

Filter Feeding

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I. Filter Feeding and the Marine Environment

A fundamental necessity for any organism 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 number of foraging techniques. Filter feeding, found in the mysticete whales and three species of pinnipeds (crabeater seals, *Lobodon carcinophaga*; leopard seals, *Hydrurga leptonyx*; and Antarctic fur seals, *Arctocephalus gazella*) is the most unique of these adaptations for feeding, and is not found in any terrestrial mammals.

Filter feeding allows these marine mammals to exploit extremely abundant, but small schooling fish and crustaceans by taking many individual prey items in a single feeding event. This adaptation arose in response to the unique patterns of productivity and prey availability in marine ecosystems. Low standing biomass and high turnover of small-sized primary producers that respond rapidly to nutrient availability characterize marine food webs. Due to spatial differences in the physical dynamics of marine ecosystems, productivity tends to be more patchy and ephemeral than in terrestrial systems. Consequently, marine grazers (e.g., schooling crustaceans and fish) often occur in extremely high densities near these patches of high primary production. Most marine mammals are primary carnivores and feed on these dense, patchily distributed aggregations of schooling prey. The spatial and temporal patchiness of this prey means that marine mammals must often travel long distances to locate prey, and the larger body size of marine mammals likely plays an important role (Croll *et al.*, 2005).

Initially, thermoregulatory requirements selected for larger body sizes as mammals returned to the ocean. However, once dependent upon marine prey, large body size also provided a buffer for the patchy and ephemeral distribution of marine prey. Thus, larger individuals could endure longer periods and travel longer distances between periodic feeding events on patchy prey. While adaptive for exploiting patchy prey resources, a consequence of larger body size is a higher average daily prey requirement. For marine mammals that feed on patchy and ephemeral resources, this requires individuals to take in large quantities of prey during the short periods of time it is available (Berta and Sumich, 1999; Bowen and Siniff, 1999).

Filter feeding is a foraging strategy that allows individuals to capture and process large quantities of prey in single mouth full, thus allowing them to acquire energy at high rates when small prey are aggregated. Indeed, for mysticetes, large body size is probably a prerequisite for attaining a sufficiently large surface area for filter feeding. Thus, the interaction of availability of prey resources, high concentrations of prey in schools, and selection for large body size likely led to the evolution of filter feeding. Ultimately, large body size and filter feeding allowed some marine mammals to exploit the extremely high densities of schooling prey that develop at high latitudes during the spring and summer, but fast during the winter when these resources disappear. Large body size provided an energy store for wintering and long distance migration without feeding (Berta and Sumich, 1999).

Due to this dependency on patchy but extremely productive food resources, it is not surprising that filter-feeding whales are believed to have 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. This increased productivity provided a rich resource of zooplankton that could be effectively exploited through filter feeding (Berta and Sumich, 1999). Recently, the discovery of a late Oligocene fossil archaic mysticete that was a macrophagous predator casts doubt on the suggestion that the initial radiation of mysticetes was linked to the evolution of filter feeding (Fitzgerald, 2006).

Present-day filter-feeding marine mammals concentrate their foraging in polar regions and highly productive coastal upwelling regions. The southern ocean is still the most important foraging area for filter-feeding marine mammals. Prior to their exploitation by humans, the highest densities of mysticetes occurred in highly productive southern waters. Crabeater seals, Antarctic fur seals, and leopard seals are 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 nearly as extensive in pinnipeds as in mysticetes.

Only three pinniped species regularly filter feed: crabeater seals, leopard seals, and Antarctic fur seals (Riedman, 1990). When filter feeding, all the three species feed almost exclusively on Antarctic krill, *Euphausia superba* in the Southern Ocean where it is large in size, 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). Once the mouth closes around a small group of 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 are performed during the night and deeper dives during the 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 found in shallow waters. Gray whale, *Eschrichtius robustus*, diet consists primarily of benthic gammarid amphipods, although they can forage

