MARINE MAMMAL MIGRATIONS AND MOVEMENT PATTERNS

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Introduction

Marine mammals are renowned as great travelers. The migrations of some whales and seals span ocean basins, but other species have home ranges limited to a few square kilometers. Factors that influence marine mammals' movements strongly include how they give birth and mate, and how their food is distributed in space and time. These differ substantially across the marine mammal groups, and so they are dealt with separately in this chapter.

Marine and terrestrial ecosystems differ substantially as environments for air-breathing homeotherms. The density of sea water leads to far lower energetic costs of locomotion for animals living in marine systems. Living in a dense medium also allows mammals to grow to larger sizes than is possible on land, and the energetic cost of travel decreases exponentially with an animal's size. These factors, coupled with the connectivity of oceans, mean that marine mammals generally have far larger ranges, or longer migratory routes, than terrestrial mammals.

However, marine mammals' need for gaseous oxygen means that, unlike most marine animals, they must return regularly to the air–water interface to breathe. Also unlike most marine vertebrates, mammals give birth to live young. These young need to breathe immediately after birth, so they must either be remarkably good swimmers at birth or be born on land. Cetaceans, sea otters, and sirenians give birth at sea, but pinnipeds and polar bears give birth on land. This leads to major differences in their movements.

Locomotion represents an energetic cost to animals, so all individual animals are selected to balance the cost of travel against the benefits gained by travel. Unlike air, which is distributed evenly at the water surface, the food resources of marine mammals are found in patches of differing scales, varying in both space and time. Other marine species are distributed through the oceans' depths, so marine mammals have a third dimension available for their travel. Changes in the density of sea water with depth mean that marine mammals may expend little energy when descending in deep water, but must display physiological adaptations to deal with the extreme pressure associated with these deep dives.

Animals' movements can be considered on several temporal and spatial scales. Migrations, generally on an annual cycle, involve persistent movement between two destinations. An animal's home range is that area within which it carries out most of its normal activities throughout the year. Classically, home ranges are not considered to include migratory movements.

Cetaceans

Two factors appear to be responsible for substantial differences between the movement patterns of mysticetes and odontocetes. Most mysticetes feed in polar or cold temperate waters, highly seasonal environments. Therefore, mysticetes' prey are more heavily based on an annual cycle than the prey of most odontocetes. Also, although all cetaceans give birth aquatically, the location for giving birth appears to be particularly important to mysticetes.

Mysticetes

The annual cycle of most baleen whales is characterized by migrations between polar or cold temperate summering grounds and warm temperate, subtropical or tropical wintering grounds. In general, whales feed on their summering grounds and breed on their wintering grounds. These migrations include movements of nearly 8000 km by some humpback whales, the longest known annual movements of any mammal. Generally, whales' longitudinal (east–west) movements are relatively small when compared with their latitudinal (north–south) movements. Individual animals tend to return to the same summering and wintering areas over several years.

Some species – right (*Eubalaena* spp.), gray (*Eschrichtius robustus*), and humpback whales (*Megaptera novaeangliae*) – migrate relatively close to coastlines. *Balaenoptera* spp. tend to migrate further offshore, and their movements are less well known than those of the coastal migrators. Species also vary in the distance over which they migrate; for

example, right whales tend to cover less latitudinal range than humpback or gray whales.

Variation in Migratory Patterns

Not all species of baleen whale demonstrate this annual cycle. Bowhead whales, *Balaena glacialis*, undertake substantial longitudinal movements around the coasts of Alaska, Canada, and Siberia, but the southernmost extent of their movements remains close to the pack ice edge. At the other thermal extreme, some tropical Bryde's whales, *Balaenoptera brydei*, may not migrate at all. A population of humpback whales in the Arabian Sea also appears not to migrate.

There can be great intraspecific variability in the distances traveled by baleen whales. Humpback whales that congregate in Caribbean waters to breed come from discrete feeding groups in Atlantic waters, including western Greenland, off Newfoundland/Labrador, the Gulf of St Lawrence, off the northeastern USA, Iceland, and from north of Norway (**Figure 1**). From Antarctic waters, some humpback whales migrate into equatorial waters in the Northern Hemisphere, but others seem not to migrate north of approximately 15°S.

Individuals of migratory species do not necessarily migrate every year. Some female and juvenile humpback whales, and female southern right whales do not arrive at their wintering grounds every year. Large baleen whales were sighted south of the Antarctic Convergence in winter by early expeditions, and Antarctic minke whales, *Balaenoptera bonarensis*, have been seen inside the pack ice during winter. There are records of blue (*B. musculus*) fin (*B. physalus*) and humpback whales wintering in high latitude waters of the North Atlantic.

