

SPERM WHALE

Physeter macrocephalus

HAL WHITEHEAD

Sperm whales are animals of extremes. They have unusually large body sizes, sexual dimorphism, brain sizes, home ranges, dive depths, and dive times; they have an ecological role that may be unrivaled in the ocean; and their vocalizations, social structure, and historical relationship with humans are all remarkable.

A potential key to the sperm whale's simultaneous possession of a wide range of extreme biological attributes lies in a series of remarkable parallels with the African elephant, *Loxodonta africana* (Weilgart et al., 1996). These include large body sizes, brain sizes, substantial sexual dimorphism, similar life history variables, large ranges, remarkably congruent matrilineally based social systems, and breeding systems in which males roam between groups of females and generally only mate successfully when in their late twenties or older. The highly evolved spermaceti organ may have paralleled the trunk (another extreme nose) in allowing the animals efficient access to a wide range of resources. Meanwhile, in these animals, large sizes and cooperative societies gave efficient defense against predators, allowing long lives. Long, safe lives, in turn, promote the formation of significant long-term relationships among animals. Thus elephants and sperm whales evolved in highly social populations, near carrying capacity, and became dominant members of their ecological guilds. However, such animals are not well adapted to recovering from sudden depletion. Both the elephant and the sperm whale have been heavily influenced by humans, and, because their social structures are so important, exploitation has had consequences beyond animals killed directly.

I. Characteristics and Taxonomy

In 1758, Linnaeus described four sperm whales in the genus *Physeter*. It soon became clear that all refer to the same species, but there has been a long, and sometimes contentious, debate as to whether *Physeter catodon* or *Physeter macrocephalus* has precedence. Currently, most, but not all, authorities prefer *P. macrocephalus*.

The common name, "sperm whale," seems to have resulted from whalers misinterpreting the function of the spermaceti oil found in the massive forehead of the whale, or because cooled spermaceti has some physical resemblance to mammalian sperm.

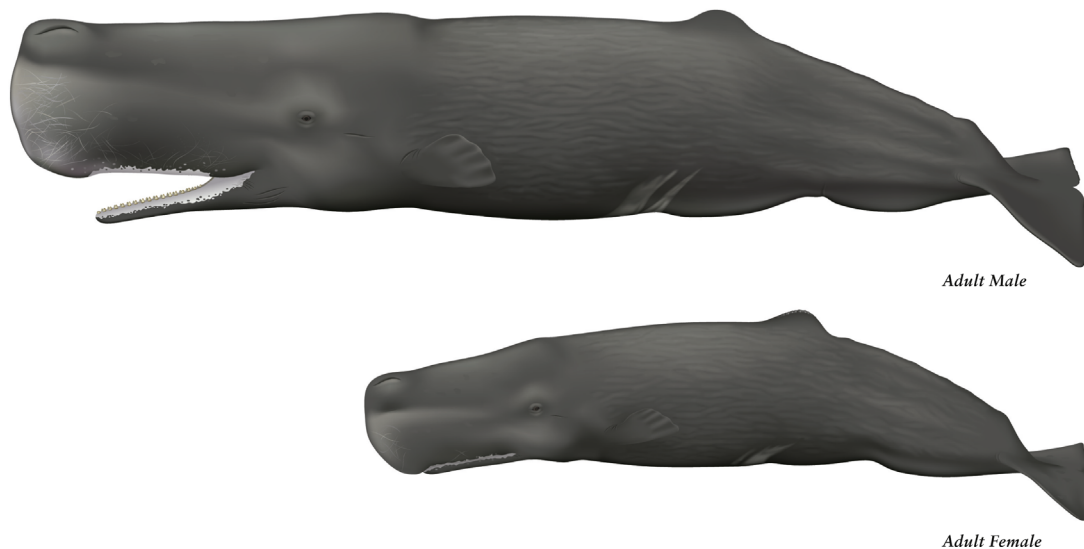
The closest living relatives of the sperm whale are the much smaller dwarf and pygmy sperm whales (*Kogia breviceps* and *Kogia sima*). Sperm whales seem to have separated from other odontocetes early in modern cetacean evolution, about 20–30 million years ago. See Sperm and Beaked Whales, Evolution for more information.

Sperm whales are the largest of the odontocetes (Fig. 1), and the most sexually dimorphic cetaceans in body length and weight. While adult females reach about 11 m in length and 15 t, a physiologically mature male is approximately 16 m and 45 t (Rice, 1989).

The most distinctive feature of the sperm whale is a massive nasal complex (Fig. 2; Ellis, 1980), one quarter to one-third of the length of the animal, situated above the lower jaw and in front of the skull (Cranford, 1999). It principally contains the spermaceti organ, which is enclosed in a muscular "case" (Fig. 2). This is a roughly ellipsoidal shaped structure made of spongy tissue filled with spermaceti oil and bounded at both ends by air sacs. Between the spermaceti organ and the upper jaws is the "junk," a complex arrangement of spermaceti oil and connective tissue. Spermaceti oil, which has the properties of a wax, differs chemically from the oils found in the "melons" of most other odontocetes.

There is considerable asymmetry in the parts of the skull and air passages that surround the spermaceti organ. This is externally manifested most clearly by a blow which is pointed forward and to the left from the tip of the snout. Compared with the blows of similarly sized baleen whales, the blow of a sperm whale is comparatively weak, low, and hard to see.

Behind the sperm whales skull lies a brain, which, together with that of the killer whale (*Orcinus orca*), is the largest brain of any animal (mean of 7.8 kg in mature male sperm whales) (Ridgway and Hanson, 2014). However, as a proportion of body size, the sperm whale's brain is not remarkable, and we have no direct information on the sperm whale's cognitive abilities, although its complex social system is consonant with those found in other cognitively advanced mammals.



