recruitment – and progress is currently in hand to integrate these into the overall management process.

Recent papers have linked variations in krill distribution and standing stock to climate change and El Nĩno–Southern Oscillations through their effects on the ACC and sea ice regime. The CCAMLR management scheme implicitly takes account of such long-term environmental change because its regime can be adjusted to compensate as the monitored species and variables change with time.

See also

Crustacean Fisheries. Current Systems in the Southern Ocean. International Organizations. Krill. Marine Mammals, History of Exploitation.

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SPERM WHALES AND BEAKED WHALES

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Introduction

Sperm whales and beaked whales are among the largest and most enigmatic of the odontocetes (toothed whales). These species tend to live far offshore in regions of deep water, and perform long, deep dives in search of their squid prey. This has generally made the study of these animals much more difficult than that of more accessible, nearshore cetacean species. In addition, the pygmy and dwarf sperm whales, and many species of beaked whale, have superficially similar external morphology, and so are often difficult to identify to species level in the wild. The study of many of these species has therefore been based primarily on examination of stranded and beachcast animals. As a result, we currently know little about many of these relatively large mammals. For example, one species of beaked whale, Longman's beaked whale, has been identified only from two skulls in Australia and Somalia. Another putative species, *Mesoplodon* species 'A' has only ever been observed at sea, and knowledge of its morphological characteristics remains far from complete. New species of beaked whales are still being discovered. For example, the pygmy beaked whale and Bahamonde's beaked whale were only identified in the last decade from specimens collected in Peru and Chile, respectively. Likewise, the dwarf and pygmy sperm whale were only recognized as separate species in the 1960s.

The sperm and beaked whale species about which we know most are the sperm whale, the northern bottlenose whale and Baird's beaked whale. Much of the information about these species has come from scientific research programs conducted in conjunction with historic whaling operations. Longer-term, nonlethal studies of wild populations only began in the early 1980s. These focused initially on sperm whales, and today include research on populations of northern bottlenose whales and dense-beaked whales. Such studies help provide important behavioral information about these species which was previously not available from studies of dead animals.

Taxonomy and Phylogeny

There are three superfamilies within the odontocetes: the Physeteroidea (sperm whales), the Ziphioidea (beaked whales), and the Delphinoidea (river dolphins, oceanic dolphins, porpoises, and monodontids). The superfamily Physeteroidea encompasses two families: the Physeteridae which contains the sperm whale, and the Kogiidae which contains the pygmy sperm whale and the dwarf

Table 1 Sperm and beaked whale species, approximate demographic distribution and size

Species		*General location*	*Adult size* (m)	*Notes*
Family Physeteridae				
Sperm whale	*Physeter macrocephalus*	Global	12–18	
Family Kogiidae				
Dwarf sperm whale	*Kogia simus*	Tropical and temperate oceanic	2.7–3.4	
Pygmy sperm whale	*Kogia breviceps*	Tropical and temperate, continental shelf and slope	Up to 2.7	
Family Ziphiidae				
Baird's beaked whale	*Berardius bairdii*	North Pacific	11.9–12.8	
Arnoux's beaked whale	*Berardius arnuxii*	Southern Ocean	Up to 9.7	
Cuvier's beaked whale	*Ziphius cavirostris*	Global, common in eastern tropical Pacific	7–7.5	
Northern bottlenose whale	*Hyperoodon ampullatus*	North Atlantic	8.7–9.8	
Southern bottlenose whale	*Hyperoodon planifrons*	Southern Ocean	7.2–7.8	
Tropical bottlenose whale	*Hyperoodon* sp.	Tropical Indian and Pacific Oceans	4–9	Sightings only
Shepherd's beaked whale	*Tasmacetus shepherdi*	Southern temperate	6.6–7	Few stranded specimens
Longman's beaked whale	*Indopacetus pacificus*	Australia, Somalia	Over 6	Two skulls
Blainville's beaked whale	*Mesoplodon densirostris*	Temperate global	Up to 4.7	
Gray's beaked whale	*Mesoplodon grayi*	Southern temperate circumglobal	Up to 5.6	
Ginkgo-toothed beaked whale	*Mesoplodon ginkgodens*	Temperate/tropical Indian and Pacific Oceans	Up to 4.9	
Hector's beaked whale	*Mesoplodon hectori*	Southern temperate, extralimital in S. California	4.3–4.4	
Hubbs' beaked whale	*Mesoplodon carlhubbsi*	North Pacific	Up to 5.3	
Sowerby's beaked whale	*Mesoplodon bidens*	Northern North Atlantic	5.1–5.5	
Gervais' beaked whale	*Mesoplodon europaeus*	Temperate/tropical Atlantic	4.5–5.2	
True's beaked whale	*Mesoplodon mirus*	Temperate N. Atlantic and temperate Southern Ocean	Up to 5	
Strap-toothed beaked whale	*Mesoplodon layardii*	Southern temperate	5.9–6.2	
Andrews' beaked whale	*Mesoplodon bowdoini*	South Indian and Pacific Oceans	4.6–4.7	
Stejneger's beaked whale	*Mesoplodon stejnegeri*	North Pacific	Up to 5.3	
Pygmy beaked whale	*Mesoplodon peruvianus*	Eastern tropical Pacific	Up to 3.7	Few strandings; tentative sightings
Bahamonde's beaked whale	*Mesoplodon bahamondii*	Peru	Estimated 5–5.5	Partial skull
Mesoplodon species 'A'	*Mesoplodon sp.*	Eastern tropical Pacific	5.5	Sightings only

