of direct handouts of fish offered by people, and many species of odonotocetes remove either bait or fish from fishing lines. In the Bering Sea and off Southern Brazil, killer whales may damage over 20% of the fish captured by longline fisheries. However, a number of dolphin species from coastal (e.g., *Tursiops truncatus*, *Sousa teuzii*) and riverine (e.g., *Orcaella brevirostris*, *Inia geoffrensis*, *P. gangetica*) habitats also enhance coastal fisheries where both dolphins and fishermen take advantage of dolphin foraging.

Both the diversity of habitats in which marine mammals live and the flexibility of individuals have led to the wide variety of foraging tactics exhibited by the group. Further studies of these tactics are still of great interest, especially systematic investigations of the function and use of particular tactics and the circumstances in which they are employed. Such detailed studies will improve the ability to predict influences of anthropogenic changes to marine habitats and prey availability on marine mammals, and aid in efforts to conserve them.

See Also the Following Articles

Behavior, Overview ■ Feeding Morphology ■ Filter Feeding ■ Tool Use

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FILTER FEEDING

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I. Filter Feeding and the Marine Environment

A critical necessity for organisms is acquiring sufficient food for maintenance, growth, and reproduction. This search for food likely drove the return of mammals to the ocean where they were able to exploit highly productive coastal waters. With their return to the sea, marine mammals evolved a wide range of physiological and morphological adaptations for feeding in water. Filter feeding is exhibited by baleen whales (Mysticeti) and three species of pinnipeds (crabeater seals, *Lobodon carcinophaga*; leopard seals, *Hydrurga leptonyx*; and Antarctic fur seals, *Arctocephalus gazella*). Although filter feeding is not found in terrestrial mammals, it has evolved independently in multiple lineages of aquatic invertebrates and vertebrates.

In marine mammals, filter feeding facilitates the exploitation of extremely abundant, but small schooling fish and crustaceans (e.g., krill or copepods) by capturing many individual prey items in a single feeding event. This is useful in marine systems because they have low standing biomass and high turnover of small-sized primary producers that respond rapidly to nutrient availability, and because marine ecosystems tend to be more patchy and ephemeral than terrestrial systems due to spatial differences in physical dynamics. Thus, the abundance and distribution of schooling fish and crustaceans reflects the spatial dynamics of marine primary production. Most marine mammals are primary carnivores and rely on these dense, patchily distributed aggregations of schooling prey. The patchiness of prey means that filter feeding marine mammals must often travel long distances to locate prey, and annual migrations to seasonal feeding grounds is a hallmark of baleen whale life history. Long distance migration across ocean basins is facilitated by the large body sizes of marine mammals, especially mysticetes, that provides low mass-specific metabolic rates and low cost of transport (Croll et al., 2005). Thus, large body size buffers for the patchy and ephemeral distribution of marine prey because larger individuals can survive longer periods and travel longer distances between feeding events. However, a consequence of larger body size is a higher absolute daily prey requirement.

Filter feeding allows individuals to capture and process large quantities of prey in a single mouth full, thus allowing them to acquire energy at high rates when small prey are at high densities (Goldbogen et al., 2011). Large body size in mysticetes is associated with a relatively larger mouth enhancing intake capacity for filter feeding (Goldbogen et al., 2010). The combination of large body size and filter feeding allows some marine mammals to exploit extremely high densities of schooling prey that develop at high latitudes during the spring and summer and in other areas of high productivity. If resources are not available in the winter, large body size provides an energy store for fasting in place or for long distance migration without feeding (Brodie, 1975).

Due to this dependency on patchy but extremely productive food resources, it is hypothesized that filter feeding whales first evolved and radiated in the Southern Hemisphere during the Oligocene at the initiation of the Antarctic circumpolar current (ACC). It is generally agreed that the initiation of the ACC led to cooling of the Southern Oceans, increased nutrient availability, and thus increased productivity. Although this increased productivity may have provided a rich resource of zooplankton that could be effectively exploited through filter feeding, the discovery of a late Oligocene fossil archaic mysticete that was a nonfilter feeding predator casts doubt on the suggestion that the initial radiation of mysticetes was linked to the filter feeding (Fitzgerald, 2006).

