

Cetacean species exhibit a wide range of distribution patterns. The family Balaenidae includes one antitropical species group (*Balaena* spp.) and one circumpolar Arctic species (*B. mysticetus*). The gray whale and the various species of balaenopterids are mostly latitudinal migrants in both hemispheres, although the Bryde's-like whales (*Balaenoptera brydei*, *B. omurai*, and *B. edeni*) are restricted to tropical and warm temperate waters, and some primarily migratory species include isolated populations that may be non-migratory (e.g., *Megaptera novaeangliae* in the northern Indian Ocean). In addition to the widespread common minke whale (*Balaenoptera acutorostrata*), the Southern Hemisphere also contains an endemic species of minke whale (*B. bonaerensis*). Similarly, the Southern Hemisphere is also home to two distinct forms (considered subspecies at present) of blue whale (*B. musculus*). In both of these cases, it is not known if the two southern forms represent divergent lineages that arose within the southern ocean or if they were the result of independent dispersal events across the equator.

Sperm whales (*Physeter macrocephalus*) are virtually cosmopolitan, and the kogiids (*Kogia sima* and *K. breviceps*) are worldwide in tropical and warm temperate waters. Beaked whales show a variety of distribution patterns, including pan-tropical species (e.g., *M. densirostris*), antitropical species pairs (*Berardius* spp.), and ocean basin endemics (e.g., *M. bidens*). Some (e.g., *M. peruvianus*) are only known from a few strandings within limited geographic areas. For most species of sperm whales and beaked whales, so little is known about their habits and ecological needs that it is difficult to hypothesize about the mechanisms that have led to their present distributions.

Three of the four species of river dolphins (*Inia geoffrensis*, *Lipotes vexillifer*, and *Platanista gangetica*) occur only in freshwater in specific tropical river systems, with the fourth species (*Pontoporia blainvillei*) having a restricted marine coastal range. The two species of monodontids (*Monodon monoceros* and *Delphinapterus leucas*) are circumpolar in the north, and are among the few resident polar cetaceans, although fossil species of this family occurred as far south as San Diego, California.

Apart from a single Indo-West Pacific coastal species that also ranges into freshwater (*Neophocaena phocaenoides*), the phocoenids are strictly marine and cold temperate to warm temperate in distribution, some with very restricted ranges (e.g., *Phocoena sinus*). Only one phocoenid, *P. phocaena*, has invaded the North Atlantic, becoming very widespread in both oceans of the Northern Hemisphere and even establishing isolated populations in the Black Sea and off West Africa.

The most speciose family of marine mammals, the delphinids, shows a wide variety of distributions, from pan-tropical species (e.g., *Stenella attenuata*) to ocean basin endemics (e.g., *Lagenorhynchus albirostris*) to species with wide-ranging but disjunct populations (e.g., *Delphinus capensis*). Many delphinids are pelagic, although some inhabit coastal waters (e.g., *Cephalorhynchus* spp.) and some even invade freshwater (e.g., *Sotalia fluviatilis*). Only one, *Orcinus orca*, seems to regularly range to the pack ice in the far north and south. For the many pan-tropical/warm temperate species, the continental landmasses effectively separate the populations inhabiting the Indian and Pacific Oceans from those inhabiting the Atlantic Ocean, raising the question of how they came to inhabit all the ocean basins. It has been hypothesized that during warm climatic periods, warm water extended far enough south to allow interchange and range expansion around the Cape of Good Hope. This would enable some species to become pantropical in their distribution, and the subsequent retreat of the warm water and isolation of populations could provide a speciation mechanism for the establishment of the tropical species endemic to the Atlantic Ocean (*S. frontalis* and *S. clymene*).

V. Conclusion

Why do species live where they do? Answering such a simple question requires the examination of clues from the past as well as the present. Biogeography involves such diverse disciplines as geology, paleontology, ecology, physiology, behavior, and systematics. For marine mammals, studying biogeographical patterns presents real challenges. There is a paucity of information about past distributions and habitats, gaps in our knowledge of contemporary and recent distributions, uncertainties about evolutionary relationships, and a tremendous amount to learn about the basic ecology and physiology of many marine mammals.