Compiled from Jefferson *et al.*, 1993.

sperm whale. The Ziphioidea encompasses only the family Ziphiidae, which includes at least 20 species of beaked whales (**Table 1**).

Although some genetic studies have challenged the relationship of the sperm whales to other toothed whales, the analytical methods used to determine this have been questioned, and there is general agreement between morphological and other molecular data that the sperm whales and beaked whales are basal odontocetes (**Figure 1**). Physeterids appeared in the fossil record in the early Miocene deposits of Argentina (approximately 25–30 Ma). In the past this family included a diverse array of genera, but today it is represented only by the sperm whale. The kogiids are thought to have diverged from the physeterids in late Miocene and early Pleiocene (approximately 5–10 Ma). The earliest ziphiids have been found in deposits from the middle Miocene (10–15 Ma). Relationships among the beaked whales are not clear. The six genera in this family have previously been separated into two tribes grouping *Berardius* and *Ziphius*, and grouping *Tasmacetus*, *Indopacetus*, *Hyperoodon* and *Mesoplodon*. However, it has also been suggested that *Tasmacetus*, with a full set of teeth in upper and lower jaws, may be the sister group to all other

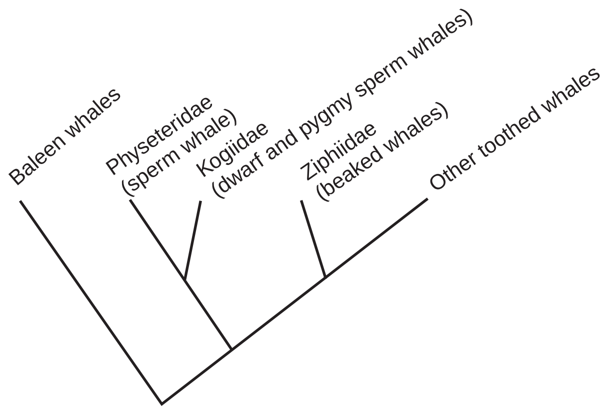

Figure 1 Phylogenetic diagram showing relationship of sperm whales and beaked whales to other cetaceans. (Based on Heyning, 1997.)

living species. Current work investigating the systematics of this group by DNA sequence data should shed further light on their phylogenetic relationships.

Anatomy and Morphology

Beaked whales are characterized by the possession of a long and slender rostrum resulting in a prominent beak in most species. An evolutionary trend in ziphiids has led to the reduction in number of teeth in all genera except *Tasmacetus*. Most species have retained only one or two pairs of teeth, set in varying positions in the lower jaw (**Figure 2**). In most beaked whale species these teeth only erupt in adult males. From observations of scarring patterns on the animals, these teeth appear to function as weapons in intra-specific combat, and have become much enlarged in some species. Other features which distinguish beaked whales from other groups include the possession of two conspicuous throat grooves or creases which form a forward-pointing V-shape, and the lack of a notch in the flukes. The skull morphology of beaked whales is also unique, exhibiting elevated maxillary ridges behind the nasals.