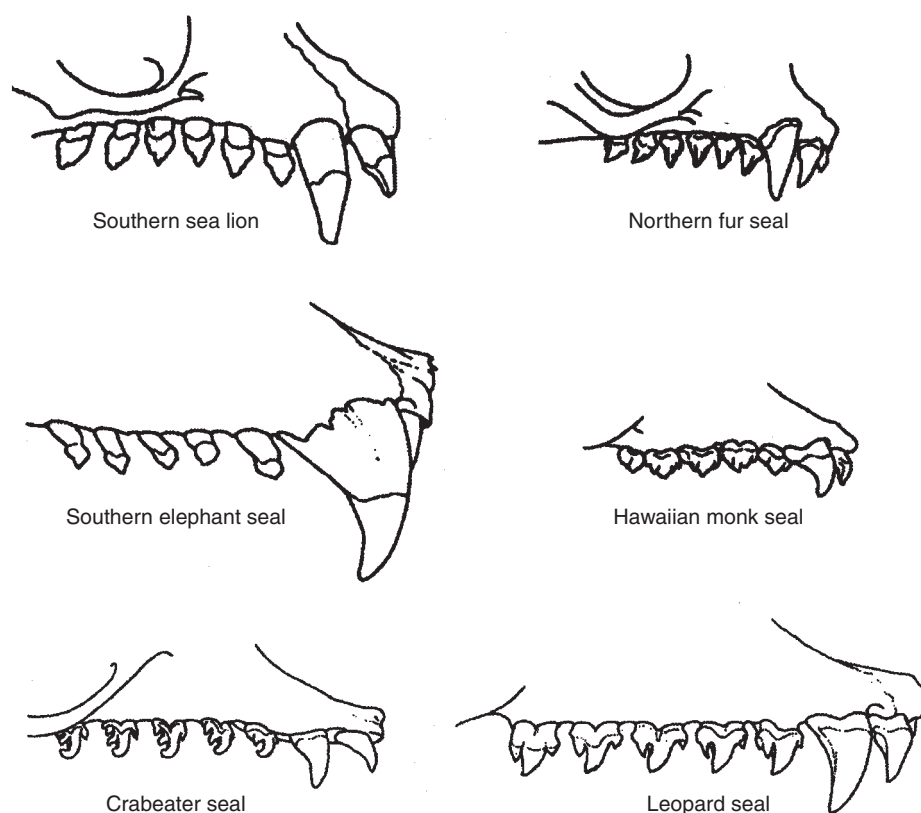


Figure 1 Dentition patterns in pinnipeds. Note modified cusps in postcanine teeth in filter-feeding crabeater and leopard seals. From Berta and Sumich 1998.

on a wide variety of prey, including schooling mysids in some areas. Right, *Eubalaena* spp., and bowhead, *Balaena mysticetus*, whales primarily feed on copepod crustaceans of the genus *Calanus*. All of the 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, *Balaenoptera borealis*), and schooling fish (minke, *B. acutorostrata*, Bryde's; *B. edeni*, humpback; *Megaptera novaeangliae*; and fin whales, *B. physalus*) (Berta and Sumich, 1999).

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. Similar to fingernails, the plates grow continuously from the base, but are worn by the movements of the tongue. As the edges of the plates wear, hair-like fibrous strands emerge as fringes. 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, the density of fibers (number of fibers/cm²), number of baleen plates, and length of baleen plates varies between species, and is related to the prey species captured in the filtering mechanism. Because gray whales feed primarily upon sediment-dwelling 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 that feed on small copepods have a fine filtering mechanism composed of more than 350 baleen plates that can

exceed 3 m in length. The fibers of right whale baleen are very fine, forming a dense mat capable of capturing copepods that are less than 5 mm (Berta and Sumich, 1999). The strong, flexible, and light characteristics of baleen plates made them commercially important in the nineteenth century where they served some of the roles of today's plastics.