Adult Male

Adult Female

Figure 1 Sperm whale, *Physeter macrocephalus* (Illustrations by Uko Gorter).

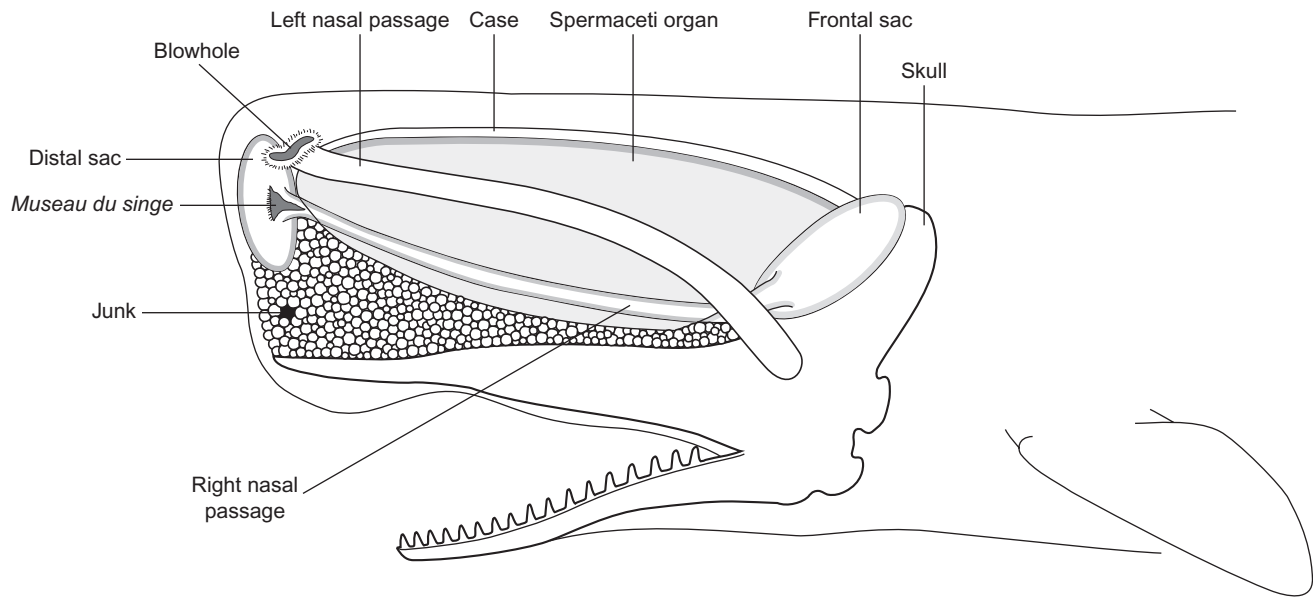


Figure 2 A diagram of the head of a sperm whale. From Ellis, R. (1980). *The book of whales*, Knopf, New York.

The sperm whale has 20–26 large conical teeth in each rod-like lower jaw. These teeth do not seem to be necessary for feeding, as they do not erupt until near puberty, and well-nourished sperm whales have been caught that lack teeth, or even lower jaws. The teeth in the upper jaw seem to be vestigial and rarely erupt.

Large corrugations cover most of the body behind the eye, but the surface of the head and the flukes are smooth. The majority of the body is dark gray in most sperm whales, but there is often a bright white lining to the mouth and sometimes white patches on the belly. The occasional sperm whale has larger white patches, especially in mature males, around the head. The flippers are relatively small and paddle shaped, and the flukes are fairly flat and triangular shaped. The dorsal fin is low, thick, and usually rounded. Especially in mature females, it may be topped by a white or yellowish rough callus. The dorsal ridge, behind the dorsal fin, consists of a series of large crenulations.

II. Distribution and Abundance

With the exception of humans and killer whales, few animals on Earth are as widely distributed as the sperm whale. They can be seen near the ice-edge in both hemispheres and are also common along the equator, especially in the Pacific. As with so many aspects of sperm whale biology, the sexes have very different distributions.

Although sperm whales have been sighted in most regions of deep water, there are some areas which the whalers called “grounds,” where they are more abundant. Many of the grounds coincide with areas of generally higher primary productivity, usually resulting from upwelling, although there are grounds in apparently unproductive waters, such as the Sargasso Sea (Jaquet, 1996).

Concentrations of a few hundred to a few thousand sperm whales can be found in areas a few hundred kilometers across characterized by a relatively high deep water biomass and usually situated within grounds. Sometimes aggregations of 50 or more sperm whales can be found within a few kilometers, presumably the result of concentrations of food.

Female sperm whales almost always inhabit water deeper than 1000m and at latitudes less than 40° (except 50°N in the North Pacific), corresponding roughly to sea surface temperatures greater

than 15°C (Fig. 3) (Rice, 1989). Although sometimes seen close to oceanic islands rising from deep ocean floors, most female sperm whales are far from land.

Young male sperm whales accompany the females in tropical and subtropical waters. On leaving their female relatives, sometime between 4 and 21 years of age, the males gradually move to higher latitudes: the larger and older the male, the higher the average latitude. Large males may be found near the edge of pack ice in both hemispheres, although they return to the warm water breeding grounds on an unknown schedule.

The large males of high latitudes can be found over almost any ice-free deep water, but, like the low latitude females, they are more likely to be sighted in productive waters, such as those along the edges of continental shelves. However, in some areas, such as off New York and Nova Scotia, the large males are sighted regularly in waters less than 300-m deep.