The Physeteroidea are characterized by several features of the skull, including a large supracranial basin. This basin holds the 'spermaceti organ', a fat-filled structure, which lies behind the melon in the forehead, and is unique to these species. This structure was named for the presence of spermaceti, an oily substance thought to resemble semen (after which it was named). It is generally thought that this organ functions in sound transmission.

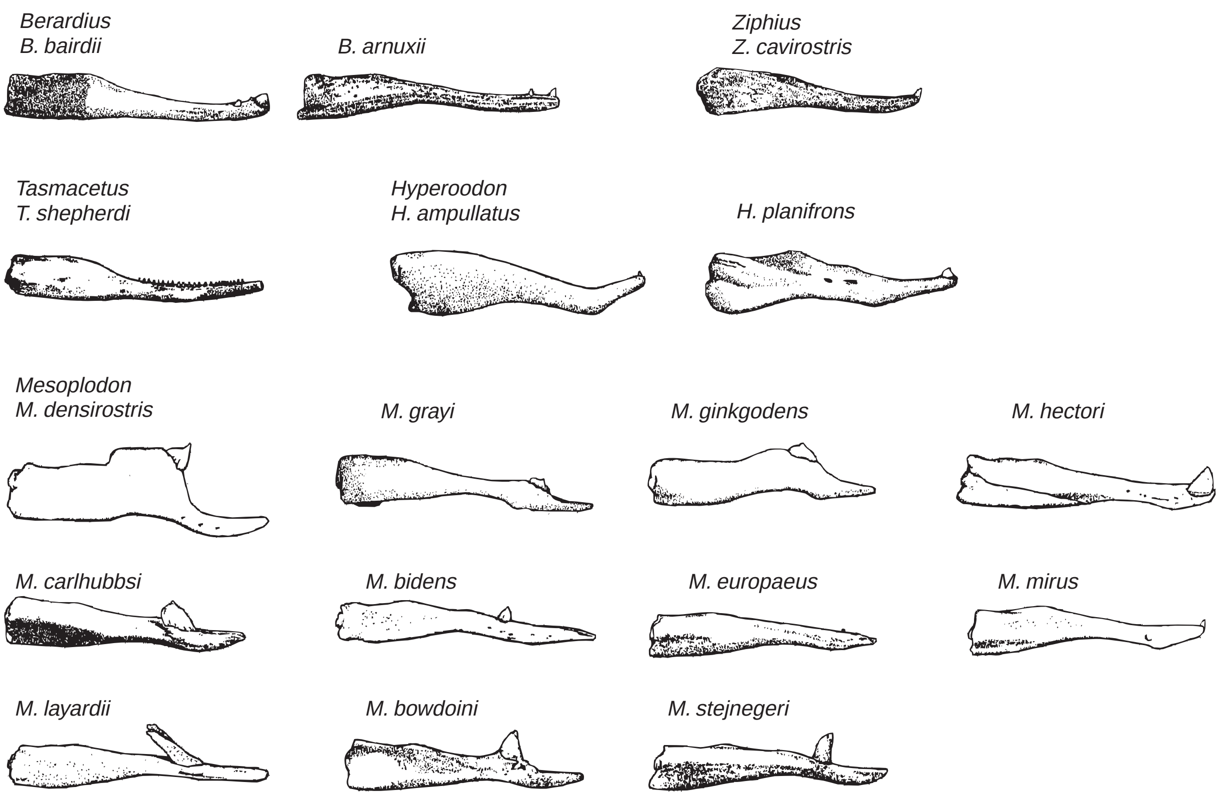

Figure 2 Variation in position, size, and morphology of the lower jaw teeth of adult male beaked whales shown for the majority of recorded beaked whale species. (Reproduced with permission from Jefferson *et al.*, 1993.)