There are records of remarkable longitudinal movements by some baleen whales. Tagging pro-

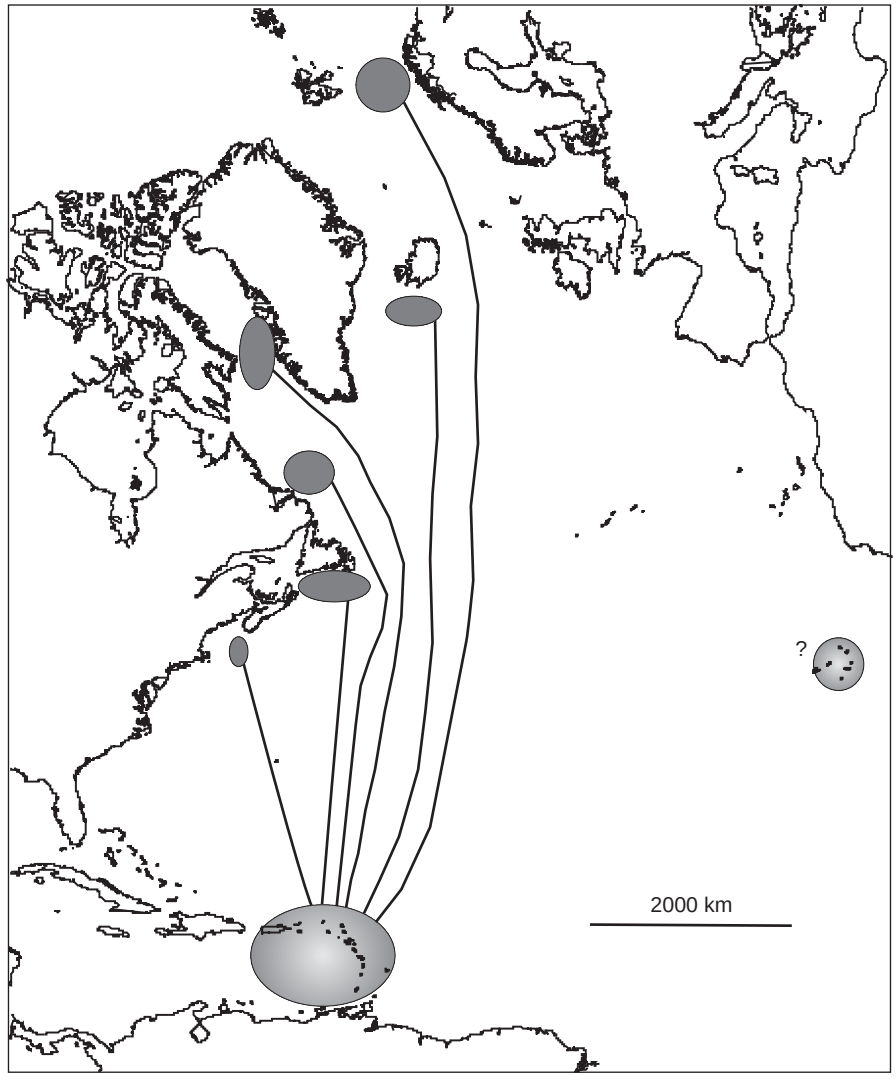

Figure 1 Migratory paths of humpback whales in the North Atlantic.

grams during Antarctic whaling demonstrated that individual blue whales could move around the Antarctic continent. Individual humpback whales, apparently males, have been observed overwintering in Hawaiian and Japanese waters in different years. Individual southern right whales have moved between the coast of South America and islands in the central South Atlantic.

As some populations of baleen whales recover from previous overhunting, further variability in migratory behavior is becoming evident. Some gray whales now feed in waters off British Columbia, well south of their primary feeding grounds in Arctic waters. Wintering southern right whales off the east coast of Australia are occurring in more northern waters. Further recoveries of baleen whale populations should reveal more behavioral variability at both wintering and summering grounds.

Why Do Baleen Whales Migrate?

Why baleen whales use high latitude feeding grounds is clear – polar systems produce incredible quantities of baleen whales' prey in the warmer months. The enigmatic aspect of baleen whale migration is why most whales travel to low latitude breeding grounds. Current hypotheses regarding why baleen whales migrate relate to calf survivorship: that calves are born away from polar waters so that in the first few weeks of life they avoid either cold waters, stormy waters, or predation by killer whales, *Orcinus orca*. Information available at present does not allow definitive conclusions on which of these competing (although not mutually exclusive) hypotheses is correct.