Extrapolation from surveys of sperm whale density that covered 24% of their global habitat suggests a current population of about 360,000 animals (CV = 0.36), down from a prewhaling population of about 1110,000 whales (Whitehead, 2002).

Information on stock structure in sperm whales is confused, but rather few differences have been found between animals in different ocean areas (Dufault et al., 1999). Studies of microsatellites indicate very little geographical differentiation in nuclear genes at any scales, whereas mitochondrial genomes are strongly differentiated by ocean basin, and in some cases by areas within ocean basins (Alexander et al., 2016). This reflects the presumed much wider movements of males, compared with females. There is remarkably low diversity worldwide in the mitochondrial genome (Alexander et al., 2013). Explanations for this feature (also found in pilot, *Globicephala* spp., and killer whales) include a historical population bottleneck, a demographic consequence of the result of these whales’ matrilineal social system, increased selection on the mitochondrial genome, or the indirect effects of selection of matrilineally transmitted cultural traits (see Culture and Social Learning). Indeed, the cultural division of sperm whales into clans (see below) seems more pronounced than any putative genetic or geographic stock structure (Rendell et al., 2012).

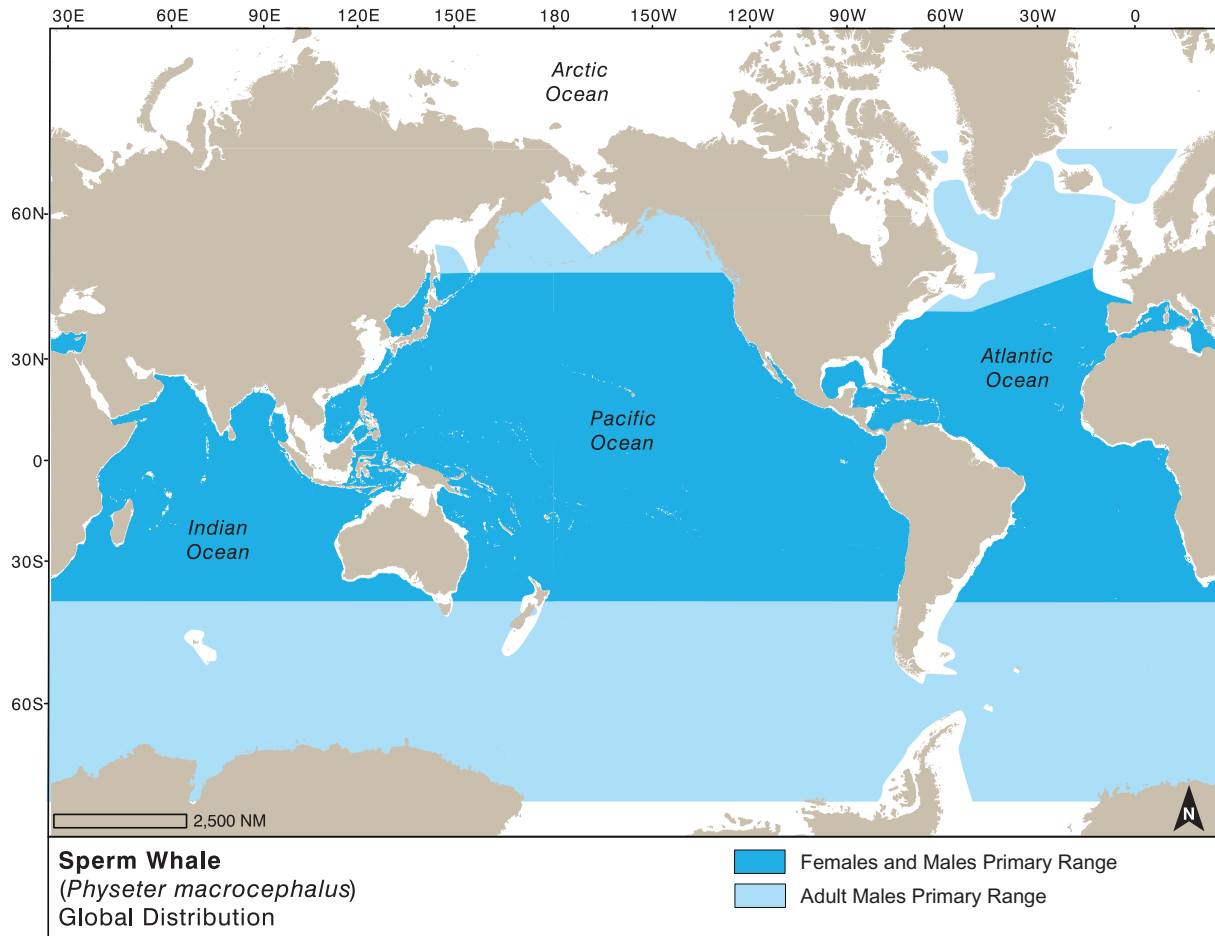


Figure 3 Sperm whale distribution. Adapted by Nina Lisowski from Jefferson, T.A., Webber, M.A. and Pitman, R.L. (2015). "Marine Mammals of the World: A Comprehensive Guide to Their Identification", 2e. San Diego, Elsevier.