Externally, sperm whales can be differentiated from other species by their narrow lower jaw, and an upper jaw which extends well past the lower. This group also has reduced dentition compared with many other odontocetes. The sperm whale has teeth (18–25 pairs) only in the lower jaw. The dwarf and pygmy sperm whales have reduced numbers of teeth in the lower jaw (generally 12–16 pairs in the pygmy sperm whale, and 8–11 pairs in the dwarf sperm whale). Some teeth may be present in the upper jaw of both dwarf and pygmy sperm whales, although this is less common in the pygmy sperm whale.

The sperm whales show highly pronounced asymmetry of the skull. Most beaked whale species also have asymmetrical skulls, although *Berardius* and *Tasmacetus* have nearly symmetrical cranial characteristics. This suggests that such symmetry is the ancestral characteristic and that cranial asymmetry in beaked whales has evolved independently from that in sperm whales.

Distribution and Abundance

All sperm whales and beaked whales are deep-water oceanic species. However, there is wide variation in species coverage. The sperm whale is found throughout the world's oceans, from the tropics to the poles. The pygmy and dwarf sperm whales also have fairly cosmopolitan distributions, and are found in temperate and tropical waters worldwide. In contrast, many beaked whale species have quite limited distributions and only two species, the dense-beaked whale and Cuvier's beaked whale, show similar ranges to the sperm whales (**Table 1**). Many other beaked whale species are limited to a single ocean basin, and several species pairs show an antitropical distribution, e.g. *Hyperoodon* species (*H. ampullatus* in the North Atlantic and *H. planifrons* in the Southern Ocean) and *Berardius* species (*B. bairdii* in the North Pacific and *B. arnuxii* in the Southern Ocean).

There are very few estimates of abundance for sperm and beaked whales. Many of these species are difficult to detect and identify at sea, and so are probably more common than sighting records would suggest. The status of all sperm and beaked whales as currently listed by the IUCN (International Union for the Conservation of Nature) Red Book is 'insufficiently known'.

Foraging Ecology

The majority of sperm and beaked whales are thought to feed primarily on squid. The reduced dentition of these species is thought to be due to this dietary specialization. One exception to this is Shepherd's beaked whale, in which both sexes possess a full set of functional teeth, and the diet appears to consist primarily of fish.

The reduced dentition of the beaked whales, together with their narrow jaws and throat grooves, have been suggested to function in suction feeding. Among the males of species such as the strap-toothed whale, the elaborate growth of the strap-like teeth may limit the aperture of the gape to a few centimeters, and it is difficult to see how prey capture techniques other than suction feeding could be successful. The same mechanism is thought to be used by sperm whales, which also have a comparatively small mouth area. Anecdotal evidence suggests that the lower jaw teeth of the sperm whale are not required for feeding, as apparently healthy animals have been seen with broken and badly set lower jaws resulting from past injuries.

Sperm whales and beaked whale species are known to be excellent divers. Dives of up to an hour have been recorded from several beaked whale species, although many of these records have been based on surface observations of diving whales. Similarly dives of up to 25 minutes have been recorded from *Kogia* species. Two studies have used time-depth recorders to monitor dives in more detail from these species. Acoustic transponder tags on two sperm whales recorded repeated dives to depths of 400–600 m (including a dive to 1185 m), for durations of 35–45 minutes. Similarly deployments of time-depth data loggers on two northern bottlenose whales showed regular dives to depths of over 800 m (maximum 1452 m) for durations of 30–40 minutes (maximum 70 minutes), with dives approximately every 80 minutes. Both these species are thought to forage at these depths in search of deep-water squid.

The similarity of ecological niches among beaked and sperm whales might be expected to lead to competition between these species. The relatively discrete distributions of many beaked whale species may have resulted from this. For example, several *Mesoplodon* species coexist in the North Atlantic, but have separate centers of distribution, with little overlap in range: Sowerby's beaked whale has a more northerly distribution than True's beaked whale, which in turn is found to the north of Gervais' beaked whale. On a much smaller spatial scale, there is some suggestion of competitive exclusion between sperm whales and northern bottlenose whales in habitat use of a submarine canyon area off eastern Canada. Prey species (mainly squid) identified from the stomachs of stranded *Kogia* specimens suggest that these species occur primarily along the continental shelf and slope in the epi- and meso-pelagic zones. Although the diets of both species overlap, the relative contribution of prey types suggests that the dwarf sperm whale feeds on smaller squid in shallower waters and thus occurs further inshore than the pygmy sperm whale.

