

Whales, porpoises and dolphins

Order Cetacea

Compiled by P.G.H. Evans

An order of mostly marine mammals, with a few freshwater species, distributed throughout the oceans of the world: 84 species arranged in c.40 genera [558, 922, 989, 1245]. Divided into 2 suborders: Mysticeti, baleen whales, mostly very large marine mammals, filter feeders with baleen plates but no teeth; Odontoceti, a more varied group of small (porpoise), medium (dolphin) and large (whale) species, mostly toothed, some of which occur in fresh water. Phylogenetically, Cetacea are very closely related to Artiodactyla, especially (among extant mammals) Hippopotamidae, and could formally be classified as a family of Artiodactyla; phylogenetic classifications group them as an Order Cetartiodactyla. This relationship is indicated not only by genetic analyses (e.g. [733, 962]) but also by a series of fossils (Pakicetidae) from the early Eocene–Oligocene of Pakistan which show limb reduction, skull and dental changes bridging the transition from terrestrial ungulates to aquatic whales [1145]. The conservative retention of an Order Cetacea for this handbook is a compromise between practical and theoretical mammalogy.

Cetaceans are highly modified in all aspects, physiological, anatomical and ecological, from the basic mammalian form. The skin is essentially naked (a few whiskers may remain on the snout of juveniles), and cetaceans rely on a subcutaneous fat layer (blubber) for insulation. Their front limbs are reduced to flippers, the wrist bones are reduced to small unrecognisable discs of bone and the hind limbs are apparently absent (tiny internal vestiges of their skeleton in baleen whales are all that remain). Vertical undulation of the elongate body provides the propulsion for their swimming, aided by horizontal tail flukes that contain no skeleton. Most species have a mid-dorsal fin, which also lacks any skeletal support.

The skull is elongate, the nostrils relocated mid-dorsally as a blowhole, and the braincase compressed anteroposteriorly, so that the occipital (posterior) surface meets the frontal bones. The eyes are very low on the side of the head. Mysticetes have long, toothless jaws, and keratinous (compressed hair) baleen plates hanging from the upper jaws. These are frayed internally, producing a filtering fringe that separates plankton or fish from a mouthfull of water. Most

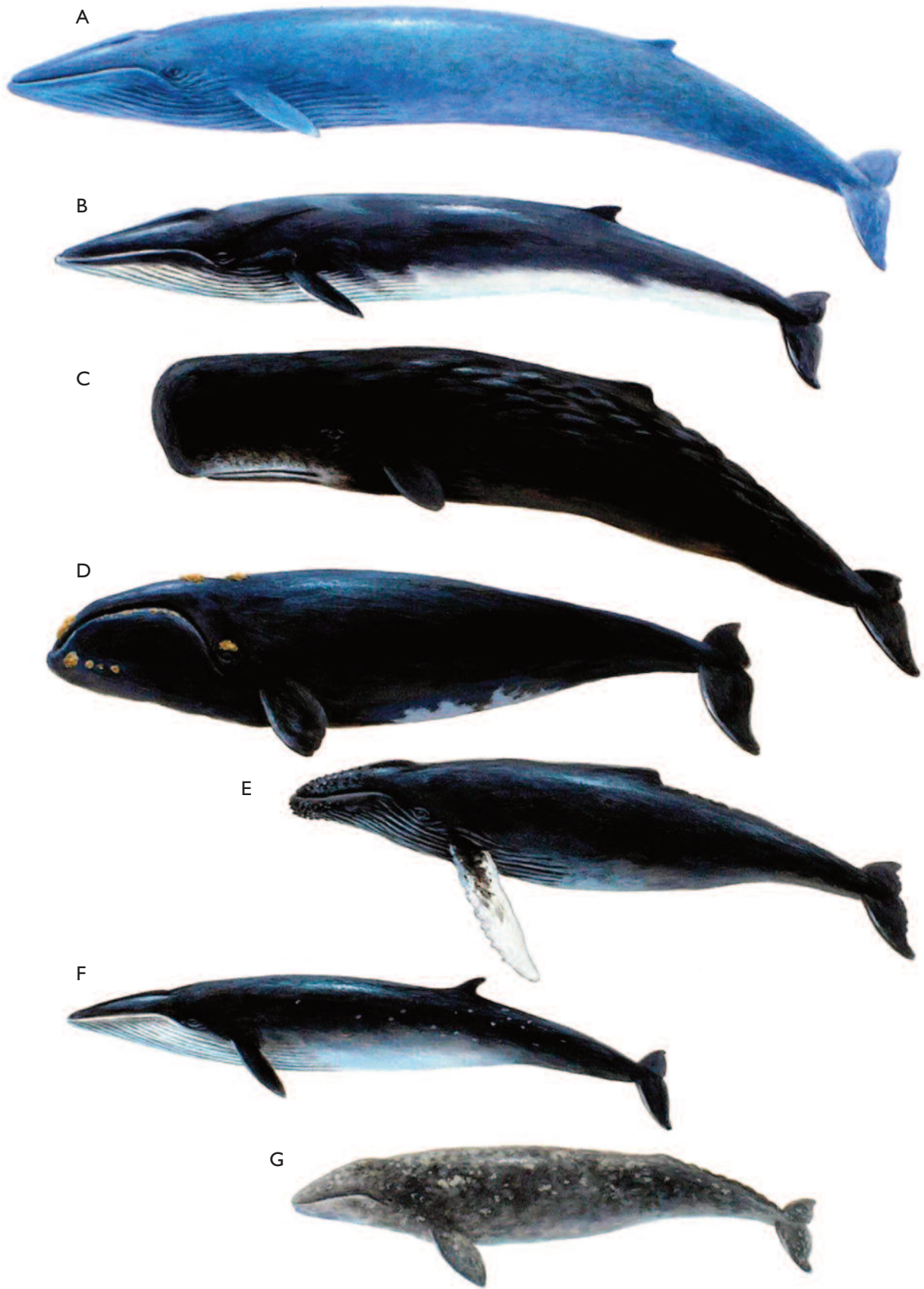
odontocetes have numerous identical teeth (up to 210, 45–65 in each jaw, in *Stenella longirostris*), strongly contrasting with the differentiated teeth (incisors, canines, premolars, molars) that characterise most mammals, and indeed paki-cetids and early whales; some (females) are essentially toothless, and their males have only a pair of tusks (modified canines?). The snouts are usually elongate, but the jaws are slender, for cetaceans swallow their food whole, do not (cannot) chew it, so have simple-looking jaws, slender jaw muscles and loose jaw joints with slight condyles and shallow glenoids.

Odontocetes, at least, use echolocation to locate their prey, producing clicks that are transmitted out through the bones of the snout, and perhaps concentrated (beamed) by a fatty melon on top of the face. Returning echoes are transmitted well through water, poorly through air, but because soft tissue is essentially water, their bodies are 'transparent'; to overcome this problem, and give directional hearing, the inner ear is encased in dense bone but separated from the rest of the skeleton by pockets of air. Sound travels into the inner ear through a solid ear canal, thus left and right ears hear sounds differentially. There is no evidence that mysticetes use echolocation, but they certainly use sounds extensively in communication, and their inner ears are modelled similarly.

Externally, most cetaceans have no obvious neck, the body being smoothly tapered, and internally the neck vertebrae are compressed, often partially or completely fused. The thoracic vertebrae and ribs are about as numerous as in terrestrial mammals (9–16 pairs, but usually 12–13 pairs), but the lumbar and caudal vertebrae are more numerous, flat-ended, with tall dorsal spines on most of them. The large whales suffocate when stranded because their rib cages are too slight to support their weight; compression of their chests, forcing air from the lungs into the more rigid bronchii, is one of their adaptations to diving.

Many species, baleen whales in particular, move to higher latitudes to feed in summer on the rich plankton and the fish associated with it, but travel to tropical waters to calf during the winter. Tropical waters are largely devoid of plankton, so little feeding is possible, but the warmer waters

Plate 13: Cetaceans



A Blue whale *Balaenoptera musculus* B Fin whale *B. physalus* C Sperm whale *Physeter macrocephalus*
D Northern right whale *Eubalaena glacialis* E Humpback whale *Megaptera novaeangliae*
F Sei whale *B. borealis* G Gray whale *Eschrichtius robustus*

12 Whales, porpoises and Cetacea: Order Cetacea

are more suitable for young calves. This means that southern and northern populations are 6 months out of phase. Atlantic and Pacific populations are also somewhat isolated, though contact is possible through the Indian and Southern Oceans. This has permitted a degree of separation of stocks, allowing partial or complete speciation. However, conventional taxonomy of such large, elusive mammals has been and remains challenging, though molecular markers are yielding valuable insights. It is often still uncertain whether populations in tropical or higher latitudes, Pacific or Atlantic, N or S hemispheres, are in complete genetic contact, partially isolated or separated into several species. Specific taxonomy is therefore uncertain in many genera, and changing rapidly as new genetic techniques reveal unsuspected differences.

The larger whales, in part because of their thick blubber, have been severely persecuted by humans since at least the Middle Ages, and commercial whaling in the late 19th–early 20th centuries reduced all the larger, more vulnerable species to commercial extinction. This was successively true of the right and bowhead whales, then in turn the gray whale, humpback, blue, fin and sei whales [342]; the sperm whale was also severely persecuted, but its largely tropical range and deep-diving behaviour offered it some sanctuary. International agreements made by the International Whaling Commission (IWC) successively gave them protection from 1935 (right whale), 1966 (humpback), 1967 (blue whale), 1985 (sperm whale) and 1986 (fin, sei, minke), though even that was, we now know, flouted by some whaling fleets [87, 1255]. Some stocks of most species have shown a modest recovery over the last 40 years, but this has prompted renewed pressure from some whaling nations, who wish the IWC to allow some reopening of commercial whaling. A small amount of scientific whaling was in any case permitted, and Iceland, Norway and Japan in particular have availed themselves of this exemption; coastal whaling in national waters seems likely to resume in the N Atlantic, facilitated by the establishment amongst whaling nations of the North Atlantic Marine Mammal Commission (NAMMCO) in 1992.

From the Middle Ages, cetaceans stranded on British coasts were legally 'Royal Fish', and belonged to the crown; originally, they provided a source of meat, oil and other products, but latterly became a nuisance; their legal status was exploited to require the notification of strandings to the British Museum (Natural History), resulting in a valuable sequence of reports on stranded cetaceans for most of the 20th century

[404, 406–408, 485, 1073, 1074]. This recording system persists, but is now supplemented by routine sea-watch surveys from headlands, dedicated cruises and survey flights, and the results of commercial as well as impromptu whale-watching, so that the distribution of live, as well as dead, cetaceans is better documented [973]. Distributions around the British Isles have been mapped specially for this account by P.G.H. Evans. Other study techniques for cetaceans include, for live animals at sea: direct observations [354, 477], photo-ID [354, 477], and acoustic monitoring [450]; and for stranded, bycaught and captured individuals: pathology, toxicology, morphometrics, genetic and dietary methods (see [661] for reviews of post-mortem methods for sample collection).

Legislation has also progressed. Several of the coastal species are now protected within national and European waters, while larger species, once hunted commercially off the W coast of Ireland [367] and off NW Scotland [181, 1148], are now protected by a moratorium on commercial hunting under IWC auspices. International protection for cetaceans includes Appendix I or II of the CMS Agreement on the Conservation of Migratory Species of Wild Animals (Bonn Convention, 1983); Appendix II or III of the Bern Convention on the Conservation of European Wildlife and Natural Habitats; and Annex IV Animal and Plant Species of Community Interest in Need of Strict Protection of the EC Habitats Directive (1992). Species are listed on List C1 of Council Regulation and since 1985, have largely been treated by the European Community as if on CITES Appendix II (trade controlled to prevent overexploitation). See Table 12.1.

Cetaceans are protected under the Wildlife and Countryside Act 1981 and the Wildlife (Northern Ireland) Order 1985. The international Agreement on the Conservation of Small Cetaceans in the Baltic and North Seas (ASCOBANS) (1992) applies to all odontocetes besides the sperm whale (see Chapter 4).

Table 12.1

Conservation status of cetacean species recorded around the British Isles

Species	Bonn Convention	Bern Convention	CITES	EU Habitats	ASCOBANS	IWC	IUCN
Northern right whale	I ^a	II	I	IV	–	Protected	EN
Minke whale	–	III	Ic	IV	–	Lim Catch	LR/nt
Sei whale	I ^a	III	I	IV	–	Protected	EN
Blue whale	I	II	I	IV	–	Protected	EN
Fin whale	Ia	II	I	IV	–	Protected	EN
Humpback	I	II	I	IV	–	Protected	VU
Sperm whale	I & II ^a	III	I	IV	–	Protected	VU
Pygmy sperm	–	II	II	IV	–	–	LR/Ic
Northern bottlenose	–	II	I	IV	+	–	LR(cd)
Sowerby's	–	II	II	IV	+	–	DD
Blainville's	–	II	II	IV	+	–	DD
True's beaked whale	–	II	II	IV	+	–	DD
Cuvier's beaked whale	–	II	II	IV	+	–	DD
Beluga	II	III	II	IV	+	–	VU
Narwhal	II	II	II	IV	+	–	DD
Long-finned pilot whale	II	II	II	IV	+	–	LR/Ic
Killer whale	–	II	II	IV	+	–	LR(cd)
False killer whale	–	II	II	IV	+	–	LR/Ic
Melon-headed whale	–	III	II	IV	+	–	LR/Ic
Risso's dolphin	II ^b	II	II	IV	+	–	DD
Common dolphin	I ^a	II	II	IV	+	–	LR/Ic
Striped dolphin	–	II	II	IV	+	–	LR(cd)
Fraser's dolphin	–	III	II	IV	+	–	DD
Atlantic white-sided dolphin	II ^b	II	II	IV	+	–	LR/Ic
White-beaked dolphin	II ^b	II	II	IV	+	–	LR/Ic
Bottlenose dolphin	II ^b	II	II	II & IV	+	–	DD
Harbour porpoise	II ^b	II	II	II & IV	+	–	VU

^a The species, or a separate population of that species, or a higher taxon which includes that species is included in Appendix II of the Convention.

^b North Sea and Baltic populations.

^c Except population of West Greenland.

IUCN Categories: DD, Data Deficient; EN, Endangered; VU, Vulnerable; LR, Lower Risk; nt, near threatened; cd, conservation dependent; lc = least concern.

SUBORDER MYSTICETI (BALEEN WHALES)

A small group of *c.* 13 species, nowadays arranged in 4 families: right whales Balaenidae, pygmy right whale, Neobalaenidae, gray whale Eschrichtiidae and rorquals Balaenopteridae [989, 1245]. Validity of Eschrichtiidae in question [494].

FAMILY BALAENIDAE (RIGHT WHALES)

A small family of 2 genera, 2–4 species [1245], the Arctic bowhead *Balaena mysticetus* and 1–3 species of right whale, *Eubalaena*, one of which occurs, now rarely, in the NE Atlantic. Pygmy right whale *Caperea marginata* (S hemisphere) sometimes included. Have very long baleen plates, suspended from highly arched upper jaws; sieve plankton by swimming slowly, at surface.

Northern right whale *Eubalaena glacialis*
Balaena glacialis Müller 1776, North Cape, Norway.
Balaena britannica Gray 1870, Dorset, England.
Fiormhiol mór na bioscáine (Irish Gaelic).

RECOGNITION

Large head, narrow rostrum with highly arched lower jaws, dark skin and absence of dorsal fin render them unmistakable (Plate 13). Have light-coloured callosities on their heads (see below). Seen along animal's axis, blow distinctively V shaped, can reach 7 m high. Feeding, occurring at surface, may lead to reports of sea monsters, as these whales skim with their mouths wide open, narrow rostrums raised in the air, and baleen plates partially exposed above the water. Broad all-black flukes are raised above the water on diving (Fig. 12.1).

DESCRIPTION

Relatively rotund, squarish in the chin, generally black, occasionally with white belly and chin patches. Head forms 25% of the total body length in adults, up to 35% in juveniles. Narrow, strongly arched rostrum and strongly bowed lower jaws are characteristic of the species. The skull can be up to 5 m in length and weigh as much as 1000 kg, with a distinctive supraoccipital bony shield. Vertebral formula C7, D14, and L11 (10–12) [1163].

Grey or black thickened skin patches, callosities, found on rostrum, behind the blowholes, over the eyes, on the corners of the chin, and variably along the lower lip and jawlines. Their arrangement is unique to each right whale, can be used for individual recognition [475]. Callosities appear light yellow or cream coloured

due to large infestations of whale lice *Cyamus*; consist of spikes of columnar epithelial tissue, appearing barnacle-like, but no barnacles have ever been found on N Atlantic right whales. Baleen plates black or brown, 205–270 plates on each side; very long, average 2–2.8 m long but relatively narrow (up to 18 cm) (Fig. 12.2). No grooves along the throat. Tail broad (up to 6 m tip to tip), all black.

MEASUREMENTS

Length: newborn *c.* 4.4–4.8 m; on reaching maturity *c.* 13.0–16.0 m; adult typically 14–16 m (max. 18 m), females averaging *c.* 1 m longer than males [27, 967]. Weight *c.* 50–56 t, occasionally to 90 t. Blubber layer up to 20 cm thick, provides both insulation and energy storage.

RELATIONSHIPS

Genetic data [1013] clearly separate *Eubalaena* (right whales) from *Balaena* (bowhead), identify 3 *Eubalaena* species (*japonica*, N Pacific; *australis*, S hemisphere; and *glacialis*, N Atlantic), and suggest that *Eubalaena* populations in N and S Atlantic have been separated for *c.* 1 million years [1044].

VARIATION

Morphological variation between populations in different ocean basins, with differences in callosity patterns and maximum adult sizes reported. However, within N Atlantic, genetic data from historical samples suggest ocean-wide interbreeding [1014]. Recent re-sighting off Norway of known individual from New England demonstrates the relative ease with which this whale can traverse large distances [561]. Suggests that local variation within N Atlantic population likely to be confined to coloration (white vs black ventral patterns) and callosity patterns.

DISTRIBUTION

In N hemisphere, normally restricted to between 20° and 70° N (mainly temperate zone) [651]. In E North Atlantic, once ranged from NW Africa, Azores and Mediterranean, N to Bay of Biscay, W Ireland, Hebrides, Shetland, Faroes, Iceland, and Svalbard. Since 1920s, sightings sporadic: from Canaries, Madeira, Spain, Portugal, British Isles and Iceland [182, 346, 353, 1168]. Historically, good evidence that E North Atlantic right whales calved in Cintra Bay, (W Sahara) during winter [964]. Whaling records indicate occurred off Hebrides and Ireland in early summer (mainly June), possibly having spent winter in Bay of Biscay (the Basque fishery operated mainly between October and February); may have moved on to Scandinavian feeding areas later [11, 273, 367, 1148]. Recent findings identify an historic



Fig. 12.1 Flukes of four large whales that usually show them on diving: (a) Northern right (*photo S.Kraus*), (b) blue (*photo P.G.H. Evans*), (c) humpback (*photo P.G.H. Evans*) and (d) sperm (*photo F. Ugarte*) whales. The pattern of black and white under the humpback whale's tail is very variable, and used for individual identification.



Fig. 12.2 Baleen plates of species of mysticete recorded around the British Isles (a) right; (b) minke; (c) sei; (d) humpback; (e) fin; (f) blue (*drawn to scale by D.W. Yalden, after [1212]*).

12 Whales, porpoises and Cetacea: Order Cetacea

right whaling ground off Norway in the 1600s [1103]. The few recent sightings in British and Irish waters have all occurred May–September [346, 360].

In W North Atlantic, range extended from Texas, Florida, and Bermuda in S, to the Gulf of St Lawrence and the coasts of Nova Scotia, Newfoundland and S Greenland in N. Most cows give birth in coastal waters of SE USA during winter [656]. Males and adult females without calves rarely seen there; whereabouts during winter remain unknown. In spring, aggregations observed in the Great South Channel, E of Cape Cod, and in Massachusetts Bay [1046, 1249]. In summer and autumn, observed in the Bay of Fundy, between Maine and Nova Scotia, and in an area on the continental shelf 50 km S of Nova Scotia [651, 652, 1127].

Individuals seen off Iceland and Norway matched animals seen in W North Atlantic [641], and preliminary genetic data indicate that separation between E and W Atlantic stocks unlikely. Given few sightings in E, best hope for the return of right whales to European waters is re-colonisation from W North Atlantic population

HISTORY

Little fossil material is available on *Eubalaena* from the N Atlantic.

Hunting right whales, started by the Basques >1000 years ago [972], led to development of all whaling [11]. Continued until 1935, when international protection given to this species by the League of Nations [967] (see Relations with humans, below).

HABITAT

No specific contemporary habitat identified in E North Atlantic. Historical whaling data suggest that most taken off GB and Ireland were <40 km from land, over the continental shelf [340, 972, 1148]. Historical whaling records identify a former right whale summering ground off Norway [1103]. Some calving certainly occurred in the coastal waters of Morocco (formerly W Sahara) in winter months, late 1800s [966]. Northern areas presumed to be feeding habitats for the few right whales that survive.

In W North Atlantic, several habitat types recognised. Feeding grounds have been identified as areas with high concentrations of copepods [615, 764]. Scotian shelf hypothesised to be a breeding ground because of the high proportion of courtship groups present there [1127]. Coastal waters of SE USA have been shown to be a calving habitat, with few males present, and no feeding activity [654].

Although nearly all right whale cows in W North Atlantic give birth off SE USA, substructuring evident within population. From genetic and photo-ID data inferred that one group of cows (representing about 1/3 of the population) does not bring its calves to Bay of Fundy nursery area [1044]. Subsequent work suggested strong maternally directed site fidelity in right whales [737], with offspring returning to the mother's summer habitat. Implies another, unknown, summer–autumn nursery area; most of coastal zone of E North America has been surveyed over the past 25 years, so this unknown location is probably offshore and/or further N. Suggests a group of whales under-represented in photo-ID surveys, could alter population estimates.

SOCIAL ORGANISATION AND BEHAVIOUR

Poorly understood. Seen either singly or in pairs, except for courtship activity. Pairs of apparently unrelated individuals sometimes associate for several weeks at a time. In feeding areas, large aggregations of whales sometimes seen, but these appear to be acting independently, with few interactions. Echelon feeding in Cape Cod Bay of 2 skimming right whales reported. Engage in many typical whale behaviours, such as breaching, fluking upon diving, flipper slapping, and lobtailing (slamming the tail down on the water surface).

Courtship groups can be large and boisterous (up to 40 animals), appear to be multiple males competing for access to a single female. Courtship and mating activities occur at the surface, with associated underwater acoustic signals [899].

Speculation that males engage in sperm competition [185], and that females actively solicit competition among males to ensure the best mate [650, 898]. Mature males ($n = 11$, N Pacific population) had testes with a combined average weight of 972 kg, and penis lengths that averaged 2.3 m [185]. Mother–calf bonds strong for the first 10 months; subsequent interactions appear to be rare.