Present-day filter-feeding marine mammals concentrate foraging in productive high-latitude and coastal upwelling regions, with the Southern Ocean recognized as one of the most important foraging area for filter-feeding marine mammals. Indeed, prior to their

exploitation by humans, some of the greatest densities of mysticetes occurred in highly productive waters of the Southern Ocean. Crabeater seals, Antarctic fur seals, and leopard seals are also found primarily in the Southern Oceans where seasonally dense aggregations of krill develop (Berta and Sumich, 1999).

II. Diet, Filter-Feeding Structures, and Prey Capture

All filter-feeding species feed on prey that form dense aggregations (primarily pelagic schooling fish and crustaceans or densely aggregated benthic amphipods). Two feeding adaptations have evolved to allow the exploitation of these dense aggregations: baleen (mysticete whales) and modified dentition (seals).

A. Seals—Diet, Feeding Morphology, and Behavior

Unlike mysticetes, pinnipeds evolved in the Northern Hemisphere where krill was not likely an important component of their diet, and adaptations for filter feeding are not as extensive in pinnipeds as in mysticetes.

Only three pinnipeds are thought to filter feed on small zooplankton: crabeater seals, leopard seals, and Antarctic fur seals (Riedman, 1990; Hocking et al., 2013). When presumably filter feeding, all the three species feed almost exclusively on Antarctic krill, *Euphausia superba*, in the Southern Ocean where it is large, abundant, and forms extremely dense aggregations. Of the three species, crabeater seals are most highly specialized with krill comprising up to 94% of their diet, while krill comprises approximately 33% of the diet of leopard seals and Antarctic fur seals. The most remarkable adaptation for filter feeding in pinnipeds is found in

the dentition of crabeater and leopard seals. In both species elaborate cusps have developed on the postcanines in both the upper and lower jaws (Fig. 1) (Berta and Sumich, 1999). Using suction as a potential engulfment mechanism (Hocking et al., 2013), the mouth closes around a small group of prey (i.e., krill), water is filtered out through the cusps, trapping krill in the modified teeth. Little detailed information is available on the behavior used by filter-feeding pinnipeds to capture prey. However, data from Antarctic fur seals and crabeater seals indicate that they track the diel migration of krill: shallow dives during night and deeper dives during day (Boyd and Croxall, 1992).

B. Mysticetes—Diet and Feeding Morphology

Most mysticetes feed primarily on planktonic or micronectonic crustaceans (copepods and krill) and pelagic schooling fish. Gray whales, *Eschrichtius robustus*, however, feed primarily on benthic gammarid amphipods. Right, *Eubalaena* spp., and bowhead, *Balaena mysticetus*, whales primarily feed on copepod crustaceans of the genus *Calanus*. All rorquals feed on euphausiids (krill) to some extent, and blue whales, *Balaenoptera musculus*, feed almost exclusively upon euphausiids (see section on krill). The other rorquals have a more varied diet that includes copepods (sei whales, *B. borealis*), and schooling fish (minke, *B. acutorostrata*, Bryde's; *B. edeni*, humpback; *Megaptera novaeangliae*; and fin whales, *B. physalus*) (Nemoto, 1970; Berta and Sumich, 1999). Little is known about the diet or feeding behavior of pygmy right whales (*Caperea marginata*).