Mysticetes have evolved three types of filter feeding: sediment-straining (gray whales), skimming (right and bowhead whales), and lunging or gulping (rorquals). The morphology of mysticetes reflects these different strategies. Gray whale heads are straight and relatively short, contain short, coarse baleen, and their throat regions possess only a few grooves (3–5) in the gular region that allows limited distension for taking in bottom sediment, water, and amphipods. Right and bowhead whale's heads have a strongly arched rostrum that allows them to have very long- and fine-textured baleen within a relatively blunt mouth. They have no throat grooves for distension and instead feed by swimming slowly (3–9 km/h) with their jaws held open for long periods while skimming prey from the water. The shape of their baleen minimizes the pressure wave in front of the whale that develops while swimming slowly through prey and enhances prey entry into the mouth (Werth, 2004; Lambertsen *et al.*, 2005). Rorqual heads are large and contain enormous mouths that extend posteriorly nearly half of the total body length. Their mouths contain relatively short baleen that ranges from fine (sei whales) to medium texture (blue, fin, humpback, and minke whales). The heads and bodies of rorquals 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 for feeding is the presence, in rorquals, of

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Figure 2 Skim-feeding in right and bowhead whales. From Berta and Sumich 1998.

70–80 external throat grooves. During gulping, these grooves open like pleats to allow the mouth cavity to expand up to 4 times in circumference, taking in a volume of water equivalent to about 70% of the animals' body weight or greater (Croll *et al.*, 2001; Acevedo-Gutierrez *et al.*, 2002; Goldbogen *et al.*, 2006; Goldbogen *et al.*, 2007). The filter-feeding strategy of Balaenids appears to focus upon enhanced filter area whereas Baleaenopterid strategy allows for greater filter pressure.

C. Mysticetes—Feeding Behavior

Observations of feeding gray whales in the Arctic and Bering Sea have shown that the whales roll to one side and suck benthic invertebrate prey and bottom sediments, with some distension of the mouth cavity through the 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 gray whales that do not migrate as far north where they feed on a variety of benthic invertebrates and schooling mysids. This benthic foraging behavior creates scrapes of 1–5-m deep in the ocean floor, and several studies have shown that the disturbance is an important factor in the ecology of soft-bottom benthic communities of the Arctic and Bering Seas. Observational and direct measurement studies have shown that most gray whales and rorquals exhibit a strong right-side rolling preference while filter feeding (Woodward and Winn, 2006). For gray whales this right-side preference has been identified by shorter baleen and fewer parasitic barnacles on the right side.

Right and bowhead whales forage by skimming with their mouths open through concentrations of crustaceans near the surface and deeper in the water column. As the whale swims, water and prey enter through a gap between the two baleen plates in the front of the mouth and water exits along the sides of the mouth. Prey are swept into the back of the mouth by the dynamically controlled flow of water through the mouth and the side-to-side sweeping action of the large muscular tongue (Fig. 2). When the mouth is opened, the large lower lip abducts to 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.

Rorqual lunge feeding has been described as the largest biomechanical event that has ever existed on earth (Croll *et al.*, 2001). Rorquals capture food by initially swimming rapidly (3–5 m/s in fin whales) at a prey school and then decelerating while opening the mouth to gulp vast quantities of water and schooling prey (Fig. 3). To maximize the opening, the lower jaw opens to almost 90° of the body axis. This is possible because the lower jaw has a well-developed

coronoid process. This process is where the large temporalis muscle inserts, and provides an anchor and mechanical advantage for control of the lower jaw while maximizing the gape for prey capture. It is not developed in other whale species, and a tendinous part of the temporalis muscle, the frontomandibular stay, enhances and strengthens the mechanical linkage between the skull and the lower jaw (Lambertsen *et al.*, 1995). The expansion of the mouth during each lunge greatly increases drag and brings the body of the whale almost to a stop. As a result, it appears that filter feeding in rorquals is an energetically costly behavior (Croll *et al.*, 2001; Goldbogen *et al.*, 2006; Goldbogen *et al.*, 2007).

With the mouth open, the onrush of water and prey are accommodated by the distending ventral pleats. The tongue invaginates to form a hollow sac-like structure (cavum ventrale) which lines the inside of the gular region and the ventral pleats distend fully. After engulfing entire schools of prey, the lower jaw is closed. The tongue and the elastic properties of the ventral walls of the throat act in concert to force water out through the baleen (Fig. 3) (Lambertsen *et al.*, 1995; Goldbogen *et al.*, 2006).

