Marine Mammal Biology

An Evolutionary Approach

EDITED BY

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Preface

Whales, porpoises and dolphins (cetaceans), seals, sea lions, fur seals and walruses (pinnipeds), manatees and dugongs (sirenians), sea otters and polar bears (carnivores) are all classified as marine mammals. Although the groups of mammals that inhabit the marine environment are taxonomically diverse, the sea is a powerful and in some ways unifying influence. For this reason it is useful to explore the similarities and differences among the various mammalian species that have adapted to life in the oceans. This evolutionary approach is the theme of this book, and it is relevant to all aspects of marine mammal biology. At the same time, the evolutionary history of the terrestrial ancestors of each of these groups has an important influence on the life history of individual species in the marine environment. Cetaceans were the first to adapt to a wholly marine existence, with the earliest fossil species dating back to the Eocene. Their closest terrestrial relatives are ungulates, but fully aquatic species first appeared as early as 50–60 million years ago. Among marine mammals, cetaceans and sirenians show the most extreme physical adaptations to aquatic life (and represent the earliest radiations), but retain numerous characteristics common to all mammals. These include giving live birth to dependent young, homeothermy and the need to breath air; and such factors limit and shape the evolutionary potential of marine mammal species. The other major taxonomic group is the pinnipeds, which radiated more recently in the Oligocene. These species remain comparatively similar to their carnivore terrestrial relatives, and have amphibious life histories, returning to land to breed and moult. A key objective of this book was to consider all aspects of the biology of marine mammal species in light of their adaptation to aquatic habitats, and to use a comparative approach to assess the role of phylogenetic history and evolutionary potential. A further objective was to provide an inclusive, advanced text on the biology of a set of species that are of great interest for their diversity, behaviour and interactions with us.

The book begins with an overview of the various species and their global distribution, followed by a review of their evolutionary history. The next few chapters describe the physiological and anatomical adaptations that evolved to meet the challenges of the marine environment, including thermoregulation, osmoregulation, streamlining, the capacity for deep diving, sensory adaptations, and changes in neural anatomy and function. Further chapters build on this foundation with detailed treatments of energetics, vocal anatomy and behaviour, echolocation, feeding ecology, an ecological perspective on social behaviour, and problem solving and memory. A review of life history and reproductive strategies is integrated with chapters on patterns of movement and population genetics. Finally, our interactions with these species, and our influence on the fate of their populations are discussed in a chapter on conservation and management.

By far the most taxonomically diverse (and most studied) of the marine mammals are the cetaceans and pinnipeds, and much of this volume focuses on these species. However, the authors have created a truly comparative analysis, incorporating data on all species we know as marine mammals. This volume provides the background and reference base a student new to the subject would require, but the authors have also made an effort to highlight the discussions and analyses at the forefront of their respective disciplines. There are also frequent illustrations and extensive summary tables providing easily accessible details on aspects of marine mammal biology and life history.

I would like to thank the authors for their excellent contributions to this volume, and their patience and responsiveness during various rounds of revision. I also thank those who critically reviewed chapters: Ian Boyd, Greg Donovan, Peter Evans, Ewan Fordyce, Stefania Gaspari, Jonathan Gordon, Phil Hammond, Sam Ridgeway, Sean Twiss, Graham Worthy and Louise Wynen. I thank the staff at Blackwell Science, especially Ian Sherman, Sarah Shannon, Cee Brandson, Jane Andrew and Katrina McCallum for good advice and enthusiastic assistance. The authors of Chapter 8 would also like to thank Stacey Reese for technical assistance and Deborah Austin and Carrie Beck for helpful comments. The authors of Chapter 13 thank Colleen Reichmuth Kastak and Robert Gisiner.

A. Rus Hoelzel, 2001

CHAPTER 1

Diversity and Zoogeography

Anthony R. Martin and Randall R. Reeves

1.1 INTRODUCTION

An examination of marine mammal diversity—in terms of morphology, ecology, life history and geographical distribution—reveals much about these animals and the processes which brought about today's complement of species. It is important to bear in mind, however, that in studying the present-day fauna, we are only looking at a snapshot in geological time. For reasons that will be explored in this and later chapters, the array of organisms presently inhabiting the world's oceans, estuaries, lakes and rivers differs from that of a thousand years ago, and dramatically from that of 1 million and 10 million years ago. Similarly, were we to revisit the planet a thousand or a million years in the future we would probably see differences (e.g. in numbers of species and their geographical ranges) that would cause us to change any conclusions and predictions based on what we see now. The earth's marine mammal fauna is dynamic, changing slowly but continuously in normal circumstances, yet much more rapidly within the past few centuries due to the influence of our own species on the planet's aquatic ecosystems.

What, exactly, is a 'marine mammal'? The usual interpretation of this term, adopted here, is that it covers animals within the orders Cetacea and Sirenia, three families of Carnivora (the pinnipeds), plus two other carnivores—the sea otter and polar bear. However, one or more species from each of the three major groups live in fresh water, so the term *aquatic* mammal would be more correct. Regardless of the collective name used, there is no reason to exclude the freshwater species as they are derived from, and closely related to, animals living in marine habitats. In some cases (e.g. Saimaa and Baikal seals) their isolation in enclosed waters occurred in fairly recent geological time.

Rather more than 120 living species of marine mammals are currently recognized: 84 cetaceans, 36 pinnipeds, 4 sirenians, the sea otter and the polar bear. But specialists disagree on how many species there are, and the number varies as new genetic or morphological information throws further light on systematic relationships (see Chapter 2). Similarly, the number of races or subspecies is neither universally agreed nor stable (see Chapter 11). For consistency of approach, we have largely adopted the conclusions of Rice (1998), who provides an excellent review of the literature on this subject.

1.2 DIVERSITY

1.2.1 Introduction

Although marine mammals vary greatly in form and function, one over-riding factor has influenced and constrained their appearance: they live for much or all of their time in a much denser medium than that inhabited by terrestrial mammals. The most profound differences between living in water and air for mammals are: (i) the inability to exchange lung gases at all times; (ii) the increased rate of integumentary heat loss; (iii) relative weightlessness; (iv) greater resistance to movement; (v) changed characteristics of sound propagation; and (vi) low-light conditions in all but near-surface waters. The degree of adaptation to an aquatic lifestyle depends, not surprisingly, on the proportion of time spent in water.

Fig. 1.1 Representative mysticetes: 1, pygmy right; 2, right; 3, blue; 4, minke; and 5, humpback whales.