See Also the Following Articles

Climate Change ■ Systematics

References

- Berta, A., Sumich, J., and Kovacs, K. (2006). "Marine Mammals—Evolutionary Biology," 2nd edn. Academic Press, San Diego.
- Brown, J. H., and Gibson, A. C. (1983). "Biogeography." Mosby, St. Louis, Missouri.
- Cox, C. B., and Moore, P. D. (1985). "Biogeography," 4th edn. Blackwell Scientific Publications, Cambridge, Massachusetts.
- Davies, J. L. (1963). The antitropical factor in cetacean speciation. *Evolution* **17**, 107–116.
- Lincoln, R., Boxshall, G., and Clark, P. (1998). "A Dictionary of Ecology, Evolution and Systematics," 2nd edn. Cambridge University Press, Cambridge, UK.
- Myers, A. A., and Giller, P. S. (eds) (1988). "Analytical Biogeography." Chapman and Hall, London.
- Nelson, G., and Rosen, D. E. (eds) (1981). "Vicariance Biogeography: A Critique." Columbia University Press, New York.
- Read, A.J., Halpin, P.N., Crowder, L.B., Best, B.D., Fujioka, E. (eds). (2007). OBIS-SEAMAP: Mapping marine mammals, birds and turtles. World Wide Web electronic publication. <http://www.seamap.env.duke.edu>. Accessed on October 15, 2007.
- Rice, D. W. (1998). "Marine Mammals of the World: Systematics and Distribution." Soc. Mar. Mamm. Spec. Pub. **4.**, Society for Marine Mammalogy, Lawrence, KS.
- Wiley, E. O. (1988). Vicariance biogeography. *Ann. Rev. Ecol. System.* **19**, 513–542.

Blubber

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Blubber, a dense vascularized layer of fat beneath the skin, is one of the most well-known and universal characteristics of marine mammals. Although it is not strictly present in polar bears (*Ursus maritimus*) or sea otters (*Enhydra lutris*), all cetaceans, sirenians and pinnipeds have blubber and it may comprise up to 50% of the body mass of some species at certain life stages. Blubber has long been recognized as the primary and most important site of fat, and thus also energy, storage in marine mammals. However, blubber also has a number of other important functions. The blubber layer serves as an insulator in mammals living in often cold marine environments and is thus central to their entire process of thermoregulation.

Blubber also affects buoyancy and functions as a body streamliner and elastic spring for efficient hydrodynamic locomotion. Although blubber is a dynamic tissue, which can reflect both nutritional state and life history stage of individuals, the tissue itself has likely evolved to best suit the lifestyles, stresses and constraints of specific groups and even individual species of marine mammals. Hence, the study of blubber can provide unique insights not only into phylogenetic relationships and environmental adaptations, but also into aspects of individual feeding habits, foraging ecology, species distribution, and demography that are otherwise difficult to study.

I. The Structure of Blubber

A. Tissue Characteristics

Blubber is a specialized subcutaneous layer of fat found only in marine mammals and is different from other types of adipose tissue in that it is anatomically and biochemically adapted to serve as an efficient and adjustable thermal insulator. The blubber layer is almost continuous across the body of marine mammals, lying over but not tightly fixed to the underlying musculature but absent on appendages. Although nearly continuous, the thickness, structure, and biochemical composition of the blubber can vary greatly over the body of an individual in some species and these differences are likely associated with localized differences in function. Consistent with its role as an insulator, there also usually exists a thermal, as well as biochemical, gradient through the depth of the blubber layer. The outer layer (nearest the skin) is usually cooler than the inner layer (nearest the muscle or body core) and activities of individual enzymes in each of these locations may be adapted to function at the different respective temperatures. The polar bear also deposits huge quantities of fat subcutaneously, which likely provides some degree of insulation. However, this superficial adipose tissue does not appear to be a specific anatomical adaptation for that purpose as it does not differ in structure from the superficial fat depots of other large terrestrial carnivores (Pond *et al.*, 1992).

Blubber, like other adipose tissue, is composed of numerous fat cells called adipocytes. Adipocytes develop prior to filling with fat and are composed, like other cells, of mostly protein and water. Once developed, adipocytes can alternately fill and empty with lipid and thus can change greatly in size. Mature adipocytes are generally large and spherical and packed densely into adipose tissue. The cells are surrounded and held in place by a mesh of structural collagen fibers. Although most other types of adipose tissue contain small to moderate amounts of collagen, blubber is distinct in being greatly enriched in collagen and elastic fibers. This gives blubber a firm, tough, and fibrous character from which it derives much of its mechanical and functional properties. The histological structure of the blubber in pinnipeds is relatively uniform throughout its depth. However, in some cetaceans, there is a distinct stratification of the tissue into an inner, middle, and outer layer based on the size, shape, and metabolic characteristics of adipocytes, as well as on the lipid and collagen content of the tissue. Blubber also contains numerous blood vessels and specialized shunts called arterio-venous anastomoses (AVAs), which allow larger and swifter blood flow than would be possible through capillaries alone and are important to the thermoregulation process. The blubber of manatees has been considered unusual in that a layer of muscle is imbedded in the middle of the ventral blubber layer, however, a similar arrangement has also been found at certain body sites in some otariids. A possible functional significance for this arrangement is not known.