Although the process described above is fundamentally the same in all rorquals, some species exhibit modifications and additional adaptations. Sei whales skim-feed in a manner similar to right whales, as well as feeding by lunging. Fin and blue whales often feed in pairs or trios that have a consistent echelon configuration. Humpback whales have a diverse diet and a wider variety of feeding behaviors. They have been observed bottom feeding, and while feeding on schooling fishes have been observed to produce a cloud of bubbles and feed cooperatively to assist in prey capture.

Laboratory experiments have shown schooling fish to 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 produce 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 appears to be fairly constant through time. Humpbacks thus likely enhance prey capture success by both using bubbles and foraging cooperatively. A variation of bubble cloud feeding has been observed in humpback whales feeding on sand lance off New England. Here the bubble-cloud feeding is followed by a tail slap—believed to cause the sand lance to aggregate more densely.

D. Mysticetes—Feeding Ecology

All filter-feeding whales exhibit distinct migration patterns linked to seasonal patterns in prey abundance. Seasonally dense aggregations of prey are probably necessary for successful filter feeding. For example,

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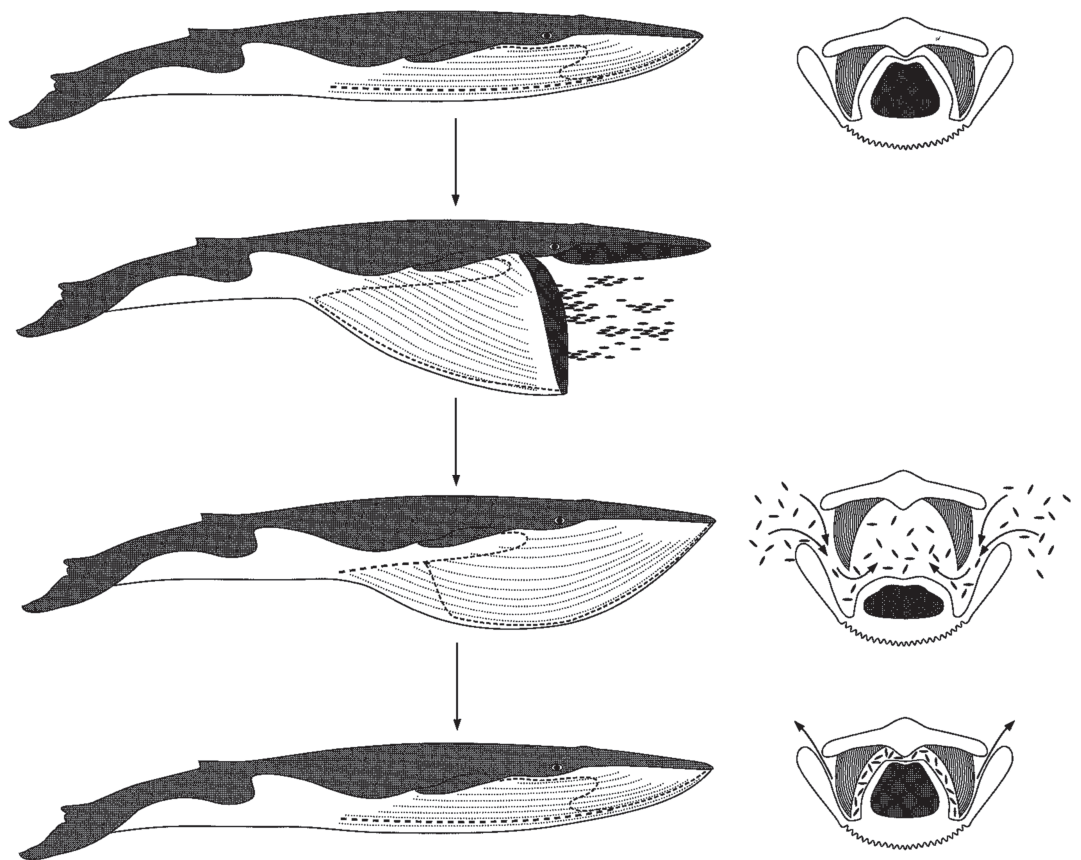


Figure 3 Lunge feeding in rorqual whales, demonstrating expansion of the throat pleats in invagination of the tongue. From Berta and Sumich 1998.