Odontocetes

Most odontocetes are smaller than mysticetes, and do not show their annual migratory patterns, nor move over ocean basins. Sperm whales, *Physeter macrocephalus*, are the exception to this. The movements of most odontocete species are not well known.

Sperm Whales

Baleen whales travel long distances latitudinally, but sperm whales are known more for their deep foraging dives. However, male sperm whales also undertake significant latitudinal movements. Females with calves and juveniles live in matrilineal groups in tropical and subtropical waters. These groups occupy home ranges with a long axis in the order of 1000 km. Young males leave their natal groups and move into higher latitude waters with conspecifics

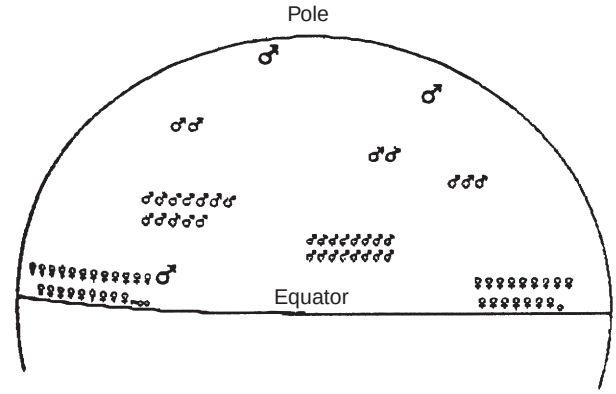

Figure 2 Diagrammatic representation of the latitudinal distribution of sperm whales in the Northern Hemisphere. (Reproduced with permission from Mann *et al.*, 2000.)

of similar age. As they mature, male sperm whales become less sociable and move into polar waters. Mature males migrate from their high latitude feeding areas to tropical waters to mate, but whether these are annual migrations is unclear (**Figure 2**).

Despite these long-distance migrations, small areas can be important. On one well-studied (and highly productive) feeding ground of only 20×30 km, up to approximately 90 males can be seasonally resident. Females' foraging ranges are larger, and it appears that their large ranges are a strategy to cope with interannual variability in environmental productivity.

Delphinids

Bottlenose dolphins Bottlenose dolphins, *Tursiops truncatus* and *T. aduncus*, are among the best studied of the delphinids. They are found from temperate to equatorial waters and from shallow waters by the coast to the deep ocean. Throughout their range, two ecotypes occur: inshore and offshore forms, with offshore animals being more robust. The relationship between these two forms and the two species of *Tursiops* is unclear, confounding comparisons. Bottlenose dolphins ranging patterns vary from animals with relatively small home ranges to migratory animals.

Bottlenose dolphins living in sheltered coastal waters, particularly bays, tend to have home ranges of several tens of square kilometers, varying in size with gender, age, and reproductive status. Most individuals appear to remain within these ranges throughout their life. Animals living in shallow waters off open coasts (e.g. California, South Africa) can range over > 100 km of coastline. Elsewhere (e.g. eastern Australia) dolphins in shallow waters off open coasts can have small home ranges,

similar to those of bay animals elsewhere. In some areas, populations of bottlenose dolphins undertake relatively long migrations. Some inshore dolphins off the US east coast migrate annually over approximately 400 km of coastline, while offshore animals in the same area move even further.

Most information on bottlenose dolphins comes from studies of individually identified animals. Logistically, these studies are likely to concentrate on animals with relatively small ranges. Satellite tracking offshore for bottlenose dolphins has started to reveal the extent over which they can range. Two animals tracked off Florida traveled 2050 km in 43 days, and 4200 km in 47 days. As these animals were rehabilitated after stranding, the extent to which their movements are representative of normal movements is debatable, but they demonstrate the ranging capacities of offshore bottlenose dolphins.

Killer Whales

Killer whales are found in all the world's oceans, from polar to equatorial waters, but their densities in polar waters are substantially higher than in tropical waters. There are two genetically distinct forms of killer whales: residents, feeding mainly on fish, and transients, that are marine mammal predators. Although these forms are best described from the waters off British Columbia, similar forms have been reported from Antarctic waters. Despite the names, the differences in ranging of these two forms of killer whales are not necessarily great. Off British Columbia and Washington, the ranges of transient pods extend to approximately 140 000 km^2 and those of residents to 90 000 km^2. As with bottlenose dolphins, logistics limit knowledge of the extent of killer whales' ranges.