III. Ecology

The sperm whale has a most catholic diet consisting of many of the larger organisms that inhabit the deeper regions of the oceans. Females appear to principally eat squids weighing between 0.1 and 10 kg. Favored taxa include *Ommastrephidae*, *Onychoteuthidae*, *Gonatidae*, *Pholidoteuthidae*, *Octopoteuthidae*, *Histioteuthidae*, and *Cranchiidae* (Kawakami, 1980). Of these, the histioteuthids, mesopelagic gelatinous pelagic cephalopods weighing about 0.1–1 kg, have featured at or near the top of the list of preferred food items in several studies of sperm whales. Females will eat much larger prey, such as the giant squid (*Architeuthis* spp.) and the jumbo squid (*Dosidicus gigas*), as well as noncephalopod prey, especially demersal and mesopelagic fish.

Males use the same squid taxa as females, but tend to eat larger individuals. Additionally, they eat species that are largely restricted to higher latitudes such as the colossal squid (*Mesonychoteuthis hamiltoni*) of Antarctic waters (Clarke, 1987) and are also more likely to eat demersal fish (including sharks, rays, and gadoids) than females. Off Iceland and in the northern Gulf of Alaska, their primary food is fish.

Sperm whales have competitors for many of these food items—beaked whale (Ziphiidae) and elephant seals (*Mirounga* spp.) also eat mesopelagic squid—and there may be important nonmammal predators of the species that the sperm whales use. For instance, the jumbo squid eats the smaller histioteuthid squids. Although

we know virtually nothing of the quantitative ecology of the deep ocean, sperm whales, because of their size and numbers, seem to dominate this trophic level in terms of biomass removed (Clarke, 1987; Whitehead, 2003). Rough estimates of the worldwide consumption of prey by the world's sperm whale population, about 100 million metric tons per year, are comparable with the current annual catch by all human marine fisheries. In the Southern Oceans where productivity is iron-limited, defecation by sperm whales may return iron to surface waters thus stimulating primary production and carbon uptake (Lavery et al., 2010).

Killer whales have been observed attacking sperm whales. They were usually unsuccessful, although at least one sperm whale was killed during a well-documented encounter off California (Pitman et al., 2001), and sperm whale remains have, very occasionally, been found in the stomachs of killer whales. Pilot whales have been seen harassing sperm whales on a number of occasions, but whether they are any real threat to the much larger sperms is uncertain. Large sharks are also potential predators, especially of young animals (Best et al., 1984).

IV. Behavior and Physiology

A. Vocalizations

The principal function of the spermaceti organ and its associated structures (the junk, air sacs and passages, and the *museau de singe* clapper system at the front of the organ) (Fig. 2) is to form,

and focus, the sperm whale's click making an extremely powerful ECHOLLOCATION system (Cranford, 1999; Möhl et al., 2000). The vocalizations of sperm whales consist almost entirely of clicks, although a few relatively quiet "squeals" and "trumpets" are made. The clicks are used both for foraging (see below) as well as social signals.

"Codas," stereotyped series of 3–20 clicks lasting 0.2–2 s, are heard in social situations (Watkins and Schevill, 1977). Groups of females are delineated clearly into clans by distinctive coda repertoires (Rendell and Whitehead, 2003). Coda repertoire is probably acquired culturally from within family units.

Whereas codas are heard principally from social females, another form of click, the "slow click" or "clang," in which distinctively ringing clicks are repeated every 6–8 sec, is largely or entirely produced by large males (Weilgart and Whitehead, 1988). The function of slow clicks is not clear, but they may attract females, repel other males, or be used to ECHOLLOCATE off other whales.

B. Movement

Scientists have studied the movements of sperm whales using photoidentification, satellite tags and artificial marks, as well as by following groups over periods of a few days (Whitehead, 2003). Sperm whales usually move through the water at about 4 km/hr. When feeding conditions are poor, their tracks are straight, resulting in daily displacements of about 90 km/day. However, when food is plentiful, the animals stay in much smaller areas 10–20 km across. Female home ranges seem to be generally of the order of 2000 km across. Some males roam more widely, but others are found quite consistently over several years in restricted coastal waters.

Migrations of the sperm whale are not as regular or as well understood as those of most baleen whales. In some midlatitudes there appears to be a general seasonal north–south migration, with whales moving poleward in summer, but, in equatorial and some temperate areas, there is no clear seasonal migration (Whitehead, 2003).

C. Social Structure

The life of a female sperm whale is overwhelmingly social. She is always in the company of other females, some of whom are her relatives. The basic element of sperm whale society is a family unit, consisting of about 10 females and their young (Whitehead, 2003). Most females spend their lives in the same unit, with their close female relatives. However, units may contain two or more matrilineal and there are recorded instances of females switching units. Two or more units may travel together for a few hours or days as a cohesive group of about 20 animals.

Units have preferred associations with other units, forming clans. These clans have distinctive sets of coda vocalizations as well as movement, foraging, and social behaviors (Cantor and Whitehead, 2015; Rendell and Whitehead, 2003; Whitehead and Rendell, 2004). In the Pacific several clans may be found in an area, whereas in the North Atlantic clans overlap less obviously (Gero et al., 2016).

Within the social units there is communal care for the young, with females suckling calves who are not their own offspring (Gero et al., 2013). Young sperm whale calves do not seem to be able to dive to foraging depths for as long as their mothers. Instead they remain at or near the surface, moving between the members of their group while they are breathing. This babysitting begins soon after birth. Members of groups with young calves seem to intentionally stagger their dives, thus providing better babysitting for the young (Whitehead, 1996).

When faced with predators, particularly killer whales, female sperm whales quickly cluster. Two defensive patterns have been described. In the "marguerite" or "wagon wheel" formation, the members of the group place their heads together at the hub, with the bodies radiating out like spokes. In contrast, when adopting the "heads-out" formation, the sperm whales face their attackers, tightly aligned in a rank, and seem to principally use their jaws for defense. Young calves stay toward the center of whichever defensive formation is adopted. Females have been observed risking themselves to assist unit members in peril during a killer whale attack (Pitman et al., 2001).