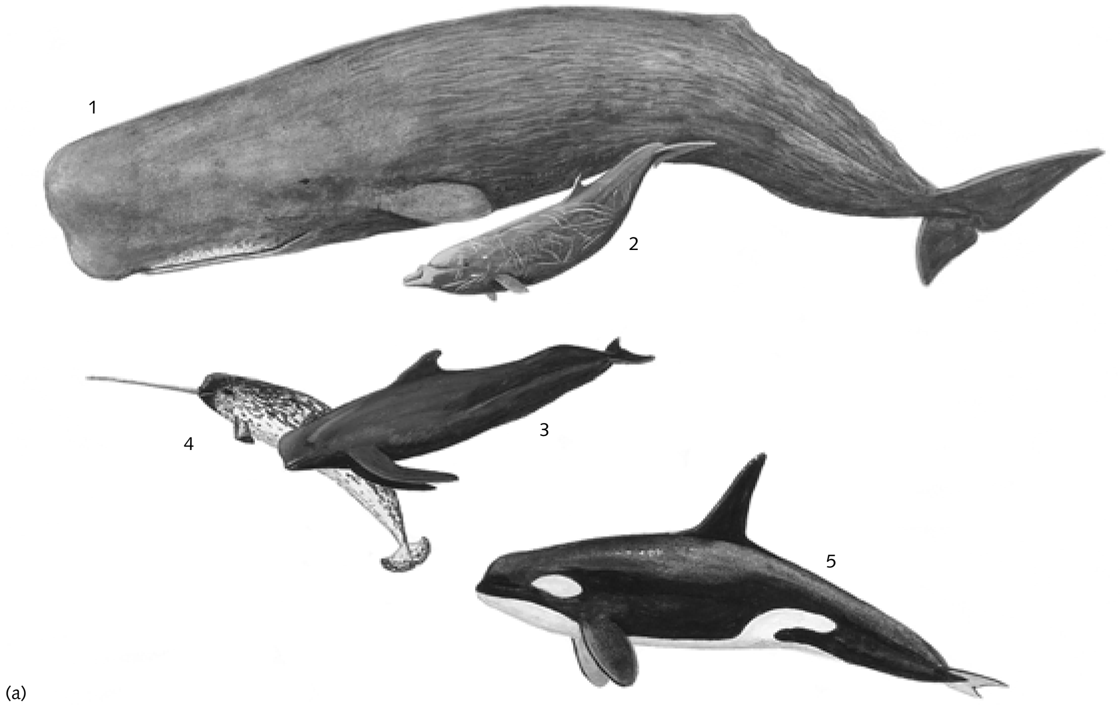
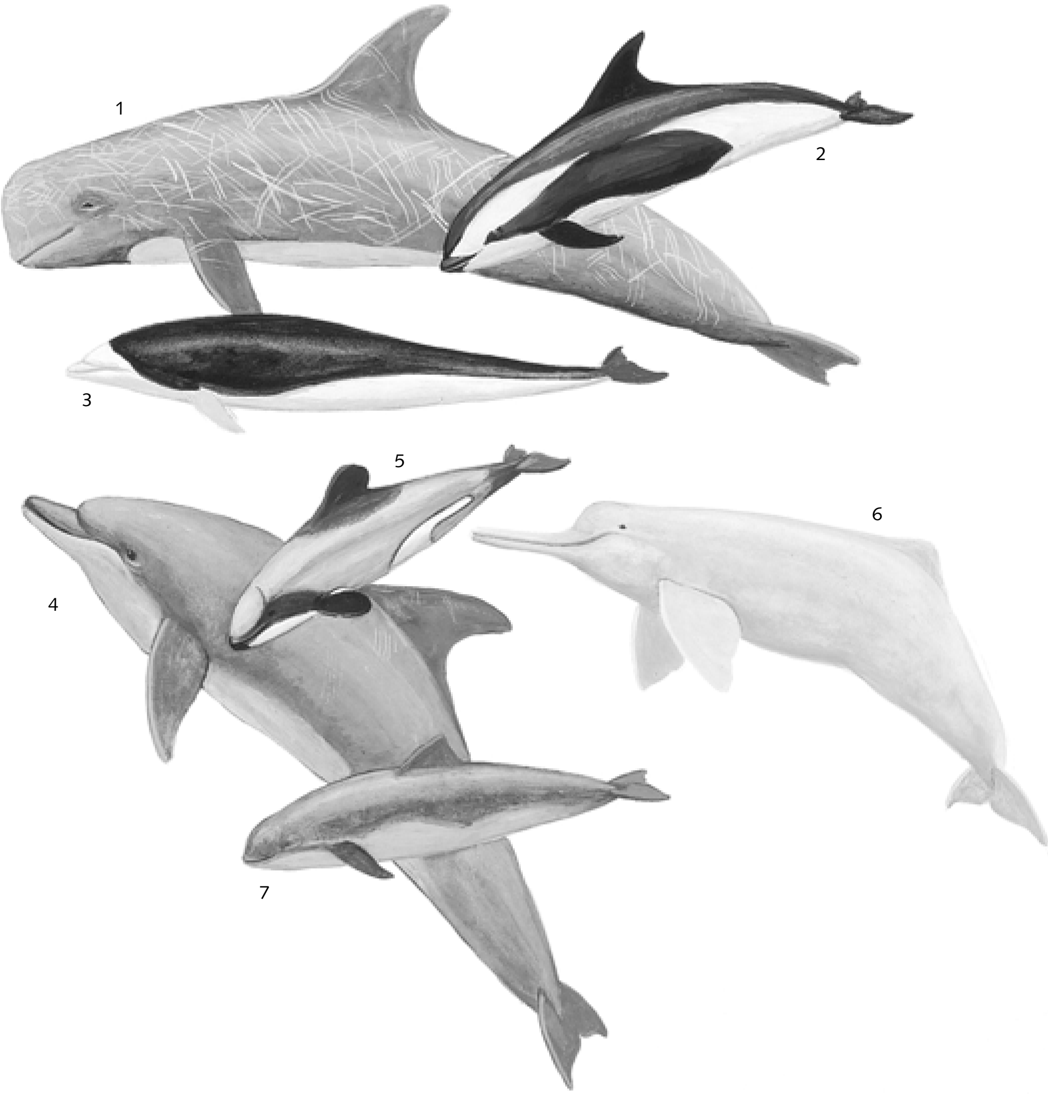


Fig. 1.2 Representative odontocetes. (a) 1, sperm whale; 2, Hubbs' beaked whale; 3, long-finned pilot whale; 4, narwhale; and 5, killer whale. (*continued*)



(b)

Fig. 1.2 (*cont'd*) (b) 1, Risso's dolphin; 2, hourglass dolphin; 3, southern right whale dolphin; 4, bottlenose dolphin; 5, Hector's dolphin; 6, boto; and 7, harbour porpoise.

Whales, dolphins and porpoises (collectively known as cetaceans) (Figs 1.1 and 1.2), which spend their entire lives in water and are unable to live on land, demonstrate extreme morphological adaptations. Cetaceans breathe through nostrils on the dorsal surface of their head, permitting rapid gas exchange without pausing at the water surface, and have breath-hold capabilities (more than an hour in some species) far exceeding those of land mammals. Their thick layer of insulating blubber also serves as a depot for fat storage, and heat loss is further reduced by vascular heat-exchange systems (Chapter 3). Some cetaceans grow to extraordinary size; this is possible because they do not need to support their own weight. Their smooth skin, rigid bodies, internal genitalia and lack of hind limbs all help reduce drag. Broad, horizontal tail flukes driven by strong musculature provide powerful and efficient

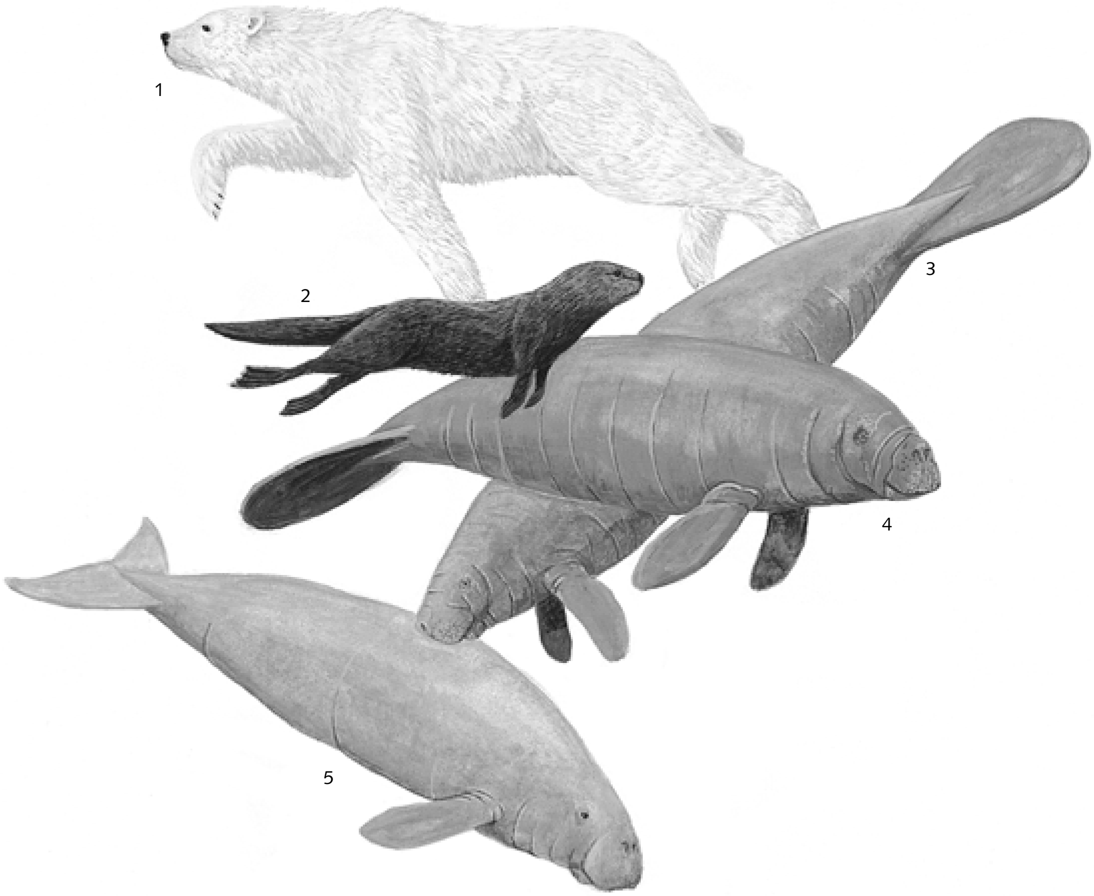


Fig. 1.3 Sirenians, polar bear and sea otter: 1, polar bear; 2, sea otter; 3, West Indian manatee; 4, Amazonian manatee; and 5, dugong.

propulsion through water. A dorsal fin provides rotational stability for most species. Finally, most cetaceans (the odontocetes at least) have sophisticated sound-processing systems, allowing them to interpret received sounds and propagate their own signals for echolocation (Chapter 6). The majority of cetaceans use sound, not light, as the primary means of gathering environmental information.