Vocalisations: Relatively vocal; substantial information on N Atlantic right whale [899, 900, 1149, 1173]; see also [1205]. Produce mainly moans in the range 400–3200 Hz, lasting 0.5–6.0 s, often with both pulsive and tonal components [254, 907]. Maximum source level 182 dB re 1 μ Pa @ 1 m [1204]. More complex calls are often associated with sexual activity; described as usually very harsh, strident or like a growl [254, 898]. These are AM moans, with major energy around 0.05–0.2 kHz. 3 classes of right whale sounds have been described: blows, gunshots, and

tonal calls [898]. Most common call is an FM upsweep with major energy around 0.05–0.2 kHz; thought to be a contact call because all whales produce it, but only when separated. Also common is the high call, an FM sweep with major energy at 0.2–0.5 kHz, with multiple frequency shifts, and greater harmonic structure, made during social activity. During social interactions, other broadband sounds made, including blows (with major energy 0.1–0.4 kHz) and slaps (major energy 0.05–1 kHz); only made during social interaction, and may serve as threats [255, 899, 900].

FEEDING

Skim feeders on zooplankton, both at the surface and at depth, depending on patch locations and density [106]. Feed primarily on copepods but also occasionally on euphausiids [616, 764, 881, 1206]. In N Atlantic, identified feeding grounds are areas of high concentrations of copepod *Calanus finmarchius*, specifically the larger stages (C4, C5, and adult) [106, 627]. Feeding documented by observing open-mouth skimming at the surface, or defecation, in all 4 of the northern habitats in W North Atlantic, but not in the calving grounds off the SE USA. No feeding documented recently in E North Atlantic.

BREEDING

Calves born in winter, early December–late March, although newborn calves occasionally reported outside this season [656]. Gestation estimated at 12–13 months [128]. Infants born at 4–5 m, grow rapidly, attain 8–9 m by end of their 1st year [473]. Lactation lasts 10–12 months, although juveniles may rarely suck up to 17 months. Average age at sexual maturity for females is probably 9–10 years, although one female gave birth at 5 years [474, 656].

Cows give birth to a single calf every 3–5 years. Calving intervals increased from slightly over 3 years in the 1980s to >5 years by the late 1990s, but returned to *c.* 3 years after 2001 [656]. Causes of this variation unknown.

POPULATION

Since 1980, have been studied using photographic identification of individuals from both aerial and shipboard surveys [180, 475]. Individually identifiable from their callosity patterns. In total, 500 right whales are catalogued in the N Atlantic population, but because of known and estimated mortality, currently estimated to number *c.* 400 animals. Despite increases in survey effort, few new adult individuals have been added each year to the catalogued population since 1985, suggesting that most of W North Atlantic population is currently documented.

In E North Atlantic, scattered sightings suggest

that the eastern stock, if it survives, is represented at most by a few tens of individuals. At least 134 right whales killed in whaling activities 1900–1926, mostly around the British Isles [182]. One cow and calf killed off Madeira, 1967 [762]. Sightings few; comprise 23 sightings of 48 whales reported, 1901–1980 [182], and a few additional sightings reported to right whale researchers over the last 20 years. Special efforts should be made to photograph any observed in E North Atlantic, for comparison with W North Atlantic catalogue.

Right whales have been sexed on appearance of the genital area, or, for cows, the long-term association with a newborn calf, and by using genetic techniques [179]. Of 60 calves sexed since 1980, 28 were females and 32 males, not significantly different from 1:1. Is seasonal segregation by sex in this population. Primarily adult females use the calving ground off SE USA, and males are rarely observed there; cows with calves rarely observed in the summering Scotian shelf area, which is dominated by males [179].

MORTALITY

Mortality rates estimated at 26–31% in year 1, 10% in year 2, 5% in year 3, and 1–4% for the next 7 years [808]. Adult mortality rates apparently very low; only 3 adults are known to have died of natural causes in this population since 1970. Longevity remains unknown, although at least one N Atlantic female had a sighting history extending over 60 years. Over 50% of mortality in this population caused by human activities, primarily ship collisions and entanglements in fishery gear [649, 655, 808].

May be low levels of predation by killer whales; *c.* 7% of the N Atlantic population displays scars from their attacks, but anecdotal reports of orca/right whale encounters suggest that right whales can defend themselves adequately. No fatal diseases or epizootics reported, although lesions and parasites, thought to be related to illness, have been reported [472, 1010, 1011].

PARASITES

3 species of cyamids reported: *Cyamus ovalis*, *C. gracilis* and *C. erraticus*. Appear to have no long-term effect, although living on the sloughing skin of the whales [1020]. Both *Giardia* spp. and *Cryptosporidium* spp. reported [1010]. Diatom *Cocconeis ceticola* common on baleen plates. No recent review of endoparasites, but 3 species of helminths reported from N Pacific right whales [637].

RELATIONS WITH HUMANS

Right whales so called from being the right whale to kill: gave high yields of oil and baleen, slow

moving and floated after death. During early 20th century, Scottish whale fishery took 94 off Outer Hebrides and 6 off Shetland, 1903–1928, although only 3 after 1918 [1148]. None obtained when whaling resumed 1950–1951 [181]. In W Ireland, 18 caught 1908–1914, but none in 1920 or 1922 [367]. Right whaling in the N Atlantic well reviewed in [972].

Contemporary threats to right whales more insidious, but no less devastating. Over 50% of all mortality due to collisions with large ships and entanglement in fishing gear [639, 649, 655, 808]. Almost 75% of all right whales in N Atlantic display scars from entanglement in fishing gear some time in their lives. Lines from lobster or crab pots and groundfish gill nets appear to be primarily responsible, although all fixed gear presents a risk [581]. Extensive efforts in USA currently under way to develop alternative fishing methods and strategies for managing shipping to reduce kills. Cumulative impacts of all human activities not well understood, may be affecting health and reproduction of this species [651]. In addition, consequences to right whales from global climate changes may be anticipated [612].

Studies currently under way worldwide to gain better understanding of biology and conservation needs of *Eubalaena* spp. Most rely on individual identification [475, 653, 908]. Aerial and shipboard photographic surveys, as well as studies on life history, genetics, feeding behaviour and habitat use, are all currently used in research on N Atlantic right whales [106, 180, 410, 475, 617, 642, 737, 764, 1044, 1095].

Listed by IUCN as Endangered and has full international and national legal protection (see Table 12.1), including complete protection under IWC; large-scale violations of this protection in the 1960s by the Soviet whaling fleet apparently did not occur in the N Atlantic.

Where locally abundant (S Africa; Argentina; Bay of Fundy, Canada), thriving whale-watching businesses have developed. Concerns over disturbance from boats remain untested. Is an icon of humanity's failure to manage any marine 'resources'.

LITERATURE

Good overviews of historical topics [186]. Habitat and feeding reviewed in [615]. Up-to-date review of the conservation status and biology of N Atlantic right whales [651].

PRINCIPAL AUTHORS

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FAMILY ESCHRICHTIIDAE (GRAY WHALE)

Nominally, a family with 1 genus and species. Genetic evidence clusters this species within *Balaenoptera*, closer to big rorquals than minke whale [494].

Gray whale *Eschrichtius robustus*

Balaenoptera robustus Lilljeborg 1866; Gräsö, Sweden.

Rachianectes glaucus Cope 1869.

Californian gray whale, scrag whale.

RECOGNITION

A moderately large baleen whale (males average 12.2 m, females 12.8 m) with a grey back, mottled white (Plate 13). Baleen plates short (40–50 cm), grey with a white fringe. Throat with just 2 grooves. Skull without the high arched rostrum of a right whale, but with a narrower snout than a rorqual.

DISTRIBUTION

Confined to N hemisphere. Found in both W and E Pacific. E Pacific population migrates from winter breeding grounds in warmer waters off Baja California, N up Pacific coasts of USA and Canada to feed in summer in shallow seas of Bering Strait and further N. W Pacific population less well known, but may have bred off S Korea, and summered in the Sea of Okhotsk. Atlantic population extinct; may have bred off Florida and in the Bay of Biscay, feeding in summer in the Gulf of St Lawrence and the Baltic Sea, but too few records to do more than speculate.

HISTORY

Extinct in Atlantic, and nearly exterminated in the Pacific as well. As a coastal species, was very vulnerable to hunting, during migration and on S breeding grounds. In Pacific, believed to have recovered now to c.20 000 in American waters, but only 2000 in Asian waters.

Evidence for former presence in Atlantic derives partly from some rather uncertain descriptions by early whalers of the 'scrag whale', which had no dorsal fin but several knobs along its back – features of this but no other baleen whale; better descriptions from early Norse writings [697]. Definite subfossil remains of 10 specimens from American E coast [777] and 7 from European coasts [189], most of which now radiocarbon dated; another, Dutch, specimen currently under study. Latest in America dated 275 bp, i.e. 1675 AD. The 2 latest from Europe are from Pentewan, Cornwall (1329 bp) and Babbacombe Bay, Devon (340 bp, i.e. 1610 AD). These strongly support notion that the species just

survived into era of commercial whaling; uncertain whether a longer history of aboriginal hunting contributed to its decline.

Original description of (*E.*) *robustus* based on European subfossil, acceptance that Pacific *Rachianectes glaucus* was conspecific required about a century [990].

Reintroduction barely feasible, but global warming and opening up of NW passage round N Canada may offer opportunity for natural recolonisation.

GENERAL ECOLOGY

Unusual among baleen whales in feeding largely on bottom fauna, especially amphipods. W Pacific population feeds for 4 months in summer in shallow Arctic waters. Migrates S, starting late September, passing Californian coast in December, to reach shallow lagoons on the coasts of Baja California. Calves born January, accompany mothers on migration back N starting February. Mating also takes place January, gestation lasts 12 months. Females breed at 2 years old, have 1 calf every other year [585, 990].

Presumed that European population would have fed in Baltic or White Sea, migrating S to breed in Bay of Biscay or along Moroccan coast.

AUTHORS

A.C. Kitchener, J.M. Mead & D.W. Yalden

FAMILY BALAENOPTERIDAE (RORQUALS)

A small family, usually accorded 2 genera, *Megaptera* and *Balaenoptera*, which includes the largest known mammals. Shorter baleen, less bowed upper jaws, than Balaenidae (Fig. 12.2), but strongly pleated throat which expands to allow intake of large volumes of water containing prey; water squeezed out through baleen plates by large muscular tongue, leaving prey caught on baleen.

GENUS *Megaptera*

A monospecific genus [494, 1021]; morphologically distinguished from *Balaenoptera* by very long pectoral flippers, bulkier body.

Humpback whale *Megaptera novaeangliae*

Balaena Novae Angliae Borowski, 1781; type locality coast of New England, USA.

Megaptera longimana moorei Gray, 1866; R. Dee estuary, Cheshire, England.

Míol mór dronnach (Irish Gaelic).

RECOGNITION

At close range, impossible to mistake for any other whale. Flippers, 1/3 body length, are the longest of any cetacean; knobs (tubercles) on the head are diagnostic (Plate 13). At a distance can be confused with any large rorqual; however, habit of raising tail before a deep dive separates it from all rorquals except blue whale (typically larger, bluish, not black) (Fig. 12.1). Trailing edge of tail prominently serrated, frequently has much white on underside (cf. sperm, right whales, which also raise their tails on diving; right whale lacks a dorsal fin, sperm whale differs in colour and overall form, and usually in habitat). Back is prominently arched before a dive, accentuating the dorsal fin. Blow often bushier than for other large rorquals, and lacks V-shape of right whales.

DESCRIPTION

Flippers very long and narrow, generally all or largely white; rounded knobs (tubercles) present on rostrum, on both upper and lower jaws; 270–400 baleen plates per side (up to 70 cm long × 30 cm wide), generally black with black or olive-black bristles (Fig. 12.2). Skin generally black dorsally; ventrally varies from white to mottled to black. Flukes scalloped on trailing edge. Dorsal fin highly variable in size and shape, from almost absent to high and falcate. Body more robust than other balaenopterids. From 14 to 35 ventral grooves, up to 38 cm wide, extending almost from tips of lower jaws to umbilicus. Females and males are not distinguishable dorsally, but females possess a grapefruit-sized lobe at rear end of genital slit, absent in males.

Tail flukes butterfly-shaped, more rounded (less obviously triangular) than those of right or sperm whales. Flukes distinctly notched, with distinctive serrations on trailing edge (Fig. 12.1). Pigmentation of underside of tail variable, from all white to all black; these markings unique to each whale, widely used for individual identification. A large catalogue of identified individuals exists for N Atlantic and other oceans.

MEASUREMENTS

Length: newborn calf 4.0–4.6 m; at independence (*c.* 1 year) 8–10 m [251]; at sexual maturity 13.9 m (females), 13.0 m (males) [236]. Females *c.* 1–1.5 m longer than males [236]. Reliably recorded maximum lengths 15.5 m (female) and 14.75 m (male), though pre-whaling populations may have contained some larger individuals. Adult weights to *c.* 45 t.

DISTRIBUTION

Worldwide, occasionally to ice edge. Highly migratory; feeds in summer in high latitudes, mates and calves in winter, in tropical waters,

12 Whales, porpoises and Cetacea: Order Cetacea

though a few overwinter on feeding grounds. Strong individual fidelity to feeding areas; in N Atlantic, include the Gulf of Maine, Gulf of St Lawrence, Newfoundland/Labrador, Greenland, Iceland and Norway. Matching of photographically and genetically identified individuals indicates E North Atlantic population migrates primarily to West Indies [740, 1121], though some animals winter near Cape Verde islands [565, 980]; genetic analysis suggests a 3rd, unknown, breeding area. Despite fidelity to specific feeding grounds, whales from all N Atlantic areas mix spatially and genetically in the W Indies in winter.

Sightings from around the British Isles have increased markedly since the early 1980s; occur in 3 main areas – N Isles, S to E Scotland; N Irish Sea to W Scotland; and Celtic Sea between S Ireland, W Wales and SW England [340, 346, 360]. Since 1980, have also been 7 strandings around British Isles, all but one (Kent) in those same regions [120, 574, 1074]. In shelf waters, humpbacks occur mainly May–September, but some sightings extend through winter (November–March), confirmed by acoustic detection with SOSUS hydrophone arrays in the Atlantic W of the British Isles [235, 256]. Sightings in Ireland, mainly along S coast, increase through summer to peak in September, rapidly declining thereafter [122].

Regional whaling catches (76 animals, 1903–1929) occurred off Shetland, Outer Hebrides and NW Ireland, all on continental shelf, mainly in July–August [181, 1148]. The small number taken may reflect unimportance of the region to the species, or depletion from earlier exploitation.

HISTORY

The frequently coastal distribution of the humpback made it easy prey for whalers; often the first species to be depleted in an area. Most populations under study appear to be recovering well. Catches in the Scottish whale fishery amounted to 51 (Shetland) and 19 (Outer Hebrides), 1903–1929 [181], but none taken in the latter area in 1950–1951. In W Ireland, 6 humpbacks were taken 1908–1914, but none 1920, 1922 [367]. No subsequent records around British Isles until 1966. Many more humpbacks taken off Norway in the late 19th century, may have affected the local stock.

SOCIAL ORGANISATION AND BEHAVIOUR

No strongly organised social structure [247]. Typically found in small unstable groups or alone, though large feeding aggregations can occur in summer and large competitive groups of males can form around females in breeding areas. Group size

in summer often correlated with size of exploited prey patch.

Vocalisations: Produce 3 kinds of sounds: (1) songs produced solitarily, ranging from <20 Hz to 4 kHz (occasionally to 8 kHz) with source levels estimated at 144–174 dB re 1 μ Pa @ 1 m; (2) group or 'social' sounds often associated with agonistic behaviour among males, ranging from 50 Hz to >10 kHz (though mainly below 3 kHz); (3) sounds made in summer during feeding bouts, at c.20 Hz–2 kHz, and 0.2–0.8 s duration, with estimated source levels of 175–192 dB re 1 μ Pa @ 1 m [993]. In winter (and occasionally at other times), males sing long, complex songs, the primary purpose of which is probably to attract females [906, 1166]. Songs change markedly over time in length, form and content, yet all whales within a population sing essentially the same song. Song regularly recorded in recent years during winter in deep water off W Scotland and Ireland, and probably originates from humpbacks migrating SW from Norwegian waters [235]. Breeding males frequently engage in aggressive contests with each other over females, but mating almost never observed, thus details of female mate choice remain unclear.

Humpbacks are known for their frequent high-energy aerial displays, which include breaching, lobtailing and flipping; these behaviours occur at all times of year and in widely different contexts; likely to perform a variety of social or other functions.

FEEDING

Diet: Euphausiids (krill) (*Meganyctiphanes*, *Thysanöessa*, *Euphausia* and *Pseudoeuphasia*), also small schooling fish, notably herring and sprat *Clupea* spp., sandeel *Ammodytes*, and capelin *Mallotus*.

Feeding methods: Vary with prey type, but always end with lunges of varying speed. Humpback blows clouds or nets of bubbles to entrap prey (especially fish). Specialised variations on this technique are often individual-specific; a common example is lobtail feeding, in which the whale slaps the water surface, perhaps to create bubbles or stun fish. No feeding on breeding grounds in winter.

BREEDING

Strongly seasonal, with most births in low latitudes in winter (peak January–March). Gestation period c.12 months. Lactation up to a year. Calving intervals typically 2–3 years, with occasional annual calving [247]. Age at sexual maturity varies by population, from 4 to >10 years for both sexes [236, 246, 414].

POPULATION

Longevity at least 48 years [236]; possibly much longer. Annual population growth rate *c.* 3.1–6.5% in W North Atlantic, annual juvenile/adult mortality *c.* 4% [98, 1122]. Overall, N Atlantic population has recovered well from exploitation, estimated at 10 400–11 570 in 1992 [1102, 1122]. Status of E North Atlantic population unclear, although clearly larger than was once thought. However, remains relatively uncommon around British Isles [360, 973].

PARASITES/COMMENSALS

Heavily invested with barnacles *Coronula* and *Conchoderma* spp. and whale lice *Cyamus* spp. Large number of endoparasites recorded, including trematodes, cestodes, nematodes and acanthocephalans [288]. Nematode *Ogmogaster ceti* commensal on baleen plates.

RELATIONS WITH HUMANS

Heavily exploited by whaling, population reduced by >90%. Little whaling in British waters. Protected in N Atlantic since 1955, and worldwide from 1966 (though USSR continued to hunt humpbacks illegally until 1973) (see Table 12.1). Vulnerable to ship strikes, entanglement in fishing gear and disturbance from industrial noise [668, 694, 971].

LITERATURE

Detailed species review [249].

AUTHORS

P.J. Clapham & P.G.H. Evans

GENUS *Balaenoptera*

A genus currently comprising 7 species, 4 of which occur in NE Atlantic, but perhaps more species if some S populations distinct from N. Genetic evidence clusters *Eschrichtius* within *Balaenoptera*, possibly also *Megaptera* [494, 1021]. Differs from *Megaptera* in shorter flippers, more streamlined body, from *Eschrichtius* by many more pleats on throat (85–90).

Minke whale *Balaenoptera acutorostrata*

Balaenoptera acutorostrata Lacépède, 1804; Cherbourg, France.

Lesser rorqual; little piked whale; *morfil pigfain* (Welsh); *muc-mhara-mhionc* (Scottish Gaelic); *miol mór mince* (Irish Gaelic).

RECOGNITION

Smallest baleen whale around British Isles. Blow low (2 m), inconspicuous, not always visible; typically seen at same time as 30 cm tall, re-curved dorsal fin situated 2/3 along back. Typical breathing sequence 3–6 blows at intervals of <1 min, followed by a longer dive typically lasting 6–12 min. Flippers have diagonal white band on upper surface (Plate 14). Head slender, pointed, triangular, with straight rather than curved borders to rostrum. Pale chevrons sometimes seen between blowhole and dorsal fin.

DESCRIPTION

General form similar to fin and sei whales, but sharply pointed snout. Baleen plates short (max. 20 cm long × 12 cm wide), yellowish white; 230–



Fig. 12.3 Minke whale lunging through surface, showing distended throat typical of feeding rorquals. Note also white blaze on flipper showing through the water splash (photo P. Anderwald).

12 Whales, porpoises and Cetacea: Order Cetacea

342 on each side of upper jaw (Fig. 12.2). Plates sometimes with black streaking; fringed with fine white bristles. General body colour dark grey to black on back, lightening to white on belly and undersides of flippers. Light chevron across dorsal surface in 2 parts: one thin and crescent-shaped, just above and behind flippers, the other larger and usually more diffuse, between flippers and dorsal fin. Flippers approximately 1/8 body length, narrow, have distinctive white band on upper surface. 50–70 throat grooves, ending just behind flippers, but in front of navel. Dorsal fin a little more than 1/3 anterior to tail flukes, tall relative to body (compared to fin and blue whales), and usually distinctly sickle shaped (Plate 14). Tail flukes broad with small median notch.

RELATIONSHIPS

Smallest of 7 nominal species of *Balaenoptera*; molecular phylogenies suggest may be basal to rest of family (*Eschrichtius*, *Megaptera* and the larger *Balaenoptera*) [494, 1021].

MEASUREMENTS

Length: newborn *c.*2.4–2.8 m; at sexual maturity *c.*7.3–7.45 m (female), 6.8–7.0 m (male); adult *c.*8.5 m (female), *c.*8.0 m (male). Adult weight 5–14 t (data from Norwegian/Icelandic specimens).

VARIATION

In N hemisphere, average *c.*0.5 m smaller than in Antarctic. On morphological [879, 1032] and genetic evidence [526, 1188, 1189], Antarctic form now recognised as separate species, *B. bonaerensis* [187, 945]. Dwarf form in S hemisphere more closely related to N hemisphere animals than to *B. bonaerensis* [542, 1189]; *B. acutorostrata* thus divided into 3 subspecies: *B. a. acutorostrata* in N Atlantic, *B. a. scammoni* (formerly *davidsoni*) in N Pacific and dwarf form (unnamed) in S hemisphere [37, 187, 526, 542, 758, 931, 932].

In N Atlantic, morphometric differences between minke whales from W Greenland, Icelandic and Norwegian waters [243], supported by isozyme and microsatellite evidence [47, 291, 292]. However, microsatellite analyses [55] suggest only weak genetic differentiation between areas, and DNA studies of minkes from Iceland and N Norway suggested mixing of these breeding stocks [90, 891]. Mixing of breeding stocks on feeding grounds clearly demonstrated in N Pacific, where Korean (= Asian coastal) and W North Pacific stocks mix seasonally in Sea of Okhotsk [452, 1188].

DISTRIBUTION

Commonest of all baleen whales, both in N

Atlantic and around British Isles, mainly in temperate and polar regions. Widely distributed along Atlantic seaboard of GB and Ireland, W and N Norway, Faroes and Iceland, often seen close to coast. Also in N and C North Sea, regularly S to Yorkshire coast. Small numbers in Irish Sea, but rare in S North Sea, Channel, and Bay of Biscay [340, 346, 360, 857, 973].

Is the baleen whale most likely to be observed from land, particularly from headlands along coasts of W Scotland and N Isles (Fig. 12.4). Most sightings July–September, but can be seen any time May–October, and some remain in coastal waters year-round [360, 973]. General offshore movement in autumn, possibly associated with breeding, although breeding locations unknown. Unknown whether extensive migrations occur, although one satellite-tagged immature individual entrapped in fishing gear in Danish waters travelled to N and W of British Isles, then to Azores, Canaries and finally into W Mediterranean [1140].

HISTORY

Fossils of balaenopteroid whales discussed in [1118], but none known of this species.

HABITAT

Occurs mainly over continental shelf of temperate and subarctic regions, often very close to land, sometimes entering estuaries, bays or inlets. Often feeds around banks and in areas of upwelling or strong currents around headlands and small islands, primarily during summer. In Scottish waters, feeding minke whales in late summer commonly associated with flocks of auks, Manx shearwaters, kittiwakes and various *Larus* gulls. Breeding areas unknown.

