer feeding areas. The cycle starts in winter in low latitudes and warm waters with ovulation and conception leading to pregnancy, during which the females migrates to summer feeding grounds in higher altitudes. The female returns to low latitudes to give birth in winter. The calf is weaned when the female migrates to summer feeding grounds in high latitudinal waters for feeding during the summer of the second year. Exceptions to this cycle are the minke whales, which may reproduce annually while balaenids reproduce only once every 3 or 4 years. Baleen whales may live between 60 and 97 years, depending upon the species, and may have up to 40 pregnancies in their lifetime. Quite in contrast with the large odontocetes, these massive animals mature relatively young (4 to 10 years), carry the fetus for only about 10 to 12 months, and nurse for a brief 4 to 10 months.

Only a proportion of females (usually 20% of the adult ones) will conceive every year. There is some evidence that at least some of the inshore whales are polyestrous if conception failed to occur. The fetus in mysticetes grows faster than in other mammal, and particularly in the latter stages of gestation. The accelerated growth generally coincides with arrival on the feeding grounds. When the young are born they are

therefore relatively large, and rapid growth continues for several months, nourished by their mother's milk with its high fat content. Lactation lasts between four and up to ten months depending upon the species and in that time the suckled young may increase its weight by five to eight times. Ovulation is usually suppressed during this period, so it is not possible for the female to conceive again until at least towards the end of lactation. This imposes a minimum reproductive cycle of two years for all but the minke whale, and some studies suggest that three years or more is likely to be more typical for most species.

For age determination air plugs are used. When cut, these plugs expose growth layers in the core, appearing as alternating light and dark bands. Each pair constitutes a growth layer and in most species (the possible exception being the humpback) is apparently deposited annually.

Table 18.2. Some reproductive data for mysticete species

Species	Peak months of conception	Gestation period (mo.)	Peak months of Birth	Lactation duration (mo.)	Age of sexual maturity (yr)
Blue (Antar.)	6-7	11	5	7	5
Fin (Antar.)	6-7	11	5	7	10 -> 6-7
Sei (Antar.)	7	11-11.5	6	6	11 -> 8
Minke (Antar.)	8-9	10	5-6	4	14 ->6-7
Bryde (S. Afr.)	Year-round	12	Year-round	?6	8-11
Humpback (Antar.)	7-8	11.5	7-8	10.5-11	4-5
Gray	12	13.75	1-2	7	8
Bowhead	5	12-13	4-6	7	8
Pygmy right	?	12	?	?5-6	?
Right (S. Hemisphere)	8-10	10	5-7	?	?

Odontocetes: Size sexual dimorphism goes both ways among odontocetes. Male sperm whales are 1.6 times larger than their female counterparts. In other species is the other way around, while in others there is no real difference. The testes are intra-abdominal and lie ventral to the kidneys. The testes in *Phocoena* and certain other species become so enlarged during the mating season that they exceed the kidneys in size and weight.

Veins carrying cool blood from the dorsal fin and flukes are juxtaposed to arteries supplying the testes. The genders can be distinguished by the difference in the configuration of the genital fold; the male usually has two openings, one behind the other, separated by a bridge of tissue. The female has a longer, more prominent slit which encompasses the closer-spaced genital and anal openings and is flanked by a small slit on each side containing the nipples. An object inserted into the genital opening of a female will be directed toward the head, and in a male, toward the flukes. In males of *Phocoena* and *Kogia*, the genital aperture is situated much closer to the umbilicus than to the anus. Cooling action allows the production and storage of viable sperm under otherwise unsuitably high body temperatures.

Reproductive seasonality is not very strong among toothed whales. Virtually all species have a breeding and calving season, but unlike the baleen whales, the season is often protracted. Sperm whales breeding season occurs between October and December in the southern hemisphere and April and June in the northern hemisphere. At that time, the estrus synchronizes with the arrival of the adult bulls. Gestation lasts between 14 and 15 months in this species. The true lactation period is usually between 18 and 20 months, but some females may be suckling up to 7.5 years of age while males up to 13 years of age! Solid food may be consumed when they are 6 months old. This may explain some of the extreme close social bonds in many species of dolphins.

Gestation varies between 10 and 17 months (the latter figure for orcas). Lactation can be very variable, and rather than lasting a few months, can last for several years as is the case for sperm and pilot whales. In these species the reproductive interval can be of up to 13 years in some species. Life span is between 25 and 60 years (depending upon species). Among phocoenids whose life span are the shorter, simultaneous lactation and pregnancy has been observed. The little harbor porpoise, with a life span of only 7 to 15 years, becomes sexually mature at age 4 to 6 and has a gestation period of 10 to 12 months, followed by 6 to 8 months of nursing. Sperm, killer and pilot whales, at the other end of the range, possibly live to 60 years or more; they reach sexual maturity at 8 to 10 years. The pregnancy lasts 14 to 16 months, and calves may nurse for 2 years or more; the females of such species may have a long post-reproductive life.

Females become sexually mature at the age of seven to twelve years and males between 9 and 11, but sexual maturity is not achieved until they are 18 to 19 years of age. Gestation periods for most odontocetes are between 10 and 12 months, although some species such as sperm whales gestation periods is extremely long, between 15 and 16 months, may be up to 19 months. This seems to be particularly true for species that consume squids that may result from the longer time needed for fetal growth arising from a lower energy content of squid. An alternative explanation is that squid predation is a very specialized type of feeding that requires certain level of maturity before trying to pursue successfully.

Age determination is done by sectioning teeth and counting the growth layers in the dentine.

Table 18.3. Some reproductive data for some odontocete species

Species	Peak month(s) of conception	Gestation period (mo.)	Peak month(s) of birth	Lactation duration	Age of sexual maturity ♀/♂ (yr)
Sperm whales	10-12	15-16	2-3	>2	19/9
Beluga	5-6	>11	4-5	?	6-7/4-7
Long-finned pilot whale	5-9	12	5-8	3.67	14/9
Short-finned pilot whale	8-1	14-16	12-1	2-3	16/5
Killer whale	10-12	12-17	12	1-3	15/8
False killer whale	?	15.5	?	1.5	16/17
Bottlenose dolphin	Spring-6	12	3-6	1.6	10-15/10
Striped dolphin	Summer and winter	12	Summer and winter	0.67-1.67	14/14
Harbor porpoise	6-8	10-11	5-7	0.67	3-4/3-4
Dall's porpoise	8-10	11.4	8-9	0.5-3.5	5-6/3-4

18.2.2. Pinnipeds

Pinnipeds are characterized by (a) delayed implantation, (b) highly seasonal, synchronized reproductive cycles in most species, and (c) the production of a single offspring at any reproductive attempt.

Almost all pinnipeds have an annual reproductive cycle. Exceptions are the Australian sea lion, (18 mo.), the walrus (15 mo. gestation, 2 yr. reproductive cycle), and the Hawaiian monk seal (6 mo. reproductive interval).

The gender of a pinniped is easily determined. In the female, the anus and vagina lead into a common opening ventral to the base of the tail. The male has two widely separated openings, with that for the penis a few cm behind the umbilical scar. There is a well-developed baculum (penis bone). The distinction between young males and females usually requires close examination and manipulation. As the animals mature, there are often prominent secondary sexual characteristics that can be discerned at a distance. For example, the males are usually larger and more robust and, in otariids, may develop sagittal crests and manes.

Females of most pinniped species become sexually mature by about 4 to 6 years of age, with some as early as 3 years (northern elephant seal) and the walrus as late as 6 to 9 years. Males reach sexual maturity at about the same age or slightly older, but may not breed successfully until several years later. This is particularly true of highly gregarious species. Age of sexual maturity, thus, varies between species and within species depending upon environmental factors.

There are three phases in their reproductive cycle: estrus, delayed implantation (embryonic diapause), and fetal growth. Estrus lasts 5-8 days among otariids and 4-60 days in phocids (depending upon lactation). Males also show cycle of fertility with mature sperm and testosterone levels appropriate only for a limited period of time beginning before and ending after the breeding season. Outside that period of time there is testicular regression. Delayed implantation varies between 3 and 4 months. It is highly dependent upon photoperiod and body fat content in the female. The 11- to 12-month pregnancy period includes a 2- to 4-month phase during which the newly fertilized egg develops into a blastula, they remains dormant until the mother's hormonal levels allow development to proceed. By delaying implantation, the female can give birth during the same brief time each year when conditions are ideal for both mating and rearing pups. This synchrony is particularly important in polar environments. The walrus, which breeds every 2 or 3 years, has a pregnancy period of around 15 to 16 months, including 3 to 4 months of delayed implantation.

Often the males arrive on the breeding ground a few days or weeks before the females and take up territories ashore (this is always the case with eared seals). The breeding females, carrying conceived the previous season, come ashore only shortly before giving birth. In elephant seals, for example, this period is about a week, but in Harbor seals, which have their pups on sandbanks or half-tide rocks, it may be only a few minutes. Birth is a speedy process in all pinnipeds, as the pup forms a convenient torpedo-shape package, which can slip out with equal facility either head or tail first.

Pregnancy rates vary from 0.46 to 0.89. Gestation lasts between 6 and 8 months. Fetal growth rate is constant and independent of body size, e.g., the fetal growth of the largest pinniped, the southern elephant seal, is approximately 10 times of that of the smallest, the Galapagos fur seal. Sexual ratio at birth is approximately 1:1. Otariid lactation lasts from 4 months to more than a year. In phocids it lasts 4 to 60 days. Milk has high fat concentration (40%).

Just like in cetaceans, all species of pinnipeds, without exception, typically produce a single young. Twin fetuses are extremely rare and when that happens one of both usually die. The newborn pup is covered with a specialized birth coat or lanugo. This is molted after two or three weeks in true seals, or two or three months in eared seals. In the Harbor seal, the lanugo is molted while still in its mother’s womb. Typically, pinnipeds breed in the spring or early summer. After a period of intensive feeding, they assemble at the chosen breeding site. All the northern true seals except the harbor and the monk seal, and all the southern seals except the Northern and Southern elephant seals breed on ice. None of the eared seals breed on ice. Walruses are ice breeders, but do not usually breed far off shore.

Usually, a few hours elapse before the mother first feeds her up. There is much variation in suckling patterns. Ice-breeding true seals, such as the Harp seal suckle their pups for as little as nine or ten days; the instability of the ice pack may be a factor in this.

In other true seals lactation is longer, about three weeks in Grey and elephant seals, or six weeks in Ringed seals. Many true seal mothers do not feed themselves at all while suckling their pups. At the end of the lactation, the mother comes into season and is mated, weans her pup abruptly and deserts it. There is no further contact between mother and pup except casually. In eared seals, the mother-pup association lasts somewhat longer. About one week after birth, the female comes into season and is mated by the nearest dominant bull. She then departs for a series of excursions between which she returns to feed her pup. The pup may be independent after 4-6 months, but often continues to receive some milk from its mother almost till the arrival of the next pup, or beyond it.

The nursing period of phocids is typically 3 to 6 weeks but has been compressed to an impressive 4 days in the hooded seal 11. Females of most species remain with their pups continuously until weaning; harbor and ringed seal mothers may leave to feed for brief intervals. Otariids provide maternal care for a few months to a year or more.

During this time the female periodically makes lengthy foraging trips. Walrus calves may begin to feed upon bottom-dwelling invertebrates as early as 5 to 6 months of age, but usually continue to suckle, at least as a dietary supplement, until about 2 years old.

18.2.3. Sirenia

Sirenians show little sexual dimorphism with the distance between the genital opening and the anus as the most reliable index of gender. In females it is closer to the anus. Manatees seem to reach sexual maturity between the ages of 2.5 and 6 years. A focal female in estrus may be surrounded by up to 22 males among manatees. Gestation lasts between 12 and 14 months. They usually give birth to only one young with twining happening 4% of the times of either or both sexes. Sex ratio is about 1:1. Calving lasts between 1 and 2 years. Average pregnancy takes place between 2 or three years during sexual maturity. Up to 9 placental scars have been counted in a dugong uterus. Placental scars do not persist in manatees so they cannot be used for fertility determinations. Sirenians show a mild seasonality in their reproductive cycles.

18.2.4. Sea Otters

It is largely non-seasonal. Gestation lasts from 6 to 8 months. Birth intervals last about a year because pups are normally nursed for between 4 and 8 months. Twins are rare.

18.2.5. Polar Bear

It is highly influenced by that annual cycle of sea ice. Breeding season is between March and May when females with yearling or, more often, 2-year-old cubs comes into estrus. Their period of delayed implantation last between 4 and 5 months when females enter their winter dens in late September or early October. Gestation lasts only 3 to 4 months. Polar bears are poorly developed (altricial). Mean litter is between 1.7 and 1.9 cubs. Only 13% of sexually mature females give birth every season. Suckling young seem to

inhibit estrus. Interval between births is between 3.1 and 3.6 years. Body mass has been correlated with reproductive success; females with low fat contents show the lowest.

18.3. Natural Mortality

Here we will study mortality by natural causes only. Mortality caused by humans will be seen later.

Lifespans: Natural adult mortality rates seem to decline in various baleen whales as the size of the species increases. Among odontocetes, smaller species have shorter life spans. Here are some examples:

species	life span (years)	
harbor porpoise	15	
bottlenose dolphin	25	
spotted dolphin	40-50	
narwhal	50	
killer whale	50+ (male)	80+ (female)
sperm whale	75	
humpbacks	30	
minke	40-50	
sei	65	
fin	85-90	

Among pinnipeds the average age is 20, but the Baikal seal may pass the 50 year old mark.

18.3.1. Cetaceans

Little is known about natural mortality in cetaceans, because it is difficult to garner such basic information as population size, calf production and survival data, and accurate age estimates. The type of long-term observations made on orcas in British Columbia waters or Florida bottlenose dolphins are not feasible for most species. Instead, information comes from stranded animals, those harvested commercially, and some taken incidentally in fisheries operations.

Following the general mammalian pattern, mortality is high in the very young, decreases sharply with maturity, and increases again in advanced age. Species that provide longer maternal care have greater juvenile survival. Mortality rates seem higher in males than females in species presumed to be polygynous (i.e., dominant males mate with a number of females), including pilot and sperm whales. Some mortality is related to environmental conditions. Cetaceans in high latitudes occasionally become trapped in ice, and may subsequently die of starvation or fall victim to predators or hunters. As many as 3,000 beluga whales at one time have met this fate, as have narwhals, gray whales, bowheads, and white-beaked dolphins.

Predation: Cetaceans have few predators besides humans: sharks, killer and false killer whales. Actual observation of predation are not that common although scars in some species seem to indicate that such attacks may be include from 3 to 18% of the individuals of some species.

Parasitism and disease: Parasitism is very common in some species. Several baleen species have conspicuous infestations of barnacles and amphipod crustaceans (called whale lice although they are not insects) attached to their skins. Barnacles are not species specific while whale lice tend to be. A number of nematodes and tapeworms live in the stomach and intestine of odontocetes and mysticetes and the same species may occur in different species. Some of these can cause severe infections that can be lethal by congestion of the kidney and consequence renal failure. Moderate infections could also cause extensive injury to the vascular system.

Strandings: There is not simple, clear explanation about the phenomenon of strandings. Some species seem to be inclined to strand with certain frequency (e.g., pilot whales) other are never been seen stranded; some places seem to be more common for stranding phenomena while other parts of the world such strandings are very rare, to say the least. Among the explanation given, there are suicide, infection of the ear canals and/or nervous system, epidemics, pollution, 'confusion' regarding the depth and nature of the bottom, anomalies in the magnetic fields, animals hit by boat propellers, drown in nets, old or too young individuals, etc. We do know that most stranding species are strongly social and tend to be pelagic. Still, there is much to learn.

18.3.2. Pinnipeds

As in other mammalian species, mortality in pinnipeds is high in the very young, decreases rapidly with maturity, and increases again in advanced age. Generally between 10 to 20 percent of pups die before they are weaned, and 20 to 50 percent of all newborns may not survive the first year. The leading causes of pup mortality are accidental separation or premature abandonment due to storms, crowding, trauma, illness, insufficient food, or human disturbance, followed by starvation.

Rookeries can be dangerous places for pups and adults when population density increases. Young northern elephant seals, Hawaiian monk seals, Steller sea lions and Pacific walruses are bitten or trampled by adults, which also are victims of aggressive encounters. Injured animals may die of their wounds, or through ensuing infection, starvation or increased predation.

The security of a rookery is also undermined by weather conditions. Storms, unusually high tides, and persistent and extensive ice cover have resulted in the loss of nearly the entire season's pups of northern elephant seals, northern fur seals, and Steller sea lions. Polar species are threatened by ice that can crush them or trap them out of water. The only known natural mass harp seal mortality followed a severe winter storm in the Gulf of St. Lawrence in 1973, in which hundreds, perhaps thousands, of dependant pups and their mothers were crushed by broken ice. One of the more elusive factors affecting population vitality is the gradual or sudden decline in available food. For example, Galapagos fur seals and sea lions faced widespread starvation when the

abundance and quality of prey declined profoundly in waters warmed by the 1982-83 El Niño event.

'Pinniped hyponatremia,' a fatal disease induced by stress, was diagnosed in free-ranging Arctic ringed seals at a time when persistent ice interfered with food production. Pacific walruses have evidently reached or exceeded 'carrying capacity' -the number of animals the environment can support. The resulting nutritional stress, together with disease, is believed to be responsible for the increased juvenile mortality observed since the mid- to late 1970's.

Predation: Predators take their toll on certain species. At sea several species of marine mammals prey upon other species of marine mammals such as killer whales and even other pinnipeds (leopard seals). Some sharks also prey on several species of marine mammals. On land ravens, red and arctic foxes, wolves, jackals, dogs, pumas, and polar bears. Foxes in some Arctic regions consume or kill as many as 40 percent of ringed seal pups hidden in the illusionary safety of their birth lairs. Polar bears and walruses prey on juveniles and adults. Steller sea lions, killer whales and sharks eat northern fur seal pups. Harbor and gray seals in the Northwest Atlantic, Hawaiian monk seals and California sea lions are also taken by sharks, while coyotes kill significant numbers of harbor seal pups in certain coastal regions of Washington. Predator-inflicted injuries may bring pinnipeds ashore, and eventually into rehabilitation centers.

Injuries sustained in intrasexual combats may also lead to premature mortality without being fatal at the time of fighting.

Parasitism and disease: True lice, mites, nematodes, cestodes, trematodes, seal pox and other viral and bacterial diseases. Many of these are transmitted from the mother; others are the result of the food (usually fish) already carrying the disease, particularly when carrying nematodes.

Toxins produced by marine algae can be carried through the food chain, poisoning a predator somewhere along the way. As captain of the schooner Antarctic in the early nineteenth century, Benjamin Morrel recorded a mass mortality of Cape fur seals at Possession Island in\ southwest Africa. A fresh appraisal of Morrel's findings suggests the event might have been caused by toxic dinoflagellates. Clusters of northern fur seals and, in one instance, Hawaiian monk seals died in circumstances also suggestive of natural poisoning.

Competition and the Response to Exploitation

Because of the above data, it is not very difficult to come up with the assumption that heavy predation from humans is going to make these species very difficult to recover. For example, in 60 years, from the beginning of this century, the numbers of blue whales were reduced from 200,000 to 6,000. Some species seem to try to accommodate to these circumstances by advancing the time of conception and increasing the proportion of pregnant females.

Yet, environmental factors can still play a detrimental role in already depleted species making recovery sometimes very difficult. In the case of manatees, for example, sea grasses are prone to large-scale episodic diebacks. Most losses, both natural and

anthropogenic are attributed to reduced light intensity due to sedimentation and increased epiphytism from nutrient enrichment. Sometimes sediment instability, dredging, and poor catchment management interact to make the process more complex.

18.4. Reproductive Patterns and Strategies

18.4.1. Introduction

Marine mammals exhibit all the variety of reproductive systems found among other placental mammals. **Monogamy** is found in some pinnipeds (e.g., hooded seals). Others (e.g., elephant seals, humpback whales, sea otters, polar bears) are extremely **polygynous**. In some cases, successful elephant seal males mate with dozens of females during the same season. Odontocetes and sirenians display **promiscuity**, i.e., several adult males are associated with a group of females for a variable period of time.

Breeding includes **mating** (mate selection and copulation) and **parturition** (calving in whales and sirenians; pupping in pinnipeds and sea otters.

18.4.2. Mating Systems

18.4.2.1. Cetaceans

All cetaceans mate and give birth in water. Consequently, our understanding of these events is most cetacean species is spotty. Only the general outlines of reproduction are documented for small odontocetes which can be observed in captivity, for species which have been exploited commercially (and for whom large numbers of carcasses have been available for examination), and for coastal tropical and subtropical species where direct underwater observations of courting, mating, and calving behaviors are facilitated by clear waters. With the advent of molecular techniques such as DNA fingerprinting, it has been possible to verify these behaviors and to determine paternity and kinship.

With few exceptions, notably cooperative feeding by humpback whales, mysticetes do not group closely together, school, or form pods. This probably reflects the need to feed more or less individually because restricted areas cannot sustain the daily food requirements of a large group. Unlike mysticetes, odontocetes exist in social groups (e.g., schools, units, and pods) of varying sizes whose structures persist longer than any individual member's lifespan. Most mysticetes show little evidence of persistent social behavior beyond mother-calf bonds, which disappear at weaning. The presence or absence of persistent social bonds between individuals can, in turn, influence the evolution of mating behavior.

Seasonal migrations:

Baleen whales need warm waters for the growth and development of their relatively small young but cannot find enough food to sustain them throughout the year. Some like the bowhead whale only make small migrations. It is possible that long migrations are a reflection of the evolutionary history of mysticetes. It is conceivable that the early baleen whales evolved alongside zones of productivity in low latitudes. Then as a result of the

retreat of the Tethys Sea, opening of various dispersal routes, and fluctuation in ocean temperature, they may have dispersed polewards following plankton concentrations but returned annually to the original regions they occupied.

Breeding areas:

There are a number of traditional breeding areas for different species of whales. Inshore of Península de Valdés, southern Argentina, and in the Gulf of California, are mating/calving ground for the southern right whale and the gray whale respectively. It seems that the major requirement for a breeding area is clam seas. Some have hypothesized that they serve as protection against predators, but observation of numerous predators (sharks, killer whales, etc.) in those areas, seems to render that explanation as very weak.

18.4.2.1.1. Social Odontocetes

Many odontocete species tend to group together in structured social groups or schools, characterized by long-term association among individuals. The size of the school varies with species and location. Observational studies in spinner dolphins in the clear waters of Hawaii and the Bahamas indicate that spinners aggregate in schools of up to one hundred individuals. Within each school are subgroups of up to a dozen individuals whose members maintain close association with each other by remaining close and synchronizing their movements. Most commonly the animals occur in staggered arrangements, or echelon formation, similar to that seen in flying formations of birds. It has been suggested that this spatial arrangement might be part of a signaling system that allows organization and transmission of information throughout the school. Spinner dolphin societies are characterized by minimal sexual dimorphism and a high degree of cooperation among individuals. Both sexes are involved in birth, maturing, instruction, and cooperative defense of the young. Mating is seasonal and apparently promiscuous, with more than one male achieving intromission with the same female in rapid succession.