Sirenians (manatees and the dugong) (Fig. 1.3) are also obligate water dwellers and share many characteristics with the cetaceans, including the basic form of the body. Their distinct genealogy (distantly linked with elephants (Chapter 2)) and lifestyle (primarily herbivorous in warm, shallow waters) have, however, ensured that sirenians differ significantly from cetaceans. They have paired nostrils positioned anteriorly on the head which precludes rapid gas exchange during locomotion, and very dense skeletal bones which help neutralize the buoyancy of the blubber. They have no echolocation ability and less sensitive hearing than cetaceans. Their dentition is appropriate for the mastication of plants, unlike all other marine mammals. The four living sirenians are of only moderate size (typically 2.5–4.5 m in length) although Steller's sea cow, which was rendered extinct by humans about 230 years ago, grew to 8 m and 3.5 t.

The amphibious lifestyle of seals and their allies (the pinnipeds) (Fig. 1.4) precludes some of the extreme aquatic adaptations seen in the Cetacea and Sirenia. Their carnivoran lineage has inevitably resulted in quite different features from the other

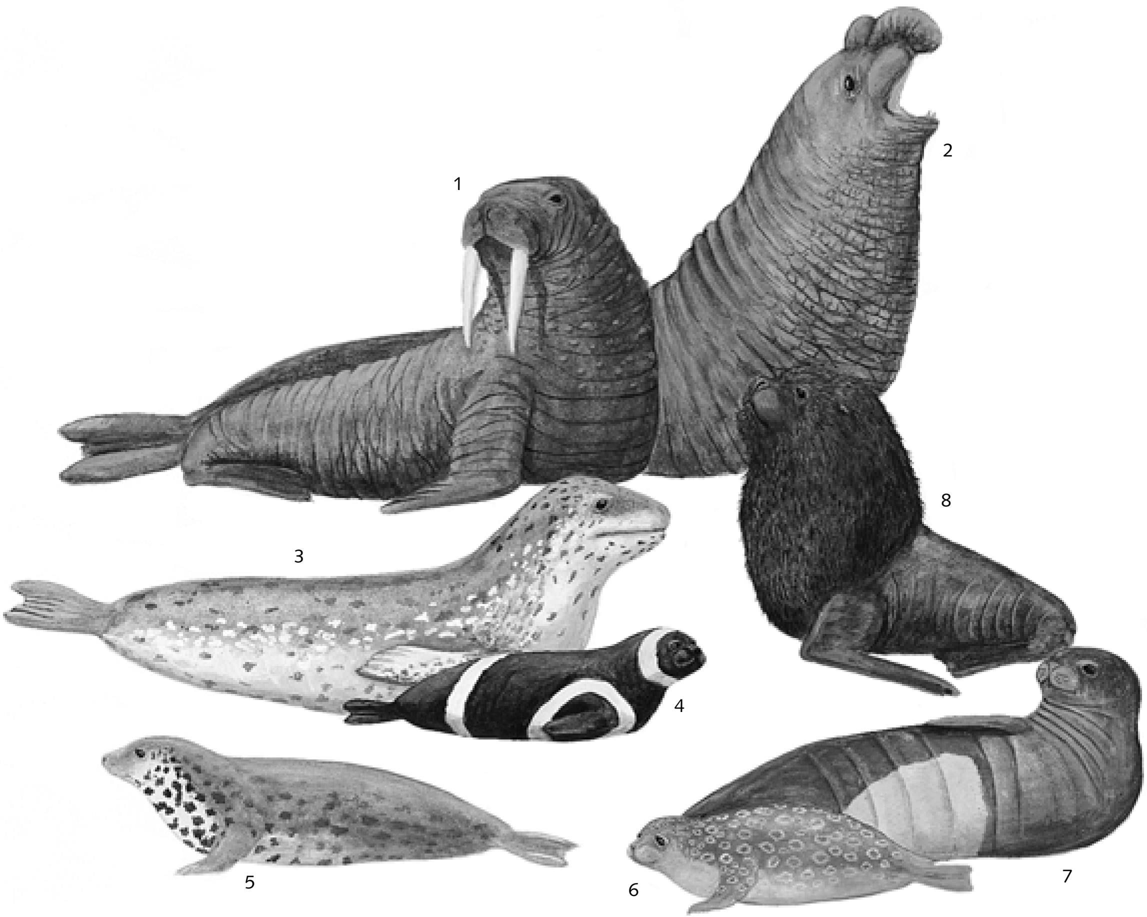


Fig. 1.4 Representative seals: 1, walrus; 2, southern elephant seal; 3, leopard seal; 4, ribbon seal; 5, grey seal; 6, ringed seal; 7, Mediterranean monk seal; and 8, South American sea lion.

two groups. The term 'pinniped' means fin-footed, and indeed these animals have hindlimbs modified to provide propulsion and forelimbs capable of assisting locomotion on land or ice as well as in water. Most also have dense fur and a flexible, streamlined body. The double nostrils are positioned anteriorly on the head as in sirenians, and the areas immediately below the nostrils are covered in typical carnivoran sensory bristles, varying in length, stiffness and density across species. The dentition of pinnipeds is more like that of other carnivores than that of cetaceans or sirenians. They have differentiated teeth, including incisors (except the walrus), canines and postcanines. Like other carnivores, pinnipeds eat flesh. Most consume fish or cephalopods primarily, but some specialize on zooplankton (e.g. crabeater seal), molluscs (walrus) or warm-blooded prey (leopard seal). Pinnipeds principally rely on vision and touch rather than sound to gather information about their environment, having relatively large eyes and no proven echolocation abilities. As a group they possess exceptional diving capability, exceeding that of cetaceans after taking into account the effects of body size (Schreer & Kovacs 1997). The largest pinnipeds are elephant seals (*Mirounga* spp.), with males reaching more than 4 m and 2.5 t (Ling & Bryden 1981; McGinnis & Schusterman 1981), but even these are small in comparison with Steller's sea cow and the great whales.

The two other carnivores considered as marine mammals, the sea otter and the polar bear (Fig. 1.3), are less adapted to an aquatic lifestyle. In fact, the polar bear has achieved greater specialization for life in a cold habitat above water than an aquatic one and should perhaps be viewed as a water-adapted terrestrial mammal. Although capable of sustained swimming, its hollow hair fibres provide too much buoyancy for prolonged diving and its long legs allow rapid terrestrial locomotion but relatively poor mobility in water. Polar bears are specialist predators of seals, but will hunt other animals (e.g. belugas and even humans) or scavenge when the availability of seals is low. Sea otters are perfectly at home in the sea, alternately diving for bottom-dwelling molluscs and crustaceans, then rafting for hours on the surface. Their hind feet are large and flipper-like, and their pelage provides an efficient barrier against heat loss.

1.2.2 Cetaceans

None of the groups considered in this volume has a greater diversity of morphological form than the order Cetacea. The largest living cetacean, and indeed the largest animal known to have lived on earth, is the blue whale (*Balaenoptera musculus*). With an adult body length of up to 33 m and a body mass of up to 190,000 kg, the largest blue whales have a mass some 3000 times greater than the vaquita (*Phocoena sinus*) or the Hector's dolphin (*Cephalorhynchus hectori*), which do not exceed 1.7 m and 60 kg. Between these extremes, an extraordinary range of body shapes and sizes reflects differing habitat and diet, social structure and behaviour. The order Cetacea comprises two very different living suborders, Mysticeti (baleen whales, Fig. 1.1) and Odontoceti (toothed whales, Fig. 1.2), discussed separately below. In the English language, cetaceans are divided into 'whales', 'dolphins' and 'porpoises' (Table 1.1). These terms broadly reflect body size (in decreasing order) rather than taxonomy, and can be confusing. For example, the killer whale (*Orcinus orca*) and the two pilot whales (*Globicephala* spp.) are actually large marine dolphins (Delphinidae).

1.2.2.1 Mysticetes

Fourteen mysticete species are currently recognized, ranging in body size from the blue whale down to the pygmy right whale (*Caperea marginata*), which reaches about 6.5 m and 3.5 t. Unusually for mammals, adult female baleen whales are larger than males, typically by about 5% in body length. Mys-

Table 1.1 Recent marine mammals. (Adapted from Rice 1998; see also International Whaling Commission 2001.)