Social Organization

The social organization of the majority of sperm and beaked whale species is poorly known, with the exception of the sperm whale. The social system of the sperm whale appears quite unlike that known for other cetaceans. Groups of females and juveniles are found in temperate and tropical latitudes (**Figure 3**). Males become segregated from these female groups at or before puberty, and migrate to higher latitudes. Younger males are found in 'bachelor schools', which consist of animals of approximately the same age. These schools decrease in size with increasing age of the members, to the point at which large mature animals are typically solitary. Sexually mature males return to the tropical waters inhabited by females in order to breed. There, these males were traditionally viewed as 'harem masters', each remaining with a single group of females throughout the breeding season. However, recent mark-recapture data, relative parasite loads, and indications of synchronous estrus suggest that instead, males rove between groups of females, and remain with any one group for only a few hours, although they may revisit groups on consecutive days.

Female sperm whales are found in groups of 20 or so individuals. These groups appear to consist of two or more stable units that associate for periods of approximately 10 days. Genetic evidence has suggested that these groups are composed of one or more matrilines. However, there are also suggestions of paternal relatedness between grouped matrilines, and recent photo-identification studies suggest that some animals occasionally switch groups, and thus may not be of the same maternal lineages as other group members.

Whalers observed that sperm whale groups often exhibited epimeletic behavior, with individuals supporting and staying with harpooned, injured, and even dead group members. It is thought that this may be a result of the close genetic ties between the individuals in a group. Sperm whales have also been observed to exhibit allomaternal care (babysitting behavior). Calves remain on the surface when a group is feeding, presumably since they are unable to dive to the depths at which adults forage, and

Figure 3 Group of female and juvenile sperm whales off the Galapagos Islands. (Photograph by Sascha K. Hooker.)

adults have been observed to stagger their dives such that it is more likely for there to be an adult at the surface with the calf, and the proportion of time that the calf is alone is reduced.

Observations of wild *Kogia* suggest that they typically form small groups of one to four animals, with occasional groups of up to 10 reported. However, almost nothing is known of the composition of these groups or of the behavior of these species at sea.

Many beaked whale species appear to show intra-specific aggression between adult males, presumably for access to females. The prominent and elaborate teeth of many beaked whale species are thought to be used in this male–male conflict (**Figure 2**), resulting in the extensive scarring seen on adult males. However, in other beaked whale species, males possess only comparatively small lower jaw teeth, and these do not appear to be used for fighting. The northern bottlenose whale is an example of this. Instead this species shows marked sexual dimorphism in skull structure and associated forehead or melon shape, which is relatively small in females, but is enlarged and flattened in adult males. Recent observations have suggested that this melon morphology is also associated with male–male competition, as adult males have been observed to head-butt each other.

Among beaked whales, the composition of social groups is not well known. The two beaked whales for which most data have been collected are the northern bottlenose whale and Baird's beaked whale. Long-term photo-identification studies of individual bottlenose whales have in fact suggested stronger associations between males than between females. However, the aggression observed between some associated males makes further interpretation difficult. Anatomical studies of groups of Baird's beaked whales taken in the continuing fishery off Japan are suggestive of a different type of social structure for this species. Among this species, both males and females possess erupted teeth, and females are slightly larger than males. Males appear to reach sexual maturity at an average of 4 years earlier than females and may live for up to 30 years longer. This has led to speculation that males may be providing parental care in this species, although further work is needed to confirm this.