B. Variation in Thickness and Proximate Composition

The thickness of the blubber layer varies among species. In general, because body volume increases more rapidly than body surface area, larger species tend to have greater maximum blubber thickness. Thus, the depth of the blubber layer can be commonly 7–10 cm in adult pinnipeds, 20–30 cm in fin whales (*Balaenoptera physalus*) and up to 50 cm in the bowhead whale (*Balaena mysticetus*). In contrast, in one of the smallest odontocetes, the harbor porpoise (*Phocoena phocoena*), blubber depth generally reaches only 2.5–3.0 cm.

Beyond general species characteristics, the amount, depth, and chemical composition of the blubber also vary with age, nutrition, and reproductive status. The adipose tissue of many newborn mammals is empty of lipid, filling quickly after birth during the lactation period. Proliferation of fat depots in immature mammals is due to an increase in both adipocyte numbers and size. However, in adults, changes in the size of fat depots are primarily due to filling or emptying of adipocytes. The same appears largely true in the case of blubber. Although neonates of large baleen whales are born with a blubber layer that is several centimeters thick, most pinniped neonates are born with very little blubber, at less than 3 mm in depth in some otariids and accounting for less than 5–6% of body mass in most phocids. Most newborn pinnipeds rely instead primarily on fur (otariids) or lanugo (downy hair grown by fetuses, which remains for short periods after birth in many phocids) and delayed entry into the water. For instance, in newborn harp seals (*Phoca groenlandica*), blubber represents less than 6% of body mass and contains only 20% lipid (Worthy and Lavigne, 1983). This rapidly changes during the 12-day lactation period, such that the blubber of a newly weaned harp seal can comprise up to 50% of body mass and contains greater than 90% lipid, representing abundant and replete fat cells. In contrast, during reduced food intake or fasting, lipid is mobilized rapidly from adipocytes and hence undernourished marine mammals are characterized by greatly reduced blubber thickness and lipid content. Likewise, during annual events associated with fasting, such as lactation or molting in some species, blubber is also reduced in depth and lipid content with fat mobilization. For instance, the sternal blubber of female harbor seals (*Phoca vitulina*) changes during the 24-day lactation period from 3.8 to 1.4 cm in depth and from 92.3% lipid, 2.2% protein, and 5.5% water to 76.9% lipid, 5.9% protein, and 17.2% water (Bowen *et al.*, 1992); i.e., the increases in protein and water content reflect the larger proportion of “emptier” fat cells. In a similar manner, lipid content of adipose tissue in polar bears has been shown to reflect reproductive status and likely changes in prey availability (Thiemann *et al.*, 2006).

C. The Lipids in Blubber

Depot lipid in animals is stored predominantly as triacylglycerols, which consist of three fatty acids esterified, i.e., linked by an ester bond to a glycerol molecule (three-carbon alcohol). The synthesis, storage, and catabolism of fatty acids are the components of lipid energy metabolism. Fatty acids in the marine food web are exceptionally complex and are characterized by high levels of long-chain polyunsaturated fatty acids (PUFA). During digestion of triacylglycerols by monogastric mammals, fatty acids are released from the glycerol backbone but not degraded and they are carried in the bloodstream and taken up by tissues the same way. These fatty acids are then either used for energy or stored as triacylglycerols in adipose tissue. Thus, fatty acids travel up the food chain intact, and

because the kinds of fatty acids that can be biosynthesized or modified in mammals are quite limited, most fatty acids found in marine mammal blubber arise from the dietary intake of fish and other prey lipids. Hence, marine mammal blubber lipid is usually characterized by high levels of long-chain PUFA as well as unique fatty acids produced at lower trophic levels of the marine ecosystem.

Marine mammals, like other mammals, can also synthesize some of their own fatty acids from sources such as dietary amino acids consumed in excess of body needs (glucose would be another source but is scarce in diets of marine mammals). These synthesized fatty acids are usually restricted to those with 16 or 18 carbon atoms and usually, at most, one double bond (i.e., 16:0, 16:1 n -7, 18:0, and 18:1 n -9). Although these fatty acids are also common in all prey items of marine mammals, some are undoubtedly deposited in marine mammal blubber from biosynthesis.

There are several exceptions to the general characteristics of marine mammal blubber lipids described earlier. In addition to the usual fatty acids that are synthesized by all mammals, one very unusual fatty acid, isovaleric acid, is also found in the blubber of some species of toothed whales (odontocetes) which can arise only from localized biosynthesis. Isovaleric acid is unusual in that it is both very short (five carbons) and branched. When present, it is found in highest concentrations in the outermost layer (nearest the skin) of blubber (Koopman *et al.*, 2003). Additionally, besides the most common form of storage lipid, triacylglycerols, some marine mammals (primarily some odontocetes) store some or all of their fatty acids in blubber as wax esters (Koopman, 2007). A wax ester is a single fatty acid esterified to a long-chain (22–34 carbon) alcohol. In general, wax esters are firm, stable, and resistant to degradation. This is why sperm whale (*Physeter macrocephalus*) oil was popular as an illuminant in the last century.