Latin name	English name(s)
Order CARNIVORA	
Family Otariidae. Fur seals and sea lions	
Arctocephalus pusillus	Tasmanian and Cape fur seals
Arctocephalus gazella	Antarctic fur seal, Kerguelen fur seal
Arctocephalus tropicalis	Subantarctic fur seal
Arctocephalus townsendi	Guadalupe fur seal
Arctocephalus philippii	Juan Fernández fur seal
Arctocephalus forsteri	South Australian and New Zealand fur seal, Australasian fur seal
Arctocephalus australis	South American fur seal
Arctocephalus galapagoensis	Galápagos fur seal
Callorhinus ursinus	Northern fur seal
Zalophus japonicus	Japanese sea lion
Zalophus californianus	California sea lion
Zalophus wollebaeki	Galápagos sea lion
Eumetopias jubatus	Northern sea lion, Steller's sea lion
Neophoca cinerea	Australian sea lion
Phocarctos hookeri	New Zealand sea lion, Hooker's sea lion
Otaria flavescens (= *O. byronia*)	South American sea lion

(*continued*)

Table 1.1 (*cont'd*)

Latin name	English name(s)
Family Odobenidae. Walrus	
Odobenus rosmarus	Walrus
Family Phocidae. Seals	
Erignathus barbatus	Bearded seal
Phoca vitulina	Harbour seal
Phoca largha	Spotted seal, larga seal
Pusa hispida	Ringed seal
Pusa caspica	Caspian seal
Pusa sibirica	Baikal seal
Halichoerus grypus	Grey seal
Histriophoca fasciata	Ribbon seal
Pagophilus groenlandicus	Harp seal
Cystophora cristata	Hooded seal
Monachus tropicalis	Caribbean monk seal
Monachus monachus	Mediterranean monk seal
Monachus schauinslandi	Hawaiian monk seal
Mirounga leonina	Southern elephant seal
Mirounga angustirostris	Northern elephant seal
Leptonychotes weddellii	Weddell seal
Ommatophoca rossii	Ross seal
Lobodon carcinophaga	Crabeater seal
Hydrurga leptonyx	Leopard seal
Family Ursidae. Bears	
Ursus maritimus	Polar bear
Family Mustelidae. Weasels and otters	
Enhydra lutris	Sea otter
Order CETACEA	
Suborder Mysticeti	
Family Balaenidae. Right whales	
Eubalaena glacialis	North Atlantic right whale
Eubalaena japonica	North Pacific right whale
Eubalaena australis	Southern right whale
Balaena mysticetus	Bowhead whale
Family Neobalaenidae. Pygmy right whale	
Caperea marginata	Pygmy right whale
Family Balaenopteridae. Rorquals	
Megaptera novaeangliae	Humpback whale
Balaenoptera acutorostrata	Northern minke whale, common minke whale (includes 'dwarf')
Balaenoptera bonaerensis	Antarctic minke whale
Balaenoptera edeni	Pygmy Bryde's whale
Balaenoptera brydei	Bryde's whale
Balaenoptera borealis	Sei whale
Balaenoptera physalus	Fin whale
Balaenoptera musculus	Blue whale
Family Eschrichtiidae. Gray whale	
Eschrichtius robustus	Gray whale

(*continued on p. 8*)

Table 1.1 (*cont'd*)

Latin name	English name(s)
Suborder Odontoceti	
Family Physeteridae. Sperm whale	
Physeter macrocephalus	Sperm whale
Family Kogiidae. Pygmy, or short-headed, sperm whales	
Kogia breviceps	Pygmy sperm whale
Kogia sima	Dwarf sperm whale
Family Ziphiidae. Beaked whales	
Ziphius cavirostris	Cuvier's beaked whale, Goosebeak whale
Berardius arnuxii	Arnoux's beaked whale
Berardius bairdii	Baird's beaked whale
Tasmacetus sheperdi	Shepherd's beaked whale
Indopacetus pacificus	Indo-Pacific beaked whale, Longman's beaked whale
Hyperoodon ampullatus	Northern bottlenose whale
Hyperoodon planifrons	Southern bottlenose whale
Mesoplodon hectori	Hector's beaked whale
Mesoplodon mirus	True's beaked whale
Mesoplodon europaeus	Gervais' beaked whale
Mesoplodon bidens	Sowerby's beaked whale
Mesoplodon grayi	Gray's beaked whale
Mesoplodon peruvianus	Pygmy beaked whale, lesser beaked whale
Mesoplodon bowdoini	Andrews' beaked whale
Mesoplodon traversii (formerly *bahamondi*)	Spade-toothed whale (formerly bahamonde's beaked whale)
Mesoplodon carlhubbsi	Hubbs' beaked whale
Mesoplodon ginkgodens	Ginkgo-toothed whale
Mesoplodon stejnegeri	Stejneger's beaked whale
Mesoplodon layardii	Strap-toothed whale
Mesoplodon densirostris	Blainville's beaked whale, dense-beaked whale
Family Platanistidae. South Asian river dolphins	
Platanista gangetica	Ganges dolphin, Indus dolphin, susu, bhulan
Family Iniidae. Amazon river dolphin	
Inia geoffrensis	Boto, Amazon river dolphin
Family Lipotidae. Chinese river dolphin	
Lipotes vexillifer	Baiji, Yangtze dolphin, Chinese river dolphin
Family Pontoporiidae. La Plata dolphin	
Pontoporia blainvillei	Franciscana
Family Monodontidae. Beluga and narwhal	
Delphinapterus leucas	Beluga, white whale
Monodon monoceros	Narwhal
Family Delphinidae. Dolphins	
Cephalorhynchus commersonii	Commerson's dolphin
Cephalorhynchus eutropia	Chilean dolphin
Cephalorhynchus heavisidii	Heaviside's dolphin

(*continued*)

Table 1.1 (*cont'd*)

Latin name	English name(s)
Cephalorhynchus hectori	Hector's dolphin
Steno bredanensis	Rough-toothed dolphin
Sousa teuszi	Atlantic humpbacked dolphin
Sousa plumbea	Indian humpbacked dolphin
Sousa chinensis	Pacific humpbacked dolphin
Sotalia fluviatilis	Tucuxi
Tursiops truncatus	Common bottlenose dolphin
Tursiops aduncus	Indian Ocean bottlenose dolphin
Stenella attenuata	Pan-tropical spotted dolphin
Stenella frontalis	Atlantic spotted dolphin
Stenella longirostris	Spinner dolphin
Stenella clymene	Clymene dolphin
Stenella coeruleoalba	Striped dolphin
Delphinus delphis	Short-beaked common dolphin
Delphinus capensis	Long-beaked common dolphin
Lagenodelphis hosei	Fraser's dolphin
Lagenorhynchus albirostris	White-beaked dolphin
Lagenorhynchus acutus	Atlantic white-sided dolphin
Lagenorhynchus obliquidens	Pacific white-sided dolphin
Lagenorhynchus obscurus	Dusky dolphin
Lagenorhynchus australis	Peale's dolphin
Lagenorhynchus cruciger	Hourglass dolphin
Lissodelphis borealis	Northern right whale dolphin
Lissodelphis peronii	Southern right whale dolphin
Grampus griseus	Risso's dolphin
Peponocephala electra	Melon-headed whale
Feresa attenuata	Pygmy killer whale
Pseudorca crassidens	False killer whale
Orcinus orca	Killer whale
Globicephala melas	Long-finned pilot whale
Globicephala macrorhynchus	Short-finned pilot whale
Orcaella brevirostris	Irrawaddy dolphin
Family Phocoenidae. Porpoises	
Neophocaena phocaenoides	Finless porpoise
Phocoena phocoena	Harbour porpoise, common porpoise
Phocoena sinus	Vaquita
Phocoena spinipinnis	Burmeister's porpoise
Phocoena dioptrica	Spectacled porpoise
Phocoenoides dalli	Dall's porpoise
Order SIRENIA	
Family Trichechidae. Manatees	
Trichechus manatus	West Indian manatee, Caribbean manatee
Trichechus senegalensis	West African manatee
Trichechus inunguis	Amazonian manatee
Family Dugongidae. Dugong and sea cow	
Dugong dugon	Dugong
Hydrodamalis gigas	Steller's sea cow

ticetes are filter feeders, consuming vast numbers of small organisms. Their teeth have been replaced by triangular plates of baleen, closely packed and rooted in the rostrum (upper jaw), one row on each side of the mouth. Baleen is formed principally of keratin and is continuously growing, its length maintained by wear at the lower (distal) end. Baleen plates are slightly curved to provide lateral strength, and are semirigid. The inner edge of each plate has a fringe of fibres, and these combine to form a dense mat lining the inside of the mouth. Food-laden water passes in through the open mouth and out through the baleen, leaving the food organisms trapped on the fibres. The diameter of the fibres varies from species to species and determines the size of prey organism which can be efficiently filtered from the water. The finest fibres are found in right whales (Balaenidae), which consume amphipods, euphausiids and copepods as small as 5 mm long.

Among the mysticete families, Balaenopteridae has the most species. Balaenopterids (commonly known as rorquals) are recognizable by having pleats, or 'ventral grooves', extending from the chin to the chest or belly. The pleated tissue is elastic and effectively forms a bag during feeding, allowing the whale to take in huge volumes of water before forcing it out through the baleen (Fig. 1.5). The huge tongue is then used to wipe prey off the mat of baleen fibres before swallowing. Whales that use this feeding technique are known as gulp feeders (Gaskin 1982). The seven species in the genus *Balaenoptera* (blue, fin, sei, Bryde's (two species), northern minke and Antarctic minke whales) share a sleek body shape, permitting rapid movement through the water (Fig. 1.1). The humpback whale (*Megaptera novaeangliae*), the only extant member of its genus, has a stockier build and much longer flippers than the other balaenopterids.