Migratory behavior of killer whales remains poorly understood. The longest movements documented to date are of three identified individual transient killer whales that moved 2660 km along the Pacific coast of North America, from 58°41′N to 36°48′N over 3 years. Soviet whaling data from the Antarctic suggest that some killer whales undergo annual migrations to at least temperate latitudes, but sightings of killer whales in the Antarctic pack ice in winter demonstrate that not all animals migrate.

Killer whales' movements seem tied to movements of their prey: north–south movements of some killer whales along the North American west coast appear to be at least partially in response to the presence of migrating gray whales. Killer whales off coastal Norway seem to follow the herring migration. Killer whales appear to move into nearshore waters at several areas in the subantarctic – Peninsula Valdes Argentina – Marion Island, Macquarie Island, the Crozet Archipelago – coincident with seal pupping, although this may reflect the limits of shore-based observation to determine killer whales' real movements.

Other Odontocetes

Some inshore delphinids seem to demonstrate the variability in ranging behavior shown by bottlenose dolphins. Some individual humpback dolphins (*Sousa* spp.) in bay and estuarine environments have small home ranges (tens of square kilometers), others in more coastal waters range along hundreds of kilometers of coastline. Along 2000 km of the open west coast of South Africa there are three distinct matrilineal assemblages of Indian humpback dolphins, *S. plumbea*. Marine Irrawaddy dolphins, *Orcaella brevirostris*, appear to have small ranges (tens of square kilometers), centered around the mouths of rivers.

Movement patterns of delphinids in offshore waters are less well understood, but it is clear that animals range over at least thousands of square kilometers. Surveys off the west coast of the USA, covering over 10 degrees of latitude and extending to 550 km offshore, demonstrated seasonal changes in the distribution of small cetaceans. For example, northern right whale dolphins, *Lissodelphis borealis*, moved into continental shelf waters of the Southern California Bight in the winter, presumably from waters further offshore. Pacific white-sided dolphins, *Lagenorhynchus obliquidens*, and Dall's porpoises, *Phocoenoides dalli*, moved into more southern waters in winter.

Belugas (*Delphinapterus leucas*) and narwhals (*Monodon monoceros*) are ice-associated odontocetes found in Northern Hemisphere waters. Both species' annual movements through Arctic waters are closely tied to the movements of pack ice. One satellite-tagged narwhal traveled > 6300 km in 89 days, moving through $> 6°$ of latitude. Satellite tagging studies of both species reveal times when they move to the vicinity of glaciers, for reasons that are unclear.

Pinnipeds

Pinnipeds comprise three families: Phocidae, the true or haired seals; Otariidae, the eared or fur seals; and Odobenidae, the walrus, *Odobenus rosmarus*. Unlike cetaceans or sirenians, pinnipeds have retained some terrestrial traits while adapting to foraging at sea. Although all pinnipeds give birth on land or ice, the importance of terrestrial sites

for suckling, rest, mating, molting, predator avoidance, thermoregulation, or saving energy varies considerably across species. Within species, individuals' movement patterns vary depending both upon local environment conditions and individuals' age, sex, or breeding status.

Breeding

Pinniped movement patterns differ from other marine mammals due to the need for females to give birth and (generally) nurse on land. Female pinnipeds exhibit three maternal strategies, 'aquatic nursing,' the 'foraging cycle,' and the 'fasting cycle.' To date, the walrus is the only species to exhibit aquatic nursing. Female walrus give birth, fast for a few days, and then take their calves with them while they forage at sea. Lactation is extended and lasts for up to 2 or 3 years. This strategy bears some resemblance to that of cetaceans and sirenians. Most phocid and several otariid species exhibit the foraging cycle strategy. In these species, females forage at sea during lactation, returning to nurse their pups. Lactation can be relatively prolonged in these cases, most otariids suckle for weeks or months. Lactation is generally less prolonged in phocid species. Harbor seals, *Phoca vitulina*, nurse their pups for 24 days, and forage at sea during the latter stage of nursing (**Figure 3**). Female phocids using the fasting strategy remain on land throughout the whole nursing period. This period is relatively short, around 18 days for gray seals, *Halichoerus grypus*, 23 days for southern elephant seals, *Mirounga leonina*, and only 4 days for hooded seals, *Cystophora cristata*. Therefore, throughout the breeding season, the movements of female seals are constrained to different degrees by the need to suckle.