II. Role of Blubber in Temperature Regulation: Heat Conservation and Dissipation

As a whole-body envelope of insulation, blubber is central to thermoregulation in marine mammals. Marine mammals, like all mammals, are homeothermic endotherms and hence need to maintain a stable body core temperature of about 37°C in cooler (usually <25°C) and often much colder (–1 to 5°C) fluid environments. Additionally, heat is always lost far more rapidly to water than to air because the thermal conductivity of water is 25 times that of air. There are several ways marine mammals have dealt with this problem. One is to increase body size, which decreases the surface-to-volume ratio and thus provides less surface area per unit volume over which to lose heat. Even the smallest marine mammals are considered large mammals, being one to two orders of magnitude larger than small terrestrial mammals such as rodents and insectivores. Additionally, and perhaps more importantly, large body size generally allows for thicker insulation (be it fur or blubber), which further decreases heat conductance.

Although fur is a far more effective insulator than blubber in air and is used as the sole means of insulation by sea otters, fur acts by trapping pockets of air (a poor thermal conductor) among hairs, which then forms the effective insulative layer. Thus, potentially when fur is wetted, but more significantly when diving under pressure (as most marine mammals do), fur is compressed, expelling the air layer and thus losing its insulative properties. In contrast, blubber does not compress with depth and it is a good insulator because, like air, it has a lower thermal conductivity than water.

Adipose tissue is also less metabolically active than other tissues and thus requires less perfusion by blood, which would otherwise tend to cause heat loss at the body surface. Nevertheless, because blubber is vascularized, circulatory adjustments allow both heat conservation and dissipation as necessary. An important means of regulating heat transfer in marine mammals is by restricting and diverting blood flow through the blood vessels and AVAs in blubber. Restricting blood flow to the blubber's surface (i.e., skin) conserves body heat and allows blubber to act as an effective insulator against cold. Conversely, increasing blood flow into the blubber allows sometimes massive redistribution and dumping of body heat in cases of either very warm water or air or during intense activity (Heath and Ridgeway, 1999).

The effectiveness of blubber as an insulative layer depends on its thickness, lipid content, and lipid composition. As an insulation layer increases in thickness, the lower critical temperature of an animal decreases and thus the animal can accommodate a broader ambient temperature range without having to increase its metabolism for heat production (i.e., to remain thermoneutral). As mentioned earlier, many marine mammals, especially those of larger body size, possess a thick blubber layer, allowing them to remain thermoneutral at most of the temperatures of the world's oceans and, for some pinnipeds, even at air temperatures of –10 to –20°C on polar ice. However, smaller species are limited in the depth of blubber they can carry and also have relatively more surface area over which to lose heat. Hence, most of the smallest cetaceans do not occur at high latitudes. Less insulation increases the lower critical temperature of an animal and requires increased metabolism for heat production. The harbor porpoise is the smallest cetacean species to inhabit temperate waters of the Northern Hemisphere. Although its blubber depth is only several centimeters thick, it is generally twice the thickness and contains more lipid than does a similarly sized dolphin inhabiting tropical waters. These properties appear to confer up to four times greater insulative capacity (Koopman, 2007).

Depletion of lipid from blubber stores will decrease the insulative capacity of the tissue and may seriously compromise an individual, especially if nutritionally stressed. Thus, small species such as the harbor porpoise must feed nearly continually to maintain metabolism and to preserve their blubber's thickness and insulative capacities. In contrast, large whales can fast and mobilize blubber reserves for weeks or months, yet can remain thermoneutral due to a low surface-to-volume ratio as well as the maintenance of a still relatively thick blubber layer. Especially in cetaceans, the thickness, structure, and insulative properties of the blubber may vary across different regions of the body and thus the function of the blubber as an insulator may also vary regionally.

Variation in the lipid composition of blubber may also confer differing insulative capacities. As stated previously, the blubber of marine mammals is composed of large amounts of unsaturated fatty acids. Unsaturated fatty acids have lower melting points than do saturated fatty acids. Thus even when the temperature of the outermost layer of the blubber and skin are near that of cold ambient temperatures, blubber tissue can remain fluid and an effective insulator if the melting point of its fatty acids is low. Saturated and monounsaturated fatty acids abundant in marine mammal blubber (e.g., 16:0, 16:1, 18:0, and 18:1) have melting points of 13–70°C. However, nutritionally important polyunsaturated fatty acids are usually plentiful in marine mammal diets and thus in blubber, conferring an overall melting point in blubber lipid of less than –15°C. Additionally, in some small cold-water cetaceans such as the harbor porpoise, Dall's porpoise (*Phocoenoides dalli*), the bottlenose dolphin (*Tursiops*

truncatus), and the beluga (*Delphinapterus leucas*), high concentrations of the very unusual branched short-chain isovaleric acid are biosynthesized and deposited in blubber (see earlier discussion). Isovaleric acid has an extremely low melting point of -37.6°C , which clearly provides fluidity to especially the outer blubber layer of these animals. Although the exact physiological function of isovaleric acid is not understood, its presence may contribute to the superior insulative properties observed previously in harbor porpoise blubber. In contrast to most other marine mammals, while manatees (*Trichechus* sp.) can also store large amounts of blubber, they generally do not tolerate temperatures below 20°C . As plant eaters, manatees must synthesize the majority of their blubber fatty acids, which would thus be restricted in their degree of unsaturation. However, little is known about the effectiveness of manatee blubber as an insulator in cold temperatures or the role that lipid composition might play in this ability.