The family Balaenidae (right whales) is a group of rotund, slow-swimming whales with huge mouths and no dorsal fins. The huge girth is due to an unusually thick blubber layer. Balaenids have the longest baleen of all mysticetes, up to 4 m, and their mouths are steeply arched to accommodate this feeding apparatus. Unlike the balaenopterids, right whales have no ventral grooves and feed by passing a continuous stream of water through the open mouth and out through the baleen during active swimming. Two basic types of right whale exist. The black right whales (genus *Eubalaena*, three species) have raised, roughened patches of skin on the head, known as callosities. The similar bowhead or Greenland right whale (*Balaena mysticetus*) has a white chin and no callosities.

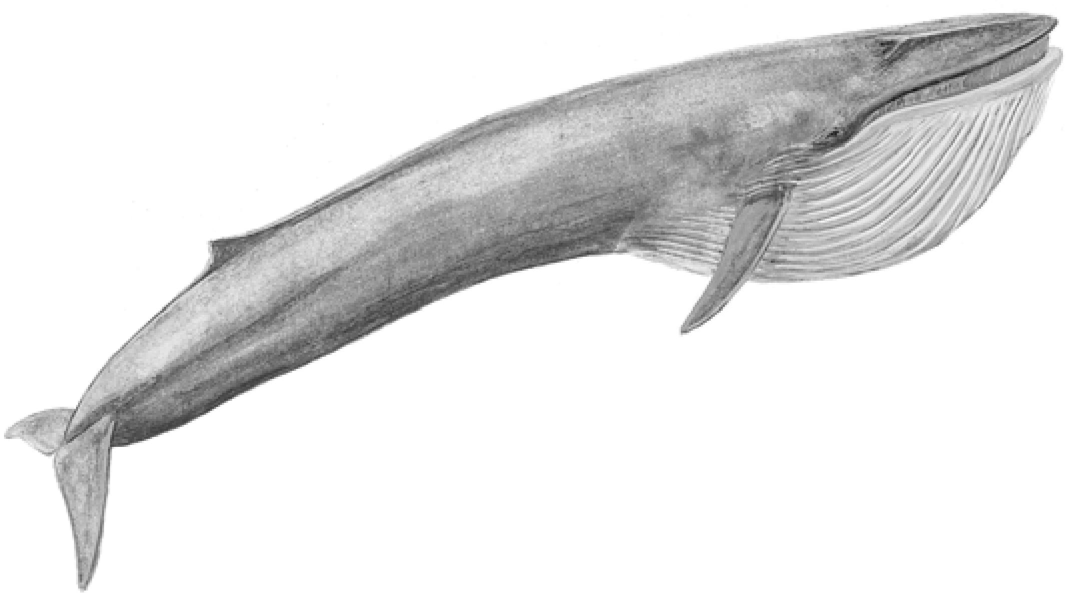


Fig. 1.5 Blue whale with distended throat.

The family Neobalaenidae has one living species, the pygmy right whale. It is much smaller and sleeker than the balaenids and has a falcate dorsal fin. But the head shape, especially the arched jaw, is recognizably similar.

The final mysticete is the gray whale (*Eschrichtius robustus*), in some respects intermediate between the rorquals and right whales. Uniquely among baleen whales, the gray whale is primarily a bottom feeder, filtering small organisms from the upper layer of the sea bed. The tongue is used as a piston to suck food items into its mouth (Ray & Schevill 1974). Gray whales have short baleen, with coarse fibres.

1.2.2.2 Odontocetes

The suborder Odontoceti, the toothed whales, embraces at least 70 species of whales, dolphins and porpoises belonging to around 10 families spanning a great range of shapes and sizes. The number, size and shape of teeth are extremely variable both across and within families. In females of some species the teeth do not even erupt past the gumline. Odontocetes are principally consumers of fish and squid, but some species (e.g. belugas, *Delphinapterus leucas*; Vladykov 1946) also take benthic invertebrates and the killer whale includes warm-blooded prey in its diet (Dahlheim & Heyning 1999). All odontocetes have a single blowhole set to the left of the mid-line, reflecting an asymmetric skull, and probably all use echolocation. Most toothed whales are sexually dimorphic in body size, with males larger than females in all except some beaked whales, the *Cephalorhynchus* dolphins and the porpoises.

The largest odontocete is the sperm whale (*Physeter macrocephalus*) (Fig. 1.2). Sexual dimorphism is extreme in this species. Males reach an average adult size of 15 m and 45 t with a maximum of 18.5 m and 57 t, while females average some 11 m and 20 t (Rice 1989). The sperm whale is also exceptional in other ways. It dives deeper than any other whale (with the possible exception of some of the larger beaked whales), and its head is proportionally bigger than that of any other species. The head is a complex structure, essentially consisting of a reservoir of oils and waxes supported by a cradle of dense bone. The mandible is slim and underslung. The functions of the various elements of the sperm whale's head, especially the spermaceti organ, have long been matters of scientific conjecture and controversy. Principal hypotheses are that the spermaceti organ acts as an acoustic lens for focusing emitted sound, perhaps to immobilize prey (Norris & Møhl 1983), and that it is used in diving to alter the animal's buoyancy (Clarke 1978).

The two species most closely related to the sperm whale are, in contrast, among the smallest animals known as whales. The pygmy sperm whale (*Kogia breviceps*) and dwarf sperm whale (*K. sima*) form the family Kogiidae. Adult *K. breviceps* reach no more than 3.3 m and about 400 kg, while *K. sima* attain only about 2.7 m and 210 kg. Both have a narrow, underslung lower jaw, but otherwise their external appearance differs from the sperm whale's. They have an upright dorsal fin and proportionally both a smaller head and longer flippers.

The family Monodontidae comprises two living species: the narwhal (*Monodon monoceros*) and the white whale or beluga. These two small whales (maximum body length about 5 m in both species) share the unusual characteristic of having no dorsal fin. Furthermore, and uniquely among cetaceans, the male narwhal grows a long spiralled tusk. This extraordinary secondary sexual characteristic is actually a tooth, rooted in the upper left jaw, which emerges horizontally through the lip and grows to a maximum length of more than 3 m. The tusk angles slightly to the left of the whale's centre line, so forward motion produces an asymmetric lateral force. To counteract this force, and to help prevent the animal swimming in circles, narwhals have fused neck vertebrae. The tusk is normally the only tooth that erupts in male narwhals, but very rarely a tooth emerges on the right side too, resulting in the 'double-tuskers' often seen in museums. Females usually have no erupted teeth. In contrast, belugas of both sexes have a full complement of peg-like teeth.

The family of beaked whales, Ziphiidae, includes at least 20 species. These small to medium-sized whales share the characteristics of a distinctively narrow rostrum with the lower jaw extending at least to the tip of the upper, a shallow or non-existent notch between the tail flukes, a dorsal fin set well back on the body and two conspicuous throat grooves which converge anteriorly to form a 'V'. They also have three or four fused cervical vertebrae and extensive skull asymmetry. All but Shepherd's and Gray's beaked whales (*Tasmacetus shepherdi* and *Mesoplodon grayi*) have only two (genus *Mesoplodon* and usually *Hyperoodon* and *Ziphius*) or four (genus *Berardius*) non-vestigial teeth, located in the mandible. For most species, these erupt only in adult males. The number, shape and position of teeth are diagnostic for most species and may be the only characteristics by which they can be identified, short of molecular analyses.

Although beaked whales occur throughout the world's oceans, they are the least-known group of cetaceans. Most are dark (brown or grey) on the dorsal surface, becoming lighter ventrally. Adults, especially males, are often covered in pale, linear scars, sometimes in parallel pairs, suggesting that the teeth are used in aggressive encounters.

The Ziphiidae are currently split into six genera, one of which (*Mesoplodon*) contains at least 13 small (6 m or shorter) species. The smallest mesoplodont (*M. peruvianus*), at < 4 m, was described only recently (Reyes *et al.* 1991). Possibly, the most distinctively patterned beaked whale is the strap-toothed whale (*M. layardii*), which has an extensive light grey blaze on an otherwise black body. This species is also unique in that males possess a flattened tooth on each side of the lower jaw which curves over the rostrum with age, eventually preventing the animal from opening its mouth more than a few centimetres. As this extraordinary tooth development does not prevent the whale from feeding, prey are probably ingested by suction.

The genus *Berardius* is represented by two whales (*B. bairdii* and *B. arnuxii*) with a maximum body size of around 13 m and 10 m, respectively. Shepherd's beaked whale (*Tasmacetus shepherdi*) is unique among the group in having many teeth in both jaws (90 or more in some specimens) in addition to a pair of more typical 'tusk' teeth at the tip of the mandible in males (Mead 1989). Measured specimens have been up to 7 m in body length, but this is one of the rarest whales and few have yet been carefully examined.