Young males leave their natal unit when between 4 and 21 years old and then are found in loose aggregations, sometimes called "bachelor schools," with other males of approximately the same size and age (Best, 1979). As the males age and grow they move to generally higher latitudes and the aggregation sizes become smaller, until the largest males are usually alone. Repeat association between males on more than 1 day is rarely observed (Letteval et al., 2002). However, mature and maturing males do strand on beaches together, suggesting significant social relationships on a scale not readily apparent to human boat-based observers.

The large mature males, in their late 20s and older, return to the tropical breeding grounds to mate, although the timing of such visits is largely unknown. When on the breeding grounds, the large males roam between groups of females, usually spending just a few minutes or hours with each (Whitehead, 2003). They are presumably searching for receptive females. There are no clear descriptions of mating itself. The breeding males seem to roam independently and generally avoid one another, although they are sometimes observed within the same group of females, and occasionally fight. These fights are rarely observed, but many large males have deep scars made by the teeth of other males.

D. Behavioral Modes

Sperm whales possess two quite distinct behavioral modes: foraging and social/resting (Whitehead and Weilgart, 1991). When foraging, the animals make repeated deep dives. Modal dives are to about 600 m and for about 45 min (Watwood et al., 2006), but dives can be much deeper (to over 1000 m), shallower (e.g., when in shelf waters 200 m deep), or longer. Between dives the whales come to the surface to breathe for about 9 min. The dive is usually signaled by the raising of flukes out of the water. The descent to depth, as well as the return to the surface, can be nearly vertical.

While foraging, sperm whales generally make regularly spaced clicks at intervals of 0.5–1.0 s, a searching sonar (Watwood et al., 2006). These are interrupted by creaks, consisting of clicks with accelerating rates, which are assumed to indicate short-range sonar during prey capture events (Miller et al., 2004). Small gelatinous squid, such as histioteuthids, are usually both relatively inactive and bioluminescent, so these can be captured using visual or acoustic cues. Larger, more muscular animals may need active chasing.

Groups of females and immatures spread out over 1 km or more of ocean when foraging, often forming a rank aligned perpendicular to the direction of travel. In contrast, males seem generally to forage independently.

Female and young sperm whales spend approximately 75% of their time foraging (Whitehead and Weilgart, 1991). However, during periods of several hours, often in the afternoon, they gather at or near the surface. At these times their behavior is highly variable. Sometimes the animals may lie still and quiet, closely clustered, for hours at a time, apparently resting (Fig. 4) (Miller et al., 2008).

Particularly at the start or end of nonforaging periods their behavior may be much more active, with breaches, lobtails, animals rolling, maneuvering and touching one another, and codas and creaks being emitted. Large males also lie quietly at the surface for long periods, but they are usually alone unless accompanying a group of females.

V. Life History

The sperm whale is the epitome of the “*K*-selected” mammal, one presumed to have evolved in an environment of competition for resources with members of its own species. It has a very low birth rate, slow growth, slow maturation, and high survival.

Young are born, almost always singly and with an equal sex ratio, at about 4 months following an approximately 14- to 16-month gestation (Best et al., 1984). Although sperm whales may eat solid food before their first birthday, they continue suckling for several years. The females reach sexual maturity at about age 9 years when roughly 9-m long, at which age growth starts to slow (Best et al., 1984). They give birth roughly once every 5 years,



Figure 4 Sperm whales in resting/social mode off the Galapagos Islands: one adult male surrounded by immatures and females (Photo courtesy of H. Whitehead lab).

although pregnancy rates have been found to vary between areas and in the same area at different stages of exploitation by humans. Female reproductive rates decline with age, and very few give birth after age 40 years. Females reach physical maturity when growth ceases, at about 30 years old and 10.6-m long.

Males, which are slightly larger than females during the first 10 years of life, continue to grow at a substantial rate until well into their 30s, finally reaching physical maturity at about 16-m long when roughly 50 years old. In males, puberty is prolonged, lasting approximately between ages 10 and 20 years old. However, males seem not to generally take much of an active role in breeding before their late twenties (Best, 1979).

Rates and causes of natural mortality are not well known. Longevity can be at least 50 years. Groups of females, males, or both, occasionally mass strand on shorelines, usually with fatal results for all members.

VI. Interactions With Humans

In the early 18th century, New Englanders began to hunt sperm whales for commercial purposes off their own shores. Over the next two centuries, sperm whaling grew to be a major worldwide industry (Ellis, 2011). By the 1830s, about 5000 sperm whales were being killed each year by whalers from several countries, especially the United States, and the oil produced was a vital element of the burgeoning industrial revolution (Starbuck, 1878). The whalers sailed all oceans of the world in their square-rigged ships. On sighting sperms, open whaleboats were lowered and rowed or sailed to the whales. The whalers threw harpoons into the animals, and then killed them using lances (Fig. 5; Beale, 1839). Dead animals were towed to the whale ship, where the oil was baled from the spermaceti organ, the BLUBBER stripped from the body and boiled to render the oil, and virtually all the remainder of the carcass discarded. In the 19th century, sperm whaling had become such a significant enterprise that it had important effects on fields as diverse as literature (Herman Melville's great novel “Moby Dick”) and ocean exploration. The open-boat hunt declined during the latter half of the 19th century because of the development of petroleum products as alternatives for sperm oil, an apparent decline in the sperm whale population, and for other reasons.