III. Role of Blubber in Energy Storage and Water Balance

Blubber, as a rich energy store, is important in the lives of marine mammals because of the critical role that stored lipid plays in their ecology, reproduction, and survival. Perhaps surprisingly, even though marine mammals obviously live in the environment within which they also forage, reproduction and especially lactation are often spatially and temporally separated from their feeding grounds. For instance, the greatest areas of feeding activity for the large baleen whales are in polar regions during the high primary productivity of summers. However, they migrate in winter to warm tropical waters of low food availability to give birth and nurse their young. In phocid and otariid pinnipeds, parturition and lactation occur on land or ice and thus these activities are also separated from the feeding environment of the lactating female. Female polar bears spend the first 3–4 months of lactation in winter dens, without eating or drinking.

In all female mammals, lactation represents the greatest energetic cost of reproduction, requiring large amounts of nutrient transfer and elevated maternal maintenance costs. Hence, lactation is usually associated with increased maternal food consumption. However, because large energy reserves can be stored in blubber in the form of lipid, baleen whales and large phocid seals are the only mammals (besides holarctic bears) that can complete much or all of lactation without feeding. Again, because a smaller body size constrains the size of blubber stores, the smaller phocids and otariids are able to fast for only portions of lactation. All species of marine mammals produce high fat milks (usually 30–60% fat) to maximize the efficiency of fat transfer from maternal blubber into milk and the subsequent efficiency of neonatal fattening and growth. In species that fast throughout lactation, females switch almost completely to a fat-based metabolism. For instance, during a 16-day lactation period, a gray seal (*Halichoerus grypus*) female draws 97% of the energy required for her own metabolic needs and 90% of the milk energy supplied to her pup solely from her blubber stores. Furthermore, the extent to which she can both maintain lactation and produce a fat pup depends on the size of the blubber layer she starts out with (Mellish *et al.*, 1999). Fasting female polar bears use their extensive subcutaneous adipose tissue in a similar manner during the first months of lactation in winter dens.

Blubber deposition is equally critical to the suckling neonate, both for thermoregulation and to act as an energy reservoir. For

example, most newly weaned phocid pups rely on blubber deposited during the suckling period to survive their own subsequent fast of several weeks or months after their mothers have departed the breeding grounds. The energy supplied from blubber is critical to survival of the young while they learn how to forage on their own.

Adult males of many marine mammal species also fast or greatly reduce food intake during the breeding season and during their annual molting period. During these times they rely on stored lipid in blubber as their energy source. Sirenians also use blubber during fasting. For instance in the Amazon, manatees (*Trichechus inunguis*) face dry seasons of up to 6 months at a time, where low waters restrict them to the deep water areas of larger lakes where the aquatic plants they feed upon are unavailable. Hence, food intake during these periods is nil.

Finally, besides being an important fat and energy source for marine mammals, blubber is a critical source of water that is essential to maintaining water balance during fasting. Each kilogram of lipid that is mobilized from blubber and oxidized for energy use by an animal generates a net production of 1.07 kg of metabolic water. In fact, oxidation of blubber yields enough water such that individuals usually do not require an additional external source. This is true even of lactating females that are exporting large quantities of water in milk daily. For instance, a gray seal female exports about 23 kg of water in milk over a 16-day lactation period while fasting and has no external access to water during this time (Iverson *et al.*, 1993). Thus, in most species, blubber functions to maintain both water balance and energy metabolism during periods of fasting.