Bottlenose dolphins inhabit nearshore waters of many temperate and warm coastlines, making many populations relatively easy to observe. One of the longest term studies of free ranging bottlenose dolphins is that of the Sarasota Bay community on the west coast of Florida initiated, in 1970. The community contains about 100 dolphins and is composed of smaller schools of socially interacting individuals. The groups are organized on the basis of age, sex, familial relationship, and reproductive condition. Although the composition of schools may fluctuate over the course o a day, many associations are relatively long term. The mother-calf bond is close and many persist for many years. Membership of the female bands is also relatively stable, and subadult and adult males may form lasting associations among themselves as well. Like adolescence, males form coalitions with one or two other adult males that last for years and may be life long. These male coalitions exist as subgroups within larger schools and forage and swim together. Similar male coalitions have been described for spinner dolphins. Coalitions of male bottlenose dolphins also aggressively attend adult females, and sometimes abduct females from other male coalitions. The extended period of calf

dependence on their mothers means that females ovulate infrequently, and it may be in the males' reproductive best interest to abduct females and keep them in close proximity until estrus occurs. In the Sarasota Bay dolphin community, males typically sire offspring from their late twenties and continue to fertilize females for about a decade. Over that time span, individual males produce offspring with several females, and different males father the calves of any one female.

Social dominance and sex differences in competitive behavior, features of societies based on long-term relationship among individuals, have been described among captive odontocetes. A zoo-based quantitative study of dominance relationships among bottlenose reveals that dominance was influence by the gender of the participants. The study confirmed earlier work, which reported male dolphins were dominant to females. Dominance relationships observed among female dolphins, however, differed from the prevalent view that female dominance relations are indistinct. The study indicated that a female's dominance status varied according to her mating partner and in some cases led to aggressiveness toward other females.

Although observations of births in wild dolphins are rare, reports of captive spinner and bottlenose births suggest that alloparenting or fostering behavior is probably common in many dolphin species. Both male and female dolphins may alloparent, although their behavior observed in captivity differs, especially in the level of apparent agonistic behavior directed toward the mother. 'Babysitting' by older juveniles of both sexes has been described for wild spinner dolphins, which suggested that the responsibility of this role is an important method for juvenile animals to practice adult behaviors that they will eventually need.

In all resident populations of killer whales so far studied, individuals exist in small stable social units known as pods. Pods are characterized by their specific dialects and foraging strategies as well as by their individual members. Orcas pods are matrilineal social groups, each typically consisting of an older mature female, her male and female offspring, and the offspring of the second generation's mature females. Mature males remain with the pod into which they were born, and movement or exchange of individuals among pods has not been documented. Mating behavior has rarely been observe, yet genetic studies support the notion that male orcas do not mate with their closely related pod members. Instead it is through that interpod matings occur when pods encounter each other in shared foraging or resting areas.

Sperm whales occur in associations of varying sizes in all oceans. Gregarious adult females and immature whales occur throughout tropical and subtropical latitudes year-round. These female/immature whale groups, or units, are structurally equivalent to pods of orcas and, like orcas, appear to be matrilineal in structure. Sperm whale social units average about a dozen whales and include closely related adult females and their offspring of both sexes. Unlike orcas, however, male sperm whales leave these female groups at 4-5 years of age and gradually drift into higher latitudes as they grow, so adult males are not permanent members of the female units. It is those large, solitary physically, mature males that participate in most matings as they move from one female unit to another seeking estrus females. In sperm whales adult males are about twice the length of females; they exhibit one of the greatest sexual size differences of any mammalian species.

Current evidence indicates that the social function of female sperm whale units is to provide a cooperative system of care for calves that are too young to accompany their mothers during deep foraging dives. Shared communal care of vulnerable calves by other adult females, also referred to as 'babysitting,' provides protection from predators as well as the possibility of communal nursing while the mother is foraging. Babysitting sperm whales seem to show alloparental care, reducing periods during which calves are unaccompanied at the surface, and thus likely increasing protection for the calf while permitting greater foraging freedom to the mother. Such communal care behavior is likely to be selected for only if individuals within a sperm whale unit are closely related and remain together for extended time periods, perhaps even entire lifetimes. The benefits of this behavior may have been instrumental in the evolution of sociality in female sperm whales. Among female and immature sperm whales, two other levels of social organization, 'groups' of associated units and even larger 'aggregations' of associated, but unrelated groups, have been recognized. Unlike units, however, temporal and geographic differences are observed in the sizes of groups and aggregations, probably caused by variations in the distribution and abundance of their food, although response to recent human exploitation may also be a factor. Sperm whales have been described as having a social system similar to elephants and bottlenose dolphin societies have been compared with those of chimpanzees.

18.4.2.1.2. Mysticetes

Baleen whales generally are observed in loose aggregations, with the basic stable unit being a cow and a calf. Usually animals occur singly or in groups of 2-6 whales, although larger groups of more than 20 have been observed both on and outside feeding grounds. Mating in most baleen whale species that have been studied appears to be promiscuous. The mating behavior of baleen whales is intimately tied to a reproductive life cycle of breeding, migration, and feeding. All mysticetes show reverse sexual size dimorphism in which females are the larger of the two sexes. This may allow the larger females to offset the energetic costs associated with rapid fetal growth and lactation, especially because much of heir time is spent in metabolically expensive cold water.

The majority of gray whales mate during the southern portion of their migration in coastal or lagoon waters of limited underwater visibility. A persistent, yet unsubstantiated, myth describes the fray whale as typically mating in trios consisting of a receptive female and two males. Although courting trios are sometimes observed, the sexes of participants are usually unknown to the observer. Based on above-surface observations of courting activities, mating appears to be promiscuous, although actual paternity is impossible to establish from direct observations of their very active and vigorous courting encounters. Courting/mating groups including as many as 17 individuals have been reported, however the intensity of the physical interactions during these courting bouts precludes determining such basic features as gender and inter-whale contact patterns or even accurate determinations of group sizes.

In the absence of direct underwater observations of gray whale mating behavior, arguments for promiscuous mating must be based on other evidence. In comparison to most other baleen whales, gray, bowhead, and right whale males have substantially larger testes weight/body weight ratios and relatively larger penises. Larger testes are presumed

to produce greater quantities of sperm. This has been interpreted as evidence of sperm competition, with copulating males competing with previous copulators by attempting to displace or dilute their sperm within a female's reproductive tract, thus increasing then probability if being the male to fertilize the female's single ovum.

Humpback whales from small, unstable groups on both summer feeding and winter breeding grounds. A unique feature of the mating behavior of this species is the performance by males of songs of extended duration. This primarily occurs on the winter breeding grounds but also occasionally on the summer feeding grounds. During the winter breeding season, the social organization of humpback whales has been described in the context of competitive groups. These typically contain a female humpback attended by another adult, termed the 'principal escort.' In the cases where gender has been determined, 'principal escorts' have been male. Other males, termed 'secondary escorts,' are sometimes present but do not play an active role in the group. Those males identified as 'principal escorts' also have been observed alone and acting as singers. 'Principal escorts' appear to be consorting with females to mate and will vigorously rebuff approaches by intruding males, termed 'challengers', by ramming or thrashing of the flukes by using trumpet blows, and by blowing bubble curtains or streams incidence of these agonistic behaviors increases with increasing density of whales in the breeding areas. The mating system, in which males display (sing) or directly compete for access to females, has been further described as being similar to both leks and male dominance polygyny. Because the mating system of humpbacks lacks the rigid spatial structure of leks, it is referred to their unique mating system as a 'floating lek.'

18.4.2.2. Pinnipeds

Pinniped mating systems cover the entire range from strict monogamy to extreme polygyny. Essentially, all species of otariids and many species of phocids are polygynous, with only a few males mating with most of the females while simultaneously denying other males opportunities to mate. Polygyny is defined as a male mating with 2-5 females (e.g., hooded seals), moderate polygyny as a male mating with 6-15 females (e.g., gray seals), and extreme polygyny as a male mating with 16-100 or more females during a breeding season (e.g., elephant seals). Polygyny is associated with moderate to extreme sexual dimorphism in adults, densely aggregated breeding groups when ashore, estrus and mating soon after pupping, and delayed implantation of the resulting blastocyst with a corresponding extension of gestation.

Two thirds of all pinniped species breed and pup on land while the remainder mate and give birth on fast ice or pack ice. Almost all pinniped species that breed on land, including gray seals, northern and southern elephant seals, and all otariids, are extremely polygynous and strongly sexually dimorphic with males showing obvious secondary sex characteristics like larger body size, elongated proboscis, enlarge canine teeth, and thick cornified skin on the neck. They prefer their pupping and mating rookeries on islands free of large terrestrial predators or on isolated mainland beaches and sandbars not easily accessible to such predators.

Species that breed in large colonies, such as the northern and southern elephant seals, Weddell seals, and Hawaiian monk seals, also exhibit **alloparenting** or fostering

behavior. Alloparenting is the attendance, care, and nurturing of a young offspring by animals other than its parent(s). Because mother-pup separations may take place frequently on a crowded rookery, there are many opportunities for adoptive behavior.

The reduced level of polygyny shown by phocids that mate in the water or on ice is explained, in part, by the difficulty of gaining access to females in physically unstable environments such as tide-washed beaches or pack ice. This also restricts pupping to a very short period of time. Since females in these species tend to be dispersed, hooded seals, for example, exhibit **mate guarding** in which the male displace one another while attending nursing females. We have little information about the reproductive behavior of species that mate in water because they are difficult to observe.

In monogamous seals, males can succeed reproductively by locating an estrus female and mating with her. With population gender ratios approximating 1:1, there will be approximately as many females available as there are males competing for them. These males are apparently limited to monogamy simply because the non-aggregated distribution of females does not allow them to access more than one female at a time or to exclude other males from access to females other than the one he is attending. The larger size and other sexually dimorphic characteristics seen in polygynous males confer no selective advantage, and monomorphism or even slight reverse sexual dimorphism becomes the norm for monogamous species. In Weddell seals, the smaller size of the male in comparison to the female has been suggested as making the males a more agile swimmer and therefore more attractive as a potential mate. In addition, ice-breeding seals have developed complex vocalization underwater to advertise attractiveness and mating receptivity.

Polygynous males, in contrast, must compete for reproductive control of females by excluding numerous other males from breeding activities. In otariids, this competition revolves around the establishment and defense of breeding territories. This type of mating system is referred to as **resource defense polygyny**. Several characteristics are common to those species that exhibit this strategy: (1): territorial males arrive before females; (2) females become receptive in close geographical proximity to where they give birth; (3) the rookery substrate is unstable and discontinuous, facilitating its defense; and, (4) there may be a relatively low level of aggressive interaction among males.

Another strategy is the one exhibit by polygynous elephant seals and gray seals that do not defend breeding territories as do otariids; rather, they establish hierarchies among groups of associating males within aggregations, or harem, of females. This type of mating is called **female (or harem) defense polygyny**. Like otariid males, elephant seals fast for the duration of the breeding season and the increased lipid stores associated with large male body mass confer clear advantages in successfully withstanding these extended periods without food. The most dominant (alpha) mal is a dominance hierarchy defends nearby females against incursions by subordinate males. Subdominant (usually younger) males in trying to gain access to females occupy less preferred breeding beaches that attract fewer males with whom they must compete. They may also try to sneak into large harems or may mob a female as she departs from the rookery and the end of the breeding season.

Mating in the water is employed by most ice-breeding seals and walruses and may give females a selective advantage that does not occur on land; directly selecting the male with whom they copulate. Pacific walruses have been described as having a lek or lek-

like mating system. During the breeding season, female walruses and calves haul-out on ice or rest in the water while one or more adult males station themselves in the water alongside a herd and perform complex underwater visual displays and produce a series of bell-like or gong-like sounds to attract females. A different mating system, female-defense polygyny rather than a lek-system, has been suggested for Atlantic walruses studies at the Dundas island **Polynya** (area of open water surrounded by stable fast ice) in the Canadian high Arctic. Under this system, a large mature male has exclusive access to a herd of walruses containing several females for 1-5 days at a tome. One or two males spend significantly more time with the herd and it was not evident that female preference was important in determining which male became the attending male. When attending a herd, a male continuously repeated a complex, stereotyped underwater song.

A major factor in the evolution of pinniped mating systems is the habitat available for pupping. Pupping habitat controls the distribution of adult females, which in turn, influences male distribution and breeding behavior. Parturition in all pinnipeds occurs out of water. Although precocious at birth, most species of pinnipeds are not immediately capable of swimming. This, combined with their reduced mobility out of water, make pups especially vulnerable to terrestrial predators. As a result, pinnipeds exhibit a strong preference for pupping on ice or on oceanic islands.

Seasonal migrations: Some seals remain near their breeding grounds throughout the year, but most disperse, either locally or, in some cases, such as the Northern fur seal, migrating for thousands of miles, During this period, seals are building up reserves to see them through the next breeding season. Juveniles and adolescents may follow the same pattern, or occupy different grounds from the adult seals. Very little is known about the life of seals at sea.

Breeding areas: Pinnipeds have failed to make the complete transition from land to water. Those adaptations that fit them so supremely well for life in the sea render them clumsy and vulnerable on land, to which they must resort to reproduce. Because seals are vulnerable to terrestrial predators when ashore, they have to adopt various strategies to ensure their safety during the period of birth and the dependence of the young. These relate to the selection of secure breeding sites, the social structure of breeding assemblies, and the duration of the period of dependence of the young.

18.4.2.3. Sirenians

Manatees and dugongs are solitary animals for most of the year. The few social interactions (apart from mother-calf pairs) observed, appear to center on reproduction. Mating and calving occur throughout the year, although some seasonality in the occurrence of newborn calves has been reported for West Indian manatees and for the more tropical dugongs. A manatee cow attracts as many as 17 males that compete for copulation rights by vigorously pushing and shoving each other. Mating may be promiscuous and participatory roles and minimum ages of competing males without a pattern have been reported.

Less is known about dugong mating. Because dugongs are not conspicuously sexually dimorphic, the sexes of participants are difficult to distinguish and usually are

interfered from behavioral patterns. The sexual behavior of dugong differs from manatees primarily in their more intense physical competition for females. 'Flighting' dugongs, with scars presumably made by the tusks of other male dugongs during courtship battles, different mating behaviors for dugong have been described. Dugongs occupying a cove in Shark Bay, Australia, exhibit a lek-strategy where males defended display territories and females appeared in the cove only in the context of courtship and mating.

18.4.2.4. Sea Otters

Sea otters are polygynous breeders, and copulation occurs exclusively in the water. When not breeding, they are segregated by gender, with adult males occupying annual home ranges at the extremes of the females' home ranges. During the spring breeding season, adult males leave these 'male areas' and establish breeding territories (usually about one km long, each running parallel to shore) within 'female areas'. As is typical of polygynous mammals, juvenile male sea otters in both California and Alaska tend to disperse faster than females. Juvenile males ultimately move to 'female areas,' while juvenile females remain within 'female areas.' Territorial boundaries and preferred resting sites within territories are related to patterns of kelp canopy cover, with some males expressing strong fidelity for the same territory over several successive years. It is not known if non-territorial males are occasionally successful at inseminating females.

18.4.2.4. Polar Bears

Polar bears are polygynous. Sexual dimorphism is not highly developed, although males are noticeably larger than females at birth. Their neck is also thicker. Possibly in relation to the dispersed nature of their seal prey, aggregations of receptive female bears do not occur, and, much like their prey (e.g., ringed seals), male bears can only attend one female at a time. Female typically do not mate when accompanied by cubs of the year. Therefore, only about one third of the adult females mate in any one year. Mating occurs in the spring and mature male polar bears travel extensively during this time on sea ice in search of receptive females. The breeding condition of females may be advertised by pheromones deposited on the ice via urine or from footpad secretions. Whatever the mechanism, males recognize the scent and follow the tracks of a receptive female (sometimes distances up to one hundred km) until she is located. Physical competition among males for available females is evidenced by scarring on the head and neck and by increased frequency of broken teeth in older males. A successful male will remain with the female for several days, repeatedly testing her receptivity for mating. Repeated matings over several days probably occur. Mated females continue to hunt and increase their body fat through the summer, they then enter maternity dens dug in snow in November. Only pregnant polar bears enter dens; mothers with older offspring and all other bears remain active throughout the year. These dens occur both on land and in multi-year pack ice. It is unclear whether pack ice denning is a result of increased human disturbance in traditional denning areas ashore.

Chapter 19

Distribution and Ecology

19.1. Introduction

Marine mammals can be found in all oceans and peripheral seas, which cover 71% of the earth's surface. Ringed seals and polar bears have been sighted at the North Pole; Weddell and crabeater seals, fin and blue whales, and several other pinnipeds and cetaceans have been seen at the front of the Ross and Filchner ice shelves at 78° S, the farthest south where open water can be found. Some species, such as orcas and sperm whales, are virtually cosmopolitan. At the other end of the spectrum are few species, such as the New Zealand sea lion, the vaquita, and the extinct Steller's sea cow, which are (or were) endemic to very limited regions. Many species are circumglobal, but are restricted to particular climatic zones; examples are the many pantropical dolphins and the bipolar, or antitropical, ranges of many baleen whales that live in the temperate or subpolar zones. Some pinnipeds, cetaceans, and sirenians also range many hundreds of kilometers up the great rivers of Siberia, Alaska, southeastern Asia, South America, and Africa, either seasonally or permanently.

19.2. Basic Ecological Concepts

As I said at the beginning of this course, we will be using the **biological species concept** to define a marine mammal species when it comes to its ecology and distribution. According to this concept, a **population** of sexually reproducing animals is usually defined as a discrete part of a species that is interbreeding and that occupies a defined geographical area. From the management viewpoint the concept used is that of a **stock**, that is, a subdivision of a population that has a very specific geographic distribution. That is a term frequently employed by organizations whose focus is on exploitation such as the International Whaling Commission.

The reproductive behavior of members of a population creates a **gene pool**, common to them but isolated from the gene pools of other populations. The characteristics of this gene pool may change due to emigration, immigration, selection, population size, and **genetic drift**. The latter occurs as a consequence of accumulation of mutations.

These are important concepts when considering the life history of individual members of our population. **Life history** represents the series of events that take place in the life of an individual from the time it is born to the time it dies, including reaching sexual maturity and reproductive and migratory habits. All populations can be characterized by their size; thus, **population size** is the number of individual found in

particular population. **Population growth rates** (either positive or negative) represent the rate at which a population size varies.

Natality is a population parameter used to denote the rate at which offsprings are produced, and it is determined by the collective birth rates of individual females in the population. **Mortality** is the rate of death in a population. It will vary according to age. The balance between natality and mortality also establishes patterns of **survivorship** and the **age distribution** of a population.

In general, marine mammals have long life spans and large body masses. They produce few offsprings and its takes long for them to mature. In many species, particularly cetaceans, nurturing is a long process that may extend up to for several years, while many pinnipeds will show a higher rate of natality, with a higher rate of mortality at an early age and much shorter nurturing period. Thus, most marine mammals are perfect examples of the **K-selected** strategy. These are species that tend to show a high degree of social behavior and group structure. This is opposite, of course, to the **r-selected** species. Although these characteristics are the ones that confer many marine mammals with an interesting social behavior, they also place them as very vulnerable to exploitation as we will be later in the course.

Birth and pregnancy rates

The number of offspring a female marine mammal produces is determined by her frequency of pregnancy (one per year), by duration of her reproductive life time, and, in polar, bear, by the number of cubs produced during each pregnancy since all other marine mammals produce only one on average. In some species, birth rates of individual females are known to change over time. Sexual maturity in most marine mammals precedes physical maturity by several years, allowing for a substantial body mass increase after a female is capable of her first reproduction. In species like elephant seals that fast for part or all of their lactation, skipping a year of pregnancy may provide a small female the time necessary to acquire additional body mass between successive pregnancies. Similar 'skips' may occur in newly mature female gray whales whose body masses are likely near the minimum size capable of supporting the energetic cost of pregnancy and lactation while simultaneously fasting.

Among short-finned pilot whales, orcas, pregnancy rates decline with increasing age of females. Female short-finned pilot whales are known to live to maximum ages of at least 63 years, yet no individual older than 36 years has been found pregnant. Finding of sperm into the reproductive tracts of females well into their post-reproductive age is not uncommon. These non-reproductive females may play a role in their populations by caring their young (which for some species may last for several years), maintain the long-duration matrilineal or **matrifocal** (aggregation of matrilines) social groups of odontocetes (seen among orcas, pilot, and sperm whales), where the older member is also a female which, in turn, may transmit cultural information along the family group. They may also play a role in fostering and baby-sitting as reported in sperm whales as mothers dive deep in search of food.

19.3. Adaptations to Major Oceanographic Factors

The base for the food chains in the oceans is the **plankton** (wanderers). These are small, mostly microscopic organisms that migrate vertically. They can be **phytoplankton** (autotrophic, e.g., Cyanobacteria and microscopic algae) and **zooplankton** (heterotrophic organisms). Phytoplankton abundance is a measure of **primary productivity**. This is the biological process of creating high-energy organic material from CO_2, H_2O, and other nutrients using solar energy (photosynthesis). Production rates vary greatly in time and space. It is measured by O_2 production and $C0_2$ consumption, using C_{14}, and also the amount of Chlorophyll a in a determined area. Satellites, using **Coastal Zone Color Scanner**, are used to determine the level of primary production. Because primary production is the base for the entire food chain in the ocean, it has a direct effect on marine mammal distribution. The only marine mammals that consume primary producers (in this case sea grasses) are the sirenians.

A number of factors affect primary production. They are called **limiting factors**, which can be classified as **biotic** (e.g., competition) or **abiotic** (e.g., light, nutrients, space, temperature, salinity) variables that may affect the survival of a species or population. Areas of great ocean productivity are coastal **upwelling zones**. These are areas where there is a great deal of mixture of nutrients near the surface. These vertical currents carry with them a great deal of nutrients, 'fertilizing' the seawater and increasing primary productivity. In these areas we can find a great abundance of zooplankton that feeds on the phytoplankton. One of the major components of the zooplankton is certain type of crustacean of the group **Euphausiaceans** (known as '**krill**') that is the main source of food for of baleen whales and the crabeater seal. Since zooplankton abundance affects directly fish abundance, they also have a direct effect on the distribution and abundance of other marine mammals, most of which are **ichthyophages**, or fish eaters. Since changes in ocean productivity is variable in time, particularly in temperate and polar seas, these variations determine the migratory patterns of many marine mammals

Sometimes, many disruptions in these patterns can be seen which have been associated with periodic events such as '**El Niño**' or **ENSO** (**El Niño Southern Oscillation**). This creates serious disruptions in the patterns of oceanic productivity affecting the abundance and distribution of marine mammals in the entire Pacific Ocean. During a typical **El Niño** event, cold water currents of the eastern Tropical Pacific Ocean slow down and, thus, upwelling events are diminished in intensity, reducing, thus, the productivity of many coastal areas in the eastern Pacific Ocean. For example, during the 1982-1983 and the 1997-1998 **El Niño** events, 100% of the Galápagos fur seal and nearly 100% of the California sea lion pups died.