By far the largest and most diverse odontocete family is Delphinidae, embracing some 35 species of dolphins in 17 genera (Rice 1998; LeDuc *et al.* 1999). Because some of these species are extremely abundant, most of the individual cetaceans alive in the world's oceans belong to this family. Body size in delphinids varies from the tiny *Cephalorhynchus* dolphins with a length of 1.7 m or less and a mass of 30–60 kg to the killer whale, males of which can reach a maximum of 9 m and 10 t. They also vary greatly in coloration, and the family includes the most strikingly marked cetaceans. Among these are the striped and spotted dolphins (*Stenella coeruleoalba*, *S. attenuata* and *S. frontalis*), the common dolphins (genus *Delphinus*), Fraser's dolphin (*Lagenodelphis hosei*) and the *Lagenorhynchus* and *Cephalorhynchus* dolphins. They have a diversity of stripes, spots, swirls, blazes and patches in shades of black, white, grey and even tan or yellow (Mitchell 1970; Perrin 1975). At the other extreme are species with simple countershading of plain dark above and lighter below. Examples are the bottlenose dolphins (*Tursiops* spp.) (Fig. 1.2), tucuxi (*Sotalia fluviatilis*) and some races of the spinner dolphin (*Stenella longirostris*).

Six delphinids with superficially similar characteristics (body form and colour, reduced dentition in all but one, no beak and three or more fused neck vertebrae) have been collectively known as 'blackfish'. The group varies in size from a little over 2 m for the pygmy killer whale (*Feresa attenuata*) to the killer whale, in which the adult male has a greatly exaggerated dorsal fin and is twice the mass of the female. The black body coloration is broken in several species with white patches on the ventral surface, and the killer whale is immediately recognizable with its postocular blaze and entirely white chin and throat. The three 'killer' whales (*Orcinus*, *Pseudorca* and *Feresa*) and the two pilot whales—long-finned (*Globicephala melas*) and short-finned (*G. macrorhynchus*)—have thick, widely spaced teeth in both jaws, effective for grasping prey. The melon-headed whale (*Peponocephala electra*) differs from the rest of the group, having 20–25 pairs of small teeth in each jaw compared to 8–13 pairs for the other blackfish.

Most of the other delphinids share a 'classic' dolphin shape, with a distinct beak and prominent dorsal fin, two or more fused cervical vertebrae and 20 or more pairs of teeth in the upper jaw. None is more than 4 m long. The 'classic' dolphins embrace eight genera, of which four (*Steno*, *Sotalia*, *Tursiops* and *Lagenodelphis*) are represented by only one or two living species. *Lagenorhynchus* and *Stenella*, with six and at least five species, respectively, are the most diverse of these genera.

The four diminutive *Cephalorhynchus* species lack a well-defined beak and have characteristically rounded dorsal fins, but are otherwise perfectly dolphin-like. The highly gregarious northern (*Lissodelphis borealis*) and southern (*L. peronii*) right whale dolphins are extremely slim, and neither has any vestige of a dorsal fin. Both species are black above and white below with clear lines of demarcation between the two colours.

The Irrawaddy dolphin (*Orcaella brevirostris*) has external similarities to the beluga and has been placed by some systematists in the Monodontidae, but recent morphological and genetic evidence indicates that it is a delphinid and may be most closely related to the killer whale (see Chapter 2). *Orcaella* has a rounded head with no beak, a flexible neck allowing unusual mobility of the head and a low number of peg-like teeth in both upper and lower jaws. In common with only the beluga, this species can 'pucker' the lips and shoot a directed stream of water from the mouth; this ability may be useful for foraging in mud or bottom sediments.

The family Phocoenidae, the porpoises, comprises six species of very small cetaceans (all < 2.2 m) with small flippers and no beak. Five porpoises have small dorsal fins, but the finless porpoise (*Neophocaena phocaenoides*), as its name suggests, has no dorsal fin at all. Porpoises differ from other odontocetes in having laterally compressed or spatulate teeth which collectively form a cutting edge. There are three porpoise genera: *Phocoena*, *Phocoenoides* and *Neophocaena*. The harbour porpoise (*Phocoena phocoena*), vaquita (*P. sinus*), Burmeister's porpoise (*P. spinipinnis*) and finless porpoise are uniformly grey or black on the dorsal surface, fading to a lighter shade ventrally. The first three also have a dark eye patch and flipper stripe (axilla to lower lip), and some finless porpoises have white lips.

The remaining two porpoises—spectacled (*Phocoena dioptrica*) and Dall's (*Phocoenoides dalli*)—are strikingly marked with black dorsally and white beneath, though in *P. dalli* the head and neck are black too. Dall's porpoise differs from all other porpoises in having a robust shape with a very 'deep' body.

The final odontocetes to consider are some of the most ancient—the river dolphins. The term 'river dolphin' applied in a taxonomic sense is, though, somewhat of a misnomer for two reasons. Firstly, one member of this group, the franciscana (*Pontoporia blainvillei*), does not live in rivers; secondly, some cetaceans which have populations living in rivers (e.g. *Sotalia*, *Orcaella* and *Neophocaena*) are excluded because they are taxonomically distant from these long-beaked species.

The river dolphins grow to an adult body size of no more than 2.5 m and 200 kg. They differ morphologically, behaviourally and physiologically from all other cetaceans. Characteristics common to the four species currently recognized include a very long, narrow forceps-like beak, large spatulate flippers, small eyes and flexible necks. The *Platanista* dolphins of the South Asian subcontinent are effectively blind due to the evolutionary loss of a crystalline lens. They have some 120 long, interlocking teeth for grasping fish and unique cranial processes thought to be related to echolocation.

The boto or Amazon river dolphin (*Inia geoffrensis*), also known as the pink dolphin because of its body colour in some parts of the range, is the only extant odontocete with differentiated dentition. Anterior teeth are simple, peg-like structures, but the posterior teeth have cusps on the inner face. These teeth indicate an unusual diet, and indeed the boto is capable of crushing both armoured fish and turtles (da Silva 1983). Its extremely flexible body, with broad, rotatable flippers and low dorsal fin, allows this species to swim and manoeuvre within an unusual habitat—the tangled vegetation and root systems of the Amazonian flooded forest.

1.2.3 Sirenians

The order Sirenia embraces two distinctly different groups of animals—the manatees (three extant species) and the dugong (one extant species) (Fig. 1.3). The manatees' structures are more generalized and adapted for slow movement in quiet and confined spaces, while the dugong's tail musculature and cetacean-like flukes provide for rapid acceleration and active swimming in exposed waters (Domning

1977; Anderson 1979). Manatees have two crescentic nostrils on top of the snout, a bristly muzzle with drooping jowls and a 'normal' mouth. In contrast, the dugong's face is dominated by a bizarre, downward-orientated rostral disk, which is really a modified and greatly expanded upper lip (Fig. 1.3). The male dugong has a pair of tusks that protrude a few centimetres just behind the corners of the facial disk. These incisors are worn into a chisel shape but are not known to be used as weapons (Nishiwaki & Marsh 1989).

Differences in facial structure reflect the differing diets of manatees and dugongs (Wells *et al.* 1999). Manatees are capable of feeding throughout the water column and reaching above the surface to crop emergent water plants and overhanging terrestrial ones, while dugongs are obligate bottom feeders. The forelimbs of manatees, in particular, are manoeuvrable enough to be used for stuffing food into the mouth, as well as for 'walking' along the bottom, sculling, turning and braking. Dugongs sometimes use their pectoral flippers as props while maintaining position on the sea floor.

1.2.4 Pinnipeds

As a group, the pinnipeds are less morphologically diverse than the cetaceans (Fig. 1.4). Body size ranges from the small lake seals in Eurasia (Baikal seal (*Pusa sibirica*) males reach no more than 1.5 m and 70 kg) to the elephant seals in which males reach 4 m and 2.5 t—thus a 2.5-fold difference in length and a 35-fold difference in mass, compared with 19- and 3000-fold differences, respectively, in cetaceans.

There are only three extant pinniped families, one of which, Odobenidae (walrus), is monotypic. The walrus (*Odobenus rosmarus*) is the only pinniped with long external tusks (Fig. 1.4). Both sexes have these highly modified upper canines, which are used for combat and threat displays, for anchorage or leverage while resting beside or clambering onto an ice floe or, in exceptional cases, to kill phocid prey (Lowry & Fay 1984). The walrus's mouth and face are uniquely adapted for foraging on clam beds. A highly enervated muzzle, covered with stiff bristles, is used to sense the substrate and detect food. A 'vacuum pump', with the tongue as the piston, is used to suck the siphons and feet of clams and other molluscs from their shells (Fay 1982).

Walruses have thick skin (up to 4 cm in adult males), an ample blubber layer (5–10 cm) and no external ears. Males can be over 3 m long and weigh 1200 kg; females are substantially smaller. The walrus's flipper structure permits the animal to move quite swiftly on land or ice when necessary, in a similar way to otariids (see below).

The Otariidae, or eared seals, are distinguished from other pinnipeds by their external ear flaps (pinnae); long, hairless or sparsely haired fore-flippers with splayed digits and vestigial nails; and relatively large hind-flippers that can be rotated beneath the body. Their flipper structure allows otariids to 'walk', albeit awkwardly. Sexual dimorphism is pronounced in these polygynous seals, with males considerably larger than females in all species. Adult males develop a thick, robust neck region, and in many species they have a mane of longer hair reminiscent of a lion's. Their large size and powerful neck are essential for establishing and maintaining dominance on the breeding rookeries.