Acoustics, Sound Production, and Sound Reception

The acoustic behavior of sperm whales is relatively well documented. These whales produce broad-band clicks in the frequency range of 1–12 kHz. These clicks are thought to function primarily in echolocation, although some repetitive patterned clicks (termed codas) also appear to be used in a social context. Adult male sperm whales also produce especially loud resonant clicks (termed 'clangs') that may function in female choice or as a threat to other males. Neither *Kogia* species appears to be highly vocal, although high-frequency clicks have been recorded from the pygmy sperm whale. The social whistles characteristic of other odontocete species are absent from the physeterids, and may be absent from some beaked whale species, although they have been recorded in others. No whistles were documented in several hours of recordings from northern bottlenose whales, which appear to produce primarily echolocation-type clicks instead. These were superficially similar to sperm whale clicks, although often at ultrasonic frequencies ($\sim$20–30 kHz). Recordings made from Baird's beaked whale and Arnoux's beaked whale included frequency-modulated whistles, burst-pulse clicks, and discrete clicks in rapid series. Only a few other records of beaked whale acoustic behavior exist and the majority of these were obtained from stranded animals.

The sound production mechanism used by both sperm and beaked whales for echolocation is homologous with that of other odontocetes, consisting of a sound-producing complex (the 'monkey lips'/dorsal bursae) in the upper nasal passages. Sound is thought to propagate into the water through the melon, a low-density lipid-filled structure which has been hypothesized to act as an acoustic lens to focus high-frequency sound ahead of the animal. The echoes of this sound are then thought to be received via the fat body in the lower jaw which connects with the bulla of the middle ear.

The sperm whale head is unique in comparison with other odontocetes in that the blowhole and sound production mechanism is situated at the front of the head rather than above the eyes. The signal generated is reverberated within the front of the head, generating a decaying series of pulses, with the time interval between these pulses related to the size of the head. It is thought that female sperm whales may select males based on this inter-pulse interval (indicating the size of the male). The extreme sexual dimorphism seen in male sperm whales in both the increased ratio of head to body size in addition to the overall much larger size of adult males (up to 18 m length compared with up to 12 m length of adult females) may therefore be based on this selection pressure associated with the sound production mechanism.

Predation

It was previously thought that large size was adequate defense against predators, but female sperm whales (of 10–12 m) have been observed under lethal attack by *transient* (mammal-eating) killer whales. Additionally large sharks are thought to be a threat to these species, and particularly to juvenile animals. Various methods of defense may be employed. For such a deep-diving species, it is surprising that deep dives are not used as a method of escape from predators. This may be because young calves are unable to dive to the depths or for the same duration as adults. Instead sperm whales appear to show a behavioral response to the threat of predation and form a 'marguerite', with the adults forming a circle (heads innermost) around the calves.

Pygmy and dwarf sperm whales evacuate reddish-brown intestinal fluid when startled, in a similar manner to squids. The lower intestine is expanded in both species, forming a balloon-like structure filled with up to 12 liters (in large specimens) of this liquid. Additionally, these species possess a crescent-shaped light-colored mark, often called a 'false gill', on the side of the head behind the eye and before the flippers. Along with the underslung mouth, this can lead to the mistaken identification of these animals as sharks. However, whether this patterning functions as camouflage against predation is unknown.

Conservation

The larger species of sperm and beaked whales were all targeted by whaling operations in the past. The sperm whale was the most heavily hunted, primarily due to the prized spermaceti oil that it contained. This fishery spanned the seventeenth to twentieth centuries and at its peak (in the 1960s) average annual catches reached 25 000 animals. Northern bottlenose whales were also quite severely depleted by whaling. The northern bottlenose whale fishery began in the late nineteenth century and between 1880 and 1920 approximately 60 000 bottlenose whales were caught. The other species in this group which has been taken in relatively large numbers is Baird's beaked whale. This species has been hunted in Japan since at least the seventeenth century, but has generally been taken in relatively low numbers (a maximum annual catch of 322 in 1952, but recently averaging 40 whales per year). This fishery still continues today.