Global climatic change can also affect marine mammal distribution. The increased melting of polar ice that has been reported in the last few years has been affecting the survival of certain marine mammal species such as polar bears. Increased UV radiation on the Antarctica as a consequence of the depletion of the stratospheric ozone has been affecting zooplankton abundance, which in turn directly affects food availability for Antarctic populations of baleen whales.

Concepts to Remember

The ocean waters can be divided into a number of zones. The most important ones for the subject of this book are:

Coastal: Refers to the areas closer to the coast and on top of the continental shelf. Some species of cetaceans and all sirenians are coastal.

Pelagic: Refers to the area of the ocean beyond the continental shelf.

Epipelagic Zone or Photic Zone. It is the area nearest to the surface where light penetrates.

Mesopelagic Zone: Bottom epipelagic zone -> 1,000 m. The main sources of energy are organic material, fecal pellets, and 'marine snow.' It has been discovered, for example, that whales play a major role in some deep-sea bottom ecosystems, since their falling carcasses are a major source of organic material for the benthic organisms found there.

The **Deep Scattering Layer** (DSL) is a sound-reflecting layer of many types of organisms that migrate daily from the mesopelagic zone to the epipelagic zone. Many marine mammals locate that layer with their sonar in order to feed.

Marine mammals use some of the unique features of water to increase their range of acoustic signals. In all oceans there are **thermoclines**, a zone in the water column that shows a sudden change in temperature with depth. These layers provide an excellent physical 'wall' that humpback whales (and perhaps other cetaceans) use to increase the range of their calls.

Some marine mammals, for example, present antitropical distribution, while others have a biantitropical distribution. Some have a circumglobal distribution.

Geographic variation: For most of the widespread species of marine mammals, the number of specimens in collections is far too few to provide even a vague picture of their geographic variation. Vast areas of the world's oceans are still without representation by any cetacean specimens. Until museums acquire many more specimens from all over the world, the full extent of the biodiversity represented in the globe's marine mammal fauna will remain unknown. This may explain why marine mammals largely escaped the orgiastic naming of new subspecies that afflicted the study of terrestrial mammals in the late Eighteenth and much of the Twentieth centuries. However, recent studies reveal that most of the widespread species of cetaceans and other marine mammals do show geographic variation. At the present time only 22% of the species of marine mammals are considered polytypic, but future studies will doubtless increase the number that have been formerly recognized as subspecies.

Populations of large whales isolated in major ocean basins tend to differ; a common pattern among species with an antitropical (bipolar) distribution is morphological divergence between Northern and Southern hemisphere populations.

Small cetaceans, which are generally less migratory than the great whales, may vary sharply over sometimes relatively short distances; two major patterns are divergence between inshore and offshore populations, and between populations on the open ocean and those in enclosed seas. Among the river-dolphins, populations in different drainage basins have differentiated, and most landlocked seals differ from their nearest marine relatives.

The strongest geographical differentiation tends to develop between isolated populations. However, contiguous populations may also differ just as much: such as in the spinner dolphins of the eastern tropical Pacific. Intergradation between adjacent subspecies may be clinal over a wide zone (often correlated with ecological gradients), as in the polar bear and bearded seal, or it may be abrupt, as in the spinner dolphins. In the former situation, termed primary intergradation, the boundary line, if one must be drawn, is rather arbitrarily positioned along the midline of the character-gradient. Many of the abrupt subspecies boundaries, often with narrow hybrid zone, are thought to result from secondary intergradation, or contact between previously disjunct populations. This may be the case for the 'whitebelly' spinner dolphins in the eastern tropical Pacific, which appear to be a *Stenella longirostris longirostris* X *S. l. orientalis* hybrid swarm.

A comparison of almost any two natural populations will reveal statistically significant differences in the means of at least some parameters, but it would serve no purpose to name each slightly differentiated population as a subspecies. Each taxonomist has his/her own opinion on the amount of morphological overlap that is allowable for subspecies. The criterion most often cited is the 75 percent rule, which states that 75% of a population must be separable from all (99+ %) of the members of overlapping populations to qualify as a subspecies. An equivalent statement is that 97% of one of two overlapping populations must be separable from 87% of the other. In the past, subspecies were often based on univariate, or at most bivariate (ratios), metrics. More recently the development of multivariate statistical procedures has allowed more discriminating analyses based on multiple parameters.

Molecular genetics had now opened an additional perspective, termed phylogeography, on the process of subspeciation. Within a species, alternate alleles differ in their geographical distribution. If the phylogeny of the alleles at each of several loci is reconstructed, the resulting 'gene trees' can be compared between loci and across the various regional populations of the species. The matrilineally-inherited, haploid mitochondrial genome is particularly informative, because it evolves rapidly and does not undergo recombination. The 'genealogical concordance' or geographical congruence among the gene trees, reveals much of the historical pattern of dispersal and vicariance of the populations, and -in concert with morphological data- permits the recognition of more realistic boundaries between subspecies, So far this approach has been applied to humpback whales, minke whales, Bryde's whales, and bottlenose dolphins, populations around the globe, to populations of dolphins in the eastern tropical Pacific, and to sea otter populations in then North Pacific.

Biological species are, by definition, separated by intrinsic reproductive isolation. The evolution of complete reproductive isolation is a gradual, continuing process, and a side effect of genetic divergence between disjunct populations. However, reproductive isolation is not necessarily closely correlated with the magnitude of overall genetic or phenotypic differences. For example, the two kinds of spotted dolphins (*S. attenuata* and

S. frontalis) are so similar that cetologists did not properly differentiate them until a few years ago, yet they are clearly good species, because they coexist throughout the Tropical Atlantic; such similar species are called sibling species - a term of convenience with no particular biological significance. At the other extreme, the three kinds of spinner dolphins in the eastern Pacific (*S. l. longirostris*, *S. l. orientalis*, and *S. l. centroamericana*) differ so much that cetologists never suspected that they were conspecific, until it was found that they integrated where their ranges come together.

Since speciation is a recurrent and gradual process, it is to be expected that at any given time in the earth's history there will be many borderline situations in which it will be difficult to say whether two geographically isolated populations have become separate species, or remain subspecies of a single polytypic species. There are a number of these debatable cases among the marine mammals, in *Arctocephalus*, *Zalophus*, *Platanista*, Sousa, *Lissodelphis*, *Berardius*, and other genera. Evidence of reproductive incompatibility between these allopatric populations can rarely be established empirically. When it cannot, the usual practice is to compare the magnitude of the differences between the taxa in question with the magnitude of the differences that separate intergrading subspecies, and those that separate non-interbreeding sympatric species, preferably in the same genus. In addition to morphology, factors such as mating behavior and timing of the breeding season should be weighed. To rank questionable allopatric populations, an operational criterion is to assume that two populations are reproductively compatible, and therefore members of the same species, unless there are 100% separable on morphological features -in at least one sex or age group. It is not very important -either theoretically or practically- whether these borderline taxa are ranked as species or subspecies.

Subspecies of a species are closely related taxa that are allopatric or parapatric. Examples are the Caspian, Baikal, and ringed seals in the genus Pus, and the long-fin and short fin pilot whales in the genus *Globicephala*. The accepted formal notation for superspecies (optional) is to include the name of the first-described species in square brackets between the generic and specific names; for example the seals mentioned above could be listed as *Pusa* [*hispida*] *caspica*, *Pusa* [*hispida*] *sibirica*, and *Pusa* [*hispida*] *hispida*, with the latter species further divisible into subspecies such as *Pusa* [*hispida*] *hispida hispida*, *Pusa* [*hispida*] *hispida botanica*, etc.

19.4. Cetaceans

Historical aspects

Cetacean distributions are conditioned by factors such as water temperature, depth, salinity, topography, and food resources. Cetaceans are found from Arctic and Antarctic waters to the tropics, from high seas to coastal and freshwaters. Baleen whales tend to have a very wide distribution. Orcas and sperm whales are virtually cosmopolitan. Sperm whales and beaked whales tend to be oceanic/deep waters. Bottlenose dolphins and other delphinids are both coastal and oceanic.

19.4.1. Baleen whales

Blue whales are found at the edge of the continental shelf. Sei whales are oceanic. Fin and minke whales are both, coastal and pelagic. Bryde's whales are found only in temperate and tropical waters, both inshore and offshore. Humpback whales can be found in all oceans. The gray whale is found today in the North Pacific Ocean only, being coastal but strongly migratory; it used to be found also in the North Atlantic. Northern Right Whales are found in the North Atlantic and Pacific while the Southern Right Whales are found in the South Pacific, Atlantic, and Indian oceans; neither species moves into tropical waters. The bowhead whale is found only in Arctic waters.

19.4.2. Toothed whales

The species of odontocetes with worldwide distribution is the orca or killer whale, the bottlenose dolphin, the Cuvier's beaked whale, the sperm whale, the pygmy sperm and dwarf sperm whales.

The tropical and warm water species include the common dolphin, Risso's dolphin, and the false killer whale.

Some have highly restricted distributions such as the vaquita. The same can be said of freshwater species, i.e., the Amazon River dolphin (in the Amazon, Orinoco, Beni watersheds), the Chinese river dolphin or baiji, the finless porpoise, and the Indus River dolphin in the Indus river,

Ecology:

Some species are found associated in a number of geographic areas. It is not clear to what extent (if any) there is a real competition among those species. We do know, for example, that there is resource partitioning between pilot whales (which prefer squids) and common dolphins (which prefer fish). Some species can be seen together feeding behind boats but after they stop following the boat they separate.

Another intriguing factor is the large number of intergeneric hybrids in nature, which may speak for higher levels of associations than usually assumed.

In terms of preferred habitat, pilot whales, bottlenose and Risso's dolphins are usually found close to shore. The common dolphin is more common in waters between coastal and fully pelagic. Offshore species include the spotted and spinner dolphins.

Marine mammals can be divided into stocks. Sometimes they can be found in large groups (in the thousands of individuals) in a specific geographic area. That is the case of inshore and offshore bottlenose dolphins.

The best studied in terms of population size are the baleen whales. There are lots of differences between populations in both hemispheres. That can be epitomized by body coloration and body shape, which sometimes represent big taxonomic headaches only resolved by DNA analysis.

19.4.3. Distribution

More than 40 species of cetaceans occur in North American waters, but only some of these are found predictably in specific areas. Fin and sperm whales and Risso's dolphin, among others, are wide-ranging and have far different stranding patterns than animals with a more restricted distribution, such as the vaquita of the northern Gulf of California. Some are **coastal** year-round (e.g., gray whales, harbor porpoises, some bottlenose dolphins), while others come inshore periodically (e.g., long-finned pilot whales), during calving or migration (e.g., beluga whales, right whales) or even diurnally (e.g., Hawaiian spinner dolphins). **Pelagic** species such as beaked whales may be seen at sea so rarely that their description relies entirely on stranding records. Topographic and oceanographic conditions influence the coastal cetacean fauna. The inshore waters of the warm, shallow Gulf of Mexico, are virtually uninhabited by baleen whales at any time of the year. Northern right, fin and humpback whales do occur, however, in cool, deep waters offshore in winter.

On the Atlantic coast, the Gulf Stream occasionally brings warm temperate species such as the bottlenose dolphin and dwarf sperm whale as far north as the Canadian Maritimes, while the broad shelf keeps pelagic species further offshore. Inshore waters north of Cape Hatteras are influenced by the Labrador Current and are home to cold water species such as the harbor porpoise and Atlantic white-sided dolphin

The steep, rocky Pacific coasts allow pelagic species, such as the short-finned pilot whale, close to shore, while the California Current brings such cold-water forms as the harbor porpoise as far south as southern California. Warm temperate species (e.g., bottlenose dolphin) seldom occur north of central California.

Northern waters are a permanent home for some species, while others only visit there during the summer months. The bowhead whale, narwhal, and beluga are more or less confined to Arctic and subarctic waters, the beluga being the most wide-ranging of the group.

Wanderers from the isolated St. Lawrence River stock occasionally reach Nova Scotia and New England and have been reported as far south as Long Island Sound. During the summer, blue, fin, minke, sei, right, gray and humpback whales move into northern feeding grounds.

The Hawaiian Islands are an archipelago of steep-sloped volcanic cones, offering little in the way of a coastal shelf able to support large numbers of resident cetaceans. A wide variety of pelagic forms occur in nearby waters, as evidenced by known stranding records involving about 20 species. Some of these, including short-finned pilot whales, pygmy killer whales, rough-toothed dolphins, and pantropical spotted dolphins are common year-round in the deep channels between the islands. Nearshore species include a wintering population of humpback whales, resident communities of bottlenose dolphins, and the pelagic Hawaiian spinner dolphin that moves into coastal waters during the day.

The size of a cetacean population is not easily determined, particularly for pelagic stocks. Populations of baleen whales in North American waters are estimated to range from hundreds (e.g., blue whale, northern right whale), to thousands (e.g., humpback, bowhead whale), to tens of thousands (gray whale, fin whale). A species abundant in one area may be in peril in another (e.g., Western Arctic vs. St. Lawrence River beluga

stocks), depending on regional conditions such as habitat degradation, patterns of exploitation, and fisheries interactions that might influence food abundance, health and survival.

19.5. Pinnipeds

19.5.1. Distribution

Pinniped **demography** is tied to a crucial need for land or ice on which to give birth and rear the young, social organization (solitary or gregarious), and methods of exploiting food resources. Regional stranding patterns clearly reflect these elements of life history. Orphaned pups of coastal harbor and elephant seals as well as California sea lions come ashore near rookeries with seasonal predictability, while adults strand in a scattered procession along their migration routes. Harp, hooded and ribbon seals undoubtedly become orphaned and sick as well, but since they live far out at sea, hauling out on ice rather than land, few casualties ever reach shore. Knowledge of the normal patterns of animal distribution, habitat use and stranding is vital to recognizing unusual events.

Pinnipeds normally **range** throughout coastal areas of the United States and Canada, except in the southeastern U.S. and the Gulf of Mexico. The East Coast features only phocid seals and the walrus; the latter was once common as far south as Sable Island, Nova Scotia, but is now restricted to waters from Labrador northward. Bearded and ringed seals occur year-round in the Arctic. Hooded and harp seals breed on springtime ice floes in the Gulf of St. Lawrence and east of Newfoundland. Gray and harbor seals range from Labrador to Cape Cod and even farther south. Harbor seals are the most common type to strand along the East Coast; gray seals, which are more pelagic, trail by a wide margin. Less frequent but increasing incidents involve harp, hooded and ringed seals that stray from northern populations.

The California sea lion ranges from the Gulf of California, where it is the only resident pinniped, northward to Vancouver Island. This species accounts for the majority of strandings in California. The Steller sea lion occurs along more northern parts of the West Coast, with primary haul-out and rookery sites in British Columbia, the Gulf of Alaska, and the Aleutian Islands. Steller sea lion numbers in the western Gulf of Alaska and eastern Aleutians have declined alarmingly since the late 1950's and continue to do so, although the causes of this loss remain uncertain. The northern fur seal has a similar range. Principal fur seal rookeries in North American waters are in the Bering Sea (St. Paul and St. George islands). There is one additional rookery off southern California (San Miguel Island). Outside of the breeding season, this species is largely pelagic and rarely found ashore.

The ubiquitous harbor seal ranges in the eastern Pacific from Baja California to the Aleutians and the southern Bering Sea. They can be found along the open coast as well as in protected areas such as estuaries and rivers. The northern elephant seal, the largest of the North American phocids, resides primarily on islands off California and Mexico’s Baja Peninsula but also migrates northward to British Columbia and the Gulf of Alaska during the warmer months. Recent tracking studies suggest that summer migrations to the eastern Aleutian Islands may be usual, and one stray has been reported as far as Midway Island in the Hawaiian chain.

Farther north, the ringed seal, one of the smallest pinnipeds, is the most abundant phocid in Alaska and the Canadian Arctic. Rarely seen on land, these seals occupy shore fast ice, where they can maintain breathing holes in surfaces more than 2 m thick. Bearded seals occupy a wide range of habitats over the continental shelf, preferring depths of 25-50 m. The Pacific walrus is limited to the Bering, Chukchi, and western Beaufort seas and breeds on offshore ice.

During summer months, adult males occupy traditional haulouts on land, mainly in Bristol Bay. Females and young may haul out on land during fall migration and when ice is unavailable. Spotted seal pups and mate in pack ice in the spring but haul out on shore after the ice has retreated. The elusive and strikingly marked ribbon seal is virtually pelagic and rarely ventures near shore.

The only pinniped native to the Hawaiian Island region is the Hawaiian monk seal, which is largely restricted to the westernmost islands of the chain. This most tropical of phocids is truly in danger of extinction, facing every conceivable threat, including human encroachment, natural poisoning and predation, and, for females, mutilating sexual attacks by male monk seals. Pinniped populations in North American waters range from less than 1,500 Hawaiian monk seals 75 to about two million harp seals.

Walruses are found in moving pack ice. They prefer ice as a substrate and migrate following changes in the ice distribution.

The Baikal seal is found in the deepest lake in the world and prefers the surface of the deepest parts of the lake.

19.6. Migration

19.6.1. Cetaceans

Baleen whales need warm waters for the growth and development of their relatively small young but cannot find enough food to sustain them throughout the year. The bowhead whale does so, and other such as the fin and minke whale may make only relatively short latitudinal movements.

As we have said in previous classes, long migrations are the reflection of the evolutionary history of mysticetes since it is conceivable that early whales evolved alongside zones of productivity in low latitudes.

19.6.2. Pinnipeds

Within a few days of mating, the adult harp seals leave the whelping patch to begin a migration that takes them to their feeding ground. The seals from Newfoundland migrate up along the Labrador coast to the Davis Strait and Baffin Bay, with smaller numbers traveling to Hudson Bay. Here they disperse until in the following year their migration takes them in the reverse direction, back to the ice fields where the whelping patches are formed. The entire intraspecific association of this species is thus condensed into a period of about two weeks during which the birth of their pups, their suckling, and the mating to produce the next generation take place. Pair bonding and maternal care are minimal.

19.7. Navigation

19.7.1. Cetaceans

One of the most intriguing possibilities on how cetaceans navigate is by the use of magnetic clues in the Earth's magnetic field. Particles of magnetite are not unusual among living organisms (from bacteria to mammals, including cetaceans and even humans). Biomagnetism has been demonstrated for birds.

It has been hypothesized that dolphins may use underwater topography to recognize areas while gray whales may use terrestrial topography (by spyhopping). It is very unlikely that any cetacean uses odors or other chemicals.

19.7.2. Pinnipeds

Virtually nothing is known about navigational methods for this group.

Chapter 20

Strandings, Pollution, and Diseases

20.1. Strandings: Basic Concepts

Marine mammals found on beaches, can be classified as **beached** if they arrived dead to the coast and **stranded** if they arrive alive. All beached animals died at sea and are almost always events affecting only one individual. Strandings may occur for one or more individuals. When three or more individuals of the same species are involved in the event, it is said that a **mass stranding** has taken place. Beachings and strandings have provided scientists with valuable information, including specimens that belong to unknown species. Today, they are the focus of research in terms of contaminants present in the animal(s)'s tissue and, thus, are used to determine the environmental quality of the sea.

Beachings are more and more attributed to high levels of pollutants in the sea. In recent studies of the causes of beachings and single strandings of marine mammals on the Oregon coast, gunshot wounds were deemed the primary cause of death in 30% of the pinnipeds examined, with bacterial infections and parasitism (27% each) accounting for most of the others. The most important factors behind strandings off the Californian coast are usually predation, starvation (due to neonatal abandonment), and viral encephalitis. 'Red tides' that produce high levels of biotoxins have been implicated in mass mortality of humpback whales and manatees.

Nearly 20 species of odontocetes have been reported in mass strandings. Pilot whales are the most commonly mass stranded animals, followed by false killer whales and sperm whales. Species and stranding frequency varies geographically.

There is a long list of hypothesis trying to explain the phenomenon of mass strandings. They include:

a) Presence of debilitating but nonlethal parasitic infestations of the respiratory tract, brain, or middle ear. For the latter, it has been proposed that parasites in the auditory system of these animals may be responsible for their inability to navigate properly.
b) Panic flight responses to predators (including humans).
c) Cohesive social bonds causing the entire heard to follow one intentional strander.
d) Nearshore disorientation due to geomagnetic disturbances. This hypothesis is based on the idea that cetaceans may use geomagnetic lines or clues to navigate and that when those clues change they confuse the animal trying to use them. Magnetic

materials have been found in a great deal of organisms from bacteria to humans as well as in the brains, bone, blubber, and muscle of fin whales, humpback whales, Cuvier's beaked whales, Dall's porpoise, and the bottlenose dolphin. Although magnetic orientation has been proven for birds, the use of these magnetic crystals as 'compass' by marine mammals has yet to be proven. Analyses of mass strandings distributions and their geographic locations in relation to magnetic anomalies have proven inconclusive.

It is not uncommon that once a mass stranded has taken place, if some or most of the animals are returned to the sea due to human intervention, the same animals strand again. Usually what happens is that these animals were sick with a viral or bacterial infection and/or with a large number of parasites. Because of these, operations aimed to return animals to the sea should not be conducted unless a medical examination of the stranded animals(s) is carried out and the animals can be radio-tagged to check for any subsequent stranding. This is aimed not to extend the animal(s) suffering.

Most likely, there is not a single cause for strandings and either an epidemic and/or the social bond among the animals involved can explain most mass strandings.

In the U.S. there is a stranding network that collects information, specimens, and/or tissues from the animals involved in these events and generate valuable information about these mammals.

20.1.1. Cetaceans

Coastal animals that reside in an area or migrate through it seasonally have a stranding pattern that is predictable and more or less consistent. Bottlenose dolphins strand throughout the year in the southeastern United States, whereas newborn gray whales are likely to come ashore in the lagoons of Baja California only during the winter calving season. These trends have a long history that is rooted firmly in the biology of the species. More recently, traditional patterns have become complicated by human activities that are less direct and not always predictable. For example, a coastal fisheries operation when in full swing may have a serious impact on local cetaceans.

Stranding patterns are not quite as evident for pelagic species, although correlations with locations, tides, storms, geomagnetic disturbances and other factors have been proposed. Some species follow the inshore migration of prey. Long-finned pilot whales, for example, pursue squid into shallow waters of Cape Cod Bay during the autumn and early winter and can be expected to strand during these seasons. These events also correlate somewhat with storms that combine with monthly peak tides. Animals that strand in a cluster over a period of a few days may be victims of poisoning, infectious disease, intensive local fisheries operations, or unusual environmental events. These episodes can be of such short duration that the ultimate cause may no longer be evident by the time the investigating team takes action.