SOCIAL ORGANISATION AND BEHAVIOUR

Usually seen singly or in pairs, sometimes aggregates into larger groups of *c.*10–20 individuals when feeding. Evidence from recognisable individuals indicates seasonal site fidelity over small geographic range [326, 327, 443]. Genetic data indicate some differentiation among populations at small geographical scale [452, 1188, 1189].

Moderately fast swimmer, cruises at 5–26 km/h, capable of bursts >40 km/h. Often arches tail stock when beginning long dive, without raising flukes above surface. Frequently approaches vessels, will both bow- and stern-ride. Breaching not uncommon. Frequently feeds near other cetacean species, e.g. harbour porpoises, white-beaked and Atlantic white-sided dolphins, and humpback whales [341, 353].

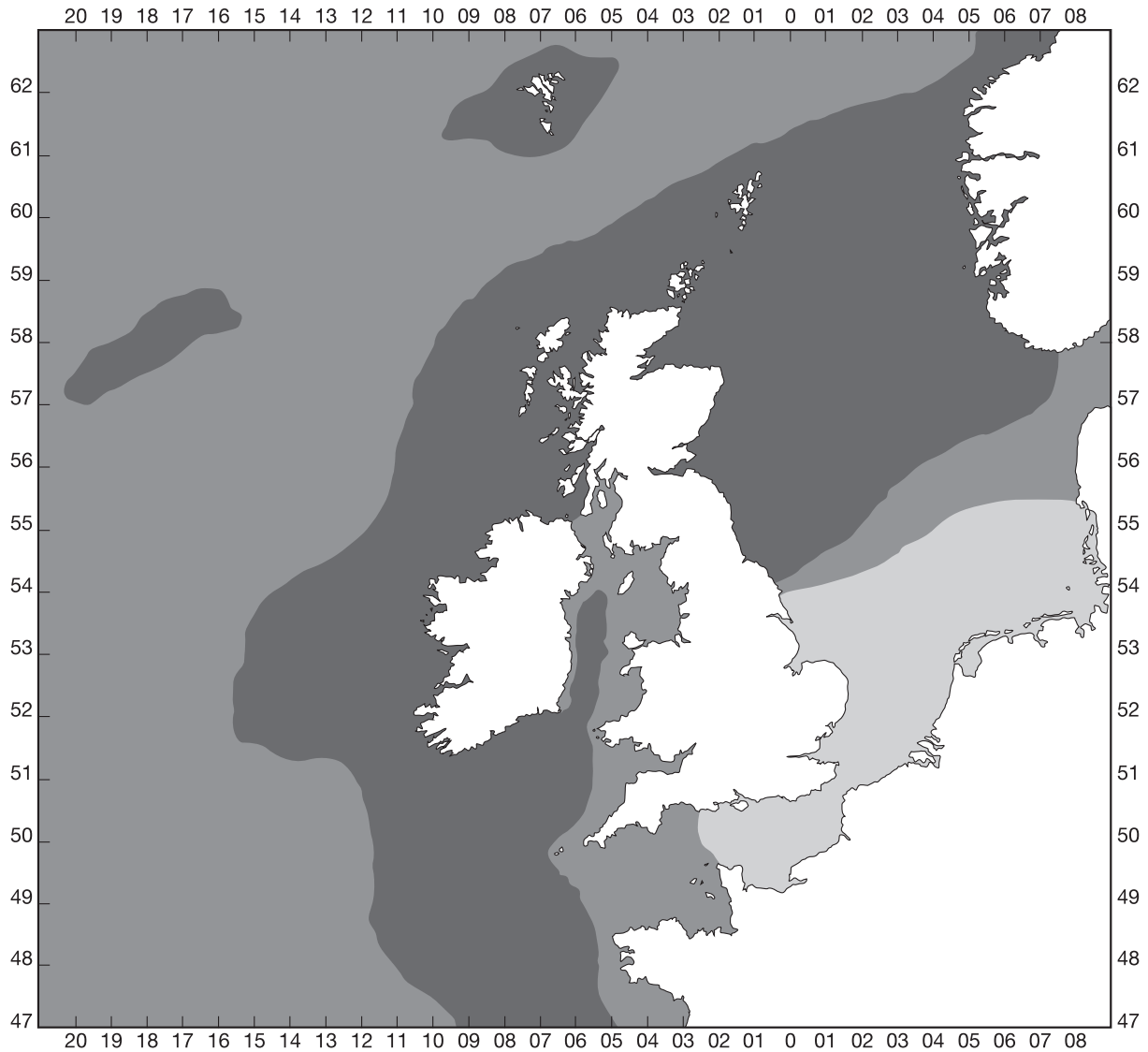


Fig. 12.4 Minke whale *Balaenoptera acutorostrata*: distribution around the British Isles.

Vocalisations: Involve intense low-frequency broadband (0.5–1 kHz bandwidth) and harmonic down-sweeps with maximum source level of 165 dB re 1 μ Pa. These include short broadband downsweeps (mainly 0.13–0.06 kHz lasting 200–300 ms); ‘grunts’ (mainly between 0.08–0.14 kHz, but up to 2 kHz, lasting 165–320 ms); and thumps (often downsweeps; mainly 0.1–0.2 kHz, lasting 50–70 ms) [337, 1047, 1149, 1247].

FEEDING

Diet: Most catholic feeder of the rorquals; in N hemisphere takes more fish (sandeels, herring, sprat, cod, capelin, haddock, saithe and whiting) than others, but euphausiids and pteropods also taken, especially in higher latitudes [157, 497, 498, 844, 852, 878, 927, 1085].

Feeding methods: Like humpback and fin whale,

minke whale uses variety of methods depending on nature of prey: engulfing prey with open mouth from behind, or side- and lunge-feeding using surface to trap fish shoals (Fig.12.3). Known individuals revisiting same bank or bay over period of several years fed at same site using same feeding strategy [529]: 2 types of foraging specialisations, used exclusively by individual whales; some fed on ephemeral patches of herring, brought to surface by feeding auks, others pursued prey in deeper water, herding them against air/water interface. Similar feeding specialization not observed off W coast of Scotland [56].

BREEDING

Births mainly around December, probably in temperate offshore waters, possibly in subtropics. Gestation 10 months. Lactation <6 months, calving interval of 1–2+ years. Sexual maturity at

12 Whales, porpoises and Cetacea: Order Cetacea

c.7–10 years, at least in Antarctic minke [544, 706, 1080, 1123]. However, difficult to read ear plugs of N Atlantic minke, due to indistinct layering.

POPULATION

Only published population estimate for minke whales in British waters is from North Sea, English Channel and Celtic Sea; line transect survey (SCANS), July 1994, estimated 8450 (95% CI 5000–13 500) [481]. More extensive line transect survey (SCANS II) over NW European continental shelf, July 2005, gave overall estimate of 16 395 (including 10 500 in area equivalent to 1994 study) [478]. Population estimate for entire C/NE North Atlantic (based on data from 1996–2001) 174 000 (95% CI 125 000–245 000) [559]. Previously, stock seasonally inhabiting Norwegian and Barents Seas estimated at 86 700 individuals (95% CI 61 000–117 000) [1052]. Assessing minke whale numbers difficult and controversial since inconspicuous at sea and may react to survey vessels.

Population changes in NE Atlantic uncertain; effort-related sightings surveys hint that increased in British shelf waters during 1980s–1990s [152, 346, 360].

Spatial and temporal segregation by sex and maturity [240, 587, 588, 1064]; of 225 minke whales caught during Norwegian scientific whaling programme (1992–1994), 45.8% males, 54.2% females [852]. Lifespan c.40–50 years, but 1 individual 57.5 years. Annual adult mortality 9–10% [873], but likely to vary between populations and times.

MORTALITY

Besides humans, main predator of minke whale is killer whale. In Antarctic waters, remains of minke whales identified in 70–85% of killer whale stomachs [196, 325, 1075]. Transient killer whales in E North Pacific also observed preying on minke in recent years. Extent of this in N Atlantic unknown, but scars seen apparently from killer whale teeth [590, 591]. Serological investigation of 129 minke whales from NE Atlantic revealed no evidence of morbillivirus antibodies [1131].

PARASITES AND PATHOGENS

Ectoparasites: Rare, but some carry whale lice *Cyamus* spp., mostly at posterior ends of ventral grooves or around umbilicus, and parasitic copepod *Pennella balaenopterae* sometimes embedded in skin, on dorsal surface or near urinogenital opening.

Endoparasites: Include 3 trematodes (*Fasciola skrjabini*, *Lecithodesmus goliath*, *Ogomogaster plicatus*), 3 nematodes (*Anisakis simplex*, *Crassicauda crassicauda*, *Porrocaecum decipiens*), 3 acantho-cephalans

(*Bolbosoma balaena*, *B. brevicolle*, *B. nipponicum*), and at least 1 cestode *Tetrobothrius affinis* [107, 127, 302, 442, 670, 874].

RELATIONS WITH HUMANS

Because of small size, not a target of Scottish and Irish whale fisheries in early 20th century. Only exploited more recently, when stocks of larger rorquals depleted and, in some cases, protected. Since late 1920s, whaling for this species carried out along Norwegian coast, expanding just before World War II to Spitsbergen and Shetland–Faroes, later extending to Barents Sea, Iceland, Jan Mayen, W Greenland and Labrador. Most whaling currently by Norway, but limited commercial fishery resumed by Iceland, 2006, after some years of scientific whaling completed in 2007. In August 2007, Iceland decided not to issue a new commercial quota for the time being. Since 1993, Norway gradually increased its catch limit year by year, taken under objection to IWC's commercial whaling moratorium; has been 1052 whales since 2006, but fewer actually caught.

Latest of baleen whales exploited by whaling industry, previously considered too small to be worth hunting. Stock reduced by whaling to 45–70% of pre-exploitation abundance [971]. In 1984, NE Atlantic Stock considered depleted by IWC, declared Protection stock. In 1986, IWC moratorium on commercial whaling came into effect with zero catch limits for all species. Legally protected in European, British and Irish waters (Table 12.1).

Sometimes gets entangled in fishing gear, mainly gillnets set for salmon and creel lines [555]. Several reports from British Isles; one photographed off W Ireland managed to get inside a salmon cage [347].

Pollutant levels of PCBs in blubber of minke whales relatively high [636, 1094]. Concentrations of PCB and DDT across N Atlantic generally increase from W to E, highest PCB levels in animals from Barents Sea [523]. Highest ¹³⁷Cs levels found in North Sea [156].

Now focus of British whale-watching industry, mainly off W coast of Scotland; also off Iceland, is most common species near Husavik, centre of Icelandic whale-watching industry. May suffer from sounds made by ship traffic (and particularly whale-watching) and seismic testing from oil and gas exploration in certain regions [338, 1202]. Collisions with vessels occur (e.g. one struck by ship in Firth of Forth, E Scotland [1]). Active sonar used by military may have killed 2 minke whales off Bahamas.

LITERATURE

Review [1123], updated in [914]; monograph

[544]; detailed research analyses [139, 1179]; popular account [528].

AUTHORS

P. Anderwald, P.G.H. Evans, A.R. Hoelzel & V. Papastavrou

Fin whale *Balaenoptera physalus*

Balaena physalus Linnaeus, 1758; Svalbard.

Common rorqual, finback; *muc-an-scadain* (Scottish Gaelic); *miol mór eiteach* (Irish Gaelic).

RECOGNITION

2nd largest of all whales, females up to 24 m in length. Uniform slate grey (Plate 13) (blue whale lighter, mottled). Generally does not show tail flukes when diving, but rolls in high arch. Relatively small dorsal fin with little curvature. White on right lower lip and palate diagnostic (all other balaenopterids symmetrically dark). Tall (4–6 m) blow, shaped like an inverted cone, followed by long shallow roll showing fin, repeated up to 7 times at intervals of 10–20 s (50 s when feeding at surface) before dive, commonly of 5–15 min, sometimes as short as 25 s (similar sei whale often rises to surface at shallow angle, does not arch its back, and dives more frequently).

DESCRIPTION

General form slender. Slender head, V-shaped and flattened from above but with prominent median ridge (cf. 3 ridges in Bryde's whale). Baleen plates relatively short (maximum 72 cm long × 30 cm wide), 260–480 on each side of upper jaw (Fig. 12.2). Plates on right side usually yellowish-white for 75–100 cm from front end. Remaining plates

of right side, and all of left side, slaty grey alternating with longitudinal yellowish bands. Fringes brownish grey to greyish white. General body colour uniformly dark grey to brownish grey above, grading to white below including lower surface of flukes and inner surfaces of flippers (cf. sei whale). Most have pale grey chevron on each side behind head, and may have dark stripe or blaze running up and back from eye, light stripe arching down to where flipper joins body. Fairly slender pointed flippers, about 1/7 body length. Throat grooves 56–100, ending posterior to maximum cross-section of body (i.e. around navel). Dorsal fin 1/3 along back from tail, c.60 cm tall (i.e. taller than in much larger blue whale) though appears relatively small compared with sei and minke whale (Fig. 12.5). Behind fin, back is ridged to tail flukes, which are broad, triangular, with slight median notch and slightly concave trailing edge.

RELATIONSHIPS

Of 7 species of *Balaenoptera*, 4 (not tropical Bryde's whale) regularly occur in European seas. Blue, fin and sei whales tend to live in deep waters, smaller minke whale occurs primarily over the continental shelf. Molecular (mtDNA) phylogeny suggests closer to humpback than blue whale [494], though rare hybrids with blue whale known [123, 1112].

MEASUREMENTS

Length: newborn c.6.4 m, but considerably smaller (5.3 m) in the Mediterranean; at sexual maturity c.18.3 m (female), c.17.7 m (male); adult usually c.20.0 m (female), c.18.5 m (male); maximum, N Atlantic, 24.0 m (female), 22.0 m (male). Weight c.20 t (15 m whale) to 80 t (25 m whale, S hemisphere) [863].



Fig. 12.5 Fin whale rolling into dive, showing small fin, placed far back (photo P.G.H. Evans).

VARIATION

In N hemisphere, average c.1–2 m smaller than in S hemisphere. DNA studies indicate genetic differences between populations in W and E North Atlantic and resident Mediterranean population [124, 894].

DISTRIBUTION

Worldwide, mainly in temperate and polar seas, both hemispheres. Although fin whales may show seasonal latitudinal migration, remaining in polar seas only during summer, those further S around the British Isles appear to be present year-round [256, 360]. The commonest large whale in E North Atlantic, Bay of Biscay and Mediterranean. Distributed around British Isles mainly along Atlantic seaboard, along or beyond edge of continental shelf (Fig. 12.6). Most sightings in coastal waters come from Shetland, Outer Hebrides, SW Ireland and the Celtic Sea between S Ireland and SW England [340, 346, 360, 941, 1125, 1126]. Most sightings in northern GB June–August, further S September–February. Some indication from sightings that move generally northwards off NW Scotland June–October [1125] when numbers may concentrate in areas like Rockall Trough and Faroe-Shetland Channel.

Of 50 verified strandings around British Isles, 1913–1992, 27 (1.35/year) occurred 1913–1932, dropping to 5 (0.25/year) 1933–1952 and 4 (0.20/year) 1953–1972, before rising again to 14 (0.70/year) 1973–1992 [120, 404, 406–408, 485, 1073, 1074]. Paucity of strandings 1932–1972 attributed to decline following intense human exploitation [408].

HISTORY

No fossil or archaeological material known.

HABITAT

Most commonly recorded in deep waters (400–2000 m depth) off the edge of the continental shelf, in some localities (e.g. lower Bay of Fundy) occurs in shallow areas (<200 m depth). Appears to favour areas with high topographic variation – underwater sills or ledges, upwellings and frontal zones between mixed and stratified waters with high zooplankton concentrations [345, 981, 982, 1252].

SOCIAL ORGANISATION AND BEHAVIOUR

Usually seen singly or in pairs (mainly mother with dependent calf), can form larger pods of 3–20, perhaps part of broader group of hundreds of individuals spread over wide area, especially on feeding grounds [794, 1233]. Aggregations usually associated with feeding; differences in group size

result from different feeding situations or from geographical segregation by sex or age class [9, 1233]. Individuals may change associations with one another over short time period, suggesting fluid relationships at least on feeding grounds [338, 1233]. Lunging behaviour frequently observed, mainly when groups present [218, 338]. Breaching occasional, whale typically landing on its belly [743]; surface sexual behaviour involving excited chases also described [1128].

Fast swimmers: 2–6.5 km/h when feeding, 6–9 km/h during normal travel, up to 30 km/h in short bursts when migrating or cruising, and up to 41 km/h when alarmed [563, 666, 704]. Tagged fin whales tracked at 4.1–12.6 km/h [1207, 1233], and averaged 6–9 km/h when tracked by laser rangefinder [861]. May dive to depths >470 m [895].

Vocalisations: Mainly low-frequency pulses (moans), usually FM downsweeps (though sometimes constant frequency, upsweeps or wavers) from c.4 to 17 Hz (but can reach 125 Hz) lasting 0.5–1 s, often repeated in series with regular interpulse intervals (5–45 s) [257, 337, 1150, 1203]. Maximum source level is 186 dB re 1 μ Pa @ 1 m [1209]. Short sequences (2–30 repetitions) produced by both sexes, probably serve for communication over distances up to 30 km, possibly more, between widely spaced individuals [1203]. Long (up to 30 h) patterned sequences of single or paired pulses with stereotyped repetition patterns (often interrupted by 20 min rest periods) produced by slow-swimming adult males, mainly October–April, thought to be reproductive song displays. Additional sounds include rumbles of very long duration (c.30 s), 10–30 Hz with extensive frequency and amplitude modulation, thought to be agonistic [337]; and high-frequency clicks (16–28 kHz, duration 8.8 s) recorded at close range [1149].

FEEDING

Diet: Feeds mainly on planktonic crustacea (mainly euphausiids, e.g. *Meganyctiphanes norvegica*, also copepods), but also take fish (e.g. herring, capelin, sandeels, mackerel, and blue whiting), and cephalopods [589, 610, 791, 1080]. Relationship between fin whale distribution and *Meganyctiphanes* abundance demonstrated in W Mediterranean [982].

Feeding methods: Uses variety of methods: engulfing prey from behind by distending the throat grooves and taking large gulp of water and prey, to side- and lunge-feeding involving some herding of prey into tight concentration. Coordinated swimming among several whales,

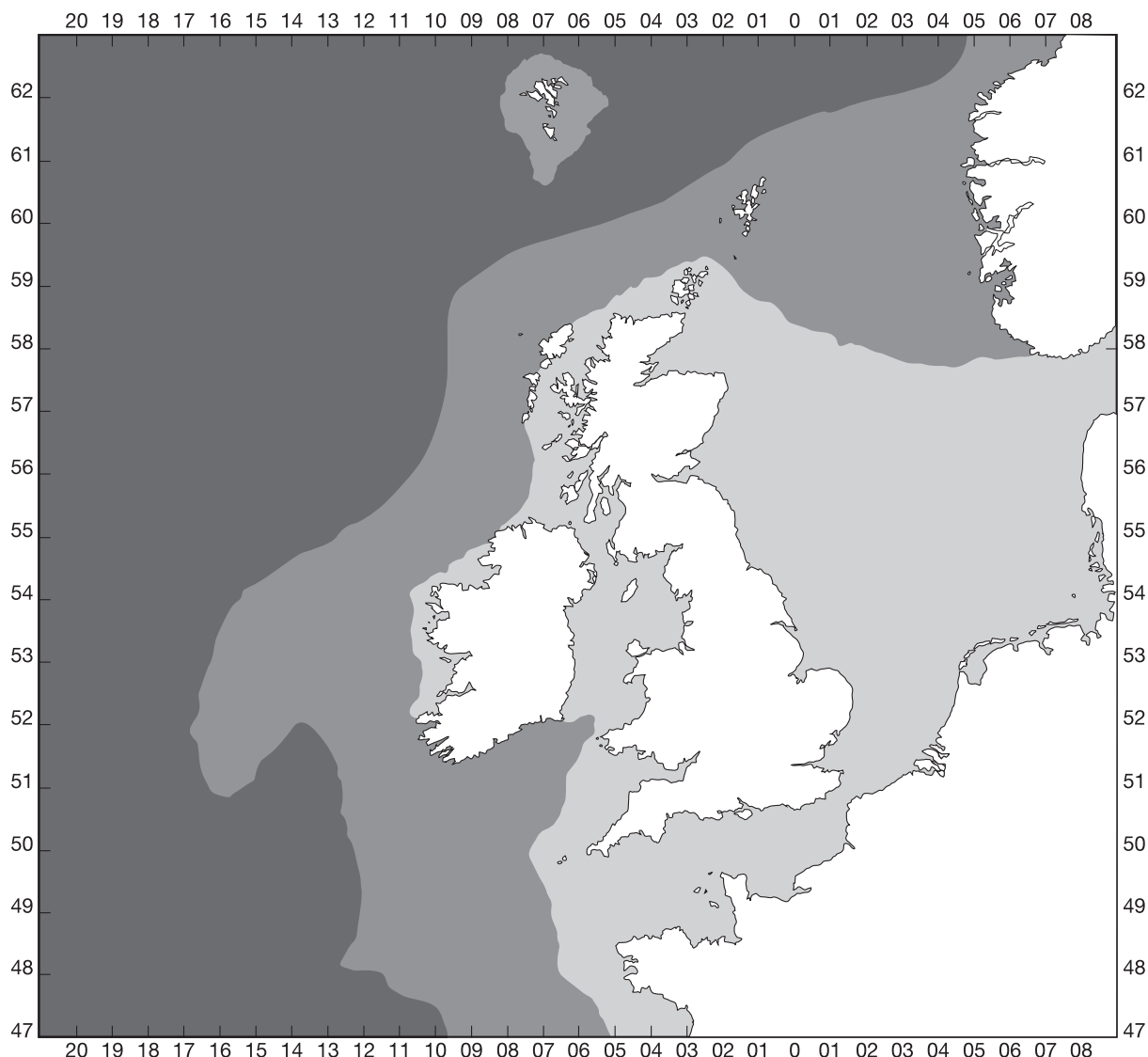


Fig. 12.6 Fin whale *Balaenoptera physalus*: distribution around the British Isles

surface-feeding on the euphausiid *Nyctiphanes couchii*, observed in S Mediterranean [218]. In NW Atlantic, fin whale's consumption of prey estimated at 533 kg/day [470].

BREEDING

Births occur mainly in autumn–winter. Gestation period 11–12 (mean 11.25) months; lactation period 6–7 months. Age at sexual maturity 6–10 years (females) and 8–12 years (males), with indication that exploited populations (such as Iceland) mature earlier [705, 1080]. Calving interval now estimated to be *c.*3 years [706]; photo-ID studies, Gulf of Maine, indicate average time between consecutive births is 2.71 years [9].

POPULATION

No current estimates for whole N Atlantic population, but recent sightings surveys suggest

>46 000 (still below its former size), including 17 000 for British Isles–Spain–Portugal stock [193, 554]. Estimate of 3500 for W Mediterranean, from sightings surveys [388]. IWC estimate for C/NE North Atlantic, 1996–2001, is 30 000 (95% CI 23 000–39 000) [559].

Can live to 85–90 years [342]. Average annual mortality estimated at 4% [873], but this varies between areas and over time.

MORTALITY

Killer whales may sometimes attack and kill fin whales [501, 573, 933, 1157].