All present-day mysticetes lack teeth and instead have rows of baleen plates made of keratin that project ventrally from the outer edges of the palate (Werth, 2000). Similar to fingernails, the plates
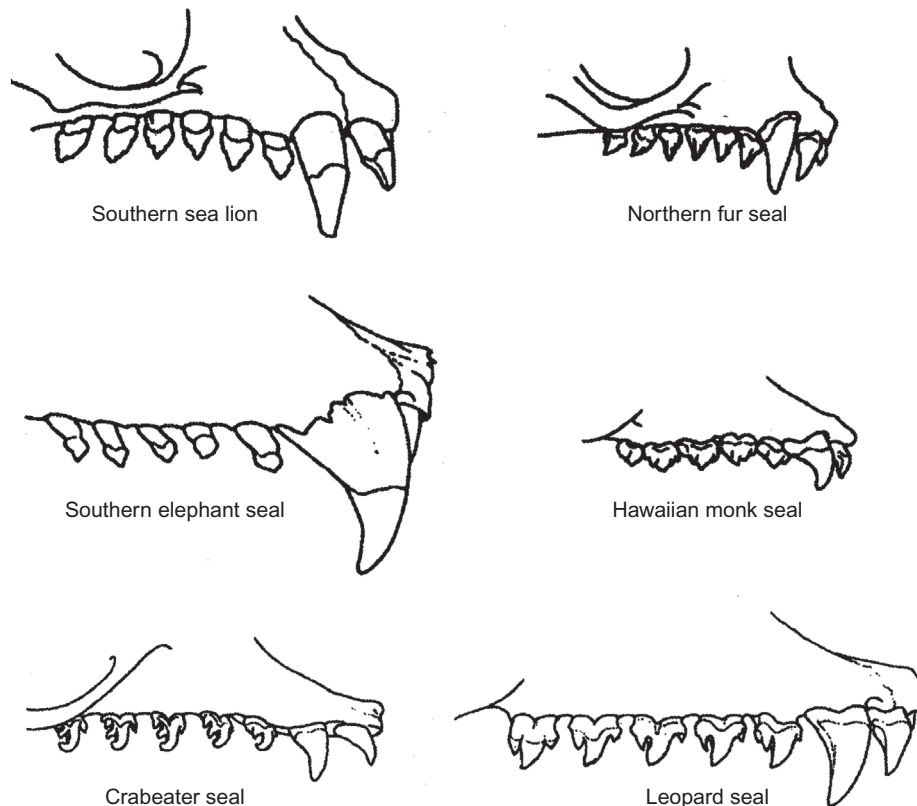
Figure 1   *Dentition patterns in pinnipeds. Note modified cusps of postcanine teeth in filter-feeding crabeater and leopard seals. From Berta, A., and Sumich, J.L. (1999). "Marine Mammals: Evolutionary Biology," Academic Press, San Diego, CA.*

grow continuously from the base, but are worn by the movements of the tongue. The outer fibers of these fringes are coarser while the inner fibers form a tangled fringe that overlaps with fringes on adjacent baleen plates. Rows of baleen plates form an extended filtering surface along each side of the palate. The coarseness of the hair-like fibrous fringes, density of fibers (fibers/cm^2), number and length of baleen plates varies between species, and is related to the prey type captured in the filtering mechanism. Because gray whales feed primarily by sucking up sediment containing benthic amphipods, they have the coarsest filtering mechanism, made up of about 100, 1-m long individual plates with very coarse fibers. This coarse filtering structure allows them to separate amphipods from bottom sediments. In contrast, right whales feed on small copepods and have more than 350 baleen plates with much smaller diameter fibers (Berta and Sumich, 1999).

Mysticetes have evolved three types of filter feeding: suction feeding (gray whales), continuous ram feeding (right and bowhead whales), and lunge feeding (rorquals). Their morphologies reflect these foraging strategies. Gray whale heads are straight and relatively short, contain short, coarse baleen, and their throat regions possess only a few grooves (3–5) allowing limited distension for taking in bottom sediment, water, and amphipods. Right and bowhead whales' heads have a strongly arched rostrum that allows them to have very long- and fine-textured baleen within a relatively blunt mouth (Werth, 2004). They have no throat grooves for distension and instead feed by swimming slowly (<1 m/s) with their jaws held open for long periods while skimming prey from the water (Simon et al., 2009). The shape of their baleen minimizes the pressure wave in front of the whale that develops while swimming slowly through prey, enhancing prey entry into the mouth (Werth, 2004). Rorqual heads are large and contain enormous mouths that extend posteriorly nearly half of the total body length (Goldbogen et al., 2010). Their mouths contain relatively short baleen ranging from fine (sei whales) to medium texture (blue, fin, humpback, and minke whales). Rorqual heads and bodies are much more streamlined than the other mysticetes, allowing them to swim rapidly into a prey school to gulp large quantities of water and schooling prey. One of the most remarkable adaptations is the ventral groove blubber and associated musculature in rorquals. This tissue has anatomical specializations for extreme extensibility (Shadwick et al., 2013). During lunge feeding, these grooves open like pleats allowing the mouth cavity to expand greatly and engulf large volumes of prey-laden water. The ram filter feeding mechanisms in right and bowhead whales, and lunge feeding in rorquals rely on flow-induced pressures from swimming, whereas the suction feeding process in gray whales is powered by the depression of the tongue muscles.