The mother/calf bond is strong and may remain so long after the end of lactation. Consequently, if both come ashore, it may be impossible to determine which led the way. Young males of some social species may appear alone at predictable times of the year. For example, juvenile white-sided dolphins strand along the northeast coast during the fall, suggesting they may have been lost or displaced from a bachelor group.

There is evidence that yearling *Tursiops* come ashore alone after being displaced from the herd during the breeding season. Animals that wander beyond their normal range, fail to migrate with the onset of winter, or make unusual appearances in bays or far up river, always generate public interest. A single male beluga whale, apparently a stray from the St. Lawrence River population, resided in Long Island Sound for over a year before it died from a gunshot wound. 'Humphrey,' a humpback whale reluctant to leave San Francisco Bay in October 1990, was finally towed out to sea after elaborate efforts failed to coax him to leave on his own. When bottlenose dolphins left their summer feeding grounds off northern Virginia in the fall of 1988 and headed south for warmer waters, 'Rascal,' a young male, stayed behind. Lingering in a shallow near-frozen bay, he extracted sympathy from every conceivable source, until he was 'rescued,' placed into a facility, and released months later. Rescue efforts following the ice entrapment of three gray whales in Alaska in 1988 became an international event. Public sentiment may override any consideration as to whether intervention in these cases is necessary, justifiable or even possible.

20.1.2. Stranding Response

Jurisdiction: All cetaceans in U.S. waters fall under the jurisdiction of the National Marine Fisheries Service and are protected by the Marine Mammal Protection Act of 1972. The sperm whale and the vaquita, as well as all baleen whales except minke and Bryde's whales, are also listed under the Endangered Species Act.

Evaluating the Event: A cetacean may be observed swimming dangerously close to shore, although for some, such as right whales, this is normal behavior. If there is no obvious injury or disability and intervention is deemed necessary, attempts can be made to direct the animal back to sea. This has been done by using boats and chains of people (under calm conditions) as a means of herding, and by creating disturbance and underwater noise (slapping the water's surface or striking objects together below it, using boat engines). Under the best of conditions, it is difficult to sustain the effort needed to herd an animal a long distance, and there is a good chance it will come ashore somewhere else, probably close to the original site. If the animal is seriously debilitated, no amount of effort is likely to avert the eventual stranding.

The response team's appropriate course of action for a stranded cetacean will depend on the animal's size, age and health, the available support, environmental conditions, and the time on the beach.

The options are to tag and release the animal if it is healthy, transport it to a facility for medical attention, euthanize it, or let it die naturally. Decisions should be timely and the action swift to relieve the animal of progressive injury and discomfort. Except for obvious abnormalities, it is not always possible to judge the health of a cetacean by its outward appearance. Even sophisticated tests may not reveal the nature of the illness, and such analyses take more time than the beached victim can spare. When circumstances do not permit an exhaustive examination, certain broad assumptions can be made to anticipate the animal's health. These assumptions are based on an understanding of life history and historical stranding patterns.

Coastal animals such as *Tursiops*, expected to be familiar with the nearshore environment, usually strand singly only when ill, although they may be occasional victims of an outgoing tide. Unless it's a simple case of refloating, their only reasonable chance of survival is in a care facility. Some offshore animals have characteristic illnesses. *Delphinus* off the California coast frequently strand because of terminal brain damage caused by the trematode *Nasitrema*; even with the best medical care, there is little chance they will recover.

Many pelagic specimens come ashore in apparent good health, or at least free of recognizable disease. Smaller ones on the beach for only a short period of time have a reasonable chance of withstanding the rigors of being returned to sea, although their long-term survival is undocumented. The larger the animal and the longer it lies on the beach, the less likely it is to survive after release. Nothing can be done to save a whale too large to handle with the available resources, or one that has suffered prolonged exposure. The animal should either be euthanized or left to die naturally; the latter is becoming more unacceptable to the general public.

Specific Equipment: Much of the equipment required for cetacean strandings is geared to moving or supporting the animals. Any specimen beyond the size of a small pilot whale will require heavy equipment. Many devices specifically designed for moving cetaceans have been cumbersome and impractical to use. Basic equipment will generally prove to be the most useful. These items include:

Foam pads or mattresses tarpaulins
Sheets, towels or blankets zinc oxide
Shovels ropes
Buckets slings
Water sprayers stretchers and poles
'Space blankets' inflatable rafts
Heavy machinery (cranes, front-end loaders)

Approach: Observe the animal's behavior and prepare a safe plan before making the approach. Advance slowly, calmly and cautiously, avoiding loud or startling sounds, abrupt movements, or bright lights. This will allow the strander to become gradually accustomed to your presence. The animal is not likely to be aggressive, but people have been bitten accidentally, and the thrashing flukes of a confused whale have wrecked more than one knee joint. Only persons with experience should approach the animal, keeping well clear of the flukes and mouth. Animals may panic in certain situations. A mother separated from her calf or attempting to protect it may become aggressive. A lone member of a social species may become frightened when separated from the pod. Consider the animal's possible response to your intended actions.

First Aid. Determining Condition: Countless procedures are used to evaluate the health of an animal, ranging from distant observation to blood and tissue analyses. Behavioral observations are quick, non-invasive, and can be done by persons with

minimum training. Behavioral criteria can be used to assign animals to one of three categories:

1. Alert (aware, responsive to environmental stimuli)
2. Weakly responsive (responsive only after much stimulation)
3. Non-responsive (not responding to noise or touch)

A stranded cetacean inevitably develops respiratory fatigue and distress. This occurs sooner in larger animals whose chest cavity will be more severely compressed by body weight. Signs include irregular and increased respiratory rates (up to 6 to 8 breaths/minute may be normal for an excited *Tursiops*; a fin or pilot whale may respire as little as once every minute or so) and audible gurgling sounds as the animal breathes in and out. If respirations are slower than expected, flushing water over the blowhole may stimulate breathing. Extensive bleeding and frothy or foul-smelling fluid from the blowhole are signs of critically poor health. Without using invasive procedures, it is possible to make a rough evaluation of cardiovascular function. Heart rate, for what it is worth, can be determined using a stethoscope in a small animal, and perhaps by placing a hand firmly under the axillary region of a larger one. Even under normal conditions, however, the rate varies considerably (e.g., from 30 to 100 beats/minute in *Tursiops*) during the breathing cycle.

One result of deteriorating cardiovascular function is poor circulation, making it difficult to obtain blood samples from the usual peripheral site. Body temperature control is also reduced when blood fails to reach the extremities where excess heat is normally dumped.

The next level of assessment requires handling the animal.

Gentle tapping near the eye should elicit a blink. Attempts to pry open the jaw, pull the tongue or tug the flipper forward should be met with firm resistance. Once the jaw is open, a finger pressed firmly on the gums over the teeth causes blanching followed by immediate return of normal pink color; a slow return or bluish discoloration is a sign of poor circulation.

Body temperature can be determined accurately enough for early assessment purposes using a deep rectal thermometer. In small to medium-sized animals, normal temperatures are about 36.5^{o} to 37 ^{o} C. In cold weather, temperature may drop rapidly below 35.6 ^{o} C, signaling the onset of hypothermia or cardiovascular shock. Temperatures above 40 ^{o} C are critical and above 42 ^{o} C probably terminal. If time permits and a clinical laboratory are accessible, a blood sample may be collected for hematologic and plasma chemical analyses. These may reveal conditions that are not readily apparent and can help establish a long-term prognosis.

Supportive Care: Volunteers can use the time between stranding and the arrival of the rescue team to relieve distress and improve the animal's chance of recovery. The key is to prevent further injury and to keep the animal comfortable while minimizing handling and disturbance.

The eyes and blowhole must be protected from blowing sand and kept moist with clean fresh or salt water. Flushing the area around the blowhole can be done only when the blowhole is closed; the best time is immediately after the animal breathes.

Inexperienced persons should observe the breathing sequence before attempting to do this. No matter where water is applied to clean or cool the animal, the source (hose, bucket, sponge) should be held close to the skin to minimize the startle reflex. It is easier to keep the blowhole free of water and sand, and presents less risk to the lungs, when the strander is placed on its belly. This can be done easily with a small animal, but in larger ones, only with some risk to the rescuers. Using a spade to burrow beneath the animal, dig holes in the sand to allow the flippers and flukes to lie in a natural position. Banking sand or placing other (non-injurious) material alongside the body will reduce the tendency to roll.

Exposure to Warm Temperatures: Animals on the beach must be protected from the elements. First aid measures on the beach. **A**. **Summer:** provide shade, drape leaving dorsal fin exposed, and keep moist; dig holes for flippers and fill with water. **B**. **Winter:** provide protection from wind, cover dorsal fin and flukes with cloths soaked in vegetable or mineral oil; dig holes for flippers. **C**. **Always:** keep blowhole unobstructed and eyes free of sand; allow flippers to assume a natural position. Prolonged exposure to wind and sun can result in excessive drying and damage to the skin, overheating at warm temperatures (hyperthermia), and hypothermia at cold temperatures. A cetacean on the beach faces the risk of hyperthermia, even on cloudy temperate days. The risk increases dramatically as the temperature rises. Dark skin absorbs heat, blubber retains it, and the circulatory system that normally helps to dissipate heat may be sluggish and not up to the task. A whale out of water has no other mechanism to cool itself. The danger of hyperthermia can be minimized by draping exposed surfaces except the blowhole with towels or sheets kept moist by periodic wetting. Lighter colored materials are preferable because they reflect light and heat, but in a pinch, items of clothing, newspapers, or even wet seaweed or mud will do. If the situation permits, a small shelter constructed over the animal will provide valuable protection. Heat loss occurs principally from the extremities, which should therefore be kept wet or cooled with ice. A trench dug in the sand around the animal can be kept filled with water through a channel connection to the sea.

An application of zinc oxide will protect skin from sun and windburn and help prevent dehydration. Oil-based compounds (lanolin), including those used in sun tanning products, retard heat loss and may do more harm than good. Skin already damaged should be kept moist, shaded and protected with zinc oxide or antibiotic ointment.

Exposure to Cold Temperatures: A good layer of blubber insulates an animal against cold. Emaciated specimens, calves and small species are at greater risk of becoming hypothermic. The diagnosis requires some expertise. On a frigid beach, provide shelter from wind and precipitation, and cover the extremities with a mineral or vegetable oil-dampened cloth.

Protection from Surf: A cetacean in the surf zone may be battered by waves, trapped among rocks, rolled onto its side or become mired. If the animal is too large to be moved into deeper water or to higher ground, shift it so it is perpendicular to the water's edge, with the head facing land. In this position, the body offers the least resistance to the surf, and the blowhole is as far from water as it can be under the circumstances. Heavy,

struggling animals can become bogged down and trapped in sand or mud that eventually fixes them into place. They are then victims of the rising tide and nearly impossible to rescue because of the difficulties and hazards of working in soft sediments.

Lacerations and Injuries: Sharp rocks and sea shell fragments can have the same effect on cetacean skin as a keen-edged knife, causing serious injury to a struggling animal. Removing or covering hazardous objects, placing padding around the body, or moving the victim to a safer place, can reduce the risk of lacerations. Efforts to calm or restrain whales under these circumstances are unrealistic. Tranquilizers and sedatives should never be used on animals that are to be immediately released.

There is no proven benefit to medicating an animal that has just stranded and is about to be released. Without opportunity for continued care, a single application of ointment, a bolus of antibiotics, or a feeding of fish has little value. However, an animal that faces a longer period out of water before it is released or transported will benefit from prompt medical care to wounds, fluid therapy to maintain hydration, and even a long-acting antibiotic.

Stress and Shock: A cetacean on the beach is almost certainly stressed. Stimulated by the pituitary gland, hormones (cortisol and aldosterone) from the adrenal cortex are released into the circulation. The presumed benefit of cortisol is to ensure a supply of blood glucose and reduce some of the adverse consequences of the inflammatory response. Aldosterone is also released, probably to maintain salt and water balance under critical conditions. Sustained high cortisol has deleterious effects on circulating white blood cells, wound healing and the immune response; prolonged high aldosterone causes excessive sodium retention, thereby increasing the animal's thirst for water.

Within a few hours after stranding, some cetaceans begin to show evidence of shock or vascular collapse. Blood pools in the thoracic and abdominal viscera, with effective circulation only to the heart and brain. The rest of the body is largely bypassed, and organs such as liver, muscle and skin, lacking blood, begin to exhibit impaired function. Compounds normally metabolized and detoxified by the liver can accumulate to dangerous levels, cortisol and aldosterone among them. Since the animal may appear to be healthy, blood studies are required to detect these changes. Only a long course of intensive care offers some hope of recovery. Whatever the reason the whale came ashore, the onset of shock further impairs its chance of survival.

Rescuers have attempted to reduce circulatory problems and muscle cramps by periodically shifting the animal's body position and rolling it onto each side for 20 minutes or so. If a stretcher is available, floating the animal in shallow water may be of some value. Some advocate massaging the muscles of the back; this procedure may benefit a small animal, but it is not likely to be effective on a larger one with thick blubber. Corticosteroids and other medications may help minimize muscle damage and delay the onset of shock.

Handling, Lifting and Moving: In any rescue operation, moving and handling are critical activities, whether dragging an animal from dangerous surf, maneuvering it into deeper water for release, or loading it onto a transport vehicle. Most procedures are potentially injurious to both the animals and personnel and should only be attempted

when supervised by trained staff and when adequate support is available. Six people might be able to carry a medium-sized bottlenose dolphin on a stretcher, whereas a beluga or pilot whale may require 16 or stronger bodies. Several methods are useful for moving small whales and dolphins. An animal can be placed or rolled onto a tarpaulin or stretcher (or plastic 'snow sheet'), then lifted or dragged. Field stretchers should be large and strong enough to bear the weight of any reasonably large animal, which means a small one will be safely enveloped in it.

When the whale will remain in the stretcher for more than 15 or 20 minutes, openings must be provided for the flippers (to prevent crushing and overheating) and the genital region (to prevent urine burns). For short rescue procedures, the flippers may be more conveniently kept within the stretcher. Fabrics should be smooth and easy to clean and sterilize; canvas, woven plastic, and netting are commonly used. Lining with towels or sheeting ('lambskin' liners are heavy when wet and trap sand) further reduces the chance of skin injury. Once the animal is in the stretcher, care should be taken to ensure no seams or creases press into the skin. Dragging is an acceptable option only when lifting is impossible.

Slings positioned under the body behind the flippers can be used to drag the animal on the beach or to support it in the water; on land, extra support under the head may be necessary. Ensure that such slings are well padded and wide enough to distribute pressure sufficiently to minimize injury and discomfort when the animal is pulled. Never use naked rope as a sling. Drag only over smooth terrain after all obstacles have been removed.

Although it has been suggested to be an effective means of moving cetaceans, rolling is not recommended. An animal healthy enough for release can be expected to react violently. This procedure will certainly be stressful and may result in damage to the flippers or dorsal fin. If an animal is small enough to roll, it is small enough to maneuver onto a stretcher or sling. Cranes and other heavy lifting equipment are needed for moving large specimens and for loading them onto transport vehicles. Secure the animal in the stretcher with enough rope or straps to prevent thrashing, and attach guide ropes or 'tag lines' that will enable handlers to hold the stretcher steady. Make sure that no one stands directly underneath the load.

Immediate Release. General Considerations: Coordinate the animal's release with an incoming or high tide, and assure that personnel and equipment are adequate for operating in the surf zone and perhaps deeper water. Choose a route that is free of obstacles such as shallow reefs or sandbanks, by first consulting a hydrographic chart or persons familiar with the area. Under some conditions, transport to an alternate site - perhaps miles away- may be necessary. When weather or tide conditions are unsuitable, the animal may be placed in a tidal pond or fabricated pen enclosure and released when circumstances improve.

Make every effort to keep a mother and calf together during release. A free-ranging dolphin may remain with her dead offspring for weeks suggesting that returning even a dead calf to the water with its mother may help to prevent her restranding. Orphaned maternally-dependant young should not be released under any circumstances. Calves whose mothers cannot be verified should be considered orphaned.

Lone animals of a social species are not good candidates for release, unless there is a good chance they will regain contact with a herd.

Marking and Tagging: Any animal returned to sea should be marked or tagged and the details of its release carefully documented. Only then can observers determine whether or not the animal survived and if rescue procedures were effective. Dorsal fin tags are easy to apply with the appropriate attachment devices. They can be made in various colors, shapes and sizes. Every team should be equipped with a quantity of colored or numbered plastic cattle ear-tags, and a small boring device for attaching the tag through the dorsal fin. Freeze brands are effective for long-term marking but are not immediately visible and must be combined with some other type of tag. Radio (satellite or Very-High-Frequency [VHF]) tags provide much more information but are costly and require specialized tracking equipment. Only trained personnel can apply tags. Natural marks (e.g., unusual fin or fluke shapes, scars) should be photographed to assist in later identification of restranded animals, or as a way to monitor individuals from small, local populations.

Acclimating Animals in the Surf: There is more to releasing a stranded whale than hauling it back to sea. Without careful planning, handling and treatment, rescue attempts can end in disaster. In preparation for its release, the animal on the beach should be kept wet and cool to avoid a quick change in temperature that might evoke a startle reaction. Once in water, the body should be kept upright and the blowhole clear of the surface. One person alone may be able to handle a harbor porpoise (assuming reserve help is on hand), but certainly more are needed for a larger species. Acclimation is not complete until the animal is able to surface on its own to breathe. The process can take a long time and puts rescuers at risk of hypothermia. Proper gear (e.g., wet suits) and a relief team must be available. A mother and calf should be acclimated together. Gentle side-to-side rocking of an animal that is not fully coordinated when refloated, has the presumed benefit of restoring blood circulation and muscle tone. Some species, such as false killer whales, tolerate this handling well, while others, such as striped dolphins, react violently. Abandon the procedure or use a more gentle approach if the animal resists. After about 30 minutes of rocking, try again to move the animal into deeper water. Many cetaceans restrand with frustrating persistence, each time compounding the damaging effects of the last stranding, until their condition is irreversible. The rescue team should know when to quit and pursue another alternative.

Herding and Towing: The animal, even when acclimated, may need to be directed outward to sea. Doing this by swimming alongside is risky because a cetacean's behavior is unpredictable. Kayaks and surfboards are light, portable, and work well in shallow water. 'Jet' boats are quiet, maneuverable, have no propellers that might cause injury, and are also suited to inshore work. Once the whale is farther offshore, sturdier craft are needed, manned by at least one observer in addition to the pilot. Boats are generally positioned flanking and to the rear of the whale. Keep engine speed low and constant. Where conditions (e.g., estuaries or inland waterways) inhibit effective herding operations, it may be preferable to secure the animal and tow it to sea. Towing a cetacean requires skill and experience, as well as a suitable boat. Improperly placed ropes or slings can cut into the skin or prevent the animal from surfacing to breath. A

whale that suddenly makes a burst for the open sea may swamp a small boat or escape before it can be properly released from its harness. Accounts of restranded animals with rope wounds around necrotic tails are testimony that not all towing attempts are successful. The first rule is to tow headfirst. Towing backwards by the tail can damage the flukes, dislocate vertebrae, and result in suffocation.

Towing headfirst and orienting the animal seaward may help prevent this from occurring. With all methods of towing, it is certain that a whale, sensing freedom of movement in the water, may decide on its own course. Better than ropes, a harness with wide banding and substantial padding will help to distribute pressure due to the force of towing. For example, a length of cloth or strapping can be draped over the back; the two ends are then passed behind and underneath the flippers (one on each side) and attached to the towline. This arrangement tends to lift the animal's head when tension is applied. A similar procedure with more technical detail incorporates a broad sheet for maximum distribution of pressure, a swivel to prevent the towline from twisting, and a spring in the towline to minimize speed surges inevitable in swells. All ropes and harnesses must allow for rapid release when the need arises.

The towline must be sturdy; long enough to keep the whale a safe distance from the engines, but short enough to allow maneuverability. A longer line will help keep the animal level and reduce its tendency to rise up and pitch forward into the water. Towing speed should not exceed 1 knot. Stop intermittently (e.g., 20 seconds moving, 10 seconds stop) to allow the whale to breathe. The animal can be placed in a flooded inflatable raft and towed, or into a specially designed stretcher supported by two rafts or pontoons, which is then towed as a unit or fastened alongside a boat. Cetaceans can also be 'towed' in a stretcher or sling fixed to the side of an adequately large boat. A net sling has the advantages of minimum resistance and easy release.

How far to drive or tow an animal offshore will depend largely on the topography of the region. A few kilometers will normally be enough if the beach is open, the coast straight and the water deep. Strong coastal currents and complex topography may require that the animal be towed a considerable distance offshore before it is released.

Helicopters and Boats: Helicopters have been used to move animals off the beach quickly. In one incident, *Tursiops* were trapped by a receding tide in a bay on the South Island of New Zealand. A cow and a calf were placed together in a sling, flown offshore, and tethered near a waiting fishing boat. All the remaining animals were transported in rapid succession and released in the vicinity of the tethered cow. When the operation was completed, the cow was released and the entire pod swam calmly into deeper water. The rescue was presumed to have been successful. In a similar manner, small cetaceans can be carried on the decks of fishing boats and released at a suitable site. Such methods have the advantage of moving animals directly to a specific location -one far enough offshore to discourage re-stranding. Where the stranding area is inaccessible to land vehicles, helicopters and boats may also be useful for moving animals to alternate holding or release sites.

Observing and Monitoring: The success of a release can only be measured by knowing exactly what has happened to the animals. One cannot assume that a whale has survived simply because it has not re-stranded. Maintain visual contact as long as possible. In a

few instances, an animal can be observed from shore, but most serious efforts will require sea-going vessels or aerial reconnaissance. Unfortunately, this is expensive and often difficult to arrange. Chemical lights that are visible up to a mile or more away can be used to track released animals at night.

The lights come in a variety of colors and can be attached (using biodegradable cotton string) to the dorsal fin tag. Still, though logistically difficult, electronic tagging (satellite, VHF) is the only reliable means of determining whether the animal has fully recovered.

Transport to Care Facility: The same equipment and approach to moving a whale on the beach is used to load it for transport. The success of the operation will depend on the type of vehicle that can be driven to the scene. Animals may be transported on thick foam pads. Close-cell foam is rigid and, because it does not absorb water, remains light; it is ideal for short-term transport. Open-cell foam, preferred for longer travel, is softer; contours easily to the animal's form, but will absorb water and become heavy. Some individuals may be more comfortable on their sides. Specially constructed transport boxes are generally used for longer distances.

Protect the animal from sun, wind, and exhaust fumes, and keep it cool and wet. One or more representatives from the rehabilitation center should be involved in the handling and transport since they ultimately share responsibility for the animal's health. During transit to the rehabilitation center, attendants should monitor respiratory rate, record body temperature, and, if possible, collect blood samples and swabs for culture. This will expedite assessment of the animal's condition upon arrival, allowing therapy to begin with minimal delay.