Although male pinnipeds are not limited by the need to nurse a pup, their movements during the breeding season are constrained by their need to mate. Males either obtain access to females on land or in the water. Approximately half of the pinniped species mate on land. However, walrus, two otariid species, and 15 species of phocid mate aquatically. Land mating pinnipeds remain onshore to defend either territorial access to females, such as in elephant seals, *Mirounga* spp. or access to resources used by females, as in Antarctic fur seals, *Arctocephalus gazella*. Males of aquatic mating pinnipeds, such as harbor seals, were previously thought not to restrict their movements during the mating season. However, recent evidence has shown that males perform vocal and dive displays in small discrete areas and limit their movements to areas frequently used by females throughout the mating season (**Figure 3**). Breeding activities clearly regulate movements of both female and male pinnipeds.

Nonbreeding

There is less variation between movement patterns of males and females outside of the breeding season, although differences do exist. During this period movement patterns are more strongly governed by resource (generally prey) availability.

Pinnipeds exhibit marked variation in the distance they move in order to reach suitable feeding grounds or breeding habitats. Harbor seals remain faithful to a single site or small group of local sites and usually do not forage > 50 km from their haul-out sites. Similarly, southern sea lions, *Otaria flavescens*, forage up to 45 km offshore, with occasional longer trips extending to > 150 km. In contrast, northern elephant seals, *Mirounga angustirostris*, carry out long-distance migrations of several thousand kilometers, travelling from California to the north-eastern Pacific Ocean twice a year (**Figure 4**).

Pups and juvenile animals are unable to travel as extensively as adults. In harbor seals, mothers restrict their foraging range while accompanied by their pups. Juvenile northern elephant seals do not dive as deeply, move more slowly, and do not migrate as far as adults during the first few years of their lives.

Haul-out Sites

Most pinnipeds remain faithful to a single or small group of haul-out sites. Groups of seals at different sites within a local haul-out area may show consistent differences in sex or age structure. Seasonal changes in haul-out site result from changes in foraging grounds, seasonal availability of prey, and characteristics of haul-out sites. Frequently, females and pups predominate at certain sites during the pupping season. Sheltered isolated areas may be chosen because of the lack of disturbance or terrestrial predators. Other sites may be used predominantly during molting.

Timing of trips to sea in relation to tidal and diel cycles varies considerably both within and between areas. Seals using haul-out sites that are available throughout the tidal cycle have activity patterns dominated by the diel cycle. When seals use haul-out sites that are only available over low tide, the tidal cycle has a more dominant effect. These effects are less pronounced when pinnipeds engage in longer foraging trips.

Small-scale movements in the vicinity of haul-out areas can be affected by the risk of predation. For example, northern elephant seals approaching major