## C. Mysticetes—Feeding Behavior

Feeding gray whales roll to one side and suck benthic invertebrate prey and bottom sediments (Woodward and Winn, 2006), with some distension of the mouth cavity through expansion of the throat grooves. Water and mud are expelled through the side of the mouth (Berta and Sumich, 1999). A similar behavior is used by some gray whales feeding on a variety of benthic invertebrates and schooling mysids creating scrapes of 1–5-m deep in the ocean floor. The resulting disturbance is an important factor in the ecology of soft-bottom benthic communities of the Arctic and Bering Seas. Most mysticetes exhibit a strong right-side rolling preference while filter and bottom feeding (Woodward and Winn, 2006; Canning et al., 2011). For gray whales this right-side preference results in shorter baleen and fewer parasitic barnacles on the right side. Humpback whales show increased lip-scuffing on the right side.

Right and bowhead whales forage by ramming the water column with their mouths open through concentrations of crustaceans. As the whale swims, water and prey enter through a gap between the two baleen racks in the front of the mouth and water exits along the sides of the mouth (Werth and Potvin, 2016). Prey become concentrated as water flows through the mouth and laterally past the baleen and out of the mouth (Fig. 2). The large lower lips create a gutter-like channel to direct water flow along the outside of the baleen to draw water out via negative hydrodynamic pressure through the baleen (Werth, 2004; Lambertsen et al., 2005). While right and bowhead whales generally feed singly, at times they may feed alongside one another—a V-formation of 14 bowhead whales has been observed (Fish et al., 2013).

Lunge feeding in rorquals is characterized by the intermittent engulfment and subsequent filtration of a large volume of prey-laden water. This involves accelerating to high speed (2–5 m/s) and followed by deceleration as the water and prey enter the mouth (Fig. 3). To maximize engulfment volume, the lower jaw opens to almost 90° of the long body axis. This is possible because the jaw joints exhibit a complete loss of the typical mammalian synovial jaw joint and instead consist of a highly flexible connection between the base of the skull and lower mandibles. The expansion of the mouth during each lunge greatly increases drag, causing the deceleration. Therefore, the next lunge feeding event requires another acceleration to high speed. Both the high drag during engulfment and the repeated acceleration suggest that that lunge filter feeding is energetically costly (Croll et al., 2001; Goldbogen et al., 2006; Goldbogen et al., 2007). Despite the high energetic cost, the tremendous engulfment capacity allows for high prey intake and thus overall high energetic efficiency when feeding on high-density prey patches (Goldbogen et al., 2011).