Rehabilitation. General Considerations: The care required to rehabilitate a stranded cetacean until it is well enough for release can strain a facility's endurance and budget. An isolation pool is necessary to avoid contaminating other animals, and a skilled team is needed for care and support. The institution bearing these costs may understandably shy away from your plea for help if previous efforts were unsuccessful, as they often are. To keep the doors open, and in the interest of humane care, select animals for rehabilitation that have a reasonable chance of recovery, and respect the decision of the accepting facility.

Small young specimens lifted from the beach soon after stranding are usually good rehabilitation candidates, because they can easily be transported and handled for diagnostic and therapeutic procedures. A coastal species such as *Tursiops truncatus* has reasonable prospects, whereas stranded *Delphinus delphis*, *Stenella* spp., and other pelagic forms seem to have more difficulty adjusting to captivity, although some have adapted successfully. A pelagic animal that has come ashore in a mass stranding, which as far as we know is a behavioral and not health-related phenomenon, may have a better chance than a singly stranded animal that is more likely to be sick and debilitated.

At the center, a new arrival may be placed in shallow water where it is more easily handled for support and medications. In water of any depth, an animal unable to swim or remain upright will need assistance. A stretcher fashioned out of neoprene (wet suit material) will provide additional buoyancy and protection against heat loss for an animal that is hypothermic. Certain animals list to one side, either because they are

weak, have problems with one lung, prefer to look to the surface with one eye, or simply because the pool currents force that position. More active animals may require some measures (i.e., attendants placed strategically to guide the animal) to prevent their colliding with pool walls.

Cetaceans often fare better in pairs or groups than alone. Social groupings are seldom possible unless the animal is part of a multiple stranding. The remaining option of placing a newly arrived stranding alongside a colony animal combines the worst elements of poor husbandry and bad medical practices. A medical examination is performed as soon as the animal arrives at the facility so therapy can begin immediately. To restore salt and water balance caused by dehydration and shock, the animal can be placed for up to a week or so in brackish water of about 10 ppm, roughly equivalent to the salinity of body fluids, or in fresh water for a few hours at a time, in hopes that it will drink. Replacement fluids can also be given by stomach tube.

After a long time on the beach, larger specimens, such as pilot whales, may suffer poor blood circulation to vital organs including liver and muscle, which then malfunction. Rigorous intervention is required to control and reverse this condition-incipient shock. Sometime during the course of rehabilitation, cetaceans are often given medications for stress, as well as antibiotics to control infections and to prevent bacteria from invading what might now be a weakened subject.

Nutrition: A rigorous nutritional program may be required to restore and maintain the animal's health. First, it is necessary to restore fluid balance by tube-feeding fluids for a few days before giving whole fish or fish gruel. The effort needed for such a feeding schedule is demanding at first, but within a few days most patients will take fish or swallow the feeding tube with minimal help from one or two persons. Formulas for dependent calves have been developed but have not been as extensively tested as those for other marine mammals. However, preparations have been used successfully to rear a bottlenose dolphin that came ashore in Florida still bearing an umbilical cord and an orphaned harbor porpoise at the Pt. Defiance Aquarium in Tacoma, Washington.

Besides special nutritional needs, dependent calves require a social setting that is difficult and expensive to provide in captivity. Attempts to satisfy this need have included companion animals, such as pinnipeds and a steady stream of volunteers. Calves are also best provided with a choice of toys and gadgets, as long as the objects are too large to swallow.

Release Following Recovery: It may be months or a year or more before a cetacean is ready to be returned to sea. Criteria for judging suitability for release include medical evaluation, overall physical fitness including swimming and diving behavior, and the ability of the animal to feed on its own. There should be good evidence that any member of a highly social species will be able to interact with others of its kind. Any human-dependent behavior should be extinguished as part of the approach to preconditioning animals for release.

A young dependent cetacean has a poor chance of survival and still less of being successfully returned to sea. While rearing a calf to the point of physical independence might be feasible, 'social maturity' may be equally vital for survival and perhaps

impossible to attain in captivity. The host facility caring for an orphan may have to face accusations that the rescue effort was a veiled attempt to acquire an exhibit specimen.

Euthanasia: Saving stranded animals is not always possible. Sooner or later, the response team will find themselves faced with a situation where actions to save the victim are futile and prolong pain and suffering. Euthanasia then becomes the only humane option. Indications of a clear call for euthanasia include:
a) Disabling injuries such as a dislocated or broken tailstock, penetrating wounds in the thorax or abdomen
b) Significant hemorrhage from the mouth, blowhole, genital opening or anus
c) Rectal temperature of 42 ^{o} C or above
d) Blistering and sloughing of a major portion of the skin surface
e) Loss of reflexes (e.g., blowhole, palpebral, corneal, genital, and tongue withdrawal)
f) Loss of jaw tone, or protruding penis
Most methods of euthanasia, even when rapidly effective and considered humane, can be visually disturbing and even hazardous to onlookers. Discretion is essential. For the sake of other whales on the beach as well as the public, you should carry out the procedure behind a visual barrier when methods other than injection are used.

Injection: In many regions, the use of syringes, needles, and euthanasia solutions is regulated. A veterinarian may be required to carry out the procedure. On the beach, access to and use of solutions must be strictly controlled. Certain preparations become viscous when cold and require special handling in a winter stranding. A cetacean up to the size of a pilot whale can be euthanized by injecting a barbiturate or other lethal agent into a vein of the flippers, dorsal fin, flukes or caudal peduncle, or directly into the heart or abdominal cavity. The dose can be estimated from length measurements. More than the calculated amount may be required if the needle is not seated well enough in the vein, and almost always when an animal is in shock, because circulation to the heart and brain is impaired. At the point of death or immediately before, the tail may begin to stroke rhythmically in a swimming motion for a few seconds, a behavior known to the old whalers as 'flurrying.' The action in water may be enough to propel the animal forward, even when held by handlers. The period of flurrying may be reduced or eliminated altogether when enough agents are given quickly, and prolonged if too little is injected or if it is released slowly. Flurrying is less apt to occur if the animal is first given a sedative. It is advisable to prepare onlookers for problems that might arise with lethal injections.

An attempt to euthanize a large whale by injection into the tail vein or peripheral vessels is likely to be unsuccessful as well as prohibitively expensive. On one occasion, personnel from the South Carolina Wildlife and Marine Resources Department 79 used 1500 mL of solution (worth $1,200.00) before abandoning the approach. The animal, a 20-ton fin whale, was later euthanized quickly by an injection directly into the heart. This was accomplished using a 'needle' fashioned from 1 m of stainless steel automobile brake line (available from auto supply stores in diameters ranging from 3/16" to 5/16"). The line was sharpened to a beveled point on one end, attached by means of a rubber sleeve to a large syringe on the other, and fitted inside with a plug (trocar). Subsequent observations suggested using a needle equal in length to about one-half the diameter of the whale, inserted through an incision (made following local anesthesia) penetrating the

skin and blubber. Although the precise entry point for each species has yet to be mapped, as a rule of thumb, the heart can be reached by directing the needle from a point just behind the origin of the flipper to the same point on the opposite side of the body. The heart can also be reached by inserting the needle to either side of the sternum, at a point just posterior to a line joining the base of the flippers. The quantity of solution required will depend on its type and strength and on the condition of the animal, but will be much less than if administered into peripheral vessels.

Explosives: When euthanasia solutions or persons qualified to use them are unavailable, other methods can be employed, providing implementation is relatively painless and death is rapid. Suffocation by obstructing the blowhole is not effective or humane. Explosives can be used to euthanize large whales humanely, although the procedure must be supervised by an expert and may require special arrangement with local authorities. When placed either deep in the whale's mouth or on the cranium or nape and covered with sandbags and heavy rubber, explosion can result in immediate death without excessive noise or damage to the carcass. This method, however, is dangerous if not done properly, may be prohibited by local statutes, and is likely to be met with resistance if attempted on a public beach. Strict precautions must be taken to keep observers at a safe distance.

Shooting: Smaller specimens can be killed quickly by shooting. Use a firearm with a large bore (.303 or greater), high muzzle velocity, and a free, solid or jacketed bullet. The gun should be fired approximately 1 meter from the animal's head; a firearm discharged directly against the animal's skin may explode. Aiming down and backward through the blowhole to an imaginary point joining the flippers is sometimes recommended, but if the shot is aimed too far backwards, the bullet must pass through the thickest part of the skull. Preferably, aim slightly upward through a point midway between the eye and the ear opening, or shoot through the eye, angling the shot backwards and upwards toward a point above the opposite ear. Shooting into the heart of a cetacean with a large girth will probably not result in a quick death. After efforts to rescue a Cuvier's beaked whale failed, a policeman fired 2 clips of bullets from a submachine gun into the animal in an attempt at euthanasia; the scapula was shattered, but the whale, weakened as it was by repeated strandings, was still alive. Even in a small animal, the site for bullet entry is critical. Shooting is generally not an effective way of euthanizing whales over about 8 m in length or a sperm whale of any size (due to their cranial anatomy), and may be inadvisable in areas where rocks increase the danger of ricochet.

Exsanguination (Bleeding): Exsanguination is an option when equipment required for other methods is unavailable shooting unsafe, or there is no qualified person to administer a lethal injection. The technique is bound to generate adverse public reaction, even if the penetration site is first injected with local anesthetic.

The cetacean brain draws its principal blood supply not from the internal carotid arteries, as in most other mammals, but from a rete mirabilia network that enters through the foramen magnum, protected deep in a mass of tissue in the back of the head. The Faroe Islanders, in their pilot whale harvest, have traditionally sought that site for cutting

the blood supply to the brain. It is approached by directing\ a lance downwards from the back of the animal's neck. Inserted deep enough, the lance will sever both the vessels and spinal cord, and death will be quick. Severing the carotids 4 is not the best approach to euthanasia. A lance can also be inserted deep into the thorax to penetrate the heart and cut major vessels. Proper entry sites for each whale species have not been mapped, but they generally lie on either side of the ventral midline, behind the origin of the flippers. In some specimens, the location is marked by an obvious heartbeat. Observers should be prepared for the disturbing appearance of this procedure.

20.1.3. Pinnipeds

Human-Related Mortality: Our attitude toward pinnipeds, among other animals, is partly shaped by social and regional values that span both ends of the ideological pole. A seal just released from a benevolent recovery program may find itself in the cross-hairs of a gunsight if it chooses to invade a pen of cultured salmon. Consequently, it may reappear for a second round of rehabilitation -if lucky. Despite legal protection, some animals are shot because they are considered a nuisance or threat, among them Steller sea lions, Pacific harbor seals, and, in increasing numbers, California sea lions. Only two of the more than 2,000 harbor seals examined by the New England Aquarium since 1972 have been gunshot fatalities. A far greater number of pinnipeds is taken in native hunts-particularly phocid seals and walrus in the Bering, Beaufort, and Chukchi seas.

The number of pinnipeds killed or injured deliberately is insignificant compared to those that succumb to fishing net or marine debris entanglements. Fisheries-related mortality is high in Pacific harbor seals, Steller sea lions, Hawaiian monk seals, harp seals, and northern fur seals. Hawaiian monk seals and northern fur seals also become entangled in plastic debris, such as packing bands and straps.

Other forms of human disturbance may be as pernicious, but their effect is not always measurable. Human intrusion on beaches was blamed for an increase in pre-weaning mortality among Hawaiian monk seals on Midway and Kure atolls in the 1950's-'60's. Oil spills have contaminated seals and fouled their coats, killing some and undoubtedly harming others. Pollution has been linked to reproductive failure in certain pinniped populations and cause-effect relationship has been demonstrated.

Stranding Patterns: Most stranded pinnipeds are likely to be a species that resides in the area permanently or seasonally or that finds its way ashore at some point along its migratory route. In fact, stranding data are useful for mapping resident locations and movements of some species. Northern elephant seals and harbor seals in California faithfully reoccupy rookeries in the winter and spring months; some of their pups are certain to strand nearby. In winter, the animals may go elsewhere, as do harbor seals from maritime Canada that retreat southward to join dense colonies on Cape Cod. Armed with facts on the life history of a specific region's pinnipeds, one can reasonably predict the time and place that a given segment of the population is likely to strand. Yet, there will always be unexpected appearances. With increasing frequency, young hooded seals wander from their subarctic ice sanctuaries in northern Canada to Massachusetts, and rarely as far south as Florida. One bizarre journey, probably across the Canadian Arctic,

brought a healthy young female hooded seal ashore in southern California. Harp and ringed seals are also appearing well south of their historical ranges.

Following the general pattern of mortality, first-year pups are the most likely to strand. Most come ashore during the nursing period or soon after, particularly when that activity is interrupted by storms or other disturbances. Because their nursing period is brief, maternally dependent phocid pups appear over the course of only a few days or weeks, whereas otariid pups rely on their mothers much longer and are more apt to suffer from any disruption of the mother-pup bond. The frequency of pup strandings tapers off after weaning, through a phase where individuals may appear with residual illnesses stemming from their early days on the rookery. Juveniles and adults come ashore for myriad reasons, with little predictable pattern, except for increased strandings that are associated with a fleeting incident such as a storm, or that signal the onset of an epidemic or toxic event.

20.1.4. Sirenia

Stranding response. Jurisdiction: the Marine Mammal Protection Act of 1972 and the U.S. Endangered Species Act of 1973 protect Manatees in U.S. waters. Florida legislation enacted in 1897 and 1907 prohibited hunting, and the Manatee Sanctuary Act of 1978 recognized the manatee as the official State Marine Mammal and designated the Florida Department of Natural Resources (FDNR) as the agency responsible for its protection. In addition, federal and state agencies began in the mid-1970's to acquire lands, particularly in the Big Bend region, for manatee sanctuaries. The Florida Manatee Recovery Plan, initiated in 1980 and finalized in 1989, mandates specific strategies for the recovery of the species by coordinating all agencies involved in manatee research and management.

The network of federal and state agencies responsible for responding to manatee strandings is much more organized than that which exists for other marine mammals. The program was initiated in 1974 by the USFWS and the University of Miami, and transferred to the FDNR, Marine Mammal Section, in July 1985. The Florida Marine Patrol and officers of the Florida Game and Freshwater Fish Commission, who assist in securing the carcasses, verify reports of dead or injured manatees received by the Manatee Hot Line. Marine Mammal Section personnel are then responsible for carcass retrieval, transport to a designated facility, and necropsy according to detailed guidelines developed by the USFWS Sirenia Project. With authorization of the USFWS Endangered Species Field Office (Jacksonville), distressed animals may be taken to Sea World of Florida in Orlando or to the Miami Seaquarium for rehabilitation; Lowry Park Zoological Garden in Tampa is also authorized to receive manatees for rehabilitation. Only trained, designated personnel may remove, necropsy carcasses or rescue distressed individuals. People not specifically involved with these organizations play an understandably limited role in manatee rescue. An exception occurred in the 1982 die-off associated with red tide, when FDNR, USFWS, Sea World, and University of Miami personnel enlisted wildlife refuge staff and volunteers to assist with observation, rescue and field necropsies. As yet, FDNR has no specific contingency plan for dealing with a similar large-scale mortality.

Evaluating the Event: Manatees move slowly, often resting motionless at the surface or near the bottom. They may wander into almost any accessible waterway, even in highly populated areas. A solitary calf may be left alone temporarily while its mother feeds. Aggressive behavior during mating activities may be misinterpreted as distress. Manatees are also prone to 'bloat,' a condition that leaves them temporarily unable to submerge. Though it may cause discomfort, the condition normally 'passes' (i.e., look for bubbles) in a matter of days and requires no intervention. Careful, prolonged observation is necessary to determine whether or not an animal is actually in distress and requires help. In U.S. waters, only authorized individuals may make this decision.

While some may pull themselves onto shore, most manatees remain in the water when no longer able to function normally. Fresh propeller wounds, monofilament line wrapped around a flipper, weakness, emaciation, inability to submerge, pronounced listing to one side, reluctance to move or suckle, or labored breathing are signs of distress. (Manatees normally breathe once every 1 to 2 minutes when active and traveling and every 5 to 15 minutes when resting on the bottom.) An unaccompanied calf, or an animal far from the normal range or unable to reach warm water during the winter will also need assistance. During the 1982 red tide in Lee County, some manatees exhibited signs of neurological dysfunction, including disorientation (swimming in tight circles, colliding with pilings, docks and seawalls), inability to submerge or maintain a horizontal position, flexing of the back, labored breathing, chewing movements and flaring of the lips, and lack of response to prodding.

Manatees usually strand alone, although a calf may accompany a sick or injured female. They are unlikely to strand as a group because social bonds are unstable. While epimeletic (care-giving) behavior has been observed, particularly between cows and dead calves, manatees generally do not appear to help others in distress. Multiple deaths or strandings, not necessarily in the same location, might be anticipated following a spell of extreme cold or a red tide.

Specific Equipment:

Nets stretcher
Rope foam pad
Buckets crane or winch
Flatbed truck or trailer heated truck (live animals in winter)

Approach and Handling: The effort needed to capture a manatee depends greatly on the animal's condition. Severely debilitated manatees may offer little or no resistance, whereas otherwise healthy individuals can injure themselves or handlers by thrashing about during the rescue operation. Approaching a manatee before all preparations for capture are in place will likely scare the animal away and increase the difficulty of subsequent capture.

One method of capture is to surround the manatee with a net (30 to 35 m long, 4 m deep, with 10 cm stretch mesh) that is gradually drawn toward shore until the animal is in water shallow enough for handlers to physically restrain it. This may require 10-15 people for a healthy manatee. Handlers must use extreme caution to avoid becoming entangled in the net and being pulled into the water if the animal attempts escape. As

soon as the manatee is pulled into shallow water, it is maneuvered onto a padded platform and secured with straps. A 3.5 m-long stretcher will also do, provided it is wide enough to accommodate the animal's large girth. The risk of injury to both the manatee and the handlers is especially high when removing the animal from water, and secure restraint is essential.

Once out of the water, manatees generally become calm and may need little restraint. They should be approached quietly, from the front. Covering the eyes and wrapping a small piece of netting over the snout (do not obstruct breathing) helps to calm the animal by giving it the sense that it is still being restrained. Handlers must be cautious of sudden tail thrashings. Calves can be restrained and supported in the water by a single individual, but they must be placed securely in a stretcher before removal from the water. One person cannot safely lift a calf; they are difficult to hold and may be seriously injured if dropped.

First Aid: Once secured and moved into shallow or protected waters, or onto a sandy beach well above the water line, the animal's condition can be evaluated. Manatees struck by motorboats may have obvious skin lacerations, but just as often there may be little outward evidence of severe internal damage to ribs or lungs. In either case, little can be done on-site to treat such injuries. Open wounds or injured flippers should be protected from further injury during handling and transport. In the rare event that a manatee has been left stranded on shore by a falling tide, rescuers should provide shade from the sun and keep the animal wet to prevent overheating until qualified medical personnel can examine it. Beached manatees have been known to swim away on an incoming tide after several hours of exposure. Cold-stressed manatees should be taken into a warmer environment (i.e., heated truck or warm pool) as soon as possible. Calves are pa zrticularly\ prone to hypothermia. Some of the manatees presumed to have been affected by the red tide were so disoriented, and they required assistance to raise their heads above the water to breathe. Under most circumstances, however, attempts to help an unrestrained manatee are ill advised and dangerous.

Transport to Care Facility: Rescued manatees are generally secured in a 1QA\stretcher and transported by truck on a 15 cm-thick foam pad. Cranes are needed to lift adults. Transport time of up to 3 hours usually presents no problem for an otherwise healthy manatee, but sick or injured animals obviously may be less able to endure the procedure. During transport, the animal should be kept moist and shaded in a 20 ^{o} to 26 ^{o} C environment. Capture stress (myopathy) is not a concern, even after several hours of transport. Nevertheless, it is best to minimize pursuit, vigorous handling, and transportation time. One individual transported for 14 hours survived with no apparent ill-effect beyond a temporary increase in serum levels of muscle enzymes.

Rehabilitation: On arrival at the rehabilitation center, the manatee should receive a thorough physical examination. Blood is drawn using a 25 mL syringe with an 18- or 20-gauge, 4-cm-long needle on an extension set, from the palmar side of the flipper, between the radius and ulna; risk of infection is great if the area is not properly cleaned of algae and bacteria. Normal values for blood and urine constituents have been reported. Fecal samples should be examined for signs of dehydration or diarrhea, and cultures taken if

possible. Manatees recovered during winter should be placed in water 20°C or warmer to allow them to conserve energy. Critical care measures are particularly effective in dealing with orphaned calves. In captivity, manatees will soon need to start eating and can be offered a variety of green plants, including lettuce, cabbage, spinach, celery, carrot tops, natural water grasses and water hyacinth. An animal that refuses to eat may first require fluids administered by stomach tube, followed by a gruel consisting of ground lettuce, apples, monkey chow, and water. Artificial formulas have been used successfully to nurse orphaned manatees back to health.

Release: Few manatees are immediately released at the site. These might include trapped or entangled animals with no sign of injury, or, as in the case of manatees affected by red tide toxins those that regain strength and coordination by the time the rescue team arrives. Of 47 manatees rescued by Sea World from 1974 to 1987, only 3 were released at the site. The decision to release an animal from a rehabilitation facility is presently made on a case-by-case basis, with authorization from appropriate federal and state agencies. Some have suggested that animals captured as dependent calves should not be released, since they have not learned important behaviors for avoiding boats and finding warm water refuges during cold weather. Older animals slated for release are freeze-branded and generally fitted with a satellite transmitter to monitor their movements. Rehabilitated manatees monitored by telemetry thus far have readapted well to life in the wild. Manatees are not released from Florida rehabilitation facilities during the winter months.

Euthanasia:
Lethal injections of barbiturate have been used effectively.

20.1.5. Sea Otters

Stranding response. Jurisdiction: Sea otters were first protected in 1911 under the International Fur Seal Treaty and then by legislation introduced by the state of California in 1913. The Marine Mammal Protection Act (1972) placed them under the jurisdiction of the U.S. Fish and Wildlife Service (USFWS). California sea otters are further protected under the Endangered Species Act of 1973 and are managed by federal and state agencies. In British Columbia, the Federal Fisheries Act and the B.C. Wildlife Act and Regulations protect sea otters. The California Department of Fish and Game (CDFG) and the USFWS conduct programs to recover carcasses in California, relying on public reporting as well as surveys of certain isolated beaches. Because most carcasses are washed ashore and may lie undiscovered for days, investigations into the cause of death are not often successful.

Along U.S. coastlines, the occurrence and location of sea otter carcasses must be reported to either federal (USFWS) or state (Alaska, California, or Washington DFG) authorities.

Evaluating the Event: Unless the need for intervention is obvious, sea otters should be carefully observed for at least 15 to 20 minutes before any action is taken. Hauling out is a normal behavior in some regions, and a sea otter on shore may simply be resting, about

to give birth, or nursing a pup. While healthy animals will typically avoid humans, they may tolerate close approach by a boat. A female otter may dive for food, leaving her pup vocalizing plaintively at the surface. Most situations of this kind do not warrant action.