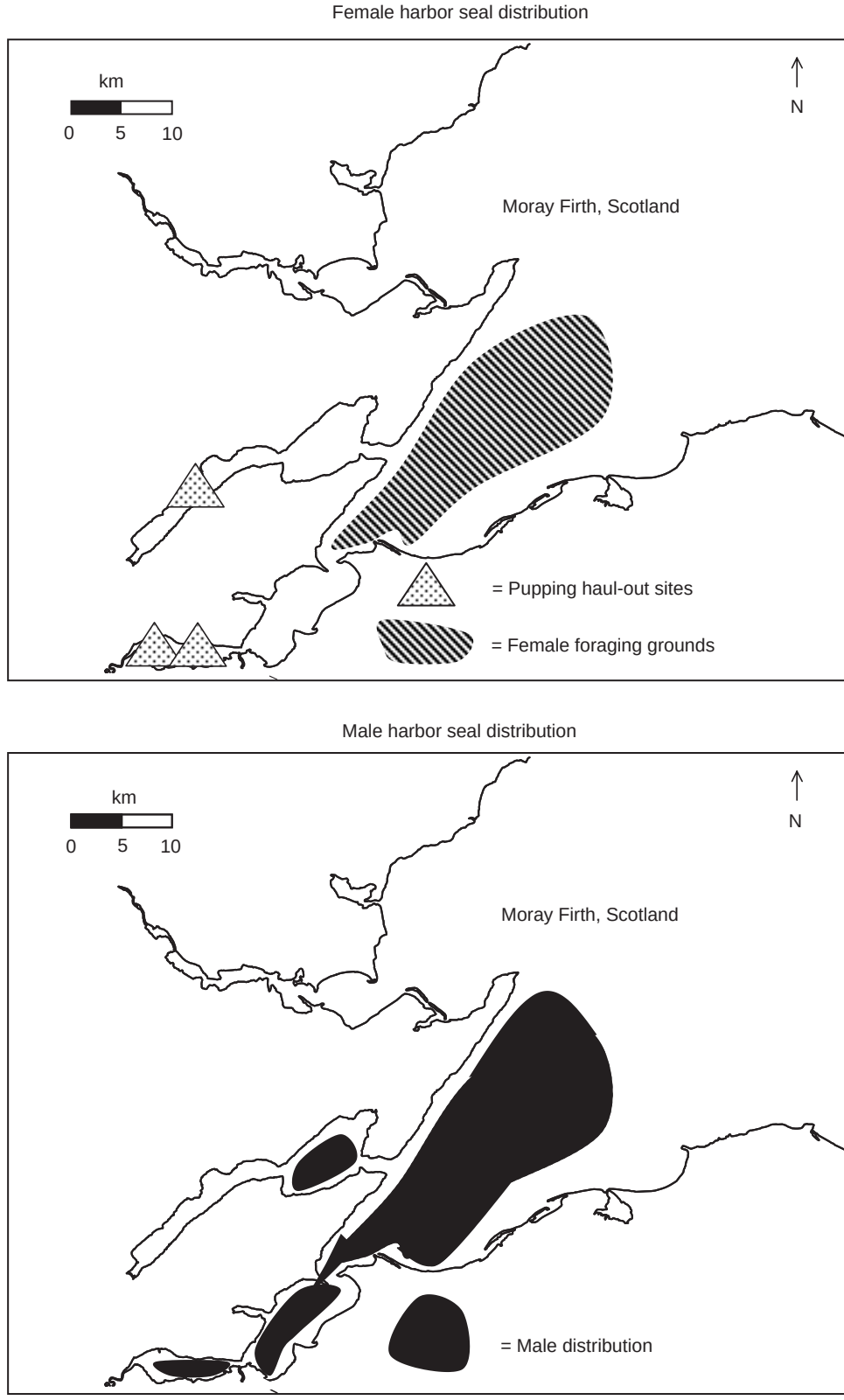

Figure 3 Ranges of harbor seals in the Moray Firth, Scotland. (From Thompson PM, Miller D, Cooper R and Hammond PS (1994) Changes in the distribution and activity of female harbour seals during the breeding season: implications for their lactation strategy and mating patterns. *Journal of Animal Ecology* 63: 24–30. Van Parijs SM, Hastie GD and Thompson PM (1999) Geographic variation in temporal and spatial patterns of aquatic mating male harbour seals. *Animal Behavior* 58: 1231–1239.)

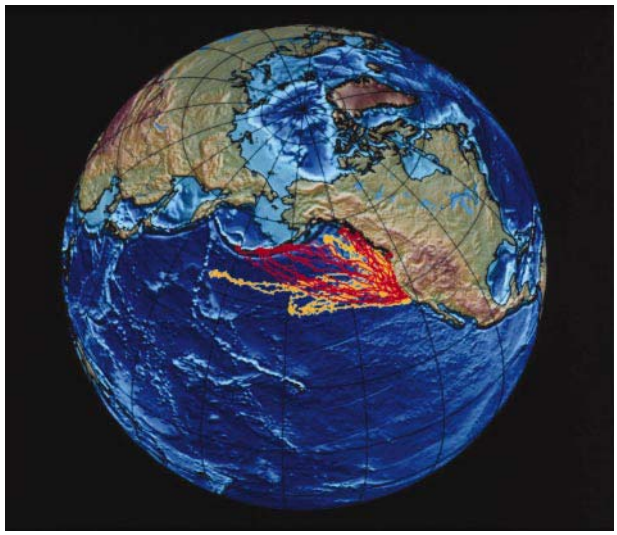

Figure 4 Movements of 22 adult males (red) and 17 adult females (yellow) tracked by satellite during spring and fall migrations from Año Nuevo, California, during 1995, 1996, and 1997. (Reproduced with permission from Le Boeuf *et al.*, 2000.)

breeding areas alter their diving behavior in a way that appears to reduce the risk of attack by the white shark, *Carcharodon carcharias*.

Pinnipeds hauling out on sand or rocky shorelines are exposed to different constraints to those hauling out on ice. Ice breeding pinnipeds often show a partiality to hauling out on a particular type of ice. As ice changes often and suddenly, they may be more constrained in the choice of haul-out site at particular periods of the year. Bearded seals, *Erignathus barbatus*, haul out on ice floes, the availability of which alters seasonally, daily, and hourly. Therefore, movements of both female and male bearded seals reflect the availability of a particular type of ice within an area.