Skimming

Figure 2   *Skim feeding in right and bowhead whales. From Berta, A., and Sumich, J.L. (1999). "Marine Mammals: Evolutionary Biology," Academic Press, San Diego, CA.*
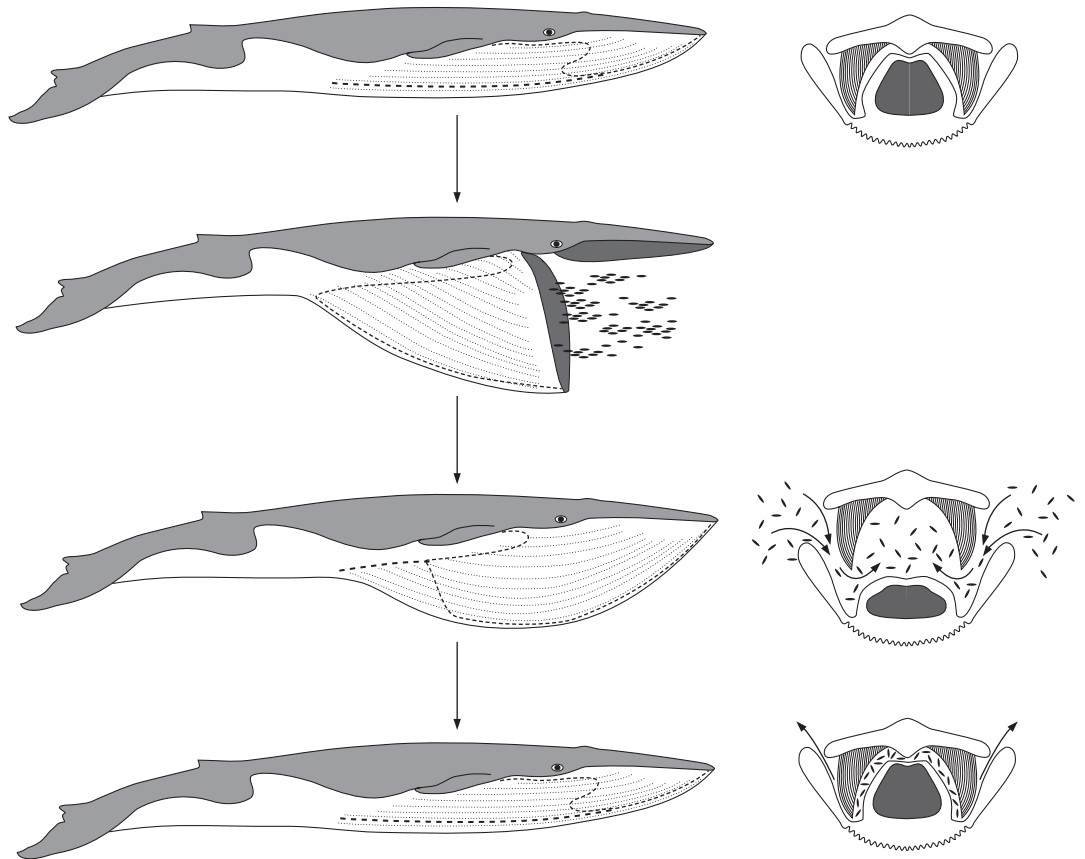
Figure 3   *Lunge feeding in rorqual whales demonstrating expansion of the throat pleats and invagination of the tongue. From Berta, A., and Sumich, J.L. (1999). "Marine Mammals: Evolutionary Biology," Academic Press, San Diego, CA.*

With the mouth open, the influx of water and prey are accommodated by the distending ventral pleats. The water entering the mouth forces the tongue to invaginate through an intermuscular space called cavum ventrale. The muscles and elastic properties of the ventral feeding pouch act in concert to force water out through the baleen, leaving prey inside the mouth (Fig. 3) (Lambertsen et al., 1995; Goldbogen et al., 2006). In addition, the level of specialization in rorqual anatomy is exemplified by a unique sensory organ between the unfused jaws that helps regulate pleat expansion (Pyenson et al., 2012), ventral groove blubber muscle with increased compressive abilities (Shadwick et al., 2013), and extensible nerves that can accommodate rapid expansion (Vogl et al., 2015).

Although this process is fundamentally similar in all rorquals, some species exhibit modifications and additional adaptations. Sei whales both skim-feed similar to right whales, and feed by lunging. Fin and blue whales often feed in pairs or trios in an echelon configuration. Humpback whales have a diverse diet and a wider variety of foraging strategies. They can bottom feed, and while feeding on schooling fishes often produce a cloud of bubbles and feed cooperatively. Laboratory experiments show schooling fish react to bubbles by aggregating more densely. Humpback whales appear to take advantage of this as one member of a group of foraging whales that form long-term associations produces a net of bubbles. The bubble cloud serves to aggregate and confuse the prey. Members of the group dive below the bubble cloud and surface together—one whale immediately adjacent to another. The location of the whales in the surfacing group is often constant through time. Humpbacks appear to enhance prey capture both with bubbles and cooperative foraging.