1.2.4.1 Otariids

The 16 otariid species are allocated to seven genera (Rice 1998). The only consistent feature that distinguishes fur seals from sea lions is the presence of a dense underfur, consisting of 30 or more secondary hairs associated with each primary hair, in the pelage of fur seals (Repenning *et al.* 1971; Warneke & Shaughnessy 1985). In addition, the sea lions generally have a broader, blunter nose than the fur seals.

The genus *Arctocephalus* embraces eight species, the southern fur seals. Morphological differences between the species are fairly subtle, especially in females and juveniles. The snout of *A. townsendi* males is markedly long and pointed, while those of *A. gazella* and *A. tropicalis* are almost blunt by comparison. Coloration is typically some shade of brown or grey, with countershading. The northern fur seal (*Callorhinus ursinus*) has proportionally longer flippers than its southern counterparts. In all fur seals, adult males have roughly five times the mass of adult females.

The sea lions are assigned to five genera, all but *Zalophus* being monospecific. Adult males are about

0.5 m longer (2.4 m vs 1.8 m) and three times more massive (300 kg vs 100 kg) than females. A striking feature of the male is its noticeably raised forehead, formed by the prominent saggital crest on the skull. Both sexes are chocolate brown, with little or no countershading.

The largest otariid is the northern (Steller's) sea lion (*Eumetopias jubatus*). Males grow to 3 m and can weigh 1 t, while females reach only about 2.2 m and 270 kg. The head and bulging neck of the bull are massive.

The three southern sea lions (South American *Otaria flavescens*; sometimes called *O. byronia*; plus the Australian, *Neophoca cinerea*, and New Zealand or Hooker's, *Phocarctos hookeri*, sea lions) are all roughly the same size as the California sea lion. Male *Otaria* have the most characteristic profile of any sea lion. Their heads are enormous, dwarfing the rest of the body, and the snout is broad and slightly upturned. The mane has very long hair and is somewhat lighter in colour than the dark brown body. Male Australian sea lions have a more complex colour pattern than the other sea lions (King 1983). The top of the head and the nape are white, in contrast to the chocolate brown body overall.

1.2.4.2 Phocids

The true or earless seals, the Phocidae, comprise the largest and most diverse of the pinniped families. Rice (1998) recognizes 13 modern phocid genera, all but four of them monospecific. Phocids are readily distinguished from otariids by their lack of pinnae (external ears); their shorter, haired fore-flippers with claws on all five digits; and their non-rotatable hind-flippers. They spend far less time in an 'upright' posture than the otariids when hauled out, and generally can only hunch or wriggle their way across the land or ice, in contrast to the ungainly walking of otariids and walruses. In most phocid species, males grow larger than females, but in some (e.g. the bearded seal (*Erignathus barbatus*), the Antarctic phocids and the monk seals) the reverse is true. Regardless of which sex grows larger, sexual dimorphism in size is much less pronounced in phocids than in otariids. Male phocids tend to be more vividly coloured than females, particularly in those species with relatively complex patterning (e.g. ribbon and harp seals, *Histriophoca fasciata* and *Pagophilus groenlandicus*, respectively). Whereas otariids have scrotal testes and four mammary teats, phocids (and the walrus) have internal testes and either two (most species) or four (monk seals and the bearded seal) teats.

Within the Phocidae, there is considerable diversity in colour pattern and body size. Harbour, spotted, Caspian and Weddell seals (*Phoca vitulina*, *P. largha*, *Pusa caspica* and *Leptonychotes weddellii*, respectively) have spotted coats as adults. Ringed seals (*Pusa hispida*), as their name implies, have light rings on a grey background (Fig. 1.4). Adult ribbon seals have three dramatic, white ribbon-like bands (Fig. 1.4), and adult harp seals have a black face and a dark horseshoe-shaped saddle across the back and flanks. Baikal and monk seals are unspotted and fairly drab in comparison. Mediterranean monk seals (*Monachus monachus*) often have an extensive white ventral patch (Fig. 1.4), and bearded seals have a variable colour pattern, sometimes with muted streaking and blotches. The bearded seal is distinguished by its impressively long, white vibrissae (thus the name 'bearded') and squarish flippers. The smaller phocids are less than 2 m long and weigh no more than 150 kg, whereas the larger ones (the bearded, Weddell and monk seals) range to about 3 m and 400 kg or more.

Two northern phocids diverge from the typical seal body form. The Latin species name of the grey seal (*Halichoerus grypus*) means 'hook-nosed' and the larger males, in particular, have a strongly arched and elongate snout (a Roman nose) (Fig. 1.4). Coloration of grey seals is highly variable, from almost black in adult males to mainly cream in adult females, with dark or light irregular spotting. The hooded seal (*Cystophora cristata*) is so named because of the adult male's remarkable inflatable nasal sac. When inflated, the hood becomes a taut, bulging, bi-lobed protuberance that dominates the entire area from behind the eyes to well in front of the mouth. The seals may inflate it when disturbed, during the pupping and mating season or even while lying quietly on the ice. In addition to the hood or crest, the male often causes its nasal septum to extrude, forming a large red balloon-like structure. The pelts of adult hooded seals have dark spots and blotches on a silvery ground colour.

These seals are 2.5–2.7 m long and weigh up to about 400 kg.

Each of the three Antarctic phocids in addition to the Weddell seal has a distinctive morphology. The Ross seal (*Ommatophoca rossii*) is a large species (to 3 m and 210 kg) with the shortest hair of any phocid, and a streaky grey coloration pattern. It has huge eyes, probably reflecting the need to collect as much light as possible in this seal's normally dark world underneath the ice. The crabeater seal (*Lobodon carcinophaga*) is long and slim, with unique dentition. The postcanines have cusps with separate, well-defined lobes, and the upper and lower ones interlock to form a sieve. This sieve allows the seal to filter its main food, krill, from sea water in a manner reminiscent of the baleen whales. Crabeaters suck food into the mouth, then press the tongue against the palate and raise the lips to let the sea water escape (Klages & Cockcroft 1990). Crabeater seals are brownish to grey on the back, shading to silver on the belly.

The leopard seal (*Hydrurga leptonyx*) is almost reptilian in appearance, mainly owing to the large head, with a marked constriction in the neck, and huge gape (Fig. 1.4). The canine teeth are exceptionally long, the postcanines massive. In form, the latter resemble those of the crabeater seal except they have three rather than four or five cusps. Leopard seals are predators on penguins and seals although they also consume krill (probably straining them much like crabeater seals), squid and fish. Female leopard seals can grow to 3.6 m and 450 kg; males are smaller. The coloration is bipartite and spotted, with dark grey on the back and light silvery on the belly.

Elephant seals (Fig. 1.4) are the largest pinnipeds, and males of the southern species (*Mirounga leonina*) are substantially larger than their northern congeners (*M. angustirostris*), while the smaller females of the two species are roughly the same size (to 2–3 m and 600–900 kg). Although not closely related, elephant seals and walruses resemble one another in the texture and appearance of their brownish, sparsely haired skin. Elephant seals share with monk seals the unusual feature of having a 'catastrophic' moult, whereby the skin sloughs away in large patches rather than having hairs fall out individually. The elephant seal's most distinguishing feature, and the reason for its common name, is its inflatable proboscis, which is highly developed in adult males and is used for display during the breeding season.

1.3 ZOOGEOGRAPHY

Our ability to understand and interpret today's marine mammal distributions has increased substantially in recent decades due to advances in other fields of science, notably plate tectonics and global climate change. Changes in the shape, size and even existence of seas and oceans over geological time have profoundly influenced the occurrence and dispersal of marine animals.

Brief examination of the distribution of marine mammals living today demonstrates the critical importance of water temperature in defining their geographical limits. The influence of temperature may be directly on the animal itself, or may be indirect if the mammal is seeking temperature-sensitive prey resources. As we shall see below, the position of the land and its surrounding shelf (if any), and water temperature, are the two over-riding influences on marine mammal distribution. Because water temperature is correlated with latitude, species often occur within latitudinal bands—sometimes in one hemisphere, less often in both. Figure 1.6 illustrates some typical distributional patterns.

Despite progress in understanding the environmental history of our planet, we remain far from having a full comprehension of marine mammal zoogeography. Not only is much of the evidence of past distribution fragmentary, but we have little idea about the ranges of some species alive today. The ziphiid whales are a case in point. For only a handful of the 20 or so extant species in this family are we reasonably confident about their precise range, and for some we have only the locations of a few strandings, separated by huge expanses of ocean.