PARASITES AND PATHOGENS

External parasites, e.g. copepod *Pennella* sp., amphipods *Cyamus*, and cirripeds including *Coronula* sp., *Conchoderma auritum*, *C. virgatum*, and *Xenobalanus globicipitis*, tend to infect whales in

12 Whales, porpoises and Cetacea: Order Cetacea

warmer waters but are lost in polar regions. Diatoms, e.g. *Cocconeis*, appear as surface films over skin of animals summering in high latitudes. Often infected by nematode *Crassicauda crassicauda*; severe infections thought to cause congestion of kidney and renal failure [669]. Other internal parasites include cestodes and acanthocephalans [416].

One stranded, Belgium, 1997, showed positive antibodies to morbillivirus [568].

RELATIONS WITH HUMANS

Heavily exploited, at least 75 000 taken (mostly S oceans) since invention of steam catcher boats and explosive harpoon gun in mid-19th century, but given full protection from commercial whaling in 1986. Original (pre-exploitation) population estimate for N hemisphere, 58 000 [342].

In 1903–1928, Scottish catches of 4536 (Shetland) and 1492 (Outer Hebrides) [1148]; further 46 caught, Outer Hebrides, 1950–1951 [181]. Irish catches 435, 1908–1914, and 157, 1920 and 1922 [367]. Seem to have depleted local stocks, species scarce in region thereafter. Most catches made off edge of continental shelf, particularly N and W of Shetlands. Until mid-1980s, whaling in Spanish waters may have reduced occurrences off SW GB and Ireland. Intense whaling conducted in Strait of Gibraltar, from 1921 to late 1950s, mostly targeting fin whales, ended with collapse of local stock [863]. Small numbers (from population numbering c.3000 in 2005) still taken by subsistence whale fishery in Greenland, but protected from commercial whaling since 1986.

Occasionally caught accidentally in fishing gear in E Canada and Mediterranean (<1 per year [555, 863]). Collapse of capelin stocks off Newfoundland, late 1970s, thought to have reduced summering populations [1234].

Levels of pollutants including heavy metals (such as mercury), PCBs and other organohalogen compounds usually low, compared to other marine mammals [13, 17, 108, 378, 379, 1027]; levels higher in N Atlantic and Mediterranean than elsewhere (DDT in blubber 0.2–10 µg/g, PCB 0.5–8 µg/g [12]).

Noise and disturbance from vessels and industrial activities may also have negative impact in some coastal areas [336, 338, 1128], and concerns expressed about impact of seismic sounds from oil and gas exploration along NE Atlantic shelf break [352]. Collisions between fin whales and vessels, particularly ferries, known, including reports in British waters, but most serious concern is in Mediterranean, in areas of heavy traffic [198, 896].

Legally protected in European, British and Irish waters and listed by IUCN as Endangered, with the

Mediterranean population proposed as Data Deficient (Table 12.1).

LITERATURE

Good reviews [12, 415].

AUTHORS

G. Notarbartolo di Sciara & P.G.H. Evans

Sei whale *Balaenoptera borealis*

Balaenoptera borealis Lesson, 1828; Lubeck Bay, Schleswig-Holstein, Germany.

Muc-mhara-sei (Scottish Gaelic); *miol mór an tuaisceart* (Irish Gaelic).

RECOGNITION

Dark steely-grey back, often with grey or white round scars. Right lower lip and mouth cavity usually uniformly grey (unlike fin whale) and no white on undersides of flippers or tail flukes (Plate 13). Prominent dorsal fin, strongly re-curved and more erect than fin whale, often visible simultaneously with blow. Blow moderately tall (c.3 m), shaped like an inverted cone. Along with dorsal fin, remains in view for relatively long periods before typically making shallow dive. May blow 2–3 times at 20 s intervals followed by dive of 5–6 min duration, or 5–6 times at 30–40 s intervals before longer dive of 15–30 min. Slender head with slightly arched forehead, though not as rounded as blue whale, with single prominent median ridge (cf. Bryde's whale which has 3 distinct ridges). Baleen plates relatively narrow (length:breadth ratio typically >2.2 whereas always less than this in Bryde's whale).

DESCRIPTION

Slender, streamlined body. Baleen plates relatively short, 300–410 on each side of upper jaw, uniformly grey-black but with fine (0.1 mm in diameter at base), almost silky white fringes (Fig. 12.2). Generally dark grey on back and sides, and rear part of belly, but greyish white on middle part of throat grooves. Relatively small pointed flippers, about 1/11 body length; c.30–60 throat grooves (averaging c.50), all ending well before navel (in fin and Bryde's whale they end at or beyond navel). Dorsal fin fairly erect, usually 25–60 cm high, strongly re-curved and located a little more than 1/3 along back from tail (i.e. slightly further forward than in fin whale and much further forward than in blue whale) (Fig. 12.7). Relatively small tail flukes, broad and triangular, with median notch.

MEASUREMENTS

Length: newborn c.4.4 m; at sexual maturity



Fig. 12.7 Sei whale rolling into dive, showing recurved dorsal fin (photo S. Kraus).

*c.*14.0 m (female), *c.*13.6 m (male); adult *c.*14.5 m (female), *c.*14.0 m (male); maximum 19.5 m. Weight: newborn 680 kg, adult *c.*20–30 t.

VARIATION

N hemisphere animals average *c.*0.5–1.0 m smaller than those found in S hemisphere. Closely related to Bryde's whale [42, 313, 315, 494, 1021, 1189], from which it was only relatively recently distinguished. Genetic studies indicate little mixing between populations of N and S hemispheres, but apparently little differentiation within ocean basins [314, 597, 1189].

DISTRIBUTION

Worldwide, mainly offshore in deep waters. Seasonal migrations from polar and cold temperate regions (mainly around Iceland, in Greenland Sea and W Barents Sea) in summer, to warm temperate and subtropical waters (off Spain, Portugal and NW Africa) in winter.

Summering populations are concentrated in deep waters of central N Atlantic, N to Iceland. In W North Atlantic, reported from 2 main locations: Scotian shelf and Labrador in summer, off Florida, Gulf of Mexico and Caribbean in winter, although some of latter may be misidentified Bryde's whales [543, 571, 592]. In E North Atlantic, thought to winter off NW Africa, Spain and Portugal and in Bay of Biscay, migrating N to summering grounds off Shetland, the Faroes, Norway, and Svalbard [346, 352, 360, 543].

Rarely seen in coastal waters of British Isles, though probably under-recorded because difficult to identify (Fig. 12.8). Most records come from waters >200 m deep, between N Isles and Faroes, and in Rockall Trough; occurs occasionally in coastal waters off Shetland, Hebrides and between S Ireland and SW England [346, 360, 973, 1216].

Around GB, off Outer Hebrides was caught mainly in June along the shelf edge near St Kilda; off Shetland waters, also from the shelf edge, mainly July–August. Recent sightings around British Isles generally in summer, July–October, particularly in August [360]. Off S Ireland, most casual sightings July–November [122]; to S, seen regularly in Bay of Biscay in autumn–winter [267].

HABITAT

Favours pelagic, temperate deep waters, 500–3000 m deep. Seems to have a more offshore distribution than fin whales or other balaenopterids [543, 1080].

HISTORY

No fossil or archaeological material known. Heavily exploited in the past; see Relations with humans, below.

SOCIAL ORGANISATION AND BEHAVIOUR

Relatively non-social species, usually seen singly or in pairs; otherwise in groups of up to 5.

12 Whales, porpoises and Cetacea: Order Cetacea

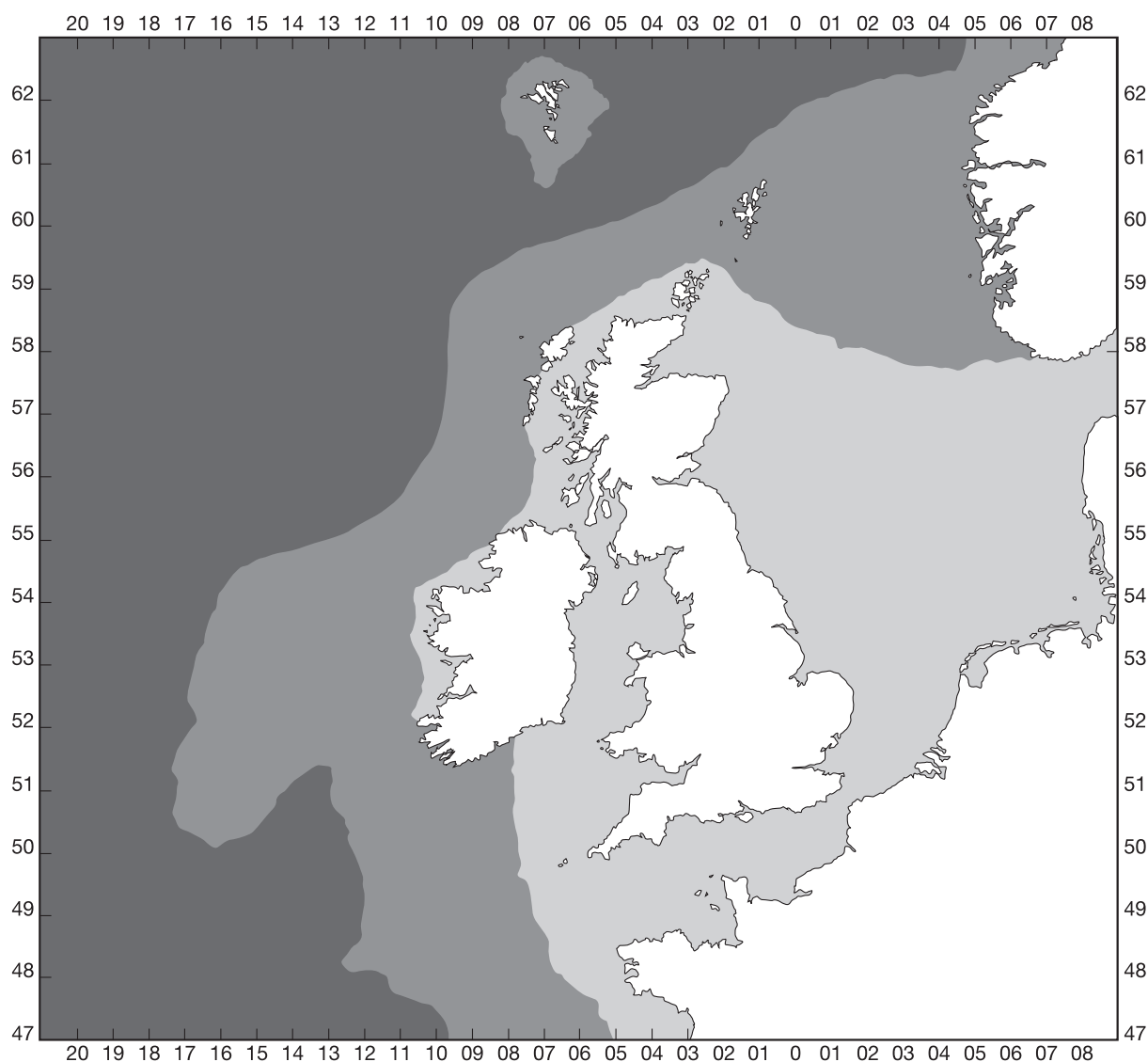


Fig. 12.8 Sei whale *Balaenoptera borealis*: distribution around the British Isles.

Occasional larger aggregations, up to 30, generally associated with feeding [195]. Some segregation by age and reproductive status likely; in S Ocean, pregnant females migrate first, and younger individuals rarely reach highest latitudes [415, 543].

Very fast swimmer (possibly fastest of all rorquals), attaining 55 km/h, though usually travels at 3.6–30 km/h [704]. Usually does not dive very deeply, and so generally surfaces and dives again at shallow angle. Sometimes breaches clear of water.

Vocalisations: Little studied, but include 3 kHz pulsed clicks each <1 s long. Recorded sounds consisted of 2 phrases of 0.5–0.8 s duration, spaced 0.4–1 s apart. Each phrase consisted of 210–220 FM sweeps in 1.5–3.5 kHz range [640, 1149].

FEEDING

Diet: In N Atlantic, mainly copepods (*Calanus*, *Eucalanus*, *Metridia*, and *Temora*); also euphausiids (*Thysanoessa* and *Meganyctiphanes*). Small schooling fishes and squid important in some areas [610, 840, 985, 1157].

Feeding methods: Prey taken near surface, captured either by taking large mouthfuls of water with plankton or by skimming close to surface with half-open mouth and then swallowing [543, 609, 610, 836, 837].

BREEDING

Reproductive biology reviewed in [417, 706, 1080]. Births mainly in winter (particularly November–December), possibly offshore from NW Africa or W of Iberia. Gestation 10.5–13 months; lactation 6–9 months; calving interval 2–3 years. Age at

sexual maturity 5.6–11.7 years (females) and 7–11.7 years (males), although in places has declined from 10–11 years to 6–8 years, following exploitation.

POPULATION

Longevity *c.* 65 years [342]. Annual adult mortality *c.* 9–10% in exploited Icelandic population [714]. Main natural predator is probably killer whale: lethal attacks witnessed, mainly in Pacific [848].

No current estimates exist for the N Atlantic population; recent sightings surveys indicate >13 500, evident depletion of stocks from some of former whaling grounds [230, 244, 594, 1079, 1080].

PARASITES/COMMENSALS

White scars in skin may be caused by copepod crustaceans of genus *Pennella*, or lesions made by the shark *Isistius* or by lampreys. Copepods *Balaenophilus* and *Haematophagus* commonly infest baleen.

Internal parasites very prevalent; acanthocephalan *Bolbosoma turbinella* common in intestine, along with cestodes *Tetrabothrius affinis* and *Balaenoptera turbinella*. Nematodes frequent in kidney and in erectile tissue of penis and urethra of males [417]. In N Pacific, often heavily infected with stomach nematode *Anisakis simplex* and trematode *Lecithodesmus spinosus*; 7% of individuals infected with a disease causing loss of baleen plates [986].

RELATIONS WITH HUMANS

Heavily exploited wherever it was common, particularly 1955–1975. Original (pre-exploitation) population, N hemisphere, estimated at 66 000 [417]. Off N Norway alone, 4000 killed, 1885–1900 [543]. Total commercial protection since 1986, but recent scientific take off Iceland, and limited subsistence whaling off Greenland.

Catches in Scottish and Irish waters earlier this century suggest that sei whales were less abundant than fin whales – still true. Off Scotland, catches of 1839 (Shetland) and 375 (Outer Hebrides), 1903–1928 [1148] with 3 more 1950–1951 (Outer Hebrides) [181]. Off W Ireland, 88 caught, 1908–1914, and a further 3, 1920, 1922 [367]. Off Outer Hebrides, caught particularly along the shelf edge near St Kilda, mainly in June; N of Shetland, mainly taken July–August.

No information exists on fisheries interactions or pollutant levels. Noise and disturbance from vessels and industrial activities potentially damaging in more heavily used areas, and seismic soundings for oil and gas exploration along Atlantic Frontier also a potential problem [352].

Legally protected in European, British and Irish

waters, listed by IUCN as Endangered (Table 12.1)

LITERATURE

Detailed account [543]; valuable summaries [417, 545].

PRINCIPAL AUTHOR

P.G.H. Evans

Blue whale *Balaenoptera musculus*

Balaena musculus Linnaeus, 1758; Firth of Forth, Scotland.

Physalus sibbaldii Gray, 1847; Yorkshire.

Sulphur-bottomed whale, Sibbald's rorqual; *muc-mhara-mhor* (Scottish Gaelic); *miol mór gorm* (Irish Gaelic).

RECOGNITION

Largest whale, reaching 28 m length. Distinctly pale bluish grey over most of body, mottled with grey or greyish white (Plate 13). Very small dorsal fin, variable in shape but usually with little curvature, distinctly more than 2/3 along back so that seen only just prior to dive, some time after blow. Tall (to 10–12 m) vertical blow, denser and broader than fin whale. Typically, makes several shallow dives at intervals of *c.* 20 s. Very broad, long body with broad, flat U-shaped head and single ridge extending from raised area forwards of blowholes towards tip of snout to form prominent 'splash guard'.

DESCRIPTION

Largest and heaviest mammal known. Body form robust with broad snout and large head up to 25% of total length. Baleen plates relatively short (90 cm long × 50 cm wide), 260–400 on each side of upper jaw, stiff and coarsely fringed, and jet black in colour (Fig. 12.2). Body generally bluish grey, mottled with grey or greyish white; sometimes has mustard yellow coloration mainly on belly (caused by diatoms from periods spent in high latitudes). Pigmentation patterns sufficiently variable to allow some individual recognition; 2 main types: dark blue-grey, mottled with sparse pale patches, or pale background mottled with sparser dark patches. Sometimes has distinct chevrons, curving down and angled back from apex on both sides of back behind blowholes. Young animals usually paler grey. Flippers long (up to 15% of body length), slim, with underside and pointed tips white or pale greyish-blue. 55–88 throat grooves, extending more than 1/2 way along body to navel. Dorsal fin >1/3 along towards tail; very small, usually <33 cm high; variable in shape from nearly triangular to moderately falcate (Fig. 12.9). Tail flukes predominantly grey on both sides



Fig. 12.9 Blue whale rolling into dive, showing small dorsal fin (photo P.G.H. Evans).

and broad, triangular with slight median notch, usually lifted only slightly before diving (Fig. 12.1). May have white patches on ventral surface of tail, also useful for individual identification.

MEASUREMENTS

Length: newborn *c.* 6–7 m; at sexual maturity *c.* 21–23.0 m (female), 20–21.6 m (male); adult *c.* 26.0 m (female), 24.0 m (male); larger in S hemisphere, to max. 33.6 m. Weight: newborn 2–3 t, adult 80–150 t [1257].

VARIATION

3 subspecies designated: Antarctic form *B. m. intermedia* is a few metres larger than N hemisphere *B. m. musculus*. Taxonomic status of small 3rd subspecies, pygmy blue whale *B. m. brevicauda*, in sub-Antarctic zone of S Indian Ocean and SW Pacific, requires confirmation. In N Atlantic, E and W subpopulations recognised for purpose of management [416]; also need confirmation by genetic studies, although photo-ID suggests that whales from Iceland and Azores do not mix with those from NE USA, E Canada or W Greenland [1058].

RELATIONSHIPS

Of 7 species of *Balaenoptera*, 4 (not tropical Bryde's whale) occur regularly in European seas. Blue, fin and sei whales tend to live in deep waters, smaller minke whale occurs primarily over the continental shelf. Molecular (nuclear and mtDNA) phylogeny suggests closer to Bryde's and sei than fin or

humpback whale [62, 494, 1021], though rare hybrids with humpback and fin whales known [123, 1112].

DISTRIBUTION

Worldwide in all seas, mainly in warm temperate–subtropical waters during winter, summering in cold temperate and polar seas.

In N Atlantic, occurs from Caribbean to Davis Strait S Greenland in W, and from Canaries, Cape Verdes and W Africa to Jan Mayen, Svalbard and Barents Sea in E. Best-known population lives in St Lawrence, April–January, where 350 individuals have been photographed [1056–1058].

Presence around British Isles evident primarily from whale fisheries of early 20th century; small numbers regularly passed W of GB and Ireland during summer in deep waters off edge of continental shelf [181, 1148]. More recently, sightings [346, 360, 973, 1216] and acoustic monitoring [234, 256] reveal small numbers in deep waters of Faroe-Shetland Channel and Rockall Trough, S to Bay of Biscay. Thought to winter in tropical and subtropical seas where they breed, then migrate to feed during summer months in cold temperate and polar waters. Supported by recent sightings in Azores and Canaries during winter–spring, and in high latitudes, May–September; but recent monitoring using SOSUS acoustic arrays suggests that some remain in high latitudes throughout winter [234, 256].

4 strandings on British/Irish coasts, 1913–1923,

but none since [408, 1072]. Only 1 recent well-documented sighting, one off NW coast of Ireland, May 1977, although also sighted over Wyville Thompson Ridge and in Faroe-Shetland Channel [346, 358, 360]. Also a few sightings in Bay of Biscay, N of Spain [20, 267, 1026].

HABITAT

Usually found in deep waters (100–1000 m); in some regions, occurs regularly close to land, in depths of 200 m or less [1055, 1080]. In Iceland, tends to be seen closer to the coast than fin or sei whales [1080].

HISTORY

No fossil or archaeological material known.

SOCIAL ORGANISATION AND BEHAVIOUR

Relatively non-social; usually seen singly or in pairs; larger aggregations of >50 occasionally occur around concentrations of food [1056, 1257]. Mother–calf pairs often observed away from schools of males and non-reproductive females [838]. Extended associations between males for as long as 3 weeks observed in St Lawrence estuary [1056]. When male–female pair approached by another whale, vigorous surface displays lasting 5–15 min observed; all 3 may race high out of water, almost breaching, and porpoising forward in explosive manner.

Fast swimmer, 2–6.5 km/h while feeding, 3–33 km/h while travelling or migrating, and >30 km/h when being pursued [704, 997].

When diving, lifts tail stock only slightly, generally dives at a shallow angle. Rarely dives to >100 m, but may go down to 500 m [416]. Only occasionally breaches clear of water.

Vocalisations: Throughout year, but with peaks from midsummer into winter. Include 17–30 Hz moans lasting 15–38 s, sometimes with higher-pitched pulses, and clicks at 6–8 or 21–31 kHz. Low-frequency sounds are very loud (c.188 dB re 1 μ Pa @ 1 m); thought to allow communication over great distances (possibly even across ocean basins) [256, 1056, 1257].

FEEDING

Diet: Feeds almost exclusively on planktonic crustaceans, mainly euphausiids (*Thysanoessa*, *Nematoscelis* and *Meganycitiphanes*; and, in Antarctic, *Euphausia* species), although will also take copepods (e.g. *Temora*), and, less frequently, amphipods, cephalopods, and occasionally small fish (perhaps accidentally) [610, 836, 839, 1157, 1257]. Observed feeding on pelagic red crabs *Pleuroncodes planipes* off Baja California [987].

Feeding methods: Thought to feed in deep waters, primarily at 100–200 m [839]. During deep dives, typically remains below surface for 8–15 min (max. 36 min). Feeding occurs primarily during summer, at higher latitudes. Although surface feeding often seen during day, more usually dives deep to plankton swarms during daylight hours, feeding near surface in evening, following ascent of prey in water column [1056]. When feeding just below surface, often surfaces slowly, belly first, exposing throat grooves of ventral pouch, rolling to breathe and expelling water from mouth before diving again. In high krill concentrations, feeds by lunging with mouth wide open, gulping large mouthfuls of plankton and water, before closing mouth and expelling water by muscular action of throat grooves and tongue through still-exposed baleen plates. If prey close to surface, lunges vigorously on sides or vertically, projecting massive lower jaw several metres up through surface [1055].

BREEDING

Reproductive biology summarised in [706, 1257]. Mating thought to occur late autumn–winter, with births during winter. Breeding grounds not known, thought to be in tropical Atlantic off NW Africa. In N Pacific, adults with young seen regularly in winter, Gulf of California. Gestation 10–11 months. Lactation 6–8 months (weaned at c.16 m long), calving interval c.2–3 years. Sexual maturity reached at 5–15 years, but mainly 8–10 years for both sexes.

POPULATION

Lifespan estimated at 30 years [1096], 80–90 years [849]. Annual adult mortality possibly c.10–12%.

Main natural predator is probably killer whale. No reports of attacks in N Atlantic, but 25% of blue whales photographed in Gulf of California have raked scars of killer whale teeth [1056].