Some behaviors signal distress. An otter on shore that appears lethargic, agitated, reluctant to enter the water, or makes no attempt to evade capture may need help. Excessive or exaggerated grooming, due perhaps to soiling of the fur, may lead to damage to the skin, ears, or eyes. Oil-contaminated otters may raise the upper part of the body out of the water and shake vigorously, although this behavior is not necessarily restricted to fouled animals.

More obvious indications of distress are emaciation, wounds, labored breathing, violent shivering, matted fur, and restricted mobility. If the fur retains a slick wet appearance after more than 10 seconds at the surface, the otter may be contaminated and should be considered a candidate for capture.

Sea otters sometimes wander beyond their normal range into unsuitable habitats, but they are unlikely to remain in areas with inadequate food resources. An animal lingering in an unusual location may require assistance, especially if it shows signs of distress or is endangered by local conditions (e.g., fishing activities, pollution).

Sea otters normally strand individually, but dozens or hundreds of animals may come ashore following severe storms, disasters such as oil-spills, or outbreaks of suspected biotoxin poisoning.

Specific Equipment:

Dip nets stuff bags
Tangle nets (modified gill nets) ice
Transport

Approach and Handling. Words of Caution: Sea otters are sensitive to and can die from the stress associated with capture, transport, and rehabilitation. The need for assistance must be carefully evaluated before subjecting these animals to unnecessary disturbance. Otters alert and active enough to avoid capture are better left alone. Chasing mothers with young may result in abandonment or drowning of the pup. Always keep pets and other domestic animals away from the area.

Appearances such as winsome face and mannerisms are definitely deceiving. Sea otters have an aggressive temperament, dexterous forelimbs, forepaws armed with sharp claws, flexible bodies with loose skin, and strong jaws with teeth adapted for crushing. They should be approached quietly, with minimum disturbance, and handled cautiously once captured. Heavy leather gloves with long cuffs should be worn to minimize serious scratch and bite injuries, bearing in mind that a sea otter can still crush a finger through a glove. Otters are so flexible1 they seem able to turn around inside their loose skin; for that reason one should never be grabbed by the tail or nape of the neck.

Techniques: Sea otters can be captured safely only by trained personnel. The most successful methods use dip nets, modified gill nets (tangle nets), or specially designed diver-held Wilson traps. Choice of method depends on the experience of the handling team, the sea state, condition of the animal and the type of habitat. Dip nets can be used

from skiffs and are effective for capturing selected individuals, particularly juveniles and lethargic adults. Older, healthy animals tend to dive to avoid capture. Dip nets cannot be used in rough seas or in kelp beds.

Gill nets (30 m long x 3-6 m deep) made of 20- to 23-cm stretch mesh net are modified by removing or reducing the weighted bottom line so entangled animals will stay at the surface. These nets work well for active animals too elusive to be taken with dip nets. Gill nets are, however, non-selective and require constant monitoring to avoid injuring trapped animals. Gill nets cannot be used in kelp beds, shallow rocky areas, or in rough seas.

Diver-held devices designed by CDFG biologist K.C. Wilson have been used successfully in California to catch animals at the surface and keep them floating there, safe but secure, until a boat arrives. These traps can be used in kelp beds 32 and have the advantage of surprise, thus minimizing the stress associated with chasing.

Sea otters should be approached quietly, and from downwind if possible because of their acute sense of smell. On land, dip nets are used to capture sleeping otters or weakened juvenile or old animals driven ashore during storms. Healthy adults are more difficult to catch, and mothers with pups tend to be more alert and to come ashore in less accessible places. Distressed otters may make little or no attempt to escape and can be caught with dip nets, tangle nets, or if weak, picked up by hand and placed into cages.

Direct communication between the capture crews, transport vehicles, and the rehabilitation center is essential, particularly in a large-scale rescue. A specialist should be present on every capture boat to assess each sea otter's condition and provide immediate supportive care. Captured otters should immediately be placed in a box or transport cage. Lining the box with a net bag will allow for easier removal and transfer to a cage, but can present problems if the otter becomes entangled. Unless judged to be hypothermic, rescued animals should be transported on a bed of ice shavings or cubes. Smaller and less aggressive animals can be picked up by the hind legs, held upside down with their backs to the handler (keeping the forepaws and head as far away as possible), and placed in a cage or restraint device. Dip nets, blankets, throw nets, or stuff bags will be needed for handling larger or more aggressive otters. The degree to which an otter must be restrained depends on its health and the objectives of the mission. Complete restraint is recommended for most physical examination and sampling procedures. This can be accomplished using transport cages or specially designed restraint cages, devices in conjunction with a stuff bag, or by chemical sedation. Avoid excessive or prolonged restraint.

First aid. Determining Condition: Sea otters should be evaluated for evidence of respiratory distress (normal rate 17 to 20 breaths/minute), dehydration, wounds, soiling of the pelage, emaciation, and diarrhea. Normal heart rate is 144 to 159 beats/minute. As a rough indication of body temperature, the hind flippers should be cool to the touch. Very warm or very cold flippers, violent shivering or panting signify thermoregulatory difficulties hypothermia and hyperthermia.

The animal's general condition may be classified as:
1. Alert and normal
2. Depressed (inactive and unresponsive to environmental stimuli)

3. Semi-comatose (responding only to painful stimuli)
4. Comatose (retaining some simple reflexes, but otherwise unresponsive)

The course of treatment may depend on the age of the animal. A rough guide according to weight is:

1. Small pup (less than 3 months, 1.0-4.5 kg)
2. Large pup (3 months-1 year, 4.5-13.5 kg)
3. Subadult to adult (>13.5 kg)

Consider in your estimate that an otter can lose as much as 25 to 33 percent of its body weight (mostly from muscle) rapidly when under prolonged stress.

Supportive Care: As soon as possible after rescue, stabilize the otter's body temperature, treat shock and dehydration, and offer food and water. Signs of dangerous hypothermia (body temperature less than 36 ^{o} C) include lethargy, lack of reaction to handling, cold hind flippers, and violent shivering (mild shivering is not a reliable sign). Place the animal in a dry cage protected from draft, and warm it gradually with a pet dryer or heat lamp, or in severe cases, place the hind flippers in warm water. Oral glucose therapy may be necessary until the otter is conscious enough to accept food.

Hyperthermia (>39.5 ^{o} C) is manifested by lethargy and warm, often flared, hind flippers. The condition may arise during captivity or transport when an active or sedated animal is confined without access to ice or water. Some oiled otters become hyperthermic through excessive grooming and in response to handling. Hyperthermia may be relieved by using cold or iced water on the hind flippers, or as a bath for immersing the animal.

Transport to Care Facility: Sea otters may be transported in uncovered plastic kennel cages with a rack placed on the bottom to keep the animal from becoming soiled. Cages of wood, fiberglass or metal with netting side panels and a raised rack in the bottom are also suitable. The wire mesh door on kennel cages should be replaced with netting to avoid injuries from chewing during longer transports. Provide ice as a source of water, particularly during warm weather, and drain accumulated water from the cage. During extended transports, offer food (e.g., shellfish meats) approximately every 2 hours. Transport otters quickly (less than 3 hours transit time) within 6 hours of rescue. Transport vehicles should be well ventilated and adequately lit so animals can be continually monitored. Ice or heaters must be readily available to allow for prompt treatment of hyper- or hypothermia. Helicopters have proven useful for moving large numbers of animals rapidly. Before transport or immediately upon arrival at the rehabilitation center, all animals should be tagged on a flipper for identification.

Rehabilitation: At the care facility, the condition of the animal should be reevaluated and a blood sample taken. The results will dictate whether to treat for hypo- or hyperthermia, hypoglycemia, dehydration, diarrhea, or shock.

General Considerations: Facilities for rehabilitating otters must include cleaning areas, dry cages, cages with pools, and floating pens for holding prior to release, all with

adequate water flow and ventilation. Enclosures should be designed to avoid injury from chewing. Secure the area from domestic pets. Sea otters are preferably kept in groups of two or more, although males and females should be separated and mature males housed individually. Females should be isolated with their pups until the pups are at least one month old. Holding pools should be filled with seawater (fresh water may be used temporarily) to a depth of at least 0.6 m to allow for adequate grooming. Maintain water temperature at 7 ^{o} to 15 ^{o} C and do not use chlorine. Recovering animals must be provided with adequate haul-out space. Sea otters kept in dry pens for more than one or two days may develop pressure sores; this can be minimized by constructing the pen floor of smooth plastic perforated with 2.5-cm diameter holes. Juvenile and adult sea otters thrive on a mixed diet of shellfish and fish consumed at a rate equivalent to 20 to 30 percent body wt/day, but they can consume more than the equivalent of 50 percent of their body wt/day when unable to maintain body temperature. Animals with serious health problems should be offered food hourly, while others may be fed every 4 hours. Avoid overfeeding healthy otters. Chips and chunks of ice are a crafty means of providing water to an animal most likely to tip over a bucket. Pups tolerate considerable handling and, after the Exxon Valdez spill, were generally found to do well if they survived the first two weeks in captivity. They need constant attention until at least three months of age, including regular temperature checks, formula feeding, and careful washing, drying, and grooming. Rehabilitation of an orphaned pup may require 6 to 9 months, including a period of weaning the otter from its attachment to humans.

Reduce stress to captive sea otters as much as possible by maintaining a clean, quiet environment, secure from domestic pets, and by minimizing handling. Providing ready access to water for swimming and grooming, and to food, ice, and canine chew-toys can curb harmful behaviors. Preoccupation with chewing may simply indicate the otter is hungry.

Caring for Oiled Otters: Oil that fouls an otter may also irritate the eyes and cause sinusitis, emphysema, anemia, and systemic toxicity. Therapy may require treatment for these conditions as well as measures to restore the insulative properties of the pelage. Heavily oiled animals should be cleaned immediately to reduce ingestion and absorption of oil. Cleaning those that are lightly oiled may be delayed for 12 to 24 hours to allow for recovery from the stress of capture and transportation and to provide food and fluid therapy.

Before cleaning can begin, the otter must be sedated, assuming it is healthy enough to withstand the procedure. Sedation allows safe handling without excessive stress to the animal and permits monitoring of rectal temperature. Oiled fur must be washed (Dawn ® dishwashing detergent [Proctor and Gamble] is recommended), rinsed and dried, and finally freed of all traces of detergent. Washing removes natural oils from the fur and greatly increases thermal conductance. Placing the otters in seawater pools for brief intervals encourages grooming and restoration of the water repellency, though it will be necessary to remove them for drying. The animals will gradually tolerate longer periods in the water without signs of chilling; after 7 to 10 days the fur should regain its insulative value.

Release: Animals with health problems that might limit their chances of survival in the wild should not be released and must either be adopted into a captive colony or euthanized.

Immediate Release: An animal that is 'rescued' but appears healthy and alert and exhibits normal behavior should be released as quickly as possible. Release should take place at the 'home' site, unless hazards there (e.g., fishing, boating activities, pollution) warrant selection of an alternate location. Dependent pups should not be returned to the water unless the mother is present. Animals captured far outside the normal range are not candidates for immediate release. Whether released from a boat or on a beach, otters should always be allowed to enter the water of their own accord.

Release Following Recovery: As soon as an animal is judged fit, it should be released, either directly into the wild or after a period of acclimation in floating pens where visual and physical contact with humans is minimal. Tagging is the only reliable method of monitoring released sea otters. Intra-peritoneally implanted transmitters have allowed tracking for up to 3 years with few problems. Transponder chips may also be implanted for permanent identification. Radio transmitters attached to flippers have allowed brief tracking, but this method is not recommended: the transmitter is too easily removed by the otter and may damage the flipper.

Euthanasia: The U.S. Fish and Wildlife Service has authorized sea otter rehabilitation centers to euthanize terminally ill animals. This is achieved by injecting a lethal substance into the distal third of the femoral vein, or into the heart or jugular vein.

20.2. Pollution: Introduction

20.2.1. Basic Concepts

There are 65,000 chemicals in common use today. 1,000 new ones enter the market every year. Some kill at contact or ingestion, others cause hormonal unbalances, weaken the immune system, cause brain damage and other neurological disorders, cause cancer, liver disease, genetic defects, etc. Due to the process of bioaccumulation, marine mammals which are the to of the trophic chain, accumulate large amounts of these toxics especially with age. Further, lactating mothers deliver these toxics to their young through the milk.

All this is particularly true in enclosed waters such as the Baltic Sea, Black Sea, North Sea, and the Gulf of Mexico. The number of reports of marine mammals containing toxics in their tissues increases every year.

For close to thirty years, most academics studying the phenomena of marine pollution have adhered to a definition developed by a UN body, the Group of Experts on the Scientific Aspects of Marine Pollution (GESAMP), who define it as the 'Introduction of man, directly or indirectly, of substances or energy into the marine environment (including estuaries) resulting in such deleterious effects as harm to living resources, hazard to human health, hindrance to marine activities including fishing, impairment of quality for use of sea-water, and reduction of amenities.'

The definition has two important qualities. First, it is action oriented. Marine pollution is conceptualized as a human activity, thereby omitting all natural activities that could potentially have damaging effects on the ocean eco-system. So, for example, earth quakes or volcanic eruptions that emanate from the ocean floor and subsequently damage or change already existing ocean eco-systems would not be considered pollution. Second, the definition is amenable to measurement. Marine pollution is harmful, and its danger can be identified in a variety of ways. For example, it is easy to see the deleterious effects that oil spills have on the sea birds and mammals who happen to run into them. Scientists likewise can readily identify various toxic substances found in the marine environment, measure their quantities, and provide estimates of their potential danger for the health of both marine life and humans.

20.2.2. Types of Marine Pollution

Probably the easiest way to organize one's thinking about marine pollution is to consider it in terms of its source. All marine pollution must originate from one of two sources, the land or the sea. Of course, because marine pollution is defined as a human activity, and humans are land creatures, it might be semantically correct to assert a land-based origin for all marine pollution. Additionally, the acid rain phenomena suggest that air based sources of pollution are equally important. Semantics aside, bear with me. Differentiating between land sea based marine pollution captures the core of marine pollution sources.

The sources of marine pollution can be broken down into five categories. Here land-based sources contribute 44% to the total amount of marine pollution, air based contributions total 33%, maritime transportation (which includes accidental and purposive oil spills, and dumping of ship garbage etc.) totals 12%, dumping (which includes all other purposive dumping such as when a garbage barge goes to sea for the express purpose of dumping its load) represents 10% of the total, and finally, offshore production (the pollution coming from oil platforms etc.) represents 1% of the total.

On the other hand, these five categories easily fit into the land and sea based classifications, albeit with a few clarification. First, the pink 'total land based' text combines the air based, land based, and offshore production totals. This classification works because the difference between land based and air based measurements are not specifically source defined. In their measurements, land based sources referred to those types of pollution introduced into the marine environment from a variety of land sources. For example, when pesticides leach into the ground water, and to rivers that eventually make their way to the ocean, they contribute to the total amount of land based marine pollution. When municipal waste plants discharge their waste (recycled or other wise) into the rivers and/or bays, they also contribute to total land based marine pollution. Air based sources refer to all the types of industrial activities that create air pollution which eventually drifts over and falls onto marine waters. Finally, as part of a legal technicality, in 1985, the Montreal Guidelines on the Protection of the Marine Environment Against Pollution from Land Based Sources added offshore production activities to the list.

The pink 'total sea based' text combines the dumping and transportation categories. Once again, some semantic differences are involved. Dumping refers to the deliberate dumping of land-based wastes at sea such as when states use their coastal

waters as dumping grounds for low-level radioactive wastes. Transportation refers to the types of marine pollution that result either accidentally or purposively from ships as part of the travel process. The best known examples in this category are oil spills, which can be deliberate (for tankers during the normal cleaning process) or accidental as in the case of some of the well known oil spills of recent times. The transportation category also includes other types of pollution activities by ships at sea. For example, when marine vessels (the navy, fishing fleets, pleasure boaters etc.) go out to sea, their crews generate garbage. Traditionally, the garbage was dumped at sea, and that waste is included in transportation totals.

When looked at from a simple land based versus sea-based differentiation, the sources of marine pollution can conveniently be labeled as predominantly land based. The statistics from Figure 1 suggest that approximately 78% of all marine pollution come from land-based sources. (It should be noted that most types of statistics associated with marine pollution are at best estimates. Even the most respected research studies make these types of claims).

20.2.3. Effects on Marine Mammals

20.2.3.1. Oil

Sources: Exploitation, exploration, accidents, oil spills, war

1991 Gulf War - 8 million tons (ca. 1 million barrels)
1989 *Exxon Valdez* - 35,000, Alaska
1983 Persian Gulf - .5 million tons
1979 Gulf of Mexico - .5 million tons
1978 *Amoco Cadiz* - 230,000 tons, France
1967 *Torrey Canyon* -118,000 tons, England

Effects: kills fauna and flora, covers rocks and sediments. Long-term biodegradable
Control: dispersants. Not perfect since affects small organisms

Oil spills, like other forms of pollution, contribute to overall degradation of habitat, can influence prey abundance and diversity, and may increase stress and susceptibility to infection. Some cetacean populations have accumulated high levels of **contaminants** that are tentatively linked with disease, including tumors and reproductive disorders.

20.2.3.2. Sewage

Sources: Domestic and industrial; raw and treated
Effects: Eutrophication, red tides

20.2.3.3. Synthetic Chemicals

Chlorinated Hydrocarbons (pesticides like DDT). They are non-degradable and persistent
PCBs (polychlorinated biphenyls) (plastics, banned in 1979 in the U.S.). Very toxic
Heavy metals: mercury (methyl mercury), lead, cadmium, copper

Low concentrations of PBC lead to suppression in the immune system responses of harbor seals. It also interferes with embryo implantation in seals, leading to fewer births, and lower birth weights. In general, marine mammals in the North Atlantic have a much higher concentration of organochlorates than those from other oceans. Belugas in eastern Canada have high concentrations of these chemicals as well as heavy metals and pesticides, and the incidences of parasitism are much higher.

Since 1989, a high number of bottlenose dolphins that have stranded on the east coast of the U.S., have been found with high concentrations of tin compounds, which are heavily used by the maritime industry.

20.2.3.4. Thermal pollution

It changes coastal ecosystems dynamics.

20.2.3.5. Solid Waste

Plastic, containers, packaging, rubber, metal

Table 20.1. Summary of the effects of objects on marine mammals

Spp. Group	Total # spp.	Spp. Entanglement records		Spp. Ingestion Records		Entanglement and/or Ingestion Records	
		#	%	#	%	#	%
Mysticetes	10	6	60	2	20	6	60
Odontocetes	65	5	8	21	32	22	34
Otariidae	14	11	79	1	7	11	79
Phocidae	19	8	42	1	5	8	42
Sirenia	4	1	25	1	25	1	25
Mustelidae	1	1	100	0	0	1	100
TOTAL	115	32	28	26	23	49	43

20.2.3.6. Radioactive

Nuclear Waste Dumping in the Arctic Ocean

We've arrived at a point in the history of the industrialized world where no place on earth is free from the scourge of pollution. Even our most remote and inhospitable areas for human habitation, the polar regions suffer from the problems commonly associated with life in the industrial world. Whereas once the adjective ‘pristine’ was unreflectively

attached to descriptions of our polar areas, today environmental discussions of the areas focus on issues such as smog, ozone depletion, water pollution, and hazardous waste.

Global response to polar pollution problems mirrors these areas' geographical placements. It's been polar opposites. The presence of a large landmass on the southern pole, coveted by various states, has led over the past three decades to a tightly knit environmental protection regime. Anchored by the Antarctic Treaty (1961), the Antarctic Treaty System now provides environmental guidelines for all aspects of the Antarctic environment, from the protection of marine mammals, flora and fauna, to the regulation of eco-tourism and waste disposal. Our northern most pole remains relatively unregulated. Save for some international agreements regulating polar bear and seal hunting, the only attempts at environmental cooperation in the Arctic have popped up during the last decade, as the states immediately bordering the Arctic agreed to informally organize around The Arctic Monitoring and Assessment Programme.

The issue of nuclear waste in the Arctic emerged in the early 1990's with revelations of the Soviet Union's intentional dumping of high-level nuclear waste during the 1960's, 1970's, and 1980's. This particular problem is one of a triple nuclear threat posed by current Russian nuclear activity.

20.2.3.7. Greenhouse Effect

Species facing extinction: Northern Right, Southern Right, Blue, Bowhead, and Humpback, giant clams, marine snails and cones, sea turtles, sharks, seabirds, seals, and sea lions

20.2.3.8. Noise Pollution

Coastal development, speed boats, jet skis, dredging, heavy shipping such as tankers an container ships, low-flying aircrafts, military maneuvers, seismic testing for oil and gas, drilling rigs, sonar, and acoustic telemetry are all to blame. Not only loudness but also frequency can be a problem. Large cetaceans are more sensitive to low frequencies and small ones to short frequencies.

It has been suggested that the increasing number of sperm whaling strandings in Britain may be linked to seismic exploration in the deep waters west of Shetland Islands. Off the coast of Newfoundland, explosions from a nearby underwater drilling operation seem to make humpback whales more likely to blunder into fishing nets.

It has also been suggested that heavy shipping traffic, and its associated noise, may be one of the reasons the endangered northern right whale population is failing to proliferate while southern right whales are increasing by about 5-7 percent annually.

20.3.3. Polar Bears and Pollution

Polluted air from Eurasia migrates to the Eurasian Arctic. North American air pollution tends toward Canada, Greenland, and the North Atlantic, leaving the North American Arctic cleaner by comparison. However, the pristine nature of the entire Arctic region is increasingly being undermined. For instance, the pesticide toxaphene, once used on

cotton – a distinctively non-Arctic commodity – has been blown by air currents into Arctic regions. Acid rain also threatens.

Polychlorinated biphenyls (PCBs), heavy metals such as mercury, and radioactive waste travel by water from the former Soviet Union's rivers and the Siberian seas to Arctic coasts. Oil spills have given Siberian coastal waters a greater pollution content than North Sea waters. The search for more sources of Alaskan oil pits environmental concerns against modern civilization's dependence upon petroleum fuels. As a result, the environmental watchdog group Greenpeace served a citizen's arrest warrant to the ARCO oil company regarding the placement of that company's oil drilling platform offshore from the Arctic National Wildlife Refuge. Other voices assert that oil companies take great pains to minimally impact their work areas.

The environmental stability of mercury and PCBs allows these substances to accumulate in living organisms. Those species at the top of the food chain have the largest concentrations of these pollutants. Because of its position at the top of the Arctic food chain, the polar bear, Ursus maritimus, has become a reservoir for environmental pollutants. *U. maritimus* may decide the extent to which the Arctic can support development by predicting the sensitivity of the Arctic ecosystem to encroaching pollutants.

PCBs were used commercially without restraint for 50 years, and as a result are now found in polar bear fat deposits. Less fat soluble than PCBs, mercury and its compounds concentrate in kidney, liver, and muscle tissue in polar bears. Because of our similar position in the food chain, humans also carry the burden of unwanted accumulated toxins. In the Canadian Arctic, Inuit women have more PCBs in their breast milk than do women of southern Quebec. A relationship has been proposed linking high breast milk PCB levels to acute ear infections in Inuit infants.