D. Mysticetes—Feeding Ecology

Filter-feeding whales generally exhibit distinct migration patterns linked to seasonal patterns in prey abundance. For example, gray whales undergo the longest migration of any mammal—foraging during the summer and fall in the Bering Sea and Arctic Ocean when dense aggregations of benthic amphipods become available with the seasonal increase in productivity. Humpback whales seasonally migrate from breeding areas to higher latitude foraging areas where schooling fish and krill become seasonally abundant (Berta and Sumich, 1999). The timing of migration patterns of California blue whales is linked to annual patterns in coastal upwelling and krill development patterns (Croll et al., 2005; Irvine et al., 2014).

Studies of the diving behavior and daily movement patterns of right whales have shown that they track dense aggregations of copepods that in turn track oceanographic features such as fronts. Zooplankton densities where right whales foraged in the southwestern Gulf of Maine were ~3× the mean densities in the region (3.1–5.9 g/m³, compared to 1.1–3.6 g/m³). Whale diving behavior is related to the depth of prey aggregations. In a year when copepods did not undergo diel migrations, dive depths averaged 12 m, with no dives exceeding 30 m throughout the day and night. In contrast, in a year when copepods showed strong diel shifts in depth (near

the surface at night, deeper during the day), whale dive depths were longer during the day (Mayo and Marx, 1990; Baumgartner and Mate, 2003; Baumgartner et al., 2003).

Rorquals also track seasonal and diel patterns in prey abundance and behavior. In general, rorquals migrate seasonally from high latitudes foraging sites to low latitudes for mating and birthing. However, blue whales in the Pacific and Indian Oceans feed at low latitude, "upwelling-modified" waters, and some individuals remain at low latitudes year-round. Diel changes in humpback whales in the Gulf of Maine indicate they adjust foraging to target the densest aggregations of sand lance (Hazen et al., 2009) switching from bubble-net feeding during the day to bottom feeding at night (Friedlaender et al., 2009). Fin and blue whales foraging on krill off North America concentrate their effort on dense aggregations of krill deep (150–300 m) in the water column during the day, and may cease feeding when krill becomes more dispersed near the surface at night (Croll et al., 1998; Croll et al., 2005).

Rorqual foraging generally occurs in regions of exceptionally high productivity, often associated with fronts, upwelling centers, and steep topography. Fin whales require estimated prey concentrations of at least 17.5g/m^3 to meet daily energy requirements of 996 kg krill/day. Krill densities where humpback whales were foraging in southeast Alaska were estimated at 910 individuals/m^3, and minimum required prey densities for humpbacks were 50 individuals/m^3 (Dolphin, 1987a,b). Krill densities where blue whales were foraging in Monterey Bay, California were estimated at 145.3g/m^3 compared to an overall mean density of zooplankton of 1.3g/m^3 in the area (Croll et al., 2005). Energetic models predict a threshold of 100 krill/m^3 required to meet the energetic demands of foraging blue whales (Goldbogen et al., 2011). At lower krill densities blue whales increased their kinematics such as 360° rolls potentially to maximize capture rates (Goldbogen et al., 2015). While blue whales likely shorten dive times to minimize oxygen expenditure (Doniol-Valcroze et al., 2011), in the presence of dense schools they increase foraging effort to maximize foraging efficiency (Hazen et al., 2015).

III. Summary

Filter feeding in marine mammals allows individuals to take in large quantities of prey. It is adaptive in marine ecosystems where prey are often small and densely aggregated, but patchy and ephemeral in space and time. Most filter-feeders feed on schooling fish and crustaceans. The large body size of marine mammals, particularly mysticetes, facilitates filter feeding by enabling a large filtering area relative to body volume and providing an energetic buffer for long distance moves between dense prey patches and long fasts between foraging events.

See Also the Following Articles

Baleen Whales ■ Feeding Morphology ■ Feeding Strategy and Tactics ■ Krill and Other Plankton

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FIN WHALE

Balaenoptera physalus

ALEX AGUILAR AND RAQUEL GARCÍA-VERNET

I. Characteristics and Taxonomy

Fin whales were initially described by Frederik Martens in 1675 and then by Paul Dudley in 1725. From these descriptions, Linnaeus created his *Balaena physalus* in 1758, which was later designated by Lacépède as *Balaenoptera physalus.*

The fin whale is very close to the other balaenopterids and shares with them the same chromosome number of $2n = 44$. Molecular studies suggest it is particularly close to the humpback whale (*Megaptera novaeangliae*), being the sister group in most phylogenies. No hybrids between these two species have been described but several hybrids have been found to occur between fin and blue whales (*B. musculus*). Although the hybridization rate between these two species has not been properly assessed, it may be in the range of one for every 500–1000 fin whales (Bérubé and Aguilar, 1998). At least in one case, a female hybrid was pregnant.