Populations everywhere seriously depleted by whaling. N Atlantic population severely reduced by over-exploitation, thought to be no more than 1500, mostly in W where are some signs of recent recovery [971]. No precise estimates for whole region; recent line-transect surveys suggested a maximum of 442 whales [1082], later extrapolated to overall population estimate of 1000–2000 animals [1080], but without details of how derived. These surveys did not cover entire N Atlantic range of species, may be misleading to extrapolate from high-density areas around Iceland. Long-term photo-ID study identified 350 individuals in Gulf of St Lawrence [1056, 1057], but not possible to derive an abundance estimate from this [480].

PARASITES/COMMENSALS

Ectoparasites/commensals: Copepod *Penella balaenopterae* found embedded in the skin; commensal copepod *Balaenophilus unisetus* found on baleen. Diatom *Cocconeis ceticola* may cover part or all of body when in cold waters [1257].

Endoparasites: Nematode *Crassicauda crassicauda*, cestodes *Tetrobothrius affinis*, *T. wilsoni*, *T. schaeferi*, *Priapocephalus grandis*, *Diplogonoporus balaenopterae* and acanthocephalan *Bolbosoma nipponicum*.

RELATIONS WITH HUMANS

Prime target of over-exploitation late 19th–mid 20th century; numbers killed worldwide greatest 1920–1940, peaking at 30 000 in 1930–1931 season. In N Atlantic, 11 000 were taken over this period, mainly off Iceland.

Off Scotland, 85 taken, 1903–1928, from Shetland and 310 from Outer Hebrides [1148]. In 1950–1951, a further 6 captured off Outer Hebrides [181]. Off Ireland, 98 killed 1908–1914, and 27 in 1920, 1922 [367]. Most captures from deep waters beyond edge of continental shelf.

Despite protection from commercial whaling in 1966, catches by USSR continued into the 1970s in secret [184, 248]. Only now is there any sign of a slight recovery of stocks, mainly in E North Pacific [250] but also possibly N Atlantic [965, 971].

Persistent contaminants such as PCBs found in blue whales off E Canada may have impact on reproduction [1056]. Little information on incidental capture in fishing gear but thought to be relatively unimportant. Sound from shipping, including whale-watching boats, may have a negative effect [338]. Collisions with ships reported, California [99]; in St Lawrence, 25% of blue whales photographed have scars attributable to vessel strikes [1056]. Seismic testing during oil and gas exploratory activities also has potential to disturb blue whales in areas like Atlantic Frontier W of British Isles, although this has yet to be demonstrated [352]. With their restricted diet of euphausiid crustaceans, could be particularly vulnerable to climate change [250, 719].

Has strong international and local legal protection (Table 12.1); completely protected since 1994 by IWC, listed by IUCN as Endangered.

LITERATURE

No detailed scientific review since [1257]. Popular reviews include [199, 416], with overview in [1056].

AUTHOR

P.G.H. Evans

SUBORDER ODONTOCETI (TOOTHED WHALES)

FAMILY PHYSETERIDAE (SPERM WHALES)

A family of only 2 genera and 3 species, 2 of which occur, occasionally, in NE Atlantic. Sperm whale *Physeter* is much the largest odontocete, but the 2 species of *Kogia* are small whales, c.3 m long. Distinguished by narrow lower jaws with numerous teeth, but toothless upper jaws. Squid specialists. Blunt heads containing spermaceti organ: large bladder full of special liquid wax. Genetically isolated within Odontoceti, perhaps closest to Ziphiidae.

GENUS PHYSETER

Monospecific. Linnaeus used both *P. macrocephalus* and *P. catodon*; former given priority by first reviser (ICZN Code Article 24) [548, 945].

Sperm whale *Physeter macrocephalus*

Physeter macrocephalus Linnaeus, 1758; European Sea, restricted to Berckhey near Wassenaar, The Netherlands [548].

Physeter catodon Linnaeus, 1758, Northern (= N Atlantic) Ocean, restricted to Scheldt Estuary, The Netherlands [548].

Muc-mhara-sputach (Scottish Gaelic); *caisealóid* (Irish Gaelic).

RECOGNITION

Readily distinguished at sea by single blowhole at apex of head, displaced to left, producing low (1.5–5 m), bushy, obliquely left, forward-facing blow (Fig. 12.10). Dark, smooth barrel-shaped ‘head’, disproportionately large, behind which is low dorsal fin (Plate 13). Forepart of head may show pronounced swollen hump, particularly on left side around blowhole. Usually raises large, triangular, flexible flukes above surface to initiate dives (fluking-up). Ashore, easily distinguished by massive head, long, thin tooth-bearing lower-jaw, with corresponding tooth sockets in upper jaw, and single S-shaped blowhole at front left side of head.

Skull: The only asymmetrical skull of this size (the left naris is much larger, and offset left) with concave premaxilla, frontal region rising to a high, basin-like structure. Mandibles very characteristic; long, narrow fused region indented with sockets for up to 25 pairs of large, peg-like or slightly re-curved teeth. Posterior end of each mandible extends to form broad, relatively thin pan bone. Each mandible resembles an upside-down rifle in shape.



Fig. 12.10 Sperm whale, showing asymmetrical blow through left nostril (photo P.G.H. Evans).

DESCRIPTION

Most striking feature is huge, barrel-shaped head; may account for up to 1/3 of body length in males, has long, thin lower jaw slung below (Plate 13). General body colour dark grey or brownish grey. Paler patches on belly in genital area. Inside of mouth, and skin on upper and lower jaw pale cream or white; particularly striking when viewed underwater. Head of male often marked by numerous pale scratches and scars inflicted by teeth of other sperm whales; round impressions due to suckers and tentacles of squid sometimes visible on head. Scarring particularly common on sexually mature males, may lead to anterior portion of head acquiring a very pale coloration with white, callous-like patches on tip of snout. After-part of the body often deeply corrugated. Short, ill-defined grooves in throat region diagnostic of *Physeteridae*. Large, rounded paddle-like flippers. Small dorsal fin (often topped by white or yellowish rough callus, particularly in mature females); often, several pronounced bumps along spinal ridge running back to insertion of triangular and deeply-notched tail flukes. Flukes quite stiff, with straight or slightly convex trailing edge (Fig. 12.1); have uniform, plain coloration, unlike patterned flukes of humpbacks. Pronounced keel runs along underside of tailstock. Lower jaw contains *c.*20–26 pairs of large (up to 25 cm and 1 kg) peg-like teeth (declining in size towards the front and back). Each fits into a deep

matching socket in upper jaw; rudimentary teeth sometimes found between these sockets, vestigial teeth sometimes just erupting. Teeth apparently not essential for feeding, erupt some time after weaning, and not at all in some females. Disproportionate size of head is due to development of 2 huge fatty bodies, spermaceti organ, and, between it and upper jaws, the 'junk' (also containing spermaceti chambers, surrounded by connective tissue), both of which are unique to *Physeteridae* and thought to be involved in sound production, and possibly also in buoyancy; in addition, the large head in adult males serves as a fighting organ.

RELATIONSHIPS

Closest living relatives are 2 much smaller *Kogia* sp. Despite suggestion that sperm whales more closely related to baleen whales than to other odontocetes [785], current genetic and morphological evidence supports traditional view that they belong within odontocetes, though occupying basal position; separated early in modern cetacean evolution, *c.*20 mya [434, 518, 763, 779].

MEASUREMENTS

Length: newborn 4 m; at sexual maturity 9 m (female), 12 m (male); at physical maturity 11 m, rarely up to 12.5 m (female), 15.8 m, rarely up to 18.5 m (male), though large bulls have become rare after selection by whalers. Weight at physical maturity 13.5 t (female), 44 t (male) [130, 988].

12 Whales, porpoises and Cetacea: Order Cetacea

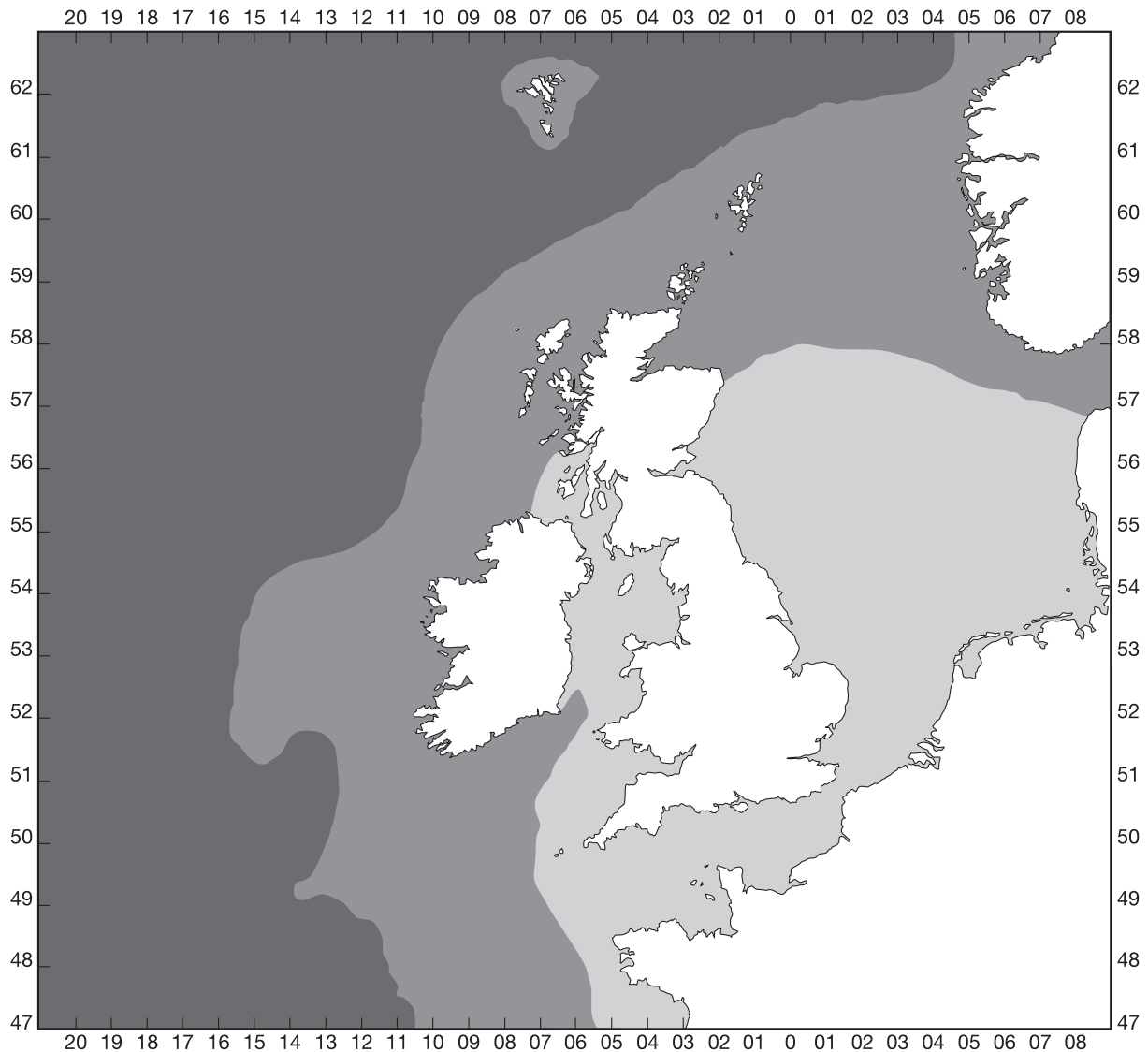


Fig. 12.11 Sperm whale *Physeter macrocephalus*: distribution around British Isles.

VARIATION

Limited understanding of stock structure. Genetic studies fail to identify distinct stocks within ocean basins [725, 727]. Surprisingly little variation even globally (using maternally inherited mtDNA); variously explained by one or more of following interpretations: historical population bottleneck, stronger selection on mitochondrial genome, the demographic consequence of matrilineal social system, or indirect effects of selection of cultural traits transmitted from mothers [725, 726, 1230, 1232].

DISTRIBUTION

Worldwide, in deep waters of all seas. Females and juvenile males have a more limited range than adolescent and mature males, confined to warmer waters, generally with sea surface temperatures (SST) $>15^{\circ}\text{C}$, between $c.45^{\circ}\text{N}$ and $c.45^{\circ}\text{S}$. Young

males accompany females in tropical and subtropical waters but from ages of 14–21 years move increasingly to higher latitudes. Only large males found in highest latitudes, sometimes even close to ice edge, but generally in most productive deep waters.

In E North Atlantic, widely distributed in deep waters off continental shelf, along Mid-Atlantic Ridge and around mid-Atlantic islands (Azores, Madeira, Canaries, Cape Verdes), from Iceland and Norway S to Iberian peninsula and E into Mediterranean. Some known preferred feeding areas for males include deeper waters along continental slope W of Portugal and N of Spain, W and N of British Isles, off Iceland, and Lofoten I. in Norway [360, 973, 1081, 1084]. Areas with aggregations of mixed groups of females with immature males include Azores, Madeira, and Canaries. Calving and mating are known to occur

there, as well as in the Caribbean and Mediterranean.

Have been no systematic surveys for sperm whales in British and Irish waters (Fig. 12.11). Some areas of predictable abundance identified, but to some extent reflect patchy distribution of survey effort. Generally, only males come as far N as British Isles; virtually all sightings come from deep waters off continental shelf. Waters around Rockall, to N of Outer Hebrides, N and W of Shetland in Faroe-Shetland Channel, and in Bay of Biscay all have relatively high densities [282, 346, 350, 360, 941, 973, 1135, 1216]. Formerly, sightings off British Isles were almost exclusively of larger males, singly or in small groups; more recently, more records of smaller individuals in larger groups noted, including mass strandings of immature males [350, 360].

Often stray into North Sea when travelling S; causes of such 'navigational errors' still unknown; often become disorientated and eventually stranded, thought to be due to poor navigation abilities in shallow water and lack of food: the North Sea has been called a 'sperm whale trap'. Strandings may concern single animals or groups of up to 16, though groups and hence strandings may become scattered in place and time. Most strandings in the North Sea occur November–February [569, 1100, 1158]; peaks recorded late 18th century and 1990s–early 21st century; poorly understood, but may partly be related to higher sea temperatures, possibly affecting the distribution of squid [928]. Number of strandings on British and Irish coasts increased markedly: 12 in 1913–1948, 31 in 1949–1986 and 53 in 1987–1994 [121, 350]. Unclear whether due to changes in whale distribution, or to increased mortality due to unknown causes. In recent years, have been several well-publicised occurrences of sperm whales (all mature or adolescent males) entrapped in enclosed waters: 2 groups in Scapa Flow (Orkney), 1 in Hebrides, and 1 in the Firth of Forth.

Sightings in British and Irish waters mainly July–December, but increasing evidence of small groups remaining at high latitudes into winter, when most coastal sightings and mass strandings take place [121, 346, 350, 360, 1100, 1158]. During Scottish and Irish whaling, early 20th century, most sperm whales caught June–August [367, 1148]. Some indication of southwards movement in late summer [360].

HABITAT

Mainly offshore either in mid ocean or over submarine canyons at edges of continental shelf or beyond; can occur close to coasts of volcanic and oceanic islands in waters >200 m (and usually

500–2000 m) depth. Concentrations occur in areas a few hundred km across, characterised by relatively high deep-water biomass resulting from increased primary productivity due to upwellings [566]. Occasionally stray into shallow waters; see above.

SOCIAL ORGANISATION AND BEHAVIOUR

Most social of the great whales. In high latitudes, typical group size is 1–2 but tight coordinated groups of 6–10 (occasionally more) may be encountered. Core social units are called 'mixed groups', believed to be matrilineal, comprising around 12 adult females plus their calves, and immature male and female offspring [1229, 1232]. Sometimes, 2 or more such groups may travel together for a few days, forming a larger group of *c.*20–30. Typically, females remain to become long-term members of these family units, but young males leave as they reach puberty (from 14–15 years onwards), forming bachelor herds. Members of mixed groups stay together for extended periods (probably for life in the case of females); show communal care (baby-sitting) of young (which possibly extends to communal suckling). Mixed groups may number tens of animals, but are usually spread over several miles while still in contact, so rarely seen together at the surface. Groups of males too, may consist of widely scattered subgroups, which join and split up frequently.

Groupings of sperm whales also spaced out over the ocean at scales of up to *c.*700 km (320 nm), associated with the presence of high relief features [566]. As males get older, form smaller and smaller bachelor groups, and range to higher latitudes. Socially mature adult males associate briefly with matrilineal groups to breed, occasionally fighting with other males. Photo-ID studies (using mainly tail-fluke margins) and radio telemetry have helped understand movement patterns. Females have home ranges generally *c.*1000 km across whereas males roam more widely, and largely seem to forage independently.

Adults spend *c.*75% of their lives in making deep dives for feeding; this continues day and night. Typically spend 10–12 min at the surface (termed 'logging'), blowing strongly and regularly every 10–15 s and moving very slowly (1–4 km/h), before fluking-up to initiate a long deep dive. Dives typically last 25–50 min, exceptionally to 138 min [448, 449, 897, 1043, 1208]. Usually reach depths of 300–1000 m; dives of >2000 m observed [1210]; depths of 3195 m inferred from observation and stomach contents [258, 703]. Members of mixed groups come together at the surface *c.*once a day

12 Whales, porpoises and Cetacea: Order Cetacea

forming tight socialising/resting aggregations of 6–30 whales. Individuals, particularly juveniles, may breach clear of the surface, or lobtail [1201].

Patterns of migration not well known. In temperate waters, females appear to show a poorly defined seasonal N–S migration; some mature males migrate from high latitudes to join female groups to breed. Recent acoustic surveys indicate that sperm whales are common off the British Isles in winter [234, 1135].

Vocalisations: Very vocal [448, 734, 1213], but makes only short, impulsive, broadband (c.0.1–30 kHz) click-type vocalisations. These can be very powerful – up to 223 dB re 1 μ Pa @ 1 m [804]. Long, regular click sequences, produced at rates of around 2/s during deep dives, are probably used for echolocation; stereotyped patterns of clicks (3 to c.20 clicks lasting 0.2–2 s), termed ‘codas’, heard from socialising female groups, may be more important for communication. Groups of females have distinctive coda repertoires, probably acquired culturally from within family units. Slow, ringing clicks or ‘clangs’ repeated every 6–8 s are produced almost entirely by large males; function unclear, may be to attract females or repel other males. Accelerating series of clicks, called ‘creaks’, are thought to represent foraging attempts towards potential prey. Typically quiet at the surface, except during periods of social activity.

FEEDING

Diet: Varied, dominated by medium-sized mesopelagic squid; males tend to take larger items than females, and more likely to eat demersal fish, from high latitudes [608, 988]. Most prey have mantle lengths of 20–100 cm; in N Atlantic, are mostly Onychoteuthidae and Ommastrephidae, although giant *Architeuthis* and bottom-living octopus also taken. In some areas (e.g. Iceland) deep-living fish, including rays, sharks, lantern fish, lump-suckers, red fish *Sebastes* and gadids, are the dominant prey [262, 747]. Crustaceans very occasionally eaten, including giant mysids and benthic crabs [608]. Stomach contents from recent European mass strandings often empty, but otherwise revealed squid *Gonatus* sp. the most important prey (likely ingested in N Atlantic); both deep-sea octopus and coastal species also frequent [1033]. *Loligo forbesi* and octopus also found in Scottish specimens, *Histioteuthis bonnellii* and *Teuthowenia megalops* in one of the Danish animals.

Sperm whales apparently dominate this deep ocean trophic level in terms of biomass removed, estimated globally at c.100 million t/year, and comparable with current annual catch by all human marine fisheries [1232].

BREEDING

Mating system poorly understood. For most of their lives, mature males and females live hundreds or thousands of miles apart. Mating takes place over an extended season (probably February–June in N Atlantic); believed that largest ‘prime’ males account for most matings, migrate to lower latitudes to achieve this, but not all mature males migrate to female areas each year. Tooth scars suggest fierce competitions take place between males. Males join mixed groups for short periods, when breeding presumably takes place. In N Atlantic, single young born mainly June–September, after 16–17 months gestation. Fetal sex ratio is c.1:1. Lactation extended, at least 19–42 months, but some young continue to take milk up to 13 years; late sucking apparently primarily for social reasons (‘comfort’ behaviour). Solid food generally first taken after 1 year. Sperm whales have one of the lowest breeding rates of any mammal, with calving intervals of 3–15 years (generally around 5 years, but varying with region and history of exploitation, and declining with age). Sexual maturity reached around 18–19 years by males, 7–12 years by female, but males generally do not play active role in breeding before their late 20s. Growth rates very slow, physical maturity not reached until around age 30 years (female) and 50 years (male). Breeding parameters reviewed in [130, 988].

POPULATION

Longevity estimated as 65–70 years, and annual adult mortality low at c.5–8% (slightly higher in males) [956, 988]. Once a common, ecologically dominant, animal in offshore waters. Numbers substantially reduced by whaling. In N Atlantic alone, over 20 000 animals have been taken since 1950. Numbers now recovering, though at an unknown rate. No reliable estimates for current N Atlantic or world populations; likely to be a few hundred thousand globally.

MORTALITY

Although killer whale and sharks are potential predators, and harassment by pilot whales has been observed, sperm whales are largely capable of driving them away. Females rapidly form a cluster either in ‘marguerite’ or ‘wagon wheel’ formation where members of group either place their heads together to form a circle or face their attackers in a tight group facing out, using their jaws for defence [1232]. Young calves remain protected in the centre, and adults may assist one another in defence.

PARASITES/COMMENSALS

Remarkably clear of external parasites. Cyamids

(notably *Neocyomus physter*) usually occur. Remora frequently attach to calves and juveniles. 24 species of parasitic helminths reported [988], though air-sinus flukes *Nasitrema*, lungworms Pseudaliidae and kidney worms *Crassicauda* surprisingly absent. Cestodes include *Phyllobothrium*, *Monorygma*, and *Tetrabothrius*; nematodes include *Anisakis simplex* and *A. physteris*; and acanthocephalans include *Bolbosoma* and *Corynosoma*.

RELATIONS WITH HUMANS

Since early 18th century, sperm whales have been especially valuable to whaling industry for waxy spermaceti (used originally for lamps and candles, later as a lubricant in engineering and textile industries), blubber, meat for fertiliser, and ambergris (an intestinal deposit highly valued as a fixative in cosmetic industry). Sperm whale populations, including those W of GB, were the target of devastating worldwide, open-boat whaling by 'Yankee' whalers in the 18th–19th centuries. Later, after populations of most baleen whale species had become depleted, sperm whales formed main target of modern whaling industry. In 1903–1929, Scottish whale fishery took 19 sperm whales off Shetland, and 76 off Outer Hebrides; 1 taken off Hebrides in 1950–1951 [181, 1148]. Off Ireland, 48 taken 1908–1914, and a further 15 1920–1922 [367]. Most catches occurred in deep waters, just off the edge of the continental shelf. Recent whaling for this species in N Atlantic occurred around Iceland, Spain, Madeira and Azores. The last catches were made in 1987.

Sperm whales are known to interact with some fisheries, including long lines and deep water trawls; in Mediterranean, young sperm whales sometimes caught in drift nets or set nets, and may be victims of ship strikes, particularly fast ferries, in areas such as the Canaries and W Mediterranean. Some killed by ingesting plastic. Contaminant levels usually somewhat higher than in baleen whales. Relatively high cadmium levels probably natural [534].