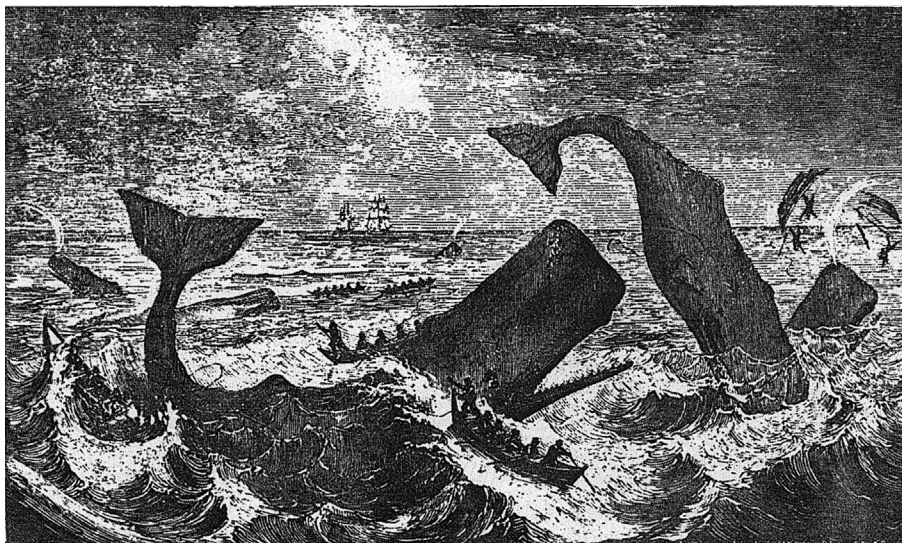


Figure 5 Open-boat sperm whaling. From Beale, T. (1839). *The natural history of the sperm whale*, John van Voorst, London.

After about 50 years of relative peace, the sperm whale populations were again hit hard following World War II. The whalers of the 20th century chased the sperm whales using mechanized catcher vessels equipped with sonar and killed them using explosive harpoons shot from harpoon guns. This whaling was also widely distributed and took a large number of sperms (up to 30,000 per year). However, unlike their earlier counterparts, the modern whalers used almost all of the whale, and preferentially targeted males. Much, but not all, of this whaling was carried out under the auspices of the International Whaling Commission (IWC). Sperm whale populations, particularly the male portions, were reduced substantially. Commercial sperm whaling declined in the 1970s and 1980s and virtually ceased with the IWC moratorium in 1988. Currently there is a small catch of sperm whales in Lamalera, Indonesia, using primitive methods and a “scientific” hunt for sperm whales by Japan which has taken 0–10 animals per year since 2000.

Nowadays most interactions between sperm whales and humans are more benign. Sperm whales are the principal subjects of whale-watching operations in several locations, including Kaikoura (New Zealand), Andenes (Norway), the Azores (Portugal), Sri Lanka, and Dominica (West Indies). Controversial “swim-with” tourism has recently been developed for sperm whales in some of these areas. Scientists study sperm whale behavior from small vessels in these and a few other locations.

The sperm whale has survived the onslaught of the whalers better than most other large whales. There are still a few hundred thousand sperm whales left in the ocean, sperm whale food is of little interest to human fishers, and their deep water home is further from most sources of pollution than the preferred habitat of most other marine mammals. However, sperm whales have very low reproductive rates even in the best of times—they do not recover quickly when depleted (Chiquet et al., 2013). Sperm whales are sensitive to some sources of anthropogenic noise (Harris et al., 2015). They are also killed inadvertently in a range of ways, including entrapment in fishing gear, choking on plastic bags, and collision with ships. The chemical pollution levels in their blubber are generally higher than that of baleen whales, but lower than in inshore odontocetes.

See Also the Following Articles

Beaked Whales, Overview ■ Cetacea, Evolution ■ Culture in Whales and Dolphins ■ Dental Morphology ■ Evolutionary Patterns ■ Pygmy and Dwarf Sperm Whales ■ Sexual Dimorphism ■ Whaling, Traditional