IV. Role of Blubber in Locomotion

Several forces act on animals swimming in fluids, and blubber plays a significant role in the way marine mammals deal with these forces. The predominant restrictive force is drag, but the vertical forces of gravity and buoyancy also exist. Drag is the force that resists the movement of a body through a medium and is much greater in seawater than in air due to seawater's higher density and greater viscosity. The single most effective way to reduce both drag and the power required for forward motion through a fluid is to have a smooth streamlined shape. Although all marine mammals tend to be somewhat streamlined in body shape as defined by their musculoskeletal system, blubber provides their form with a smooth sculpted contour. Blubber thickness is often distributed across an animal in a nonuniform manner that ensures this. For instance, the blubber over the hind end of a seal may be thicker than would be necessary for insulative purposes. The blubber layer here instead serves to taper the animal more gradually than would be dictated by the musculoskeleton. In fact, another very important means by which to reduce drag on a body is to be spindle-shaped, i.e., to have a gradually tapering tail end. This acts to reduce the wake left by the animal moving through the water and hence further reduces the forces of drag. Again, blubber creates this effect in cetaceans by a thickening and sculpting of the tailstock (Pabst *et al.*, 1999). This locomotor function may actually constrain the way in which animals utilize their blubber as energy reserves. In large baleen whales as well as the smallest harbor porpoise, blubber may be greatest in depth and fat content, even during nutritional stress, in the posterior dorsal and tail areas of the body (Lockyer, 1987; Koopman, 1998), as blubber in these areas serves important locomotory functions by both streamlining and possibly acting as a biomechanical spring, capable of temporarily storing and releasing elastic strain energy (Pabst, 1996).

Finally, blubber also plays a role in the buoyancy of marine mammals. Buoyancy is the force that acts on a body submerged in water where, if the mass of the body is greater or less than the volume of water it displaces, it will experience either a net downward or net upward force, respectively. In most marine mammals (except the sea otter), buoyancy will be determined primarily by the ratio of its adipose tissue to lean body tissue and body mass. Fat-filled adipose tissue is less dense than seawater, whereas lean tissue is more dense. Thus, the degree to which marine mammals store blubber will affect their buoyancy and thus the energy expended in moving or maintaining position in water. Although some newly weaned phocid pups may be positively buoyant at greater than 43% adipose tissue, most adult marine mammals will not be positively buoyant and thus are not likely to require any counteracting of this force when at the bottom of dives or when feeding at the benthos. However, changes in blubber stores will clearly affect the degree to which they are negatively buoyant. Studies have demonstrated that seals descend faster during diving when they are more negatively buoyant than when they are less negatively buoyant, providing evidence that seals adjust their diving behavior in relation to seasonal changes in buoyancy (Webb *et al.*, 1998; Beck *et al.*, 2000).

V. Insights from the Study of Blubber

Marine mammals are widely distributed in tropical, temperate, and cold oceans of the world and show a diversity of distributional patterns and apparent physiological adaptations. However, our understanding of these patterns, as well as of the foraging ecology of most marine mammals, is hindered by the difficulties in observing free-ranging animals that spend most or all of their lives at sea. Blubber is clearly of central importance to the structure and function of marine mammals. Due to the fact that blubber has evolved to serve complex functions, and yet the composition and amount of blubber carried by an individual can change rapidly, its study can provide unique insights into the lives of marine mammals as well as the ecosystems in which they live.

The ultrastructure, thickness, and proximate composition of blubber can provide insights into the feeding status of individuals as well as the functional significance of the blubber itself. As stated previously, the proximate composition, especially lipid content, of blubber changes radically in response to feeding and fasting behavior and thus, along with other nutritional indices, may be used to indicate nutritionally stressed vs robust individuals. Because many marine mammals go through predictable annual periods of fasting and fattening, the proximate composition of blubber can also be used to indicate the life cycle stage of an individual. In some cetaceans, the characteristics of blubber differ greatly across sites of the body and thus study of these properties can provide insight into the functions of blubber. For instance, the structure and composition of blubber at specific sites suggest that in some areas on the body (e.g., the thoracic-abdominal area), blubber may play a more important role in insulation and energy storage, whereas at other sites (e.g., the thick ridge posterior to the dorsal fin or at the caudal peduncle) blubber may serve more important roles in maintaining hydrodynamic shape and other locomotory functions (Koopman, 1998; Pabst *et al.*, 1999). Thus, the study of how blubber at these various sites is utilized during times of fat mobilization may provide further insight into adaptations of blubber structure. For example, the finding that blubber in the area of the caudal peduncle is rarely used and always thicker than needed for insulation, even during severe nutritional stress, lends support to the hypothesis that it may be more important in

that region for structural support and locomotory functions than as an insulator or energy provider.

Blubber can also provide insight into adaptation and phylogenetic relationships. For instance, the characteristic of storing blubber lipid primarily as wax esters appears to be confined to a group of the odontocetes (i.e., beaked whales and the sperm whale, *Physeter catodon*). The species in which blubber consists primarily of wax esters, although all closely related, are also all pelagic deep divers. Hence the study of their blubber may provide insight into phylogenetic patterns as well as roles that wax esters may play in deep diving animals (Koopman, 2007). The presence of isovaleric acid is likewise confined to a fairly restricted group of animals, which also may be under special thermal constraints (see earlier discussion). Thus the study of isovaleric acid in blubber may provide clues to its function and potential value in insulation. Additionally, in several species the presence of isovaleric in the outer layer of blubber increases in direct proportion with age, suggesting the possibility of using its level in blubber to estimate ages of unknown individuals in the same population (Koopman *et al.*, 2003).