Nowadays, sperm whales are the mainstay of 2 commercial whale-watching operations in the NE Atlantic. Large males can be observed off Lofoten I., and mixed groups in Azores, Madeira and Canaries. Legally protected in European, British and Irish waters (Table 12.1).

LITERATURE

Most detailed treatment is [1232], which updates and expands upon [988]; popular introduction [449]; succinct overview [1231].

PRINCIPAL AUTHORS

J.C.D. Gordon & P.G.H. Evans

GENUS *Kogia*

Contains 2 closely related species, pygmy sperm whale *K. breviceps* and dwarf sperm whale *K. sima*. Are among the least known cetaceans and were only recently separated [482]. Only pygmy sperm whale has been recorded from British and Irish waters.

Pygmy sperm whale *Kogia breviceps*

Physeter breviceps Blainville, 1838; S Africa.

Caisealóid beag (Irish Gaelic).

RECOGNITION

Both *Kogia* spp. have robust bodies. Surface slowly, with indistinct blow. May lie still at surface, showing back and dorsal fin. *Kogia* sp. difficult to tell apart at sea. Both have falcate dorsal fins but that of pygmy sperm whale proportionally smaller: typically 5–9% of snout–fin length (9–16% in dwarf sperm whale) [745]. May be confused with blunt-headed dolphins of similar size; distinguished by slower movements and square head (Plate 16). Noticeably smaller than similar-looking beaked whales. Usually has crescent-shaped, light marking on side of head between eye and flippers ('false gill'), giving head a shark-like appearance.

Skull resembles miniature sperm whale. Blowhole slightly left of midline, placed further back in pygmy than dwarf sperm whale; tip of snout to blowhole is 10.5–13% of body length (in dwarf sperm whale, <10% of body length). Lower jaw narrow, underslung, ends well behind the tip of the snout, carries 10–16 pairs of sharp pointed teeth; no upper teeth (dwarf sperm whale sometimes has 1–3 pairs of teeth in upper jaw). No reported sexual dimorphism.

DESCRIPTION

Conical head, 1/6 of body length (cf. 1/3 in sperm whale), which becomes squarer with age. No beak. Blowhole on top of head, but right naris passes through a valve structure ('museau de singe') unique to Physeteridae, thought to be used for sound production. Oil-filled spermaceti organ in *Kogia* is small, lies above skull behind a large melon [203]. Short, ill-defined grooves in throat region. Body dark blue-grey on back, outer margins of flippers and upper surface of tail flukes, lightening to pale grey on flanks and dull white belly (sometimes with pinkish tinge). Skin may have wrinkled appearance. Flippers relatively long (up to 14% of body length), wide at the base tapering to rounded point. Low, slightly re-curved dorsal fin placed just behind centre of back. Tail with concave trailing edge, distinct median notch. Low and inconspicuous blow during slow sluggish roll.

12 Whales, porpoises and Cetacea: Order Cetacea

Unlike sperm whale, no obvious sexual dimorphism. Skull of both *Kogia* spp. has an unusually short rostrum (the shortest among living cetaceans), and marked asymmetry with no independent jugal, a well-developed facial depression, and a pronounced sagittal septum extending from the narial aperture to the vertex. In pygmy sperm whale, this is broad near its apex and slopes gradually into cranial fossae on each side (dwarf sperm whale has a narrow steep-sided septum, often pinched posteriorly) [203, 1016]. Cranial fossae are elongated anterioposteriorly, posterior walls slope gradually from the dorsal rim of the skull (in dwarf sperm whale, dorsal rim of each fossa is steep, giving a cupped appearance to the skull).

RELATIONSHIPS

Dwarf sperm whale *K. sima* is closely related, only recently distinguished as a separate species; tends to inhabit warmer waters [203], in E North Atlantic, recorded from Senegal [203], Spain [1172], and France [283, 331], as well as W Mediterranean [78]; might yet occur off British Isles.

MEASUREMENTS

Length: newborn *c.* 1.2 m; at sexual maturity *c.* 2.3–2.7 m (both sexes); adult maximum *c.* 3.30 m (both sexes) [203, 937]. Typical weight 300–400 kg, although 450 kg male reported from E Canada [766].

VARIATION

No information.

DISTRIBUTION

Poorly known; apparently worldwide in tropical, subtropical and temperate seas of both hemispheres. Rarely sighted, most information from strandings, mostly on coasts of N America. Records in N Atlantic range from equatorial waters N to Nova Scotia in W and British Isles in E.

On Atlantic coasts of British Isles, 12 strandings: singles in Co. Clare, in April 1966; Co. Galway, October 1985; Glamorgan, October 1980; Devon, October 1993 and January 1997; a live stranding in Pembrokeshire, October 1997; singles in Co. Mayo, sometime in 1998 and in July 1999; an adult and calf, live stranded in Loch Ryan, Wigtownshire, October 1999; singles in Co. Galway in June 2000; Devon, January 2002; and Co. Kerry, July 2002 [120, 360, 408, 1040, 1073]. Also strandings from Netherlands [883], Atlantic coasts of France [330, 333], Spain [853], Portugal [978, 1060, 1061], and the Azores [759, 1143]. Also 3 sightings reported from waters around British Isles: 1 in North Sea off NE England, August 1979;

2 in deep waters off NW Ireland, on successive days in June 1982 [346, 360].

HISTORY

No fossils attributable to this species, but *Kogiinae* is represented in the Pliocene [53]; a few, incomplete, fossils listed in [828].

HABITAT

Occurs in deep waters; dietary analysis indicates feeding in deep zone of continental shelf and slope waters [938, 1040].

SOCIAL ORGANISATION AND BEHAVIOUR

Poorly known. Apparently not gregarious, observations mainly of single individuals or small groups of 3–4, rarely up to 6 animals [937]. Slight sexual size dimorphism, small group size and small relative testis size all suggest a promiscuous mating system [937]. Relatively easy to approach, although it rarely approaches vessels [607, 787]. Occasionally breaches, but more usually lies apparently motionless on the surface. A relatively slow swimmer, perhaps *c.* 5–6 km/h, although capable of much more rapid bursts of speed [814].

Vocalisations: Not studied in detail; echolocation clicks recorded at 60–200 kHz (dominant frequency 120 kHz) [204, 1028]. Possible sound production mechanisms suggested in [260].

FEEDING

Diet: Predominantly mesopelagic squid, such as *Histioteuthis*, *Chiroteuthis*, and *Lycoteuthis*, also fish and crustacea [759, 766, 938, 1040]. Females with calves take more inshore species whereas adult males consume cephalopods that inhabit continental shelf edge and slope [938].

BREEDING

Breeding season unknown in N Atlantic. Off S Africa, conceptions occur April–September, with prolonged calving season March–August [937]. Gestation period thought to be *c.* 11 months [787, 937]. Age at sexual maturity estimated at *c.* 4 years (both sexes), with ovulation in females occurring every *c.* 1.5 years (17.7 months, assuming 1 dentinal growth layer group = 1 year) [937]. 24% of all mature animals examined along coast of S Africa found to be simultaneously pregnant and lactating, indicating a postpartum oestrus [937]. Lactation thought to last *c.* 12 months [937]. Lifespan unknown.

POPULATION

No estimates for population size or status, nor on sex ratio, age structure or mortality rates.

MORTALITY

A few reports of evidence of attacks by killer whales and sharks, although the species of shark was not identified [1040]; false killer whale also a possible predator.

PARASITES AND PATHOGENS

Cyamid whale lice have been reported attached to infected tissue from a wound on the flanks of an individual [206]; nematodes have been found in abundance in the forestomach, and trematodes encysted in the blubber, particularly ventrally and in anal region [203, 288, 828]. Heart failure and pneumonia have each been noted in stranded animals, although their role in mortality is rarely known [166, 203, 870].

RELATIONS WITH HUMANS

The status of the species is unknown but there are reports of mortality caused by a variety of human activities. Occasionally in various harpoon fisheries, e.g. E Caribbean, Indonesia, Japan [203]. Found in fish markets in Sri Lanka [677], estimated >80/year die there in fishing gear [679]. Fisheries-related mortality also reported Caribbean coast of Colombia, coastal Brazil; Japanese squid gillnets may take incidentally, N Pacific [882, 919]. Stranded animals frequently show evidence of collisions with vessels [766]; may move away from or dive to avoid aircraft or large vessels [818, 993]. Very little information on pollutant levels; high zinc levels (163 mg/kg wet weight) in 1 female, Argentina, but generally low levels of other metals and organochlorines (DDT, PCBs) from this and 5 other individuals from SE USA, S Africa and Australia [622, 643, 673, 741]. Plastic bags in stomachs of some individuals may have prevented feeding, led to death [203, 1016, 1117].

Legally protected in European, British and Irish waters (Table 12.1).

LITERATURE

Most recent reviews [203, 765]; original biological data [1016]; genetic variation [237].

AUTHORS

R. Leaper & P.G.H. Evans

FAMILY ZIPHIIDAE (BEAKED WHALES)

A small family of 6 genera, 21 species [1245], of which 3 genera and 6 species occur in NE Atlantic. Characterised by obvious elongate beak, sharply demarcated from prominent melon, and most species have few or no teeth – none in most females, 1–2 pairs of lower tusks in males (only the southern *Tasmacetus* has numerous teeth, like other odontocetes). Mostly occur in deep water, specialise in eating squid. Occupy position in Odontoceti above Physeteridae, but basal to all others.

GENUS *Hyperoodon*

A genus of 2 species, the southern *H. planifrons* and northern *H. ampullatus*. Largest ziphiid, distinguished by enlarged, bulbous head. Males have a single pair of lower tusks at the tip of the jaws (as also in *Ziphius*, some *Mesoplodon*) (Fig. 12.12).

Northern bottlenose whale *Hyperoodon ampullatus*

Balaena ampullatus Forster, 1770; Maldon, Essex, England.

Balaena rostrata Muller, 1776.

Delphinus butskopf Bonnaterre, 1789; R. Thames.

Hyperoodon butskopf Lacépède, 1804; near London.

Hyperoodon bidens Fleming, 1828; Essex.

Hyperoodon latifrons Gray, 1846; Orkney (based on different skull morphology of males).

Bottle-nosed whale or bottlenose whale, latter favoured [551]; *miol bolgshrónach* (Irish Gaelic).

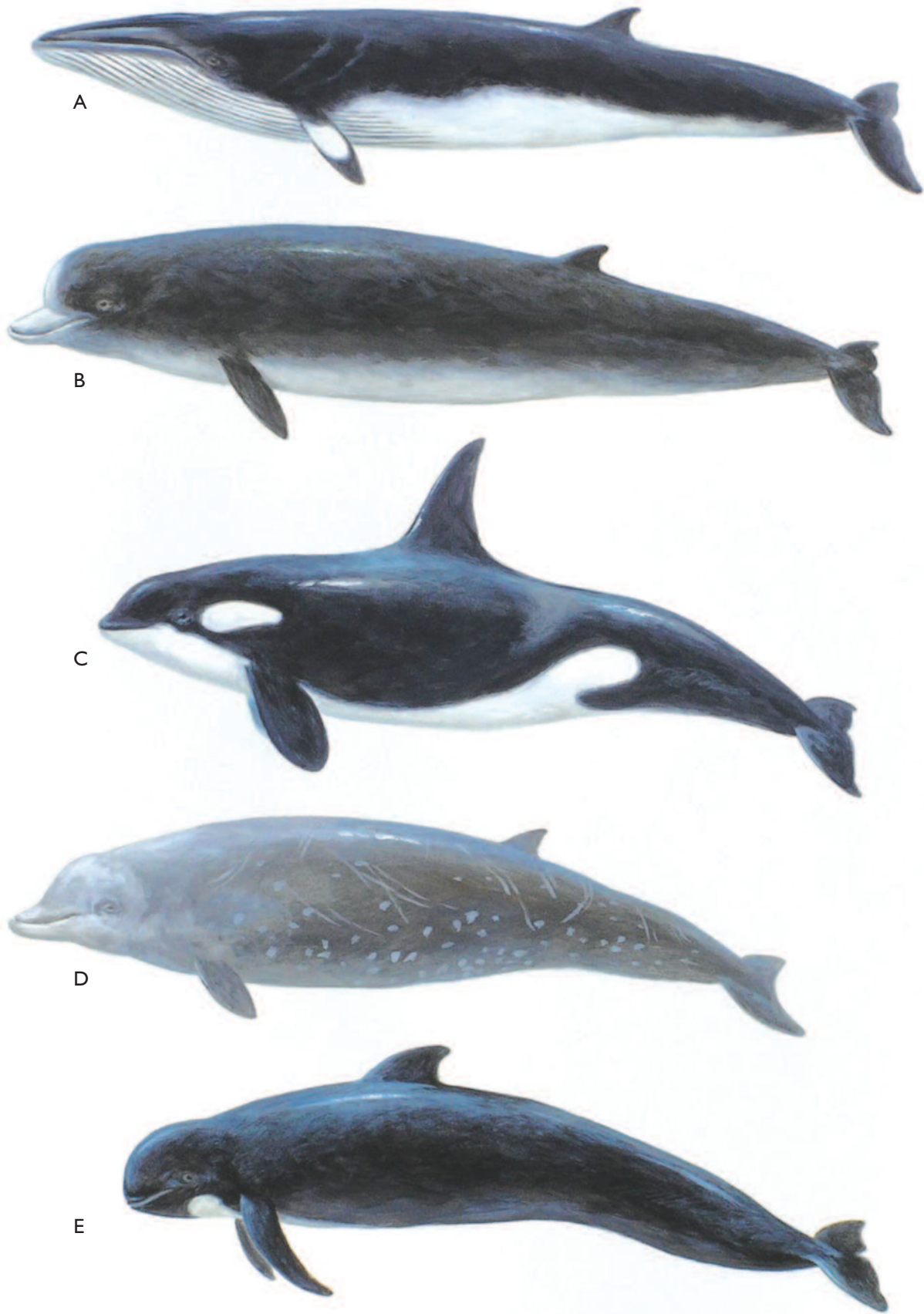
RECOGNITION

Large bulbous head (particularly in male) and short bottle-nosed beak. Usually 1 pair of teeth in lower jaw (of male, rarely visible on live animals), no teeth visible in mouth of female. Solid bony maxillary crests on sides of skull becoming larger and heavier with age, especially in males.

DESCRIPTION

Largest of British beaked whales, distinguished from other ziphiids by large bulbous forehead and distinct short dolphin-like beak (Plate 14). Older males have single pair of conical teeth (up to 41 mm long), erupting at tip of lower jaw; in females, these rarely appear through gum. 2nd pair sometimes buried in gums behind 1st; minute vestigial teeth may be embedded in gums of upper and lower jaws. Pair of V-shaped throat grooves. Coloration very variable, from chocolate brown to yellowish-brown above, caused by diatom coating on skin; lighter on flanks and belly, with irregular patches or blotches; male forehead becomes lighter with age [145, 458].

Plate 14: Cetaceans



A Minke whale *Balaenoptera acutorostrata* B Northern bottlenose whale *Hyperoodon ampullatus*
C Killer whale *Orcinus orca* D Cuvier's beaked whale *Ziphius cavirostris* E Long-finned pilot whale *Globicephala melas*

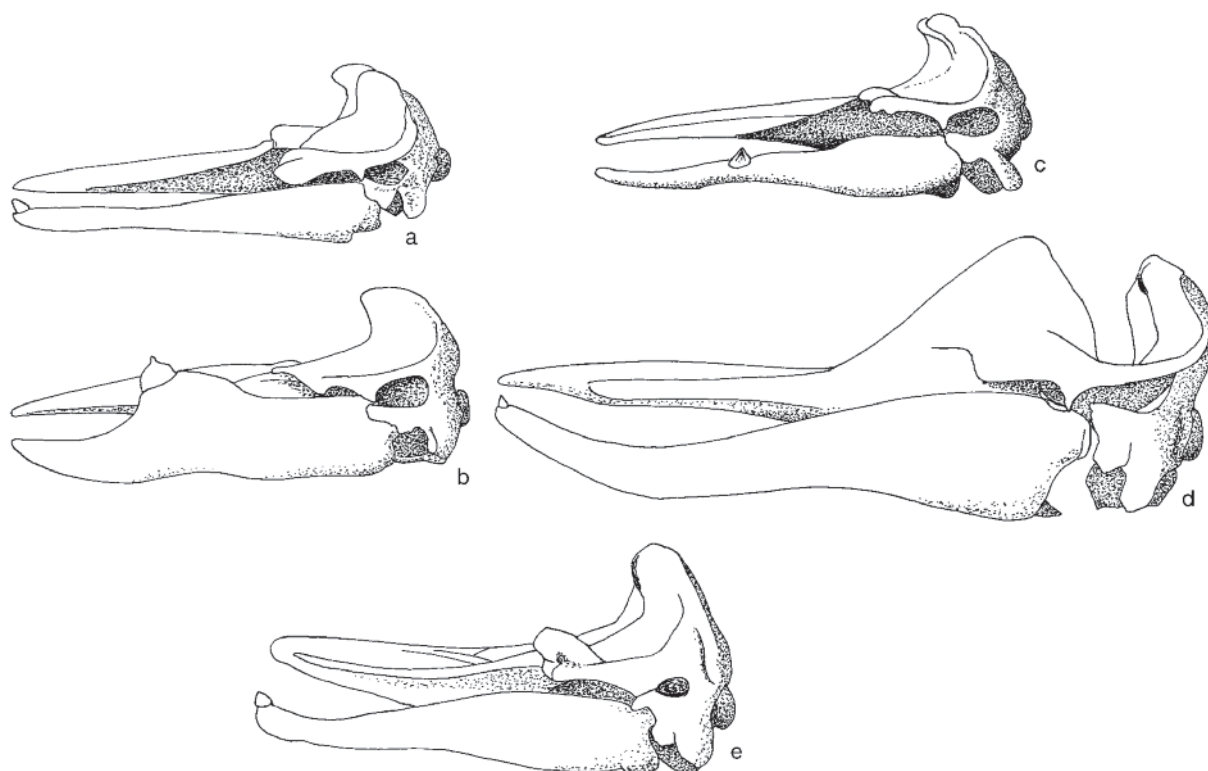


Fig. 12.12 Skulls of male ziphiids, to show position of tusks (a) True's; (b) Blainville's; (c) Sowerby's; (d) Bottlenose; (e) Cuvier's (drawn to scale by D.W. Yalden, after [1212]).

Newborn calves grey, with dark eye-patches and light-coloured head. Long, fairly robust, cylindrical body. Single crescent-shaped blowhole in depression behind forehead giving single low (<2 m) bushy blow, slightly forward-pointing. Short tapering flippers, can fold into underlying indentation in body. Falcate dorsal fin of moderate height (30 cm), 2/3 along back. Broad, un-notched tail flukes with concave trailing edge. At sea, usually seen in groups of 1–4, sometimes up to 14. Dives generally 30–40 min, max. 70 min [536]. May be confused with Cuvier's or Sowerby's beaked whales, minke whale, or sperm whale. Main distinguishing feature is shape of head.

RELATIONSHIPS

Anti-tropical distribution of northern and southern bottlenose whales prevents interbreeding; relationships to other ziphiids unresolved [763]. Supposed equatorial Indo-Pacific bottlenose whales [935] confirmed as Longman's beaked whales *Indopacetus pacificus* [289].

MEASUREMENTS

Dimorphic, males larger than females. Length: newborn *c.*3.4 m; at sexual maturity *c.*6.9 m (female), *c.*7.5 m (male); adult 7.0–8.5 m (female), 8.0–9.5 m (male). Weight *c.*6–8 t.

DISTRIBUTION

Temperate and Arctic N Atlantic, from ice-edge to Azores, particularly in deep waters. Main regions of concentration, identified from former whaling activities, appear to be W of Norway, W of Spitsbergen, N of Iceland, Davis Strait off Labrador, off Faroes and in the Gully off E Canada [968]. Majority of sightings and strandings off British coasts, July–September [352, 360, 407]. Strandings recorded on all coasts of GB and Ireland [404, 406–408, 485, 1073]. One immature female famously swam up R. Thames, London, 19–21 January 2006. In adjacent waters, sighted primarily in waters >1000 m depth, such as Faroe–Shetland Channel, Rockall Trough, and S Bay of Biscay [340, 346, 360, 973, 1194, 1215, 1236] (Fig. 12.13).

Increased stranding frequency in British waters in late summer–autumn cited as evidence of S migration from polar regions [407, 872], reported most commonly between Iceland and Jan Mayen late April–early June, then off Scotland June–July [145, 1148] However, alternative explanations equally plausible, and S migration hypothesis contradicted by sightings also off Azores during summer [264]; stomach contents of one off Faroes, August, suggested that had recently been much further S [261]. Genetic studies also show little

12 Whales, porpoises and Cetacea: Order Cetacea

link between populations that might be caused by seasonal migration [290].

HISTORY

Commercial whaling of bottlenose whales began in 1850 by Scottish whalers [776]. Commercial fishery ceased in 1973, when GB banned import of whale meat for pet food [968]. See Relations with humans, below.

HABITAT

Primarily found in waters >500 m [110, 111, 540, 973, 1194]. Perhaps associated with submarine canyons [540, 1246], possibly due to influx of squid or other food [539].

SOCIAL ORGANISATION AND BEHAVIOUR

British populations little known; most information

from 10-year study in the Gully, E Canada. Groups may contain any mix of age and sex classes. Juvenile whales (from newborn to 3 years old) seen with different escorts, although mostly associated with presumed mother. Most associations between individuals appear to be brief, but males sometimes form bonds that last for years [459]. Aggressive behaviour rare, although conflict between mature males observed [456].

Often curious, will approach vessels. Also show caring behaviour, will remain beside wounded companions, making them particularly vulnerable to hunting. Dive deeply, to at least 1450 m, for up to 70 min [536]. After a long dive, remain at the surface for >10 min, blowing regularly, but may remain at surface for hours at a time. Rarely show tail flukes at onset of dive. Rarely exhibit percussive behaviour; lobtailing seen more often than breaching.