References

- Alexander, A., Steel, D., Hoekzema, K., Mesnick, S.L., Engelhaupt, D., Kerr, I., Payne, R., and Baker, C.S. (2016). What influences the worldwide genetic structure of sperm whales (*Physeter macrocephalus*)? *Mol. Ecol.* **25**, 2754–2772.
- Alexander, A., Steel, D., Slikas, B., Hoekzema, K., Carraher, C., Parks, M., Cronn, R., and Baker, C.S. (2013). Low diversity in the mitogenome of sperm whales revealed by next-generation sequencing. *Genome Biol. Evol.* **5**, 113–129.
- Beale, T. (1839). *The Natural History of the Sperm Whale*. John van Voorst, London.
- Best, P.B. (1979). Social organization in sperm whales, *Physeter macrocephalus*. In “Behavior of Marine Animals”, (H.E. Winn, and B.L. Olla, Eds), pp. 227–289. Plenum, New York.
- Best, P.B., Canham, P.A.S., and Macleod, N. (1984). Patterns of reproduction in sperm whales, *Physeter macrocephalus*. *Rep. Int. Whaling Comm. (Special Issue)* **6**, 51–79.
- Cantor, M., and Whitehead, H. (2015). How does social behavior differ among sperm whale clans? *Mar. Mamm. Sci.* **31**, 1275–1290.
- Chiquet, R.A., Ma, B., Ackleh, A.S., Pal, N., and Sidorovskaia, N. (2013). Demographic analysis of sperm whales using matrix population models. *Ecol. Modell.* **248**, 71–79.
- Clarke, M.R., 1987. Cephalopod biomass—estimation from predation. In “Cephalopod Life Cycles”, (P.R. Boyle, Ed.), pp. 221–237. Academic Press, London.
- Cranford, T.W. (1999). The sperm whale’s nose: Sexual selection on a grand scale? *Mar. Mamm. Sci.* **15**, 1133–1157.
- Dufault, S., Whitehead, H., and Dillon, M. (1999). An examination of the current knowledge on the stock structure of sperm whales (*Physeter macrocephalus*) worldwide. *J. Cetacean Res. Manage.* **1**, 1–10.
- Ellis, R. (2011). *The Great Sperm Whale: A Natural History of the Ocean’s Most Magnificent and Mysterious Creature*. University of Kansas Press, Lawrence, KS.
- Ellis, R. (1980). *The Book of Whales*. Knopf, New York.
- Gero, S., Böttcher, A., Whitehead, H., and Madsen, P. (2016). Socially segregated, sympatric sperm whale clans in the Atlantic Ocean. *R. Soc. Open Sci.* **3**, 160061.
- Gero, S., Gordon, J., and Whitehead, H. (2013). Calves as social hubs: Dynamics of the social network within sperm whale units. *Proc. R. Soc. B* **280**, 20131113.
- Harris, C.M., Sadykova, D., DeRuiter, S.L., Tyack, P.L., Miller, P.J.O., Kvadsheim, P.H., Lam, F.P.A., and Thomas, L. (2015). Dose response severity functions for acoustic disturbance in cetaceans using recurrent event survival analysis. *Ecosphere* **6**, 1–14.
- Jaquet, N. (1996). How spatial and temporal scales influence understanding of sperm whale distribution: A review. *Mamm. Rev.* **26**, 51–65.
- Kawakami, T. (1980). A review of sperm whale food. *Sci. Rep. Whales Res. Inst.* **32**, 199–218.
- Lavery, T.J., Roudnew, B., Gill, P., Seymour, J., Seuront, L., Johnson, G., Mitchell, J.G., and Smetacek, V. (2010). Iron defecation by sperm whales stimulates carbon export in the Southern Ocean. *Proc. R. Soc. B* **277**, 3527–3531.
- Letteval, E., Richter, C., Jaquet, N., Slooten, E., Dawson, S., Whitehead, H., Christal, J., and McCall Howard, P. (2002). Social structure and residency in aggregations of male sperm whales. *Can. J. Zool.* **80**, 1189–1196.
- Miller, P.J.O., Johnson, M.P., and Tyack, P.L. (2004). Sperm whale behaviour indicates the use of echolocation click buzzes “creaks” in prey capture. *Proc. R. Soc. Lond. B* **271**, 2239–2247.
- Miller, P.J.O., Aoki, K., Rendell, L.E., and Amano, M. (2008). Stereotypical resting behavior of the sperm whale. *Curr. Biol.* **18**, R21–R23.
- Möhl, B., Wahlberg, M., Madsen, P.T., Miller, L.A., and Surlykke, A. (2000). Sperm whale clicks: Directionality and source level revisited. *J. Acoust. Soc. Am.* **107**, 638–648.
- Pitman, R.L., Ballance, L.T., Mesnick, S.L., and Chivers, S.J. (2001). Killer whale predation on sperm whales: Observations and implications. *Mar. Mamm. Sci.* **17**, 494–507.
- Rendell, L., Mesnick, S.L., Dalebout, M.L., Burtenshaw, J., and Whitehead, H. (2012). Can genetic differences explain vocal dialect variation in sperm whales, *Physeter macrocephalus*? *Behav. Genet.* **42**, 332–343.
- Rendell, L., and Whitehead, H. (2003). Vocal clans in sperm whales (*Physeter macrocephalus*). *Proc. R. Soc. Lond. B* **270**, 225–231.
- Rice, D.W. (1989). Sperm whale. *Physeter macrocephalus* Linnaeus, 1758. In “Handbook of Marine Mammals”, (S.H. Ridgway, and R. Harrison, Eds), pp. 177–233. Academic Press, London.
- Ridgway, S.H., and Hanson, A.C. (2014). Sperm whales and killer whales with the largest brains of all toothed whales show extreme differences in cerebellum. *Brain Behav. Evol.* **83**, 266–274.
- Starbuck, A. (1878). *History of the American Whale Fishery From Its Earliest Inception to the year 1876*. Government Printing Office, Washington, DC.
- Watkins, W.A., and Schevill, W.E. (1977). Sperm whale codas. *J. Acoust. Soc. Am.* **62**, 1486–1490.

- Watwood, S.L., Miller, P.O., Johnson, M., Madsen, P.T., and Tyack, P.L. (2006). Deep-diving foraging behaviour of sperm whales (*Physeter macrocephalus*). *J. Anim. Ecol.* **75**, 814–825.
- Weilgart, L., Whitehead, H., and Payne, K. (1996). A colossal convergence. *Am. Sci.* **84**, 278–287.
- Weilgart, L.S., and Whitehead, H. (1988). Distinctive vocalizations from mature male sperm whales (*Physeter macrocephalus*). *Can. J. Zool.* **66**, 1931–1937.
- Whitehead, H. (2003). *Sperm Whales: Social Evolution in the Ocean*. Chicago University Press, Chicago, IL.
- Whitehead, H. (2002). Estimates of the current global population size and historical trajectory for sperm whales. *Mar. Ecol. Prog. Ser.* **242**, 295–304.
- Whitehead, H. (1996). Babysitting, dive synchrony, and indications of alloparental care in sperm whales. *Behav. Ecol. Sociobiol.* **38**, 237–244.
- Whitehead, H., and Rendell, L. (2004). Movements, habitat use and feeding success of cultural clans of South Pacific sperm whales. *J. Anim. Ecol.* **73**, 190–196.
- Whitehead, H., and Weilgart, L. (1991). Patterns of visually observable behaviour and vocalizations in groups of female sperm whales. *Behaviour* **118**, 275–296.