Finally, the fatty acids in blubber can provide powerful insights into the foraging ecology and diets of both individuals and populations of marine mammals. As stated previously, fatty acids in the marine ecosystem are complex and diverse, fatty acids often travel up the food chain intact, and there are narrow limitations on their biosynthesis in marine mammals. Hence the fatty acids of marine mammal blubber arise in large part from dietary intake and therefore can be used to study aspects of diet and foraging ecology (Iverson, 1993). Given the dynamic nature of lipid mobilization and deposition in marine mammal blubber, fatty acids can provide insight into diets over both time and space. Studies on wild and captive animals demonstrate that there is direct deposition of dietary fatty acids in both marine mammals and their prey and that the influence of dietary fatty acid intake on blubber composition is both substantial and predictable, whether or not rapidly fattening (Iverson *et al.*, 1995; Kirsch *et al.*, 2000). Considered alone, fatty acids stored in a predator can provide powerful qualitative insight into spatial and temporal differences in foraging and diets of individuals and populations. However, recent advances have developed methods that use fatty acids in predators, along with their prey, to quantitatively estimate species composition of predator diets (Iverson *et al.*, 2004). Quantitative fatty acid signature analysis (QFASA) accounts for effects of predator metabolism on fatty acid deposition, and then determines the weighted mixture of prey species fatty signatures that most closely resembles that of the predator's fatty acid stores to thereby infer its diet. QFASA has been validated and used to estimate diets of free-ranging individuals in a number of pinniped species and the polar bear (Iverson *et al.*, 2004, 2006). A blubber biopsy (100–500 mg), or adipose tissue sample, from a free-ranging animal provides relatively non-invasive information about diet that is not dependent on prey with hard parts, nor limited to only the last meal, as are analyses of fecal or stomach contents. This is accomplished most easily in pinnipeds where, using a medical biopsy punch, one can safely obtain a complete sample through the full depth of 5–10 cm. However, in cetaceans, blubber is generally much thicker and layering of fatty acids in the blubber is more pronounced, with dietary fatty acids being most reflected in the inner and middle layers nearest the deep body core. Thus, less work has been done on live animals in these species. Nevertheless, QFASA is now being used to address broad ecosystem-scale processes and is providing new insight into foraging patterns and ecology of free-ranging marine mammals that would otherwise not be possible.

VI. Other Specialized Fats

In addition to blubber, several other unusual and specialized fat bodies exist that are unique to a single group of cetaceans, the odontocetes or toothed whales. These fat bodies occur in the forehead tissue (melon) and in and around the mandibles of the lower jaw (mandibular fats) and play important roles in hearing and echolocation. They are composed of a unique array of lipid classes and fatty acids that are likely synthesized with these head tissues (Koopman *et al.*, 2003, 2006). These unusual fats are believed to facilitate sound reception by acting in the melon to focus high frequency sound produced in the nasal passages, while in the mandibular fats, they are organized to form a channel to transmit received sounds to the ear. In all odontocetes examined, short- and branched-chain fatty acids appear to be concentrated in the center of the inner mandibular fat body and immediately adjacent to the earbones. Because sound travels more slowly through these types of fatty acids, this should cause sound entering an odontocete head to bend inwards and be directed to the ears (Koopman *et al.*, 2006). The unique arrangement of lipids within these fat bodies and their direct effect on sound transmission is an important area of current research.

In conclusion, blubber and other fats play a number of major roles in the lives of marine mammals. These fats can also be a powerful tool in trying to understand adaptive solutions of species living in marine environments as well as insights into their ecology and behavior.