Scores of marine mammal species live in Arctic and adjoining areas. US Pacific waters include the polar bear, sea otter, walrus, 11 species of seals and sea lions, and 36 species of dolphins, porpoises, and whales. However, Norway's Spitzbergen Islands in the Barents Sea are a recent focus of attention, because this Arctic region receives airflows from North America and Europe, and water currents from Russian rivers. The confluence of airborne and waterborne pollutants makes this area suitable for study; PCB levels are several-fold higher than those in Alaska or Canada. Animals exposed to high levels of exotic compounds should exhibit clearly defined toxic symptoms. The immune response and breeding patterns of polar bears will be examined. Whales, seals, and walruses will be similarly analyzed for environmental pollutants and behavioral changes. Research in the Spitzbergen/Barents Sea area will determine the intrusive effects of persistent environmental pollutants on species in Arctic regions.

20.4. Diseases

20.4.1. Cetaceans

Parasites are common among wild animals. Even humans have them. Most parasites do not kill their host. It is in their best advantage.

20.4.1.1. Ectoparasites

Conspicuous infestations are common among baleen whales but are less common in smaller cetaceans.

Callosities on the head in front of the blowhole of right whales are infested with colonies of barnacles, parasitic worms, and whale ice. The largest patch, located on the snout, was called the 'bonnet' by old time whalers and is a feature by which the species is easily recognized. The pattern of callosities is individually unique and may facilitate recognition of individuals.

a) Barnacles: Not species specific, up to 450 kg in a humpback, they dig 1 cm under the skin. Barnacles very rarely in dolphins (on teeth when cracks in the mouth)

Usually found among slow moving whales.
Three types: mound-shaped acorn barnacles (*Coronula* and *Cryptolepas*)
stalked or ship barnacles (*Conchoderma*)
Pseudostalked barnacles (*Xenobalanus* and *Tubicinella*)

They do not seem to cause any damage of inflamation or infection. They could be regarded as mutualistic or commensal: only the barnacles benefit because they feed on the whale skin?

b) Amphipod crustaceans (whale lice) Cyamid, *Cyamus* (species specific) on head, flippers flukes mostly in humpback, gray (more ectoparasites than anyone else), and right whales

They aggregate in areas of low water flow such as the long longitudinal grooves and prominent ridges covering the throat, chest, and anterior part of the central body surface of the margins of the lips, and on callosities, the raised patches of roughened skin found only on the head of right whales. Callosities, which surround a single sensory hair, may have evolved to help the whale sense its environment, although their roughened surfaces also provide good attachment sites for cyamids. The cyamids that blanket a callosity could interfere with sensory reception of a whale by covering, breaking, or bending the sensory hairs. However, it also is possible that cyamids amplify the signal to the whale by sensing a plankton bloom and changing their activity patterns which could signal to a whale that it had entered or left plankton-rich water. The whale lice require shelter where they will not be swept off the whale's surface and this is available in the depths of these body grooves. Physiologically, Cyamus needs heat and blood and hence it inhabits areas that are well vascularized. Observations indicate that cyamids feed on the epidermal layer of whale skin. Although the principal diet of cyamids is whale skin, it is possible that they also feed on plankton. Cyamids may be more accurately regarded as mutualist, rather than parasites. In association of mutualist, both the whale and cyamids benefit; the whale skin provides for food the cyamids and the cyamids inform the whale nearby food resources, In gray whales, cyamids also may actively undercut barnacles and increase their rates of detachments.

c) Copepods: skin blubber, baleen plates

d) Diatoms: Concentrated in the form of a thin yellow-green film, e.g., *Cocconeis* on the blue whale.

They acquire these ectoparasites during their summer stay in polar waters. Its presence has helped to identify the migration patterns of those species.

Breaching may have to do with getting rid of parasites (would not work for barnacles). They do not appear to be detrimental (should not be called parasites but commensals)

20.4.1.2. Endoparasites

Nematodes (roundworms) (up to 50 kg in the stomach of a sperm whale)
Platyhelminthes (tapeworms) (up to 15 m in length)
Stomach, intestine, kidneys, urogenital system, mammary glands
up to 3% of natural mortality
94% of fin whales (4-5% mortality/yr.)

Parasites in the ears/brain and strandings
May be very detrimental

Also, bacterial infections
Pneumonia in stranded animals
Fibrosis, atrophy in heart, arteriosclerosis, tumors
In captivity: Gastric ulcers, cirrhosis of the liver, pulmonary infections
Lots of DDT, PCB, other chemicals

Nearly every cetacean beyond the age of a newborn has parasites; some may even be acquired in utero. Some parasites play an arguable role in disease and mortality. Nematodes that reside seemingly innocuously in lungs and stomach can overwhelm a host facing other stressful conditions. Aberrant migrations of trematodes through the brain have been linked to strandings of common dolphins. Damage to the bones of the head, caused by nematodes of the genus *Crassicauda*, has been linked to mortality of young pantropical spotted dolphins. Other species of *Crassicauda* injure renal blood vessels 65 and mammary tissue, perhaps with serious effects. Small respiratory tract nematodes of the genus *Stenurus* are commonly found in the auditory or eustachian tubes, middle ears and cranial sinuses, but there is no firm evidence for the popular notion that they precipitate strandings.

Cetaceans have been found with cardiovascular problems, lung **diseases** not associated with parasites, nutritional disorders, and infections caused by a range of opportunistic pathogens. These conditions simply reflect the broad range of illnesses facing any species, and none is regarded as having population-wide effects. However, certain **large-scale threats** are becoming identified. The recent outbreak of morbillivirus infection that killed at least 750 striped dolphins, *Stenella coeruleoalba*, in the Mediterranean suggests that **viruses may have long been overlooked as possible causes**

of mass mortality. Fourteen humpback whales died near Cape Cod after eating fish that contained **saxitoxin** produced by the marine dinoflagellate *Gonyaulax tamarensis* (responsible for paralytic shellfish poisoning in humans). **Brevetoxin** produced by *Gymnodinium breve* was implicated in the mass mortality of bottlenose dolphins along the Atlantic coast during 1987-1988. If these events are linked to human-induced changes in the environment, they may foreshadow an emerging trend in cetacean mortality.

20.4.2. Pinnipeds

Virtually all adults and most weaned pups serve as either intermediate or definitive hosts for **parasites** of all kinds.

Ectoparasites: Sucking lice (Echinophthiridae) dwell on skin. They are obligate parasites exclusive to marine carnivores, mainly pinnipeds. Their claws may be modified for clinging to the fur or to the skin where they are found commonly on eyelids, nostrils, and the anus. Pups are more prone to infestation than adults and may serve as hosts soon after birth.

Mites occupy respiratory passages. Cestodes and nematodes are ubiquitous, and include gastrointestinal roundworms, tapeworms, hookworms, as well as heart and lung worms. Except for fatal episodes of infection by hookworm in northern fur seal pups and lung-worm in California sea lions, northern elephant seals and harbor seals, parasites seem to have little obvious effect on the well-being of a healthy host. However, stress and pre-existing illness can upset the balance, transforming innocuous parasites into serious pathogens that induce pneumonia, gastric ulcers, intestinal inflammation and a host of other ailments seen in stranded animals.

Ailing pinnipeds eventually die of diseases brought about by a variety of pathogens. Except for leptospirosis in California sea lions and northern fur seals, bacteria are not significant primary agents of disease. However, as secondary invaders, they can kill animals already stressed by habitat degradation, malnutrition, parasites and other pre-existing conditions. Infections complicate traumatic wounds, even the mild irritations that arise when a young pup drags its exposed umbilicus along a sandy beach. From a practical standpoint, we recognize that bacterial infections can mask or overwhelm the clinical picture of a stranded animal and therefore demand immediate attention.

Diseases, if severe enough, can reduce populations. Viruses, once considered insignificant in natural mortality, have suddenly emerged as serious pathogens in certain species. The 1955 die-off of crabeater seals (2,500 dead) in the Antarctic sparked an investigation that stirred the first empirical diagnosis of viral disease. The unaccounted mass mortality of Galapagos sea lions in the 1970's is also suggestive of a viral agent. In 1979-80, an influenza virus swept through the winter population of New England harbor seals, killing at least 450 animals, and influenza continues to strike there in modest form. In 1987, a type of morbillivirus (related to human measles and canine distemper) named Phocine Distemper Virus (PDV-2) killed several thousand seals in Lake Baikal. No one was prepared for the ensuing epidemic caused by another strain of the virus (PDV-1) that eventually claimed more than 17,000 harbor seals in the North Sea. In searching for the origin of the virus, investigators have noted isolated cases of disease in seals along the North American east coast and have detected antibodies in harp seals sampled from

Greenland prior to the epizootic. Why the sudden increase in virus-induced mortalities? Such large-scale events would not have gone unrecognized in recent history, suggesting that these outbreaks are indeed a new phenomenon. Circumstances are changing: protected animal populations are expanding; human occupation and industrial activity in coastal waters are increasing; sophisticated fisheries operations are competing for dwindling food resources; increasing air and water temperatures are influencing pinniped behavior and distribution; and habitats are showing the effects of chronic contamination.

Algal bloom -> red tide -> emphysema -> pulmonary edema. 17,000 died throughout Europe in 1988.

Morbilliviruses
a) CDV: canine distemper virus
b) M: measles in humans
c) PPRV: peste des petits ruminants
d) RPV: rinderpest virus
e) PDV: phocine distemper virus
f) VESV: vesicular exanthema of swine virus
g) SMSV: San Miguel sea lion virus

What had happened? During the breeding season when the reverse of fat into blubber is mobilized, contaminants such as PCB and pesticides residues suppress the immune system. This has happened among harbor seals, harbor porpoises. Gray seal seems very resistant

Chapter 21

Exploitation

21.1. Introduction

The interactions between humans and marine mammals have not been very good for the latter. For example, humans are responsible for the extinction of at least three species: *Zalophus japonicus*, *Monachus tropicalis*, and *Hydrodamalis gigas*. Also, an unknown species of pinniped disappeared from the Chagos Archipelago soon after 1786 and from the Seychelles after 1808. In addition, many populations have become either extinct or endangered in many parts of the world. We have already seen how pollutants are affecting these animals worldwide and in next chapter we will discuss the issue of captivity.

Since the 60's increased public awareness had led to a number of conservation measures worldwide; yet, many of the same factors that have led to reduction of species and populations are still there.

21.2. Encounters with Humans

Stories of friendly interactions between humans and marine mammals abound, although some of them have had tragic consequences for the latter. Here are some examples.

For about 24 years, from 1888 until 1912 a Risso's dolphin called Pelorus Jack, escorted ferry steamers through the narrow French Pass on the northern tip of the South Island, New Zealand. However, Pelorus Jack met an untimely death in April 1912 when a crew of a Norwegian whaling boat anchored offshore harpooned him. He is still fondly remembered to this day.

A bottlenose dolphin known as the 'Dingle dolphin' or Fungie appeared in Dingle harbor, County Kerry, Ireland, in the mid-1980s and has stayed ever since, becoming a great tourist attraction in Ireland.

In November 1988, two sailors were shipwrecked in rough seas of the coast of Indonesia. When their ship sank, a group of dolphins appeared. The animals nudged and guided the men throughout the night, until they finally reached the safety of dry land.

In July 1996, a man jumped into the Red Sea to swim with a group of five bottlenose dolphins. Within minutes he was being attacked by a (tiger?) shark, which lifted him nearly 5 feet out of the water. While one of his friends jumped into an inflatable boat and raced to the rescue, three of the dolphins surrounded the man, slapping their flukes and fins on the surface of the water, preventing a further attack until he could be lifted out of danger.

21.3. Whales and Whaling

21.3.1. Earlier Whalers

Regardless of cultural differences, the ultimate purpose of whaling has been to obtain meat, oil, baleen, and other materials for human consumption. Takings of marine mammals have been practiced for centuries by virtually all coastal cultures. Remains of common dolphins (*D. delphis*), bottlenose dolphins (*T. truncatus*) and the Mediterranean monk seal (*M. monachus*) have been found associated with Neanderthals of the Upper Paleolithic (40,000 – 10,000 YBP) of Gibraltar (Stringer et al. 2008). Midden remains of seals, sea lions, and nearshore cetaceans date back as far as 8500 years. Remains of manatees have been found in many archeological sites of coastal cultures on pre-Columbian America. Cetaceans were abundant in the North Sea and in the English Channel during and before the Middle Ages. Right whales and perhaps gray whales were hunted regularly in this area from at least the ninth century onward; harbor porpoises and other small cetaceans were hunted in this area before the sixteenth century.

The first large-scale, commercial whaling operation began in the twelve century by the Basque fishermen off the Bay of Biscay. It extended to the rest of the North American Atlantic waters in the seventeenth and eighteenth centuries. The Basques used all the parts of animals, even the excrement which was employed as a red fabric dye.

By the beginning of the seventeenth century Britain, Holland and other nations also realized that whaling could be a profitable enterprise and they started to compete for control of major whaling grounds. By the late sixteenth century took coastal gray whales off the Atlantic had already been exterminated.

Box 21.1.

Uses of Whaling Products

Oil: Extracted by heating the blubber to a very high temperature, whale oil was known as the 'liquid gold' of the whaling industry. It has been used to make soap, shampoo, detergent, lipstick, margarine, cooking fats, ice cream, crayons, paints, polishes, linoleum, machine lubricants, and even glycerine for explosives. Homes in Europe and North America were lit by whale-oil candles and lamps. The fat from sperm whale heads was the finest to make high quality candles and lubricants and was even used for medicinal purposes.

Baleen plates: Whip handles, riding crops, shoehorns, umbrella ribs, bristles for brushes, watch springs, store shutters, fans, fishing rods, and even tea trays, for corsets, or to use them to maintain the curls in fancy wigs.

Whale meat: Never in great demand. Ground up to be used as fertilizer or used as animal food. For many years it was thrown back into the sea. Norwegians, Icelanders, Koreans, and a few other nationalities do eat whale meat, but the main commercial market has always been Japan. Today it is sold as a delicacy in Japanese meat markets.

Others: Vikings made use of bones for furniture making. Faröe Islanders use pilot whale skulls to build their farm walls. Whales decorated and carved whale teeth, making buttons, chess pieces, snuffboxes, cufflinks, necklaces, and a variety of other fancy article.

Whale skin: It was used to make bootlaces, or turned into bicycle saddles, handbags, and shoes. The blood became an ingredient in sausages, and was used in fertilizers and adhesives. Even the tendons were turned into strings for tennis rackets and 'catgut' for surgical thread. The liver was a source of vitamin A, while the connective tissue yielded a gelatin for use in sweets and photographic film. In parts of Scandinavia the intestines were used as substitute for window glass.

Ambergris: is a waxy, solidified lump occasionally found floating in the sea or washed ashore. It is formed in the lower intestines of some sperm whales and disgorged when whales vomit. It is primarily made of ambrein, a fatty substance similar to cholesterol that hardens on exposure to air and often contains squid beaks. Whenever whalers found a lump of ambergris in the sea or removed it from a recently killed sperm whale, they whooped and cheered. It was worth its weight in gold. Originally used as medicine to treat indigestion, convulsions and a variety of other ailments, and also as a aphrodisiac, it became later as fixative in perfumes and for making cosmetics.

Since the early 1900's, some huge lumps of ambergris have been found, a few of them looking more like giant rocks or boulders than something that could have come out of a sperm whale. A British whaler found the largest ever recorded piece. It weighted 1,400 pounds (635 kg) and was found near New Zealand.

Today there is no need for any of these products since petroleum and plastics are better, cheaper substitutes of all of them.

21.3.2. 'Yankee' Whalers

The American whaling industry began soon after 1640's when the earliest colonist ventured from the green shores of New England to hunt right whales. The right whales were the 'right' whale to hunt because they were easy to approach, swam slowly, live close to shore, had a tendency to float when dead, and provided large quantities of oil, meat, and baleen.

It was a profitable but also risky business. Many ships never returned, some of them even after their maiden voyage. It was very harsh on officers and crews with many hands jumping ship. 'One voyage in a whale ship is one too many' was a common say. Typical crew consisted of 30-35 seamen: The captain, 4 harpooners, 4 mates, a cooper, a steward, a blacksmith, a cook, a cabin boy, and 15-20 ordinary seamen. The latter lived in cramped, dark, filthy conditions near the bow.

Food was horrible. They did not like whale meat. Their basic diet was salted pork or beef, with thick, hard crackers, and coffee or tea. The crew commonly floated the crackers in a hot drink, until the maggots crawled out and could be skimmed off.

Many voyages lasted for 4 to 5 years. Communications were almost non-existent despite a system of 'post offices.' In the Pacific, for example, ships would leave letters in the Galapagos Islands to be picked up by another ship in its way home. The letters were placed in wooden boxes covered by tortoise shell, ready to be picked up by other ships heading home. The rate of letters actually received was about 6%.

The combination of this bad reputation and the expansion of the whaling industry after 1815, New England seaports were soon finding it hard to recruit competent crews; that was particularly true after 1800's when the industry had to compete with the lure of gold and free land in the West.

Unscrupulous 'ship agents' were often hired to assemble ordinary seamen by rounding them up from the eastern seaboard and the Midwest, tempting them with false promises of money and adventure. Worse still, it was not an uncommon event for men to wake up after a night on the town with a massive hangover in a rock-hard bunk on their way to whaling grounds hundreds or thousands of miles from home.

Everybody received a percentage of the net value of the cargo: the ship owner's: 66%; the captain up to 10%, the mates, harpooners, and coopers up to 1% each; the ordinary seamen about 0.6%; the cabin boys no more than 0.4%. A variety of 'expenses' were deduced from these meager wages. Furthermore, whaling crews were considered the worse of any seamen on shore.

From the early nineteenth century on, 'Yankee' whales from New England were extending their reach into the Pacific and Indian Oceans, in a widening search for sperm, right, bowhead, and gray whales that swam slowly and could be killed with hand harpoons and lances. By the end of the Nineteenth century, right whales in both hemispheres as well as bowhead and gray whales, had been severely depleted. The northern right whale remains the most endangered of the great whales, numbering fewer than 300 animals, despite almost complete protection for over a hundred years. For reasons not well understood, the southern right whales are showing true sings of recovery.

21.3.3. Industrialization of Whaling

The era of modern whaling started in the 1860's with the invention of the cannon-fired, explosive-head harpoon. In combination with the development of fast steam-power catcher boats, whalers for the first time could take large numbers of the faster swimming rorqual whales (initially blue and fin whales). Whalers with hand harpoons previously had ignored these whales, for they were too fast to be overtaken in sail- or oar powered boats.

At first, whaling for rorquals was conducted from land stations and the number that could be exploited was limited. The first Antarctic whaling station was established in 1904 on South Georgia and 195 whales were taken. By 1913, there were six land stations and 21 floating factories and the total catch was 10,760 whales.

The invention of the stern slipway in 1925 allowed pelagic factory ships to haul harpooned whales aboard for processing at sea rather depending on shore stations, and

the kill of large rorquals rose dramatically. From 176 blue whales caught in 1910, the annual take climbed to over 37,000 whales (of which more than 28,000 were blue) in 1931, when 41 factory ships were working in Antarctic waters. After the peak year of 1931, blue whales became increasingly scarce. Blue whale catches declined steadily until the catch was commercially insignificant by the mid -50's. In 1966, only 70 blue whales were killed in the entire world's oceans. Only then, when substantial numbers could no longer turn a profit, was the hunting of blue whales banned in the southern hemisphere.

Whaling operations effectively ceased during World War II. The war caused a world shortage in the supply of whale oil, and the end of World War II encouraged several nations to renew their pelagic whaling activities. It was in this immediate postwar setting that discussions were held in London in 1945 and in Washington in 1946 on the international regulation of whaling. Meanwhile, without large populations of blue whales to exploit, pelagic whalers switched to the smaller, more numerous fin whales, catches which skyrocketed to more than 25,000 whales per year for most of the 1950's. By 1960, the fin whale catch also began to plummet and whaling pressure was diverted to even smaller sei whales. Between 1963 and 1964, 29,255 sperm whales were killed. The total southern hemisphere sei whale population probably never exceeded 60,000; one-third of that population was killed in 1965 alone. By the late 1960's, sei whales had followed the larger relatives to commercial extinction, and the whaling effort shifted toward the even smaller minke whales. Minke whales remained the principal target species of pelagic whalers until pelagic harvesting of baleen whales ceased completely during a moratorium initiated in 1986.

The ultimate death toll on large whales has been immense: 1 million sperm whales, 350,000+ blue whales, 250,000+ humpback whales have been killed and 2 million of all species of whales have been killed in the Southern Ocean alone. Today no more than 5-10% populations of whales remain.

There are only 300 northern right whales left, and that after more than 60 years of protection. The gray whale has bounced back in the Pacific but early whalers wiped out the one in the North Atlantic. Humpbacks and southern right whales are making a comeback as well.

Box 21.2.

Chronology of Technological Changes in Whaling

1852: The first successful explosive harpoon was invented by an armorer from Connecticut, U.S., Known as the bomb-lance, it consisted of an explosive missile armed with a time delay fuse that killed or mortally wounded the whales, normally at a safe distance of the whalers.

1857: The first auxiliary steam engines were installed in British whaling ships and, in the years that followed, many other whalers installed similar engines in their vessels.

1859: The first purpose-built steam whaling ships were successfully launched. The extrapower gave them increased speed and safety, although once on the whaling grounds the whalers continued to hunt from traditional rowing boats.

1863: Norwegian sea captain Svend Foyn (1809-1894), built a new, 82-foot (25 m) steam-driven schooner called the Spes et Fides ('Hope and Faith'). The first of the modern whale catchers, this combined the functions of the open rowing boat and the ship in a single vessel. It was relatively easy to maneuver and yet fast enough to chase the whales by itself. Now, no species of whale, no matter how fast a swimmer, was safe.

1865: A whaling captain from New Bedford, in the United States, invented the darting gun, a kind of explosive harpoon with the accuracy of a conventional harpoon.

1868: After several seasons of experimentation, Sven Foyn developed an explosive harpoon that could be fired from a cannon mounted on a swivel in the bow of a whaling vessel. The cannon was solidly made to absorb the recoil and so well balanced that it could be aimed with great accuracy. Screwed to the tip of the harpoon was a grenade consisting of a detonator and a sack of black gunpowder in a steel container equipped with barbs. The barbs were designed to open on impact, ensuring that the harpoon was firmly embedded in the animal's flesh, and the grenade exploded inside its body two or three seconds later. The awful weapon precipitated an enormous increase in whaling worldwide and is still in use today, albeit in modified form.

1925: The growth of the whaling industry was limited by a need to return constantly to shore-based stations to process the whales. The final dramatic development: floating factory ships solved this problem. The new ships were designed to accompany fleets of catcher-boats far out to sea and, with stern slipways to winch the whales on board, gave a new level of efficiency to then hunt. It was 1925 that the first factory ship arrived on the Antarctic whaling grounds.