Because the fin whale makes seasonal migrations (see later) which follow alternate schedules in each hemisphere, the northern

and southern populations do not appear to come into contact. This has led to genetic isolation and, as a consequence, two forms, sometimes accepted as subspecies, are recognized: *B. physalus physalus*, inhabiting the Northern Hemisphere and *B. p. quoyi* in the Southern Hemisphere. The whales from the Northern Hemisphere have smaller body size and shorter and broader flippers than their southern counterparts. Small variations in body proportions and coloration between fin whales from different locations in the Northern Hemisphere have also been described, and it has been proposed that North Atlantic and North Pacific fin whales may also be considered as different subspecies (Archer et al., 2013). Although not supported by genetic data, a pygmy form, dark in color and possibly with black baleen has been found to occur off the western coast of South America and temptatively named as *B. p. patachonica* (Clarke, 2004).

The fin whale (Fig. 1) is sexually dimorphic, with females being about 5%–10% longer than males (Gambell, 1985). In the Southern Hemisphere, the average body length of adults is about 26 m for females and 25 m for males; in the Northern Hemisphere the corresponding lengths are 22.5 and 21 m. The fin whale is a slender balaenopterid, its maximum girth being between 40% and 50% of the total length. The rostrum is narrow, with a single, well-developed longitudinal ridge. BALEEN plates number 350–400 in each row and their maximum length is up to 80 cm. The dorsal fin is falcate and located at 75% of the total length; it is higher than that of blue whales, but lower than in sei whales (*B. borealis*) or Bryde's whales (*B. edeni*). The ventral grooves are numerous and extend from the chin to the umbilicus. The pigmentation of the cephalic region is strikingly asymmetrical; whereas the left side, both dorsally and ventrally, is dark slate, the right dorsal cephalic side is light gray and the right ventral side is white. This asymmetry also affects the baleen plates: those on the whole left side and the rear two-thirds of the right side are gray-slate, whereas those on the front third of the right maxilla are yellowish. Particularly in adults, the skin of the flanks in the rear trunk is often covered by small round scars and stripes caused by the attachment of lampreys and other parasites or epizoites. The white ventral region of whales inhabiting cold waters may have a yellowish layer produced by infestation of diatoms.

The body mass of adult individuals typically ranges 40–50 metric tons in the Northern Hemisphere and 60–80 metric tons in the Southern Hemisphere. A general formula for estimating body weight (W) from body length (L) is $W = 0.0015\,L^{3.46}$. If the girth at the level of the navel (G) is available, a more precise formula is $W = 0.0469\,G^{1.23}L^{1.45}$.

The relative mass of body tissues varies seasonally according to nutritive condition (Lockyer and Waters, 1986). Average mass relative to total body weight is $18.4 \pm 3.3\%$ for blubber, $45.3 \pm 4.4\%$ for muscle, $15.5 \pm 2.4\%$ for bone, and $9.8 \pm 2.1\%$ for viscera. The liver is large, usually weighing 230–600 kg. The heart is similar in relative size to that of terrestrial mammals but larger than in odontocetes and weighs 130–290 kg. Kidneys are large and weigh 50–110 kg. The right lung is about 10% heavier than the left, each one weighing 100–160 kg. The spleen weighs 2–7 kg and sometimes has accessory bodies of smaller size.

The rostrum of the fin whale is sharply pointed, without the lateral curvature typical of blue whales. The zygomatic width is about 50%–55% of the condylo-premaxillary length, the width of the rostrum at midlength is approximately 30%–35% of its basal width, and the whole skull measures about 20%–25% of the total body length. Ribs usually number 16 pairs, with the last pair being smaller and not attached to the vertebral column. The number of vertebrae ranges from 60 to 63, with a typical formula of C, 7; D,