SPINNER DOLPHIN

Stenella longirostris

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The spinner dolphin, described by Gray in 1828, is the most common small cetacean in most tropical pelagic waters around the world. It can be seen at a great distance as it spins high in the air and lands in the water with a great splash.

I. Characteristics and Taxonomy

The spinner dolphin is identified externally by its relatively long slender beak, color pattern, and dorsal fin (Fig. 1) (Perrin, 1998). Four subspecies are currently recognized: the globally distributed *Stenella longirostris longirostris* (Gray's spinner, Fig. 2), the eastern tropical Pacific (ETP) endemics *Stenella longirostris orientalis* (eastern spinner, Fig. 3), and *Stenella longirostris centroamericana* (Central American spinner), and *Stenella longirostris roseiventris*, the dwarf spinner of central Southeast Asia (Perrin, 1990; Perrin et al., 1999). A form intermediate between Gray's spinner and the eastern spinner called "whitebelly spinner" occurs in a broad zone of hybridization and carries Y-chromosome alleles found in both subspecies (Andrews et al., 2013). Fig. 4 provides an overall worldwide map of distribution.

The skull can be confused with those of *Stenella coeruleoalba*, *Stenella clymene*, and *Delphinus* spp.; all have a relatively long and narrow dorsoventrally flattened rostrum, a large number of small slender teeth (about 40–60 in each row) (Perrin, 1998). It differs from the skull of *Delphinus* in lacking strongly defined palatal grooves.

The spinner dolphin is a member of the subfamily Delphininae. There are varying hypotheses of relationships among the delphinines (Perrin et al., 2013).

II. Distribution and Abundance

The spinner dolphin is pantropical, occurring in all tropical and most subtropical waters around the world between roughly 30–40°N and 20–40°S (Fig. 4, Jefferson et al., 2015). It is typically thought of as a high-seas species, but coastal populations and races/

subspecies exist in the eastern Pacific, Indian Ocean, Southeast Asia, and likely elsewhere (Perrin, 1998; Perrin et al., 1999).

Estimates of abundance exist for several regions (IUCN, 2016; Tyne et al., 2015a): whitebelly spinners in the ETP, about 800,000; eastern spinners in the ETP, about 600,000; northern Gulf of Mexico, about 12,000; Hawai'i, about 6,000; southern Sulu Sea, about 4000; and southeastern Sulu Sea, about 31,000.

III. Ecology

In the ETP, the habitat of the pelagic eastern subspecies is tropical surface water characterized by a shallow mixed layer, shoal and sharp thermocline, and relatively small annual variation in surface temperature (Balance et al., 2006). In other tropical waters, spinner dolphins are usually associated with islands and coasts, venturing out to deeper water at night to feed (Benoit-Bird and Au, 2003; Dolar et al., 2003; Karczmarski et al., 2005; Thorne et al., 2012). The Central American spinner inhabits shallower inshore water. Ecological niches defined mainly by surface temperature, depth, and other factors are sharply different among the *Stenella* species and other dolphins (Dolar et al., 2006; do Amaral et al., 2015).

In the eastern and western Pacific, the pelagic form has been shown to prey mainly on small mesopelagic fishes and squids, diving to 600 m or deeper (Perrin and Gilpatrick, 1994; Dolar et al., 2003), but a dwarf subspecies in inner Southeast Asia, *S. l. roseiventris*, consumes mainly benthic and reef fishes and invertebrates (Perrin et al., 1999). Predators include sharks, probably killer whales (*Orcinus orca*) and possibly false killer whales (*Pseudorca crassidens*), and pygmy killer whales (*Feresa attenuata*). Parasites may cause direct or indirect mortality.

IV. Behavior and Physiology

Why the spinner spins is unknown. It has been suggested that the large underwater bubble plume created by the violent spin and reentry may serve as an ECHOLLOCATION target for communication across a widely dispersed school (Norris et al., 1994).

School size varies greatly, from just a few dolphins to a thousand or more. Social organization in Hawaiian waters is fluid, with schools composed of more or less temporary associations of family units; the associations may vary over days or weeks (Norris et al., 1994). Genetic and social structure of schools are flexible traits that can vary between even closely related populations (Andrews et al., 2010). Maximum recorded movements of individuals are 113 km (over 1220 days) in Hawai'i and 275 nmi (over 395 hr) in the eastern Pacific (Perrin, 1998).

V. Life History

Gestation is about 10 months. Average length at birth is about 75–80 cm. Length of nursing is 1–2 years. Calving interval is about 3 years. Females attain sexual maturity at 8–9 years (Larese and Chivers, 2009) and males at 7–10 years (Perrin, 1998). Breeding is seasonal, more sharply so in some regions than in others. The mating system may vary among populations. This is indicated by geographic variation in morphology and testis size. For example, in the ETP eastern spinners are more sexually dimorphic and have smaller testes than whitebelly spinners, likely indicating a greater tendency toward polygyny as opposed to polygynandry (promiscuous mating) (Perrin and Mesnick, 2003).

VI. Interactions With Humans

Large numbers have been killed incidentally since the early 1960s by tuna purse seiners in the ETP; the population of *S. l. orientalis* is estimated to have been reduced to less than one-half of its original size (Wade et al., 2007). Continued chase and capture in the