See Also the Following Articles

Skeletal Anatomy ■ Swimming ■ Pinniped physiology

References

- Beck, C. A., Bowen, W. D., and Iverson, S. J. (2000). Seasonal changes in buoyancy and diving behaviour of adult grey seals. *J. Exp. Biol.* **203**, 2323–2330.
- Bowen, W. D., Oftedal, O. T., and Boness, D. J. (1992). Mass and energy transfer during lactation in a small phocid, the harbor seal (*Phoca vitulina*). *Physiol. Zool.* **65**, 844–866.
- Heath, M. E., and Ridgeway, S. H. (1999). How dolphins use their blubber to avoid heat stress during encounters with warm water. *Am. J. Physiol.* **276**, R1188–R1194.
- Iverson, S. J. (1993). Milk secretion in marine mammals in relation to foraging: Can milk fatty acids predict diet? *Symp. Zool. Soc. Lond.* **66**, 263–291.
- Iverson, S. J., Bowen, W. D., Boness, D. J., and Oftedal, O. T. (1993). The effect of maternal size and milk output on pup growth in grey seals (*Halichoerus grypus*). *Physiol. Zool.* **66**, 61–88.
- Iverson, S. J., Oftedal, O. T., Bowen, W. D., Boness, D. J., and Sampugna, J. (1995). Prenatal and postnatal transfer of fatty acids from mother to pup in the hooded seal. *J. Comp. Physiol.* **165**, 1–12.
- Iverson, S. J., Field, C., Bowen, W. D., and Blanchard, W. (2004). Quantitative fatty acid signature analysis: A new method of estimating predator diets. *Ecol. Monogr.* **74**, 211–235.
- Iverson, S. J., Stirling, I., and Lang, S. L. C. (2006). Spatial and temporal variation in the diets of polar bears across the Canadian arctic: Indicators of changes in prey populations and environment. *Symp. Zool. Soc. Lond.: Conservation Biology Series* **12**, 98–117.
- Kirsch, P. E., Iverson, S. J., and Bowen, W. D. (2000). Effect of diet on body composition and blubber fatty acids in captive harp seals (*Phoca groenlandica*). *Physiol. Biochem. Zool.* **73**, 45–59.
- Koopman, H. N. (1998). Topographical distribution of the blubber of harbor porpoises (*Phocoena phocoena*). *J. Mammal.* **79**, 260–270.
- Koopman, H. N. (2007). Phylogenetic, ecological, and ontogenetic factors influencing the biochemical structure of the blubber of odontocetes. *Mar. Biol.* **151**, 277–291.
- Koopman, H. N., Iverson, S. J., and Read, A. J. (2003). High concentrations of isovaleric acid in the fats of odontocetes: Variation and patterns of accumulation in blubber vs. stability in the melon. *J. Comp. Physiol.* **173**, 247–261.
- Koopman, H. N., Budge, S. M., Ketten, D. R., and Iverson, S. J. (2006). The topographical distribution of lipids inside the mandibular fat bodies of odontocetes: Remarkable complexity and consistency. *IEEE J. Oceanic Eng.* **31**, 95–106.
- Lockyer, C. (1987). Evaluation of the role of fat reserves in relation to the ecology of North Atlantic fin and sei whales. In “Approaches to Marine Mammal Energetics” (A. C. Huntley, D. P. Costa, G. A. J. Worthy, and M. A. Castellini, eds), pp. 184–203. Society for Marine Mammalogy Special Publication No. 1., Allen Press, Lawrence, KS.
- Mellish, J. E., Iverson, S. J., and Bowen, W. D. (1999). Individual variation in maternal energy allocation and milk production in grey seals and consequences for pup growth and weaning characteristics. *Physiol. Biochem. Zool.* **67**, 677–690.
- Pabst, D. A. (1996). Springs in swimming animals. *Am. Zool.* **36**, 723–735.
- Pabst, D. A., Rommel, S. A., and McLellan, W. A. (1999). The functional morphology of marine mammals. In “Biology of Marine Mammals” (J. E. Reynolds, and S. A. Rommel, eds), pp. 15–72. Smithsonian Institution Press, Washington, DC.
- Pond, C. M., Mattacks, C. A., Colby, R. H., and Ramsay, M. A. (1992). The anatomy, chemical composition, and metabolism of adipose tissue in wild polar bears (*Ursus maritimus*). *Can. J. Zool.* **70**, 326–341.
- Thiemann, G. W., Iverson, S. J., and Stirling, I. (2006). Seasonal, sexual, and anatomical variability in the adipose tissue composition of polar bears (*Ursus maritimus*). *J. Zool. (Lond.)* **269**, 65–76.
- Webb, P. M., Crocker, D. E., Blackwell, S. B., Costa, D. P., and Le Boeuf, B. J. (1998). Effects of buoyancy on the diving behavior of northern elephant seals. *J. Exp. Biol.* **201**, 2349–2358.
- Worthy, G. A. J., and Lavigne, D. M. (1983). Changes in energy stores during postnatal development of the harp seal, *Phoca groenlandica*. *J. Mammal.* **64**, 89–96.

Blue Whale

Balaenoptera musculus

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The blue whale is a baleen whale belonging to the family Balaenopteridae, which includes the group of cetaceans known as rorquals (Fig. 1). Common names are blue whale, sulfur-bottom, Sibbald's rorqual, great blue whale, and great northern rorqual. The largest animal known to have existed on Earth, it is found worldwide, ranging into all oceans (Yochem and Leatherwood, 1985).

I. Characteristics and Taxonomy

On average, Southern Hemisphere blue whales are larger than those in the Northern Hemisphere. The largest recorded were caught off the South Shetlands and South Georgia and were 31.7–32.6 m (104–107 ft) long. The largest recorded for the Northern Hemisphere was a 28.1-m (92-foot) female reported in whaling statistics from catches in Davis Strait. In the North Pacific females of 26.8 m (88 ft) and 27.1 m (89 ft) have been recorded. A 190-ton female was reported taken off South Georgia in 1947; however, body weights of adults generally range from 50 to 150 tons. For maximum size descriptions, female measurements are used because female baleen whales are larger than males.