The annual movements of harp seals, *Phoca groenlandica*, in the Barents Sea demonstrate their relationship with both ice and food availability. These seals breed in the White Sea in February/March, then molt in April/May in the White Sea and southern Barents Sea. In March and April, adult females seem to move westward on a short feeding migration. Between June and September, they are found in open water or in pack ice from Novaja Zemlja to Svalbard. They tend to be more associated with pack ice edge in September and October, moving east and north east to the vicinity of Franz Josef Land. Through November they seem to migrate ahead of the advancing pack to the southern coast of Novaja Zemlja, from where they move to their breeding grounds (**Figure 5**). Recently, in some years this pattern has been altered, with the westward movement of immature seals along the coast of northern Norway in winter (December–March). As these seals were in poor condition, these movements appear to be related to attempted foraging.

Sirenians

Being generally herbivorous, sirenians' foraging behavior differs substantially from other marine mammals. As animals of tropical and subtropical waters, their movements and food sources also show less seasonal variation than those of most other marine mammals. Dugongs, *Dugong dugon*, are the only extant sirenians that are truly marine, and so they will be the focus of discussion here.

Dugongs occur in shallow (generally $< 20\,m$) waters of the tropical and subtropical Indo-West Pacific. Most dugongs live in relatively small home ranges, in the order of tens to around a hundred square kilometers. Occasionally, satellite-tagged individuals undertake longer movements, up to 600 km from their home range and then, after a period of up to several weeks, return to their home range. There are no apparent age- or gender-related patterns to this, and reasons for these movements are unclear. Within their home range, dugongs' diel movements are tidally influenced, especially if seagrass beds occur in banks that are $< 1\,m$ deep or exposed at low tide. In at least one area, dugongs graze in large herds at the same site over weeks or months. This ranging and foraging pattern, termed 'cultivation grazing', encourages the growth of the pioneer seagrass species that are dugongs' preferred food. During periods of extreme food shortage in their home range, dugongs are known to travel along several hundred kilometers of coastline in search of new feeding grounds.

Glossary

Migration – Persistent movement between two destinations.

Home range – An animal's home range is that area within which it carries out most of its normal activities throughout the year. Home ranges are not usually considered to include migratory movements.

Haul-out site – Area (land or ice) where seals remove themselves from water.

Foraging – The process by which animals obtain food – includes searching for, capturing, and ingesting food.

Matrilineal (social unit) – Social system where female relatives remain associated, thereby providing the basic unit of the animals' society.