21.3.4. The International Whaling Commission

In 1946 the International Convention for the Regulation o Whaling was signed, and in 1948 ratified, establishing the **International Whaling Commission** (IWC). The aimed was 'to provide for the proper conservation of whale stocks and thus make possible the orderly development of the whaling industry.' It was formed, essentially, as an association of whaling countries in order to self-regulate their takings, particularly in the Antarctic, to make recommendations on quotas and minimum sizes, and to ban the taking of females with calves. It established an advisory Scientific Committee nominated by government members. Despite all this it lacks inspection and enforcement powers and any member can object any decision and exclude itself from the limitation of that decision. Each nation member can unilaterally issue permits to catch whales for 'scientific' purposes. As most international organizations is very weak. In fact, the IWC was responsible for the killing of more than 2 million whales during its first 30 years of existence. Now most of its nation members are pro conservation but the small but vocal group of whaling nations is very active and engaged in behind-the-scenes politicking, bribery, and threats.

Early IWC management procedures were based on the use of the **Blue Whale Unit** (**BWU**) as a means of setting catch quotas. In terms of oil yield, it was considered

that one blue whale was equal to 2 fin, 2.5 humpback, or 6 sei whales (based on their relative oil yields), with no distinction given to the actual species being harvested. In 196201963, a call from the Scientific Committee for quotas by species was rejected but the total quota was reduced to 10,000 BWUs and humpback whales were protected throughout the southern hemisphere. In 1964-1965, blue and humpback whales were given complete protection and Norway, the Netherlands, and the UK ceased their Antarctic whaling operations, leaving only Japan and the Soviet Union actively engaged in the pelagic harvesting of baleen and sperm whales.

Reductions in target population sizes, new national and international regulations, and changing market demands, as well as changing attitudes concerning the ethics of killing large whales for profit, all have contributed to the demise of large-scale pelagic whaling. A new IWC management procedure was instituted in 1974, based on the recognition that management procedures should apply to geographically localized stocks rather than to species. This new procedure also recognized a protection stock category on which no harvesting is allowed. In 1979, a proposal to end pelagic whaling for all species except the minke whale was adopted and a sanctuary was declared for the Indian Ocean outside the Antarctic.

In 1982, the IWC agreed to a deferred pause ('moratorium') in all commercial whaling beginning in 1986, with a responsibility for conducting a comprehensive assessment of large whales stocks by 1990. Norway objected to the moratorium and resumed commercial exploitation of minke whales in the North Atlantic in 1994, even thought he moratorium had not been lifted. Japan and Norway have authorized the killing of whales for 'scientific' purposes even though the IWC has questioned the value of such research. In 1994, the IWC accepted a revised procedure for estimating the number of whales that could be taken without causing the affected population to be reduced below its maximum net productivity. This **revised management procedure** (**RMP**) has been evaluated using computer simulations, but if commercial whaling is resumed it is clear that independent monitoring of the affected population will be required to verify that RMO is working.

Since the 1982 moratorium on whale killing, about 60,000 whales have been killed including minke, fin, sei, Bryde's, humpback, gray, sperm, and bowheads. The moratorium came into effect in the 1985-86 season. Since then Japan, Norway, Iceland, Russia, Korea, and the U.S. have been involved in whaling and taking whales in numbers beyond their quotas or simply providing false data about it. Whalers are very strong and have instigated many Caribbean nations to join the IWC to favor their pro-whaling positions. Many of these countries have received important fishing subsidies of Japan.

In 1994, members of the IWC approved the Southern Ocean Whale Sanctuary of about 50 million sq kilometers around Antarctica. Japan has ignored this. Japan and Norway continue to expand their whaling activities. Japan calls its whaling 'scientific' using a loophole in the IWC rules for scientific purposes. The whale carcasses are processed for meat production and that meat is sold in supermarkets. Since the moratorium Japan has killed 6,083 minke, 634 Bryde's, and 400 sperm. After the fall of the Berlin wall, it was discovered that Russia had falsified its whaling records for more than 30 years. In April 1996, 6.5 tons of Norwegian whale meat was confiscated by Japanese costume officials. It was disguised as a mackerel shipment. It was the first installment of a 66-ton shipment of whale meat due to be smuggled into the country.

In 1996 several nations announced their opposition to whaling under any circumstances. Fearing that this would split the IWC in two, in 1997 Ireland proposed limited commercial whaling in coastal waters, on the understanding that the meat could not be traded internationally and that all other whale hunts should stop.

There is also pirate whaling. Ships from eleven countries have been involved. One of those ships was the Sierra. It was impounded by South African authorities and sunk by saboteurs in 1980. A Norwegian businessman and a large Japanese fishing company jointly owned it. It was registered in Liechtenstein, flew a Somali flag, and had a South African crew. The captain was a Norwegian and had Japanese meat inspectors on board. It labels its illegal catch as 'product of Spain' and sold it through Ivory Coast to Japan.

In 1997 sailors on a transatlantic yacht approaching the Azores from the west reported dead and dying whales afloat on the surface or tied to buoys. At least one factory vessel and its catcher boat are believed to have been involved.

Table 21.1. Commercial and 'Scientific' Whale Catches under the IWC

Country	Region	Species	1994	1995	1996	1997	1998	1999	2000	2001	2002
Norway	NE Atlantic	Minke	279	217	388	289	289	650			
Japan	N. Pacific	Minke	21	100	77	100	100	100	40	100	150
Japan	Antarctica	Minke	330	440	440	438	389	439	440	440	440
TOTAL			630	757	905	827	778	1189	480	540	590

Recent Total Whale Catches by Country

	Norway Commercial	**Iceland** Commercial & scientific	**Japan** Scientific	**Russian Federation** Subsistence	**U.S.** Subsistence	**Denmark** (Greenland) Subsistence
2001	552	--	598	113	75	158
2002	634	--	684	134	50	164
2003	647	37	704	131	41	209
2004	544	25	755	112	43	204
2005	639	39	1243	126	68	193
2006*	546	37	1320	140	39	197
Total*	**3562**	**138**	**5304**	**756**	**316**	**1125**

*2006 data incomplete

‘Aboriginal’ whaling:

The IWC allows for ‘aboriginal,’ ‘subsistence,’ or ‘traditional’ whaling and establishes catch limits for this type of whaling. The problem is the exact meaning of those words.

In 1997, the IWC agreed to 1998-2002 catch limit for several whale stocks subject to aboriginal subsistence: 280 from the Bering-Chukchi-Beaufort Sea stock of bowhead whales (taken by Alaskan Inuit and native peoples of Chukotka), a total of 620 northeastern Pacific gray whales (including the take of up to 5 whales by the Makah Indian tribe of northwestern Washington State), and a total of 175 West Greenland minke whales (taken by Greenlanders). Additionally, annual catches of up to 19 West Greenland fin whales and 12 East Greenland minke whales (taken by Greenlanders) and two humpback whales (taken by natives of St. Vincent and the Grenadines) were authorized.

In the town of Point Barrow, on the northern tip of Alaska, the local Inupiat and Yup’ik people have hunted bowhead whales in the region for more than 2,000 years and, even today, they are allowed an annual quota of more than 60 whales. The bowhead is an endangered species. These whalers use motorized boats and rely on spotter planes to find the whales. They use heavy iron harpoons, including some that explode on impact, to do the killing. Then, since the modern local people do not rely on whale meat themselves, they generate a profit from their kills by selling carved baleen or whalebone to visiting tourists.

In 1996 the Makah tribe, from an isolated corner of America’s Pacific Northwest on Washington’s State’s Olympic Peninsula, persuaded the United States Government to apply for a quota that would allow them to kill 5 gray whales. The U.S. delegation brought a group o Makah to the 48th meeting of the IWC who claimed a ‘whaling tradition’ and argued that the resumption of waling could alleviate social problems by strengthening the tribe’s culture. Meanwhile, conservationists flew in another group of Makah who expressed their opposition to then hunt of the grounds that they had not been whaling since 1926; one elder told the meeting that a gray whale had been netted accidentally the previous year: ‘Nobody in the village knew how to cut it,’ she said. Conservation groups were concerned that a quota would blur the line between indigenous and commercial hunting, and would open the floodgates to any coastal community that could provide evidence of whaling in historical times. Eventually, the United States withdrew its application and in 1997, resubmitted a joint proposal with the people of Chukotka, Russia. Thus, whaling continues to be practiced with the support of the Clinton-Gore administration.

Table 21.2. Aboriginal Whaling Catches

Active Whalers	Species	1995	1996	1997	1998	1999	2000	2001	2002
Russian Federation	Gray Whales	90	43	43	126	124	116	113	134
West Greenland	Minke whales	153	164	148	166	170	145	139	139
	Fin whales	12	19	13	11	9	7	8	13
East Greenland	Minke whales	9	12	14	10	15	10	17	10
St. Vincent	Humpback whales	0	1	0	2	2	2	2	2
U.S.	Bowhead whales	57	44	66	54	47	47	75	50
Canada	Bowhead whales	0	1	0	1	0	1	0	1

Whaling outside IWC

There is a long history of whalers that have acted outside the IWC. The most infamous pirate whaling vessel was the 'Sierra', which killed thousands of protected whales before it was sunk in 1980 by protesters. The ship was reportedly jointly owned by Norwegian investors and the 'Taiyo Fishery Company' of Japan. The ship's crew was stated to have consisted of a Norwegian captain and first mate, four Japanese and several South Africans.

Protectionists accuse Taiyo of setting up fake 'front' operations in Taiwan during the 1970s to help move and process the whale meat. The 'Ming Tai Frozen Seafood Corporation' of Taiwan operated Taiyo-supplied whaling vessels, which were purchased through a third party. Most of the whales killed by Ming Tai were reportedly exported to South Korea where the meat was repackaged and sent on to Japan. This was important because, as an IWC member, South Korea could legally export to Japan while Taiwan is not an IWC member, and so cannot do so (Anon 1994).

Exposures of this type of illegal commercial whaling helped lead to the decision to impose a global ban on whaling in 1982. However, the IWC lacked any real teeth to tackle the problem of pirate whaling, which many believed was still likely to take place, despite the ban.

In 1993, investigators from the Hawaii-based Earthtrust organization carried out genetic (mitochondrial DNA) analyses of whale meat samples taken from several retail outlets in Japan, (Baker et al, 1994). The specimens analyzed produced some surprising results. In addition to finding the expected South Atlantic minke whale, the tests showed

that several other species of whales protected under the IWC were freely on sale in Japan. Four of the samples were from fin whales, one a northern hemisphere minke whale and another was from a humpback whale. Dolphin meat was also discovered being sold as whale meat. Less than a week after the Japanese Government learned of the DNA results, police arrested Japanese members of a criminal syndicate who had been operating a whale meat smuggling operation (Anon 1994).

The litany of illegal trading is enormous. In May 1993, for example, a Korean boat was seized after it tried to unload 11 tons of whale meat in Nagasaki, Japan (IWC 1995). Recently, it was discovered that a South Korean vessel, the 'Shell', had ferried 232 tons of Bryde's whale meat to Russia in 1993, where it was prepared for export to Japan. But the real scale of the trade only became apparent when the Russian Federation revealed in 1994 (IWC, 1994) that four Soviet factory ships operating between 1948 and 1980 had killed some 80,000 more whales than were ever reported to the Bureau of International Whaling Statistics. This illegal slaughter included over 48,000 humpback whales, against a reported catch of only 8,000.

Some suspect that the meat from these whales was being sent to the burgeoning Japanese market. At no time did Japanese report these illegal imports and, whilst pressing for a lifting of the moratorium had, until 1995, never officially admitted to any of these events.

Scientific whaling and whaling under Objection, (as practiced by Norway), both flout the original IWC mandate for a complete moratorium on all commercial whaling, and also allow for pirate whaling to continue. Norway's continued increase in its self-allocated quota allows for increased pressure to illegally export whale meat and products to Japan and other potential markets.

21.3.5. The Use of Small Cetaceans

The IWC has generally ignored the situation of small cetaceans (dolphins and porpoises) unless they are taken by whaling ships, such as is the case for killer whales or bottlenose whales.

In addition to intentional killings of dolphins and other small cetaceans, millions of these animals have been killed in recent years by the tuna industry in the Eastern Tropical Pacific Ocean where, for reason still unknown, dolphins and yellowfin tuna tend to be found together. Gill (drifting) nets continue to be a major source of dolphin mortality around the world

Other harvests of cetaceans, such as the Faröe Island drive fisheries of pilot whales and Japanese harvests of other small coastal odontocetes continue to this day. Dolphins are also killed in many other countries such as Venezuela using the meat as shark bait.

Belugas and Narwhals have been hunted in Arctic regions of Canada, the U.S., Greenland, and Russia for centuries. Their oil is used for lighting and cooking, their blubber and skin as a delicacy, known as *muktuk*; and their meat for human consumption and as a food for sled dogs. The long tusks of male narwhals were originally used for tent poles, sled runners, and lance shafts (instead of wood), and were marketed as the horns of the legendary unicorn. More recently, until the introduction of trade bans, they have been sold as curios to tourists.

Mainly Inuits of the Canadian Arctic and West Greenland take about 1,000 narwhals every year (many more are hit, and sink before they can be retrieved). The Alaskan Inuit take perhaps 200 belugas each year, apparently with no negative impact on the population. The Inuit of the Canadian Arctic, West Greenland, and Arctic Russia take more than 2,000 belugas each year.

Fishers in at least 60 ports of the coasts of Peru have been killing up to 20,000 dolphins and porpoises were being killed, until recently, every yea. Dusky dolphins and Burmeinster's porpoises were the hardest hit, but a number of other species also suffered severe losses. Sales of meat for human consumption were a lucrative business and, as fishers became increasingly greedy, more and more animals were being killed. After a long campaign by national and international conservation groups, the Peruvian government finally banned dolphin hunting in 1990. But no real enforcement took place until 1996.

Japanese fishers actively hunt no fewer than 16 of the 21 species of small cetaceans in their coastal waters. Small coastal vessels equipped with canons that fire explosive harpoons are used to kill about 50 Baird's beaked whales every year. Hand-held harpoons are thrown from small boats to catch Pacific white-sided dolphins and Dall's porpoises. And drive-fisheries (where fishers herd cetaceans into the shallows and kill them from shore) target striped, Risso's, bottlenose, and spotted dolphins; short-finned pilot and false killer whales; and a number of other species. In most cases, the meat is sold throughout Japan, often fraudulently as whale meat.

Long-finned pilot whales have been hunted around the Faröe Islands (a group of Danish islands in the northeast Atlantic), for several hundred years. Men in small boats herd entire pods of the 4-6 m whales into sandy bays during noisy drives that frequently take many hours. All the animals, including pregnant and lactating mother with calves, are dragged ashore with steel gaffs, which are stabbed into their heads. They are killed with long knives and the meat is distributed free to local people (although some is also sold in supermarkets and occasionally appears on restaurant menus.

Faröe hunting statistics date from 1584, with unbroken records from 1709 to now. During this most recent 287-year period, more than 250,000 long-finned pilot whales have been killed in about 1,700 different drives. The official number taken each year ranges from zero to a peak of 4,325 recorded in 1941. The average during the last few years has been 1,200 whales per year. The Faröese defend their hunt vigorously, arguing that it is a long-standing tradition and provides a free and welcome source of protein. But in truth, it is no longer necessary in such a modern society with a relatively high standard of living.

Thousands of dolphins and whales are also killed because they are considered a nuisance by many fishers. There are even organized 'culls' to wipe out as many cetaceans as possible, all that with the support of many governments.

The largest hunt designed to reduce the level of competition with fisheries has been taking place in the Black Sea since 1870. During the worst period, from 1931-1941, more than 50,000 dolphins and porpoises were being killed every year.

In the 1920's and 1930's, the Quebec government literally bombed belugas from the air; in 1956, the Icelandic government arranged for a United States naval vessel to use machine guns, rockets, and depth charges against killer whales; and in the mid-1980's, Alaskan fishers used explosives and firearms to wipe out local killer whales.

Table 21.3.

Major International Agreements Regulating the Takes of Marine Mammals

1911: International Convention on Pribilof fur seals
1931: The convention for the Regulation of Whaling
1931: The bowhead
1935: League of Nations Convention for the Regulation of Whaling
1935: Northern and Southern Right Whales
1940: Convention on Nature Protection and Wild Life Preservation in the Western Hemisphere
1946: International Convention for the Regulation of Whaling (gave rise to the IWC).
1946: Gray Whale
1966: Humpback whale, blue whale
1979: Sei whale (except in the Denmark Strait west to Iceland)
1984: Sperm whale
1986: IWC Moratorium takes place

Whaling is cruel: In 1993 a minke whale took 55 minutes to die a slow, lingering death at the hands of Norwegian whalers. It is hard to imagine the pain and suffering it experienced after an explosive harpoon had blown a huge, gaping hole in the side of its body.

Japanese whalers use electric lances to kill harpooned whales, but electric charges are grossly insufficient to induce death and, instead, causes violent muscle contractions and probably even more stress and suffering. As one ex-whaler commented: 'if whales could scream, whaling would have stopped many years ago.'

Impact of Fisheries

Cetaceans too often become trapped in fishing nets. **Entanglement associated with coastal fisheries** is a serious threat to the harbor porpoise throughout much of its range and has driven the vaquita to critically low numbers. It is also a significant cause of injury and death to humpback whales, mainly around Newfoundland. Occasional entanglements combined with ship collisions may be impeding the recovery of the northern right whale.

Pelagic fisheries, particularly in the North Pacific, are harmful to offshore species. Large numbers of spotted and spinner dolphins, and Pacific white-sided and northern right whale dolphins, among others, are taken in purse seines and drift nets. The situation in the Eastern Tropical Pacific has steadily improved over the past two decades with the introduction of new fishing techniques for tuna. Restriction of North Pacific high seas drift-net fisheries since 1987, combined with the planned global moratorium beginning in 1993, will further reduce the needless killing of pelagic marine mammals.

a) Drift netting: A single drift net can be up to 48 km in length. Normally released at dusk, it is allowed to drift with the ocean currents and winds before being retrieved the

following day, or several days later. It is virtually undetectable as it hangs in the water, and catches literally everything in its path. There are thousands of kilometers of these 'walls of death' floating around the world's seas and oceans at anyone time, more than enough to circle the Earth at the equator. In 1992 the United Nations passed a resolution banning nets larger than 2.5 km, but many fishers, particularly Japanese, continue to use large drift nets.

B) Tuna fishing: Since 1959 this industry started using purse-seine nets to catch yellowfin tuna in the Eastern Tropical Pacific. Since dolphins are commonly associated with school of this fish in that part of the world, fishers encircle dolphins in the belief - not always right- that there would be tuna underneath them. As a consequence of this, many dolphins die trapped on the net; many pregnant mothers miscarried. The final toll: between 6 and 12 million spotted dolphins died. Although the mortality rate has been reduced, the slaughter continues.

Table 21.4. The most endangered Species of Cetaceans

Species	Distribution	Population	Notes
Baiji	Yangtze River, China	<100	May become the first cetacean to extinct in recent history.
Vaquita	Extreme northern end of the Sea of Cortez	<200	Highly restricted distribution
Northern Right Whale	Western North Atlantic	<320	It has never recovered after more than 60 years of protection
Bhulan	Indus River, Pakistan	<500	Since the 1930s barrages have split the dwindling population into isolated pockets
Hector's dolphin	Coastal waters of New Zealand	<4,000	The world's rarest marine dolphin. Threatened mainly by incidental catches
Susu	Ganges, Meghna, Brahmaputra, and Kamaphuli river systems of India, Bangladesh, Bhutan, Nepal	<4,000	The population is split into two by the Farakka Barrage

21.4. Sealing and Ottering

Pinniped rookery or haul-out sites have been especially vulnerable to hunters foraging for food, clothing, and housing materials.

Midden remains of seals, sea lions, and nearshore cetaceans date back as far as 8500 years. Almost all species of pinnipeds have been hunted for oil, meat, fur and other products. One species, the Caribbean monk seal, have already become extinct. The number of fur seals taken until relatively recently has been dramatic. Some species have recovered; others have not.

Sea otters, all species of fur seals, hooded seals, both species of elephant seals, and walruses were heavily harvested for skins and oil beginning in the early nineteenth century, but these hunters left few records of the number of animals taken. By the late nineteenth century, California sea otters and northern elephant seals were thought be to be extinct. Other species, including southern hemisphere fur seals, were depleted but have recovered to pre-exploitation numbers. Baltic Sea harbor seal numbers also have increased exponentially after protection was introduced for them in the 1960's and 1970's, and as of 1986 exceeded 5000 individuals.

Pinnipeds continue to be exploited for commercial purposes. The Namibian government continues to award quotas to harvest Cape fur seals, primarily as a fisheries protection measure. As recently as 1995, the Canadian government authorized personal use hunting of harp, hooded, and gray seals along its Atlantic coast. A subsidy for landed seal meat was established to encourage the expansion of this harvest. For harp seals, the total commercial quota was raised from 186,000 to 250,000 and was justified by the dubious assumption that harp seals are a significant factor impeding the recovery of cod stocks in the western North Atlantic.

Before 1900, several agreements were made to govern the taking of seals and fur seals, mostly regarding land-based operations in the Antarctic. In 1911, the International Convention on Probilof fur seals banned the pelagic harvesting of fur seals, although harvesting of young bachelor males continued on land for much of this century. After the Convention lapsed in 1984, commercial harvesting of northern fur seals effectively ceased.

The U.S. Marine Mammal Protection Act also authorizes northern fur seals to be harvested for subsistence purposes by Aleut residents on the Pribilof Islands. Harbor seals, Steller sea lions, and the Pacific walrus also continue to be harvested by Alaska natives for subsistence.

Sea otters in Alaska are occasionally shot as quarry by native hunters or, as in California, for intruding on fisheries activities. Some, especially inexperienced juveniles, are hit by boats or become entangled in fishing nets and marine debris.

Oil spills are a particularly serious threat to sea otters. The 1989 Exxon Valdez spill in Prince William Sound claimed more than 1,000 animals. Fresh, volatile oil kills by damaging the respiratory, digestive and urinary systems. Though less acutely harmful, oil that remains at the surface presents an enduring hazard. Fouling robs the fur of natural oils that normally hold the loft that provides insulation.

Metabolic rate increases to counter the elevated heat loss. The victim becomes so intent on restoring the pelt that it forgoes feeding and resting, spending its time grooming

instead. Sapped of energy, with no stores to draw from, the otter eventually dies of stress and shock.

Literature Cited

C. B. Stringer, C.B.; J. C. Finlayson, R. N. E. Barton, Y. Fernández-Jalvo, I. Cáceres, R. C. Sabin, E. J. Rhodes, A. P. Currant, J. Rodríguez-Vidal, F. Giles-Pacheco & J. A. Riquelme-Cantal. 2008. Neanderthal exploitation of marine mammals in Gibraltar. *Proceedings of the National Academy of Sciences* (USA) **105**:14319-14324.