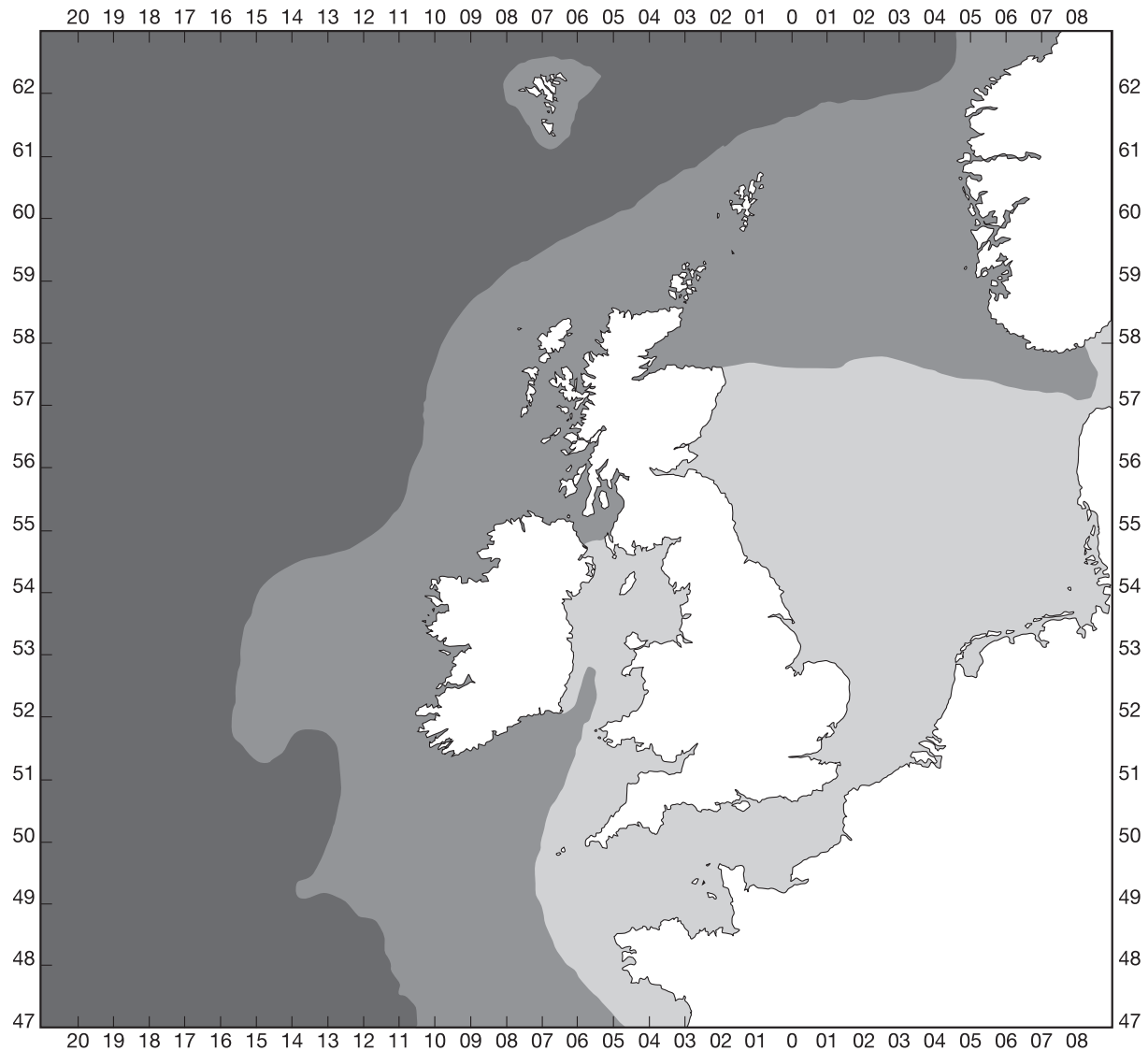


Fig. 12.13 Northern bottlenose whale *Hyperoodon ampullatus*: distribution around British Isles.



Fig. 12.14 Northern bottlenose whale, adult female and calf (photo S. Hooker).

Vocalisations: Includes high-frequency (24 kHz) echolocation clicks [537]. Whistles (3–16 kHz) and chirps (3–16 kHz) lasting 115–850 ms recorded from one encounter [1248], but nearby pilot whales may have confounded this, since not found in a more detailed study [537].

FEEDING

Diet: Mainly adult squid *Gonatus*, off British Isles likely to be *G. fabricii* [261, 538, 693, 1034]. Other squid and fish (including herring *Clupea harengus* and redfish *Sebastes* sp.) occasionally eaten [111].

Feeding methods: Appears to forage largely at or near sea floor [536].

BREEDING

Mating system unknown, though possibly some male territoriality [540]. Young born late spring–summer; gestation period >12 months [110]. Lactation period uncertain, at least 1 year, calving interval at least 2–3 years (Fig. 12.14). Sexual maturity reached at 7–11 years in male, c.11 years in female [239].

POPULATION

No detailed population estimates for N Atlantic; IWC N Atlantic sightings surveys (NASS), 1987 and 1989, suggested c.40 000 [829, 1178]. Still

locally abundant [466, 968]. Former N Atlantic stock poorly estimated, but surely heavily depleted by whaling. Sex ratio likely to be 1:1. Longevity at least 37 years [239], probably much more.

MORTALITY

Causes of mortality little known; killer whales and sharks likely predators, especially of young animals. Norwegian whalers observed attacks by killer whales on a free-swimming animal, as well as 2 harpooned animals [590, 591].

PARASITES AND PATHOGENS

Include lice and barnacles [461, 872] and several species of endoparasites mainly from the digestive system [288, 302].

RELATIONS WITH HUMANS

Previously hunted for oil and animal food. Scottish and Norwegian whalers took in total 60 000 throughout N Atlantic, 1850–1920 [535]. Since 1920, yearly catches, primarily by Norwegian whalers, much reduced and total of c.5900 taken [776]. Small numbers taken off Scotland early in 1900s, though preference given to larger rorquals. In 1908–1927, 26 captured around Shetland and 1 in Outer Hebrides [1148]. Most catches in deep waters off edge of continental shelf.

As yet no attempt at commercial whale-

12 Whales, porpoises and Cetacea: Order Cetacea

watching, due to offshore nature of distribution.

Contaminant load investigated for one stranded specimen in North Sea; PCB and DDT levels similar to other local cetaceans [541], relatively high levels of cadmium in liver [486]. Oil and gas development off Hebrides and in N North Sea may present acoustic and contaminant threats; like other beaked whales, *Hyperoodon* may be susceptible to trauma induced by mid-frequency active sonar and other loud sound sources [281, 757]. Ship collisions implicated in some strandings [120].

Legally protected in European, British and Irish waters (Table 12.1). Designated as 'Lower Risk (conservation dependent)' [971], and 'completely protected' under management procedures of IWC.

LITERATURE

Review of species [776]; summary for genus [455]; review of past exploitation and current conservation status, N Atlantic [968].

AUTHORS

S.K. Hooker, S. Gowans & P.G.H. Evans

GENUS *Ziphius*

A monospecific genus, a large whale with a single pair of tusks at the tip of the lower jaws (as also in *Hyperoodon*), head much less bulbous, skull without the huge maxillary 'wings'. (Fig. 12.12). Short beak when compared to *Mesoplodon*, leading to alternative name, goose-beaked whale.

Cuvier's beaked whale *Ziphius cavirostris*

Ziphius cavirostris G. Cuvier, 1823; mouth of the Rhône, France.

Cuvier's whale, goose-beaked whale; *miol mór le gob gé* (Irish Gaelic).

RECOGNITION

Is 2nd-largest beaked whale in European waters, with the typical ziphiid pattern (small fin located in the middle 1/3 of the back), and often pale body. In addition, it has a sloping (or slightly bulbous) forehead with short, indistinct beak and upcurved mouth line. This not easy to distinguish, can be confused with *Mesoplodon* because both tend to break the surface beak-first, making it look longer. Often pale head and anterior back (entire back sometimes white in older animals); body often scarred (Plate 14), and sometimes covered with patches of yellow diatoms. One pair of small conical teeth at tip of lower jaw in males.

DESCRIPTION

Long stout body with small head; concave or slightly S-shaped mouth line (likened to goose beak) (Fig. 12.15). Beak generally shorter than in other ziphiids, mostly ill-defined, with slightly protruding lower jaw. Single pair of conical teeth (up to c.60 mm long and c.35 mm in diameter) at tip of lower jaw, erupting only in adult males and then protruding forward from mouth. 2nd pair of teeth or tiny rudimentary teeth sometimes present [165]. Converging pair of throat grooves. Coloration variable; most commonly brownish grey but sometimes blue-grey; paler grey or even white head and (anterior) back (particularly in older males); often has linear pale scars on back and sides and cream or white oval blotches on



Fig. 12.15 Cuvier's beaked whale. Note pale body and distinctive sshape of head. (photo N. Aguilar).

sides and posterior abdomen. Sometimes yellow diatoms in patches over body. Distance from snout to blowhole less than in *Hyperoodon*, forehead far less bulbous. Low, inconspicuous blow that can be heard at a distance in calm weather. Small, narrow flippers with pointed tip, located low down on flanks, fitting in a depression of the body. Dorsal fin varying from small, triangular to relatively tall (up to 38 cm), sickle-shaped, situated about 2/3 along back. Somewhat concave tail flukes, like other beaked whales, normally lacking distinct median notch.

Skull relatively short and broad, with well-developed cranial vertex and enlarged, asymmetrical nasal bones overhanging the bony nares (Fig. 12.12). No bony maxillary crests on rostrum, but (in adult males) a densely ossified mesorostral canal and a characteristic prenasal basin.

RELATIONSHIPS

No congeners, relationships to other ziphiids unresolved [763, 962].

MEASUREMENTS

Length: newborn *c.*2.7 m; at sexual maturity *c.*5.8 m (female), *c.*5.5 m (male); max. recorded length 7.0 m (both sexes). Weight up to *c.*3 t.

VARIATION

No information on geographical variation or genetic polymorphisms.

DISTRIBUTION

Most widespread of beaked whales, probably worldwide in warm and warm-temperate seas. Like other beaked whales, appears to favour deeper waters, occurring off continental shelf edges. Apparently prefers warmer waters, rarely recorded as far N as British Isles (1 record from Iceland). Further S, is the most common ziphiid off the Iberian peninsula, in the Bay of Biscay, and the only species occurring regularly in the Mediterranean. Seen year-round in the Canaries.

Around British Isles, only 6 well-documented sightings: singles in the N North Sea, E of Orkney, August 1980; off Co. Cork, S Ireland, August 1984; SW of Mizen Head, Co. Cork, July 1987; 2–3 individuals with a mixed pod of long-finned pilot whales and bottlenose dolphins off NW Ireland, August 1987; 3 off Skye, September 1988; and 2 off Co. Cork, June 1998 [340, 346, 360]. By contrast, at least 12 sightings 1995–1998, (total of 36 individuals) from ferry surveys in Bay of Biscay (S of 46° N), 75% in February–May [1237].

On coasts of British Isles, 65 strandings in 1913–2005, of which 41 since 1963 [120, 360, 408, 1073, 1022, 1074]. All but 2 of these from the

Atlantic seaboard – SW England, S and W Ireland, W Scotland and the N Isles. Almost 50% occurred January–March. Only 6 well-documented records from the North Sea – 2 strandings on Swedish W coast, April 1867 and August 1872; 1 stranded, Scheldt Estuary, Netherlands, July 1914; 1 near Wells, Norfolk, August 1989; another at Walcott near Happisburgh, Norfolk; and 1 near Dunkerque, France in March 1980 [360, 1192].

HISTORY

Frequent fossil remains of the early ziphiid, *Choroeziphius*, found in the Tertiary North Sea area, but supposed fossil ziphiid *Ziphius (Dolichodon) geelongensis*, early Pliocene, Australia, is erroneous [397].

HABITAT

Mainly found in deep waters, possibly favouring continental or island slopes at depths of 500–3000 m. Sightings from Greece along shelf slope in waters 650–1000 m deep [943, 944]; in NW Mediterranean, most sightings from depths of 750–2000 m [815].

SOCIAL ORGANISATION AND BEHAVIOUR

Not often seen; most sightings are singletons or small groups of 2–12 (occasionally up to 25) [403, 517, 678, 685, 815]. Mean group size, NW Mediterranean, 2.3; larger groups partially segregated by age and sex [815]. Social organisation unknown; extensive scarring on dorsal surface and flanks of males, presumed due to intraspecific aggression [806].

Vocalisations: D-tag studies reveal main vocalizations to be echolocation clicks and buzzes [582]. Usual clicks are FM, have a characteristic upward sweep shape, with most energy at 30–50 kHz [1265]. Mostly restricted to deep, long foraging dives, up to 85 min and to depths of 1990 m; average foraging dives 58 min, to 1070 m [1167]. Echolocation used in the deepest part of the dives, normally >500 m; vocal phase averages 33 min [582, 1167]. Foraging dives are usually interspersed by series of shorter (mean 15 min) and shallower (mean 250 m) dives with no vocal activity. Function of these intermediate dives still unknown; may relate to processing lactic acid produced during long foraging dives [1167]. Average duration of surfacing intervals 2 min; occasionally may stay on surface for long periods and before foraging dives usually surfaces for 4–5 min. Rarely breaches, but often shows head when surfacing, presumably after a deep dive.

FEEDING

Diet: Mainly a great variety of squid; particularly

12 Whales, porpoises and Cetacea: Order Cetacea

Histioteuthis reversa and *H. bonnellii*, also *Gonatus* spp., *Todarodes sagittatus*, *Ancistoteuthis lichtensteini*, *Heteroteuthis dispar*, *Chiroteuthis veranyi*, *Octopoteuthis sicula*, *Ommastrephes bartramii*, and members of the families Brachioteuthidae, Cranchiidae, Lycoteuthidae, Onychoteuthidae, and Pholidoteuthidae; sometimes crustaceans and fish, including Gadiformes such as *Antimora* sp. and blue whiting *Micromesistius poutassou*, but the latter may not be primary prey [137, 221, 259, 304, 374, 378, 400, 685, 806, 850, 880, 939, 1035, 1017, 1157, 1197].

Feeding methods: During the vocal phase of each foraging dive, performs *c.*30 buzzes that are interpreted as prey capture attempts [582, 1167]. Average of 12 foraging dives/24 h performed during day and night.

BREEDING

Little information. Possibly protracted breeding season. No seasonal pattern found [517]. Length of largest reported fetus 267 cm; shortest calf 269 cm [774]. No information on gestation or lactation periods.

POPULATION

No population estimates. Longevity >36 years for males and *c.*30 years for females, assuming that 1 dentinal growth layer group in teeth = 1 year [1017].

Photo-ID studies suggest territorial fidelity to certain areas (Hawaii, Canaries); also observed off Bahamas, although individuals identified there not re-sighted since mass mortality in 2000, related to the use of mid-frequency military sonar [252].

MORTALITY

Killer whale observed feeding on a fresh carcass, Mediterranean [860]; oval scars, thought to be due to cookie-cutter shark *Isistius brasiliensis*, found on skin of many specimens from the Canaries [806].

PARASITES AND PATHOGENS

Commensals include barnacles *Xenobalanus* from the flukes and dorsal fin [96, 168, 806] and *Conchoderma* on erupted apical teeth [398, 435, 787]; parasitic copepods *Pennella* found in blubber of flanks [806]. Nematodes *Anisakis* [398, 618, 806, 889] and *Crassicauda* [302, 806], and cestodes *Phyllobothrium* encysted in the blubber [620, 806, 1157] recorded.

RELATIONS WITH HUMANS

Occasionally taken in fisheries for small cetaceans off Japan [850, 880] and E Caribbean [200, 205, 311]. Incidentally caught in many types of fisheries [311, 555].

Few specimens analysed for pollutants. A mature male, stranded New Zealand, had low levels of pesticides and mercury [398]. 4 mature animals, stranded Bermuda, contained moderate levels of PCBs and pesticides [638]. Single animals in S Adriatic (Italy) and W Mediterranean (Corsica) had relatively high levels of total mercury in the liver and cadmium in the kidney [411, 1129]. In 10 *Ziphius* stranded in Kyparissiakos Gulf (SE Ionian Sea, Greece) in May 1996, DDT 11.2–35.1 $\mu\text{g/g}$ wet wt (mean value 20.9 $\mu\text{g/g}$), PCBs (sum of 13 congeners) 3.0–12.4 $\mu\text{g/g}$ wet wt (mean value 7.5 $\mu\text{g/g}$) [495].

Military sonar in mid-frequency range (1–10 kHz) shown to cause mass strandings of ziphiids, particularly Cuvier's beaked whale [355, 369, 402, 403, 757].

Legally protected in European, British and Irish waters (Table 12.1).

LITERATURE

General review [517]; European information well reviewed in [1000].

AUTHORS

P.G.H. Evans, C. Smeenk & K. Van Waerebeek

GENUS *Mesoplodon*

A genus of *c.*14 poorly known species, found in deeper waters of all oceans, but mostly known from occasional strandings: many known from only a handful of specimens. All morphologically rather similar. Differ from other ziphiids in more slender (less bulbous) head and smaller size. A single pair of teeth in the lower jaws, erupting from the gum only in mature males, their shape and position diagnostic for the species; may be near the tip or up to 1/2 way back, flattened or recurved (Fig. 12.12). Believed to take mesopelagic squid and fish [775], thought to employ a sucking action when feeding; have pleated throats [520]. Phylogenetic relationships within family unresolved [763, 942].

Sowerby's beaked whale *Mesoplodon bidens*

Physeter bidens Sowerby, 1804; Moray, Scotland. Sowerby's whale, North Sea beaked whale; *miol mór gobach an tuaisceart* (Irish Gaelic).

RECOGNITION

Rarely seen at sea, difficult to distinguish from other *Mesoplodon*, but usually dark brown or grey uniform coloration on back. Shares their prominent forehead bulge, sickle-shaped dorsal fin almost 2/3 along back, and inconspicuous blow. Diagnostic features are long, slender beak and



Fig. 12.16 Sowerby's beaked whale, showing narrow elongate beak characteristic of *Mesoplodon*, posteriorly placed tusks of this species (photo J. Benney).

moderately arched lower jaw, with 1 pair of laterally compressed triangular teeth (only visible in adult male) placed slightly behind midpoint of gape (Fig. 12.16).

DESCRIPTION

Long, slender, spindle-shaped body, small head with bulge in front of crescent-shaped blowhole and well-defined slender beak, pair of deep grooves forming V-shape below (Plate 15). Relatively small flippers, 1/7–1/9 body length, often tucked into flipper pockets. Dorsal fin triangular or slightly sickle-shaped, almost 2/3 along back. Un-notched tail flukes have trailing edge slightly concave. Dark grey coloration, paler on belly, with light spots and, especially in adult males, single linear scars scattered over back and flanks. Young animals have lighter bellies and fewer spots. Pair of teeth extruding outside of mouth in adult males, set on rising curve of lower jawline slightly behind midpoint of gape; project backwards, then slightly forwards at tip, up to 3 cm exposed above gum. In females and young, are smaller, concealed beneath gum.

Premaxillae project anteriorly to nasals at vertex of skull, when viewed from above, rostrum slender, not dorsoventrally deepened. Teeth located at posterior limit of mandibular symphysis: no other N Atlantic beaked whale species has tooth sockets overlapping posterior limit of symphysis (Fig. 12.12).

RELATIONSHIPS

One of 5 species of *Mesoplodon* in N Atlantic; relationships unresolved [962].

MEASUREMENTS

Length: newborn *c.*2.4 m; adult *c.*4.5–5 m. Weight: a 2.7-m calf weighed 185 kg; adult estimated *c.*1000–1400 kg [328].

VARIATION

No information on geographical variation, intra-population differences or genetic polymorphisms.

HISTORY

No archaeological or fossil material known, but fragments of *Mesoplodon*-like animals found in Red Crag and Suffolk Crag in E England (Upper Miocene) and from the phosphate beds of N and S Carolina [775].

DISTRIBUTION

Known only from the temperate N Atlantic, mainly in European waters; distribution presumably centred on deep waters of mid and E North Atlantic, mostly N of other *Mesoplodon* species [360, 728, 973]. Although many stranded in North Sea, most probably a consequence of passive drift of carcasses. In N European waters, confirmed sightings S of Iceland, in the Norwegian Sea, W of Norway, around the Faroes, N and W of

12 Whales, porpoises and Cetacea: Order Cetacea

British Isles, in the Channel Approaches and Bay of Biscay [140, 223, 346, 360, 695, 762, 1215, 1236]. Further S and W, recorded from Madeira [1260] and the Azores [979, 1088].

Although rarely seen (or at least specifically identified), have been c.80 strandings around British Isles, 1913–2007, with 55 of these since 1963 [120, 360, 408, 974, 1073, 1074]. Occurred mainly in N Isles, N & W Scotland and along the E coast of GB, but also from English Channel, W Ireland, and other European coasts of North Sea. Occurred in all months but mostly July–November.

HABITAT

Although most strandings from North Sea, bycatches on shelf edge of NW Atlantic and distribution of sightings suggest that, like other beaked whales, mostly inhabits deep ocean basins and trenches with depths of 700 m or more.

SOCIAL ORGANISATION AND BEHAVIOUR

Very poorly known. Strandings generally of single individuals or mothers with calves; once, 3 juveniles [974]. Most sightings either singles or pairs, but with groups of 4–10 recorded [346, 353, 360, 678, 696, 1236].

Intraspecific combat between adult males inferred from development of teeth and higher incidence of scarring, as for Blainville's beaked whale [730, 731].

Fast swimmer, often at surface, and clearly mainly pelagic. Echolocating sound pulses recorded from young animals kept in a dolphinarium for a few hours. One stranded alive was reported as lowing like a cow.

FEEDING

Diet: Very poorly known, but believed to favour mesopelagic squid (e.g. members of family Ommastrephidae). Small numbers of otoliths from fish (Gadidae, Merlucciidae and Ammodytidae) found in stomachs of 3 stranded on E coast of Scotland, 1992–1996 [1030].

BREEDING

Virtually unknown. Mating and birth possibly occur in late winter and spring [678]. No data on gestation or lactation periods, or calving interval.

POPULATION

No population estimates; like other *Mesoplodon*, pelagic distribution and difficulty of observing and identification at sea mean the species may be more common than the few records suggest. No information on age structure or mortality rates.

MORTALITY

No information; killer whale and false killer whale potential predators (cf. [775]).

PARASITES AND PATHOGENS

Little information. Gooseneck barnacles *Conchoderma* found attached to teeth of males stranded on Scottish coasts [974, 1165]. Cestode *Tetrabothrius* sp. found in one stranded on English coast [442].

RELATIONS WITH HUMANS

Formerly hunted off Newfoundland [1065]. Occasionally captured accidentally in fishing gear such as gillnets [775, 792, 1050]. 12 mesoplodonts of unknown species (but probably this one) recorded as bycatches in one year in swordfish gillnet fishery along shelf edge of E USA [1219].

Oil and gas exploration W of British Isles (along Atlantic Frontier) may pose a threat [349, 352], although military sonar in mid-frequency range (1–10 kHz) likely to be more important (cf. Cuvier's whale) [355]. One washed up, Belgium, was a victim of a ship strike [632].

Legally protected in European, British and Irish waters (Table 12.1).

LITERATURE

Useful general review of *Mesoplodon* [775] but no comprehensive treatise on this species. Variation in the genus as a whole considered in [729].

AUTHORS

P.G.H. Evans, J.S. Herman & A.C. Kitchener

True's beaked whale *Mesoplodon mirus*

Mesoplodon mirum True, 1913; Beaufort Harbour, North Carolina, USA.

Miol mór gobach le clár-fiacla (Irish Gaelic).

RECOGNITION

Not yet identified with certainty at sea, because of the great difficulty in distinguishing it from other *Mesoplodon* species. Back slate grey, often with pale spots and linear scars, which may be in closely spaced pairs (Plate 15). Like others of genus, may have a prominent bulge on forehead, with sickle-shaped dorsal fin, inconspicuous blow. Diagnostic feature is short but clearly defined beak sloping into slightly bulbous forehead, with single pair of teeth (exposed above gum only in adult male) at extreme tip of lower jaw.

DESCRIPTION

Long spindle-shaped body, more robust than Sowerby's and more similar to Cuvier's beaked whale. Small head with bulge in front of crescent-shaped blowhole; short but pronounced beak, pair

of throat grooves forming V-shape below. Relatively small narrow flippers often tucked into flipper pockets and triangular or slightly sickle-shaped dorsal fin situated almost 2/3 along back. Tail flukes have trailing edge slightly concave; usually no notch, but some show slight median notch. Coloration bluish-grey on back, lighter on belly, with light spots and, especially in adult males, linear scars which may be paired; pale patches may be present in anal and genital regions. Single pair of teeth, slightly compressed laterally (25 × 13 mm), oval in cross-section, directed forward and upward at extreme tip of lower jaw; exposed above gum and outside mouth in adult males (Fig. 12.12). In females and young, are smaller and concealed below gum.