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 coastal migration patterns of the California blue whale appears to be linked to annual patterns in coastal upwelling and krill development patterns (Croll *et al.*, 2005).

Studies of the diving behavior and daily movement patterns of right whales has shown that they track dense aggregations of copepods that in turn track oceanographic features such as fronts. Zooplankton densities in regions where right whales foraged in the southwestern Gulf of Maine were approximately three times the mean densities in the region (whale feeding densities averaged 3.1–5.9 g/m³, compared to 1.1–3.6 g/m³ where whales were not foraging). In a related study using hydroacoustic surveys, zooplankton densities where right whales were foraging were 18–25 g/m³ (compared to 1–5 g/m³ where whales were not foraging). Whale diving behavior is related to the depth of prey aggregations. In a year where 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 where copepods showed strong diel shifts in depth (near the surface at night, deeper during the day), whale dive depths were significantly longer during the day (Mayo and Marx, 1990; Baumgartner and Mate, 2003; Baumgartner *et al.*, 2003).

Rorquals also track seasonal and diel patterns in the abundance and behavior of their prey. In general, the distribution and movement

patterns of most rorquals consist of a seasonal migration from high latitudes where foraging takes place to low latitudes where they mate and give birth. However, data from blue whales in the Pacific indicate that feeding also takes place at low latitude, “upwelling-modified” waters, and data from both the Pacific and the Indian Oceans indicate that some blue whales may remain at low latitudes year-round. Fin and blue whales foraging on krill off the coast of North America concentrate their foraging 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 appears to only occur in regions of exceptionally high productivity, often associated with fronts, upwelling centers, and steep topography. It has been estimated that fin whales require prey concentrations of at least 17.5 g/m³ to meet daily energy requirements. Krill densities where humpback whales were foraging in southeast Alaska have been estimated at 910 individuals/m³, and minimum required prey densities for humpbacks were about 50 individuals/m³ (Dolphin, 1987a, b). Krill densities in schools where blue whales were foraging in Monterey Bay, California were estimated at 145.3 g/m³ compared to an overall mean density of zooplankton of 1.3 g/m³ in the area (Croll *et al.*, 2005).

III. Summary

Filter feeding in marine mammals is an adaptation that allows individuals to take in large quantities of prey in one mouth full. This is particularly adaptive in marine ecosystems where prey are relatively

small and often densely aggregated, but patchy and ephemeral in space and time. Most filter-feeding species feed on schooling fish and crustaceans. The large body size of marine mammals and particularly mysticetes facilitates filter feeding by providing the ability to have a large filtering area relative to body volume. In addition, large body size likely provides an energetic buffer for animals that must move long distances between dense prey patches and endure long periods of fasting between foraging events.

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See Also the Following Articles

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Fin Whale

Balaenoptera physalus

ALEX AGUILAR

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I. Characters and Taxonomic Relationships

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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*.

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The fin whale is very close to the other balaenopterids, particularly its congeners, and shares with them the same chromosome number of $2n = 44$. It appears to be particularly close to the blue whale (*B. musculus*), from which it diverged between 3.5 and 5 million years ago, and with which several hybrids have been described. 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. At least in one case, a female hybrid was pregnant (Bérubé and Aguilar, 1998).

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The fin whale 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 26m for females and 25m for males; in the Northern Hemisphere the corresponding lengths are 22.5 and 21m. 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 70cm. 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 (Fig. 1). This asymmetry also affects the baleen plates: those on the whole left side and the rear two-thirds of the right side are gray, 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 attributed to the attachment of lampreys and remoras. The white ventral region of whales inhabiting cold waters may have a yellowish layer produced by an infestation of diatoms.

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The body mass of adult individuals typically ranges from 40 to 50 metric tons in the Northern Hemisphere and from 60 to 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 $W = 0.0469 G^{1.23} L^{1.45}$.

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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 230–600kg. The heart is similar in relative size to that of terrestrial mammals but larger than in odontocetes and weighs 130–290kg. Kidneys are large and weigh 50–110kg. The right lung is about 10% heavier than the left, with each one weighing 100–160kg. The spleen weighs 2–7kg and sometimes has accessory bodies of smaller size.

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