1.3.1 Cetaceans

1.3.1.1 Mysticetes

With few exceptions the baleen whales are migratory, occupying different parts of their range on a seasonal basis. Indeed, some mysticetes migrate further than any other mammals. The reasons for their migrations may be related to energy and

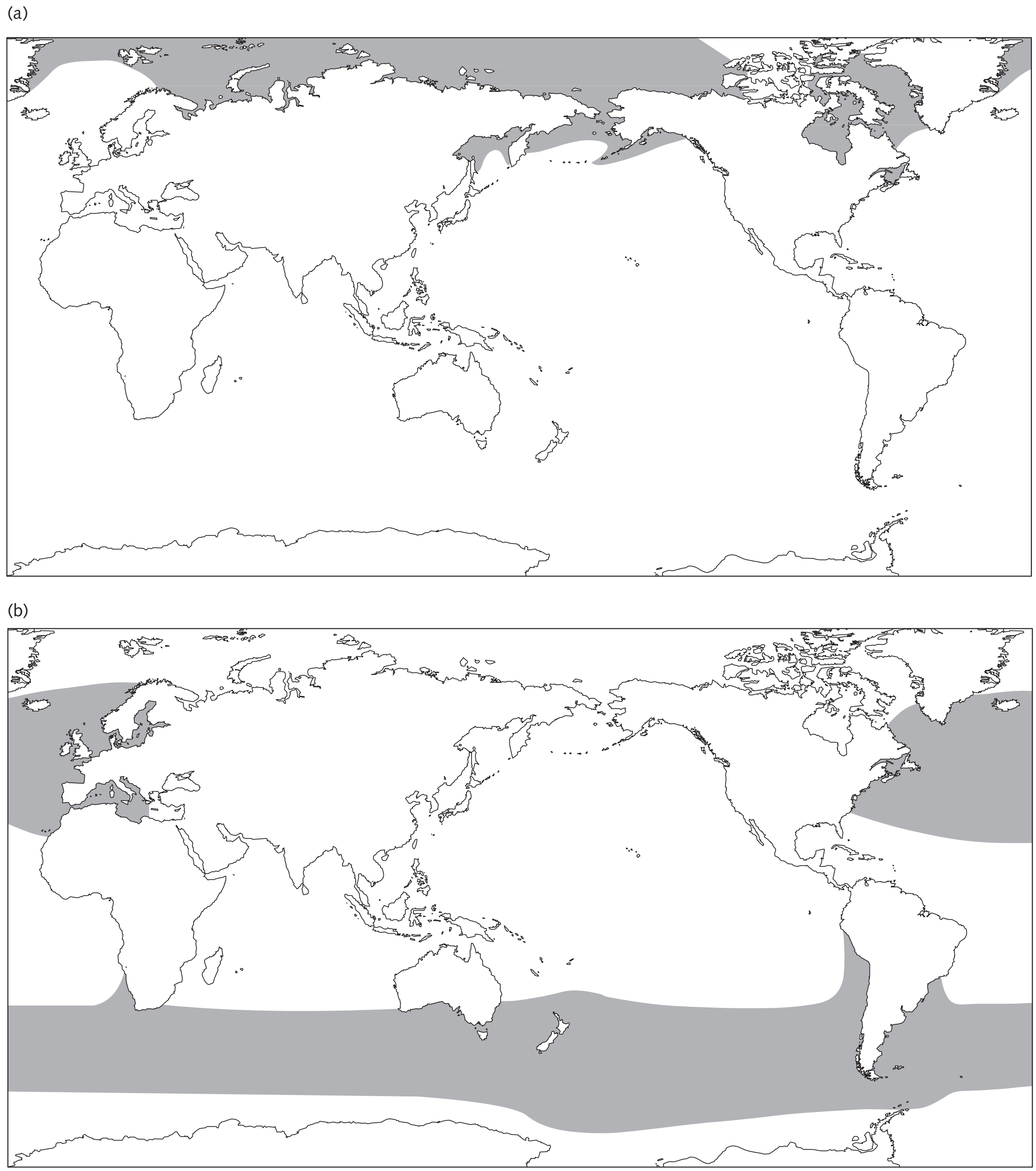


Fig. 1.6 Representative climate–zone distributions of cetaceans: (a) northern circumpolar—beluga; (b) antitropical—long-finned pilot whale. (*continued on p. 18*)

nutrition, or to the need for particular environmental conditions for reproduction. A population's winter and summer ranges can be separated by many thousands of kilometres (see Chapter 7).

The two types of balaenid whale have different distributions and migrational patterns. The bowhead is one of only three cetaceans with an exclusively Arctic range (the other two are monodontids); its migrations allow it to exploit rich high-latitude food resources during the short ice-free season. The morphologically similar right whales occupy temperate latitudes in both hemispheres. Their

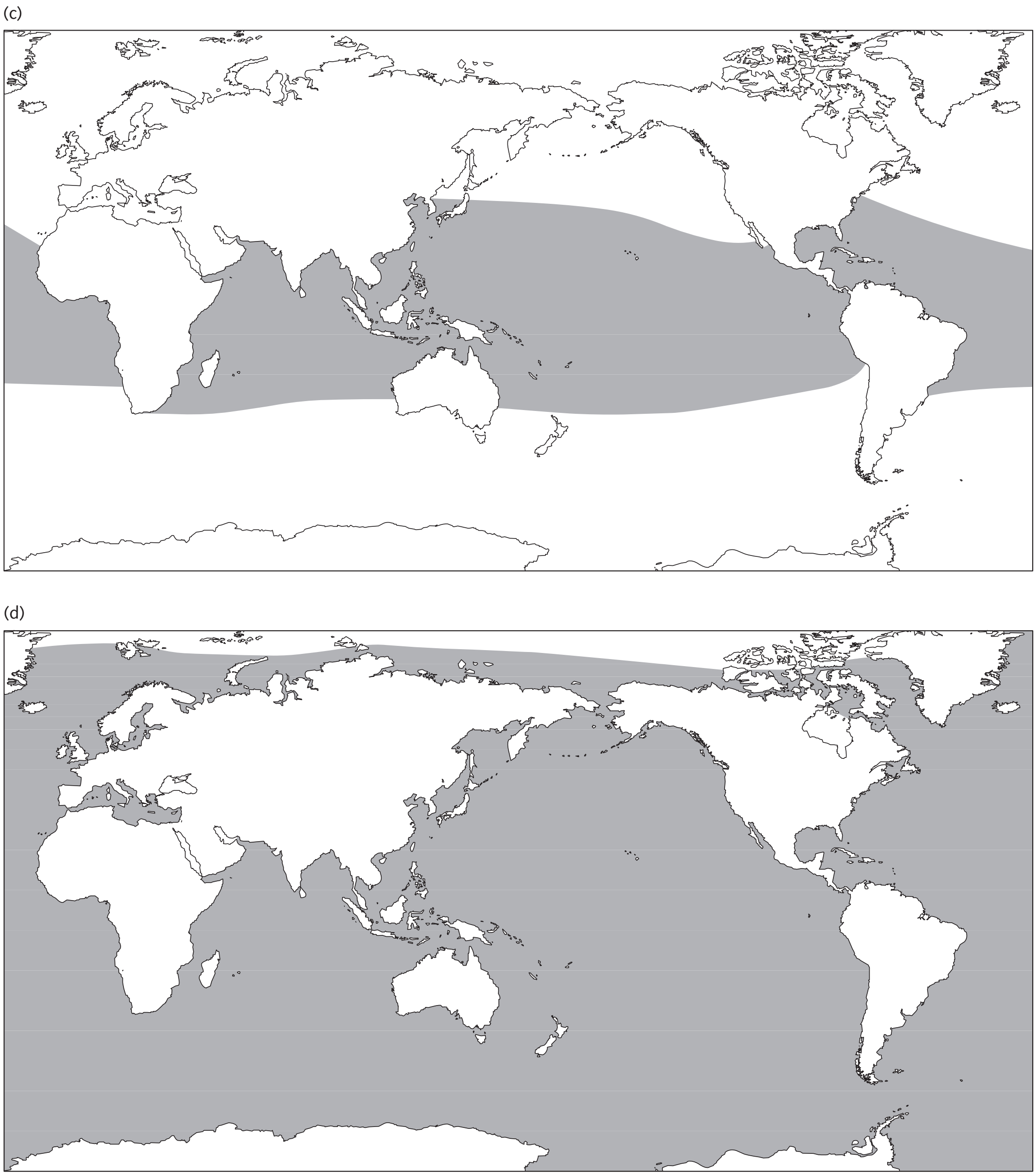


Fig. 1.6 (*cont'd*) (c) Pan-tropical—spinner dolphin; and (d) cosmopolitan—killer whale. This and all subsequent maps in Chapter 1 are intended to demonstrate patterns of distribution rather than to be precisely accurate in every detail. (Adapted from Jefferson *et al.* 1993.)

antitropical distribution ensures that northern and southern hemisphere populations remain separate, though they clearly have common ancestry (Schaeff *et al.* 1991; Rosenbaum *et al.* 2000). The pygmy right whale is also a temperate species, but is confined to a narrow latitudinal band (roughly 30–52°S).

The gray whale is restricted to shelf waters by its bottom-feeding habits and coastal migration