Current threats faced by these species range from other factors potentially causing immediate death, such as ship-strikes, to the more insidious threats of ocean plastic, chemical, and acoustic pollution. Since many sperm and beaked whales feed primarily on squid, they are very susceptible to the ingestion of plastics, apparently mistaking it for prey. Stranded animals from several sperm and beaked whale species have been found with plastic in their stomachs and in some cases, this appears to have blocked the normal function of the stomach, causing severe emaciation and probably contributing to their death. The ecological role of odontocetes as long-lived top predators also exposes these animals to increased levels of chemical pollutants. Cetaceans store energy (and pollutants) in their blubber, and have a lower capacity to metabolize some PCB isomers than many other mammals. Foreign and toxic substances are therefore often biomagnified in odontocete species, and even species living offshore in relatively pristine environments have been found to contain high levels of pollutants. These high pollutant levels can have two major effects: (1) inhibition of immune system capacity to respond to naturally occurring diseases, and (2) potentially causing reproductive failure.

There is also increasing concern about the effect of anthropogenic noise in the marine environment. Sperm whales and beaked whales appear to be particularly susceptible to the effects of such noise. Sperm whales have been observed to react to several types of underwater noise including sonar, seismic activity, and low-frequency sound. Beaked whales also appear to be susceptible to high-intensity underwater sound. Several beaked whale stranding events appear to have coincided with military naval exercises, and associated increased noise levels. As sound seems essential to their foraging and social behavior, increasing levels of underwater noise are therefore of particular concern for these species.

See also

Bioacoustics. Marine Mammal Diving Physiology. Marine Mammal Evolution and Taxonomy. Marine Mammal Migrations and Movement Patterns. Marine Mammal Overview. Marine Mammal Social Organization and Communication. Marine Mammal Trophic Levels and Interactions. Marine Mammals, History of Exploitation.

Glossary

echolocation the production of high-frequency sound and reception of its echoes, used to navigate and locate prey
epimeletic care-giving behavior
mandible lower jaw
matriline descendants of a single female

rostrum anterior portion or beak region of the skull that is elongated in most cetaceans

sexual dimorphism morphological differences between males and females of a species

ultrasonic high-frequency sounds, beyond the upper range of human hearing

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SPHENISCIFORMES

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What is a Penguin?

Penguins, with their upright stance and dinner-jacket plumage, constitute a distinct and unmistakable order of birds (Sphenisciformes). Granted there are a few embellishments here and there – the odd crest, a black line or two on the chest – but otherwise, penguins conform to a very conservative body plan. The design of penguins is largely constrained by their commitment to an aquatic lifestyle. Penguins have essentially returned to the sea from which their ancestors, and those of all tetrapods, came. In that sense, they share more in common with seals and sea turtles than they do with other birds. Their spindle-shaped bodies and virtually everything about them have evolved in response to the demands of living in water (**Table 1**).

The loss of flight associated with their aquatic makeover is the penguins' most telling modification. While isolated examples of flightlessness can be found in virtually all other groups of waterbirds, penguins are the only group in which all members cannot fly. Among birds generally, they share that distinction only with the ratites (the kiwis, ostriches, emus, and their ilk), where flight has been sacrificed for large size and running speed.

Despite earlier claims to the contrary, it is clear that penguins have evolved from flying birds. The evidence from morphological and molecular studies suggests that penguins are closely related to loons (Gaviiformes), petrels, and albatrosses (Procellariiformes), and at least some families of the Pelicaniformes, most notably frigate-birds. Despite this, the exact nature of the relationship between penguins and these groups remains unresolved: at the moment it would seem to be a dead heat between loons and petrels as to which group is the sister taxon of penguins (**Figure 1**). (On the surface, loons may seem strange candidates to be so closely allied to penguins – penguins are found in the Southern Hemisphere, loons in the Northern Hemisphere; penguins are wing-propelled divers, loons are foot-propelled divers. However, it seems that loons, or their ancestors, were wing-propelled divers in their past.)

If the relationship of penguins to other birds seems confusing and controversial, the relationships among penguins themselves are no less so. Penguins are confined to the Southern Hemisphere and the distribution of fossilized penguin bones discovered to date mirrors their present-day distribution. Fossils have been found in New Zealand, Australia, South America, South Africa, and islands off the Antarctic Peninsula. The oldest confirmed fossil penguins have been described from late Eocene deposits in New Zealand and Australia, dating back some 40 million years. However, fossils from Waipara, New Zealand, unearthed from late Paleocene/early Eocene deposits that are about 50–60 million years