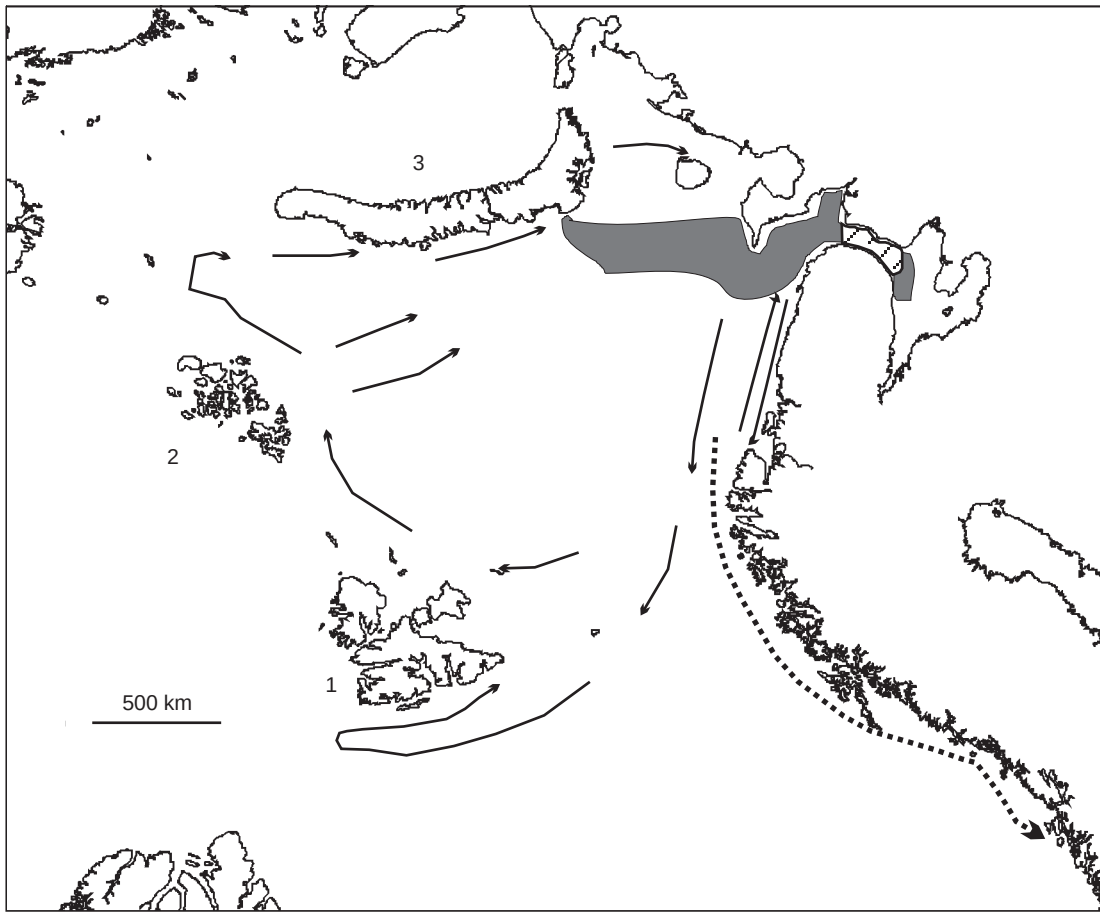

Figure 5 Annual movements of harp seals in the Barents Sea, including movements during recent invasions of the Norwegian coast. (1) Svalbard; (2) Franz Josef Land; (3) Novaja Zemlja. Gray shading shows the molting area, hatching shows the breeding area. The dashed line indicates the extent of movements of harp seals during invasions over recent years. (Data primarily from Haug T, Nilssen KT, Øien N and Potelov V (1994) Seasonal distribution of harp seals (*Phoca groenlandica*) in the Barents Sea. *Polar Research* 13: 163–172.)

See also

Baleen Whales. Marine Mammal Diving Physiology. Marine Mammal Overview. Marine Mammal Social Organization and Communication. Marine Mammal Trophic Levels and Interactions. Seals. Sea Otters. Sirenians. Sperm Whales and Beaked Whales.

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MARINE MAMMAL OVERVIEW

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Introduction

The term 'marine mammals' is an ecological grouping that lumps together a phylogenetically diverse set of mammals. The only thing linking them is that marine mammals occupy and rely upon aquatic habitats for all or much of their lives. The cetaceans and the sirenians (see the relevant Encyclopedia articles), or dugongs and manatees, live their entire lives at sea, only coming on land during perilous stranding events. Cetaceans (**Table 1**) evolved from ungulates whose modern members include pigs, while sirenians (**Table 2**) evolved from ungulates related to the modern elephant. One member of the bear family (Ursidae), the polar bear, is categorized as a marine mammal, while two members of the family Mustelidae are considered marine: the sea otter and the marine otter of Chile (**Table 3**). Seals and walruses also evolved from terrestrial carnivores. Most biologists lump the seals and walruses into a suborder called the Pinnepedia, and these are often referred to as pinnipeds, meaning 'finlike feet'. Seals are divided into two families: the Otariidae, or eared seals, and the Phocidae, or true seals (**Table 4**). Walruses are categorized as a separate family, the Odobenidae (**Table 4**). The definition of marine mammals is somewhat arbitrary – river dolphins are considered marine mammals, but river otters are not. Inclusion in this category can have real consequences in the United States, since marine mammals have special protection under the US Marine Mammal Protection Act.

Taxonomy

The basic evolution of marine mammals from carnivores and ungulates is well established, but the details of phylogeny and taxonomy at the species level are in flux, owing in part to recent molecular genetic data. Since there is a relatively well-established nomenclature that has been stable for the past 20 years or so, and which forms the basis for species management, this nomenclature will be used in the following tables, while it is recognized that the developing synthesis of molecular and morphological data will probably change some of the species relations. For example, the US and international agencies responsible for protecting endangered species split right whales of the northern and southern oceans into two species; some taxonomists lump right whales into one species, but the North Pacific and North Atlantic right whales are clearly separated and recent genetic data suggests the division of right whales into three species: Southern, Northern Pacific, and North Atlantic. Where the designation of endangered species focuses on the species level, this lumping of right whales of the North Atlantic and North Pacific, which are highly endangered, with right whales of the South Atlantic, which are doing well, could have profound policy implications.

Adaptations of Marine Mammals

The success of marine mammals is something of a puzzle. How did their terrestrial ancestors, adapted for life on land, compete against all of the life forms that were already so well adapted to the marine environment? Multicellular organisms arose in the oceans of the earth about 700 million years ago (MYa), and for the next 100 million years or so, there was a remarkable burst of evolutionary diversification, as most of the basic body plans of life in the sea evolved. By 350–400 MYa, multicellular animals expanded from the ocean into terrestrial environments, with another evolutionary radiation. Mammals only reentered the sea about 60 MYa, and thus have had less than one-tenth of the time available to the original marine metazoans for adaptation to this challenging environment.