Premaxillae project anteriorly to nasals at vertex of skull, when viewed from above; teeth slightly laterally compressed, ratio of antero-posterior to transverse breadth > 1.66 (cf. rounded oval teeth in Cuvier's beaked whale, with which it can be confused).

RELATIONSHIPS

One of 5 *Mesoplodon* spp. recorded from N Atlantic; relationships unresolved [763, 942].

MEASUREMENTS

Length c.4.5–5.5 m; shortest reported calf 2.33 m. Weight c.800–1400 kg.

VARIATION

No information on geographical variation, intra-population differences or genetic polymorphisms.

DISTRIBUTION

Range very poorly known; may be widespread in deep waters of temperate Atlantic extending to SW Indian Ocean; records from E North America, NW Europe, NW Africa and S Africa [75, 728, 769, 776, 1015].

Of 10 strandings from Europe since 1899, 9 from W Ireland (Killadoon, Co. Mayo to Long Strand, Co. Cork) [51, 120, 360, 406, 483, 484, 1002, 1181]. This includes 2 specimens, one in University College Museum, Galway [51], thought to be from a stranding in Galway Bay around 1899, and another washed ashore in 1903/1904 on Aran Is., Co. Galway, in Galway Museum [52]. Various identified as Hector's beaked whale and Cuvier's beaked whale, reassessed as *M. mirus* [483, 484] (both omitted in [120]). No definite records from GB; supposed skull from S Uist, Outer Hebrides, 1931, proved to be *Ziphius* [404, 633, 768].

One other European record, France [104], although also reported from Canaries [1187]. Sightings thought to be of this species on the basis of uniform bluish grey coloration and short but

prominent beak, October 1993, N of Canaries [1134]; July 1997, Bay of Biscay [1193]; and off Azores [1119].

Irish strandings occurred February–November, mostly June–July.

HISTORY

No archaeological or fossil material attributable to this species is known, but see *M. bidens* (cf. [775]).

HABITAT

Not known, but presumably deep ocean basins and trenches.

SOCIAL ORGANISATION AND BEHAVIOUR

No information. Putative sightings have been of singles or pairs. Intraspecific combat between adult males inferred from development of teeth and higher incidence of scarring, as for Blainville's beaked whale [731].

FEEDING

Diet: No data, believed to take mesopelagic squid and fish [775].

Feeding methods: Thought to employ suction when feeding [520].

BREEDING

No information.

POPULATION

No information; like other *Mesoplodon*, probably under-recorded, because of pelagic distribution and difficulties of observing and identifying it at sea.

MORTALITY

No information; killer whale or false killer whale potential predators (cf. [775]).

PARASITES AND PATHOGENS

A few parasitic copepods *Pennella* sp. found on flanks of 2 specimens, USA [775]. Unidentified trematodes found in liver and bile duct, and nematodes in stomach and intestine [775]. Male, stranded Co. Mayo, November 1987, had many commensal barnacles, *Conchoderma*, growing around its teeth [1180]. *Conchoderma* (usually in blubber of flanks) and cestode cysticerci *Monorhynchus* (between the peritoneal membrane and the body wall in the posterior abdomen) frequent [775]. *Xenobalanus globicipitis* reported, attached to flukes of 2 from S Africa [1017].

RELATIONS WITH HUMANS

No information. Legally protected in European, British and Irish waters (Table 12.1).

12 Whales, porpoises and Cetacea: Order Cetacea

LITERATURE

Useful general review of *Mesoplodon* [775], but no detailed treatise on this species.

AUTHORS

P.G.H. Evans, J.S. Herman & A.C. Kitchener

Gervais' beaked whale *Mesoplodon europaeus*
Dioplodon europaeus Gervais, 1855; English Channel. Gulf Stream beaked whale, Gervais' beaked whale, Antillean beaked whale, European beaked whale.

RECOGNITION

Rarely seen at sea, when it would be difficult to distinguish from other *Mesoplodon* species. Back usually uniformly dark grey, sometimes with pale linear scars. Like other *Mesoplodon*, may have a prominent bulge on forehead, sickle-shaped dorsal fin situated almost 2/3 along back, and inconspicuous blow. Diagnostic features are moderately long, slender beak, relatively straight mouthline, and 1 pair of laterally compressed, triangular teeth in lower jaw (exposed above gum only in adult male) about 1/3 along gape from tip of snout. In transverse section, rostrum ventrally flattened (cf. dorsally flattened in Blainville's).

DESCRIPTION

Long spindle-shaped body, proportionately small head with slight bulge in front of crescent-shaped blowhole and on forehead; pronounced, slender beak, with pair of deep grooves forming V-shape below. Relatively small narrow flippers often tucked into flipper pockets. Triangular or slightly sickle-shaped dorsal fin situated almost 2/3 along back. Un-notched tail flukes may have a small (c.3 cm) median projection on the slightly concave trailing edge. Coloration dark grey or indigo dorsally, sometimes becomes medium or light grey on lower flanks and belly, with single pair of scars, especially in adult males. Juveniles have a white belly. In some adult females, white patch, c.15 cm diameter, extends from just before genital slit to just behind anus. Rosy patch under the flipper in the freshly stranded Spanish specimen [1172a]. Single pair of flattened, triangular teeth (c.7–8 cm × 3–5 cm), set 1/3 of gape from tip of lower jaw, exposed above gum and outside mouth only in adult males. In females and young, teeth usually smaller, concealed below gum.

Premaxillae project anteriorly to nasals at vertex of skull, when viewed from above, rostrum slender, not dorsoventrally deepened. Teeth set back from tip of mandible, but anterior to posterior limit of symphysis. Gray's beaked whale, *M. grayi*, a Southern Ocean species recorded once from the Netherlands, has teeth similarly placed but very

long and slender rostrum.

RELATIONSHIPS

One of 5 *Mesoplodon* spp. recorded from N Atlantic; relationships unresolved [763, 942].

MEASUREMENTS

Length: newborn thought to be c.2.1 m; physically mature adults usually 4.2–4.8 m (max. probably 5 m). Weight c.600–1200 kg.

VARIATION

No information on geographical variation, intra-population differences, or genetic polymorphisms.

DISTRIBUTION

Known only from the Atlantic; apparently favours warm temperate and subtropical waters. Type specimen found floating in the English Channel, 1848, but most records come from W Atlantic, between Long Island, New York and E Caribbean; most records S of North Carolina. Is the most common *Mesoplodon* in E USA, Gulf of Mexico [570, 775].

Several recent strandings in E North Atlantic [360]. In W Ireland, a male stranded, Ballysadare, Co. Sligo, January 1989 [1007]. In Canaries, 5 strandings involving 11 specimens, 1985–1997, and 3 sighted, January 1998 [226]. Other strandings in Portugal [1061], S Spain [1172a], Azores [1119], Mauritania [999] and Guinea-Bissau [977].

HISTORY

No archaeological or fossil material known, but fragments of *Mesoplodon*-like animals in phosphate beds of N and S Carolina, and also from Red Crag and Suffolk Crag in E England (Upper Miocene) [775].

HABITAT

Not well known, but apparently deep ocean basins and trenches.

SOCIAL ORGANISATION AND BEHAVIOUR

Very little information on behaviour: nearly all records are of strandings. The 3 seen off Tenerife, Canaries (in 1700 m depth) approached the vessel and swam around it for about 10 min [226]. May associate at times with Cuvier's [1187], and Blainville's beaked whales [756].

FEEDING

Diet: Very poorly known, presumably mesopelagic squid and fish, like other *Mesoplodon* [775]. Traces of squid beaks (but no fish remains) found in stomachs of 3 stranded specimens [775]. Those

from the Canaries contained squid beaks and mandibles of the deep-sea fish *Chauliodus sloani* [756].

BREEDING

Negligible information. One specimen 48 years old (assuming 1 dentine tooth growth layer = 1 year) [775].

POPULATION

Unknown; pelagic distribution, and difficulty in observation and identification at sea, mean that may be more common than few records imply.

MORTALITY

No information for this species, but see Blainville's beaked whale.

PARASITES AND PATHOGENS

Numerous parasitic cyamids, *Isocyamus delphini*, found on a healing wound on the flank of an adult male [775]. Nematode *Anisakis* found in the stomach, and cestode cysticerci *Monorhynchium* and *Phyllobothrium* found in the posterior abdomen (between the peritoneal membrane and body wall) and the blubber (mainly of the flanks) respectively [756, 775]. Unidentified trematodes have also been found in the liver and bile duct of specimens [775]. Teeth of adult males often bear commensal barnacles: *Conchoderma* cf. *C. auritum* identified [775].

RELATIONS WITH HUMANS

Hunted off New Jersey coast, 19th century, and more recently in Jamaica [807]. Occasionally taken in the local small cetacean fisheries, E Caribbean [792]. One individual, later identified as *M. europaeus*, entangled in a pound net off New Jersey, 1905 [26] Legally protected; see Table 12.1 and Chapter 4.

LITERATURE

Useful general review of *Mesoplodon* [775] but no detailed treatise on this species.

AUTHORS

P.G.H. Evans, J.S. Herman & A.C. Kitchener

Blainville's beaked whale *Mesoplodon densirostris*

Delphinus densirostris Blainville, 1817; Seychelles, Indian Ocean.

Dense beaked whale, Atlantic beaked whale, tropical beaked whale; *miol mór gobach na h-Eorpa* (Irish Gaelic).

RECOGNITION

More commonly seen at sea than other N Atlantic *Mesoplodon* species: either quite common in some areas, or more coastal and easier to identify to species. High-arching lower jaw distinctive, surmounted in adult males by massive pair of flattened, triangular teeth; these tilt slightly forward, are often encrusted with barnacles (Plate 15). Usually dark grey or brown on the back, lighter grey on the abdomen, and commonly with large grey or pale blotches (sometimes described as pinkish) dorsally, may disappear after death. Head often flattened directly in front of blowhole, with moderately long, slender beak (in Gervais' beaked whale, the rostrum is ventrally flattened). The long beak is the first part of the body to break the surface, and its curved shape readily distinguishes this from other *Mesoplodon* species.

DESCRIPTION

Long spindle-shaped body, small head with slight bulge in front of crescent-shaped blowhole; pronounced slender beak and highly arched mouthline, with pair of deep grooves forming V-shape below. Relatively small narrow flippers often tucked into flipper pockets; triangular or slightly sickle-shaped dorsal fin situated almost 2/3 along back. Un-notched tail flukes. Coloration dark grey or brown on back and pale grey on belly; juveniles and adult females may be lighter grey on dorsal surface with white belly. Greyish white or pink blotches over back and flanks; linear scars and scratches (sometimes paired), at least in adult males, which are often covered with intricate network of pale scars, mainly between dorsal fin and blowhole. Younger males and females may also have scars, but less numerous. All sexes/ages may have yellowish patches of diatoms on the body. Lower mandible sometimes white. Brownish hue may show on the head, shading to light grey on the edge of the upper lip and on the lateral and ventral lower jaw. In adult males, single pair of flattened, triangular teeth ($c.12 \times 8$ cm) set anteriorly on apex of arch of lower jaw, up to 4 cm erupted from gum and exposed outside mouth (Fig. 12.17). In females and young, teeth smaller ($c.6 \times 3-5$ cm), usually concealed below gum [126, 515, 1171].

Premaxillae project anteriorly to nasals at vertex of skull, when viewed from above, rostrum dorsoventrally deepened. Teeth located on upward arch of stepped mandible, well behind posterior limit of symphysis (Fig. 12.12).

RELATIONSHIPS

One of 5 *Mesoplodon* spp. recorded from the N Atlantic; relationships unresolved [763, 942].

MEASUREMENTS

Limited to very few specimens. Length at birth thought to be *c.* 2.1 m; maximum probably *c.* 4.8 m; physically mature adults usually 4.1–4.8 m. Apparent age at sexual maturity *c.* 9 years (based on data from related species *M. europaeus*). Weight *c.* 700–1100 kg.

VARIATION

No information on geographical variation, intra-population differences or genetic polymorphisms.

DISTRIBUTION

One of the most widely distributed species of *Mesoplodon*, recorded from tropical and warm temperate seas of all oceans. In the Atlantic, mostly recorded from SE USA, Gulf of Mexico and Caribbean; records range from Nova Scotia to S Brazil [229, 351, 546, 570, 775, 782].

In E North Atlantic, recorded from France [219], Portugal [976, 1061], Spain [228, 1172] and Madeira [484], but most records come from the Canaries where sightings frequent [22, 224, 998]. Here, occur year-round, with individuals identified over several years, suggesting site fidelity [24, 58] as also recorded in Bahamas [252] and Hawaii [772].

Only 1 record from British Isles: adult female, stranded July 1993 at Aberaeron, W Wales [360, 515]. Considered to have a more offshore distribution than some other *Mesoplodon* [807], Welsh and another, Icelandic, extralimital record [926], perhaps carried on North Atlantic Drift. The type specimen described by De Blainville in 1817 now thought to be from Seychelles, not France [377, 462].

HISTORY

No archaeological or fossil material attributable to this species known, but see under *M. bidens* (cf. [775]).

HABITAT

Poorly known, likely to be deep ocean basins and trenches of >700 m depth. Frequently seen near oceanic archipelagos such as Hawaii, Bahamas and Canaries, where great depths occur near shore. Sightings around Hawaii were made over 700–1000 m, with depths of up to 5000 m occurring nearby [775, 1067]. In the Canaries, may approach coast near the slope, and follow this to forage at depths usually >500 m [22].

SOCIAL ORGANISATION AND BEHAVIOUR

Most sightings have been of singles or pairs [225]. Pods of 3–7 (off Hawaii) [1067], 1–7 (off Canaries) [58]. Calves or juveniles never observed alone at

the surface, groups strongly synchronous. Typically only 1 adult male, accompanied by 1 or more adult female–calf pairs and juveniles, suggests harem structure [58]. Support similar observations in Bahamas [252, 253]. Sometimes approach vessels; may lie on the surface during calm weather. Scarring incidence much higher in adult males than other sex/age groups, suggesting that males are aggressive to each other, perhaps compete for mates [731].

Spend on average only 2 min at the surface between dives. Make deep foraging dives to 800–1300 m, commonly for 45–60 min (revealed by time–depth recorders) [22, 1167]. Employ stereotyped diving and foraging behaviour, with long, deep foraging dives undertaken day and night, separated on average by 1.5 h, during which they make shallow, silent, short dives (mean 20 min) with no foraging function [22].

Vocalisations: Before 2003, only recordings came from 2 stranded animals that produced short whistles and chirps which when analysed were definitely pulsed, at frequencies ranging from <1 kHz to >6 kHz [201]. Use of attached D-tags that record sounds emitted by diving whales has revolutionised our knowledge [22, 582, 583, 736, 1167]. Uses echolocation to forage, producing long series of ultrasonic clicks interspaced by pauses and buzzes. Buzzes during dives indicate prey capture attempts; performs some 30 of these per deep foraging dive. Mostly silent <200 m depth, vocalising only in deep parts of foraging dives.

FEEDING

Diet: Little information on food preferences; presumed to favour mesopelagic and benthopelagic squid and fish [775]. Traces of squid beaks (but no fish remains) found in stomachs of 3 stranded specimens [775]. The female stranded in Wales contained the lower beak of a squid, *Histioteuthis reversa* [515]. However, S African specimens contained remains of fish *Cepola*, *Lampanyctus*, and *Scopelogadus*, and one had 2 squid beaks, *Todarodes sagittatus* and *Octopoteuthis* spp. [1017]. One stranded, in Canaries, had remains of squids *Octopoteuthis sicula*, *Histioteuthis meleagroteuthis*, *H. reversa* and *Histioteuthis Type A*, as well as myctophid and gadid fishes [1041].

Feeding methods: Thought to employ suction when feeding [520]. Tagging studies suggest that catch around 30 prey per foraging dive, with little variation in swimming speed, suggesting that targeted prey are relatively small, scarcely mobile relative to whale [22].

BREEDING

Very little information. Presumed minimum age at sexual maturity 9 years (based on data from one individual *M. europaeus* [1017]). The Welsh specimen was 21 years old, assuming 1 tooth growth layer = 1 year, and was considered to have borne a number of calves [515].

POPULATION

Unknown; recent sightings indicate that, at least in some localities (e.g. Canaries, Bahamas, Hawaii), the species concentrates in certain areas with site fidelity for many years. May be locally abundant, but populations do not seem numerous, and calves few relative to adults, suggesting slow recruitment [23].

MORTALITY

Virtually no information, but tooth scars on a female thought to have been caused by killer whale or false killer whale [775].

PARASITES AND PATHOGENS

Unidentified adult cestodes present in proximal intestine of juvenile male, New Jersey [775]; nematode *Anisakis simplex* and cestode *Tetrabothrius* sp. found in female stranded, Wales [442]. Clumps of stalked barnacle *Conchoderma* sp. recorded on teeth of male animals [353, 775, 787]. *Xenobalanus* sp. and unidentified balanoid barnacle found deeply embedded on the flank of one, S Africa [775].

Two vaginal fibromas described from a stranded specimen [376].

RELATIONS WITH HUMANS

No commercial fishery, but occasionally taken in small cetacean fisheries of Taiwan, Japan and Korea [553, 605, 775, 792]. Accidentally killed in fishing gear off Sri Lanka, Seychelles, and W coast of Australia [679, 775].

Pollutants (PCBs, DDT) present in blubber of stranded animals from NW Atlantic [1138], Wales [673] and Mediterranean [19], but levels all comparatively low.

Live-stranded individuals occasionally held in captivity for limited periods but have invariably died [775].

Major threat probably comes from use of military sonar in mid-frequency range (1–10 kHz), has been responsible for mass strandings of ziphiids, including Blainville's beaked whale [355, 369, 757].

Legally protected in European, British and Irish waters (Table 12.1).

LITERATURE

Useful general review of *Mesoplodon* [775]; for this

species, most detailed information in unpublished PhD thesis [22]. Additional information on population analysis in [252, 772].

AUTHORS

P.G.H. Evans, N. Aguilar de Soto, J.S. Herman & A.C. Kitchener

FAMILY MONODONTIDAE

Currently considered to comprise 2 monospecific genera, *Monodon* and *Delphinapterus*; both occur as rare vagrants in British waters. No biological data collected from these occasional visitors, so accounts below derived from their normal range. Closest to Phocoenidae [763]. Irrawaddy dolphin *Orcaella brevirostris* once assigned to Monodontidae, but similarities superficial, genetic evidence places it clearly in Delphinidae [684, 700].

GENUS *Delphinapterus*

Beluga Delphinapterus leucas

Delphinapterus leucas Pallas, 1776; mouth of R. Ob, Siberia.

White whale; *míol mór bán* (Irish Gaelic).

RECOGNITION

Only medium-sized cetacean lacking dorsal fin and with uniform white body colour (Plate 15) (whiteness only achieved in adulthood, but all British records are of adults). Smaller animals varying shades of grey. Stout body with small head and pronounced melon. Upper profile of skull broad and flat, distinguished from narwhal by having erupted teeth in both upper and lower jaws. Unique among cetaceans in having all, or almost all, of the neck vertebrae unfused.

DESCRIPTION

Head has slight beak, looks unusually small compared with body, due to great thickness (up to 15 cm) of blubber covering thorax and abdomen. Neck uniquely flexible and visually distinct. 8–11 pairs of simple peg-like teeth in upper jaw, 8–9 pairs in lower jaw, often curved and worn, maximum 40 in total; in old adults, may be worn flat to gumline. Melon bulbous and malleable. Skin soft, often with small transverse ridges, and frequently scarred. Adults pure white or (in early summer) yellowish. Calves grey or grey-brown, often blotched. Juveniles become progressively lighter with age (becoming pure white by age 9 years in males and 7 years in females), although females often still light grey at sexual maturity.

12 Whales, porpoises and Cetacea: Order Cetacea

Pectoral fins short, rounded; progressively turned up at their tips in adulthood. Tail fluke is deeply notched and changes shape with age, developing a lobe on each side of trailing edge. A distinct ridge takes the place of a dorsal fin.

RELATIONSHIPS

Only close relative is *Monodon*. Within species, variations in beluga body size and growth parameters [317, 1124], mtDNA and microsatellite analysis [740], contaminant patterns [550], and vocal dialects suggest some geographical differentiation, although evidence for limited gene exchange weak [865] and may be result of sampling separate stable pods comprising family units [893]. However, mtDNA confirms that belugas tend to return to their natal areas year after year, dispersal among summering concentrations limited even where there are few geographical barriers [183, 866]; satellite tracking supports this [991].

MEASUREMENTS

Size varies geographically, larger further N [1124]. Vagrants to GB probably derive from either Svalbard or White Sea populations, which contain some of largest individuals. Length: newborn *c.* 1.6 m [176]; at sexual maturity (varies between geographical areas) *c.* 270–379 cm (female), *c.* 310–415 cm (male) [505]; adult female typically 3–4 m (max. 4.7 m), male 4–5 m (max. 5.7 m) [317, 505]. Weight: newborn 79 kg [176]; adult typically 400–1000 kg (female), 1000–1700 kg (male) [317, 505].

DISTRIBUTION

Arctic, circumpolar. Normally occurs at or near ice-edge, seasonal distributions largely dictated by annual sea-ice cycle. Most S population resident in Gulf of St Lawrence, Canada.

Only stranding on British coast, October 1932, in R. Forth near Stirling. Most reliable sightings from N North Sea. Singletons off Clare Island, Co. Mayo, September 1948; off Soay, Skye, in 1950; between Orkney and Burray, October 1960; in Gourock Bay, late summer 1964, and possibly same individual at Arrochar, Loch Long; off Yorkshire coast, Whitby, June 1987, with possibly the same animal off Northumberland, March 1988; in Cork harbour, June 1988; off Applecross, W Scotland, April 1995; and singles in Shetland, September 1996 and August 1997 [360].

Single belugas also seen from mainland European North Sea coasts. Some may involve the same individuals of this highly visible and unmistakable species.

HISTORY

Fossils in Pleistocene clays in NE North America

reflect successive range expansions and contractions associated with glacial maxima and minima. Earliest monodontid is extinct beluga *Deuebola brachycephala* from late Miocene, Baja California, Mexico, indicating that this family once occupied temperate zone [100].

HABITAT

Cold marine waters near or within sea ice. Enters estuaries and river mouths for brief periods in summer, probably linked to annual synchronised epidermal moult. In many Arctic regions (e.g. E Canadian Arctic and W Greenland), believed to migrate ahead of advancing polar ice front [373], but in some areas (e.g. White, Barents and Kara Seas) occurs year-round, remaining in polynyas in deeper water during winter [635].

SOCIAL ORGANISATION AND BEHAVIOUR

Gregarious, rarely seen alone, so single vagrants to temperate waters are geographically and socially abnormal. Basic social unit is mother–calf pair, but previous calf also sometimes present. Medium-term associations between adult males shown by radio-tracking [755]. Aggregations often hundreds, even thousands of whales, but within these are smaller groups of 2–20, often of similar ages or reproductive status. Mating system not known; probably promiscuous, since no indication of any long-term male–female relationships. Mature males and females appear to mix only during breeding season on winter grounds [1106].

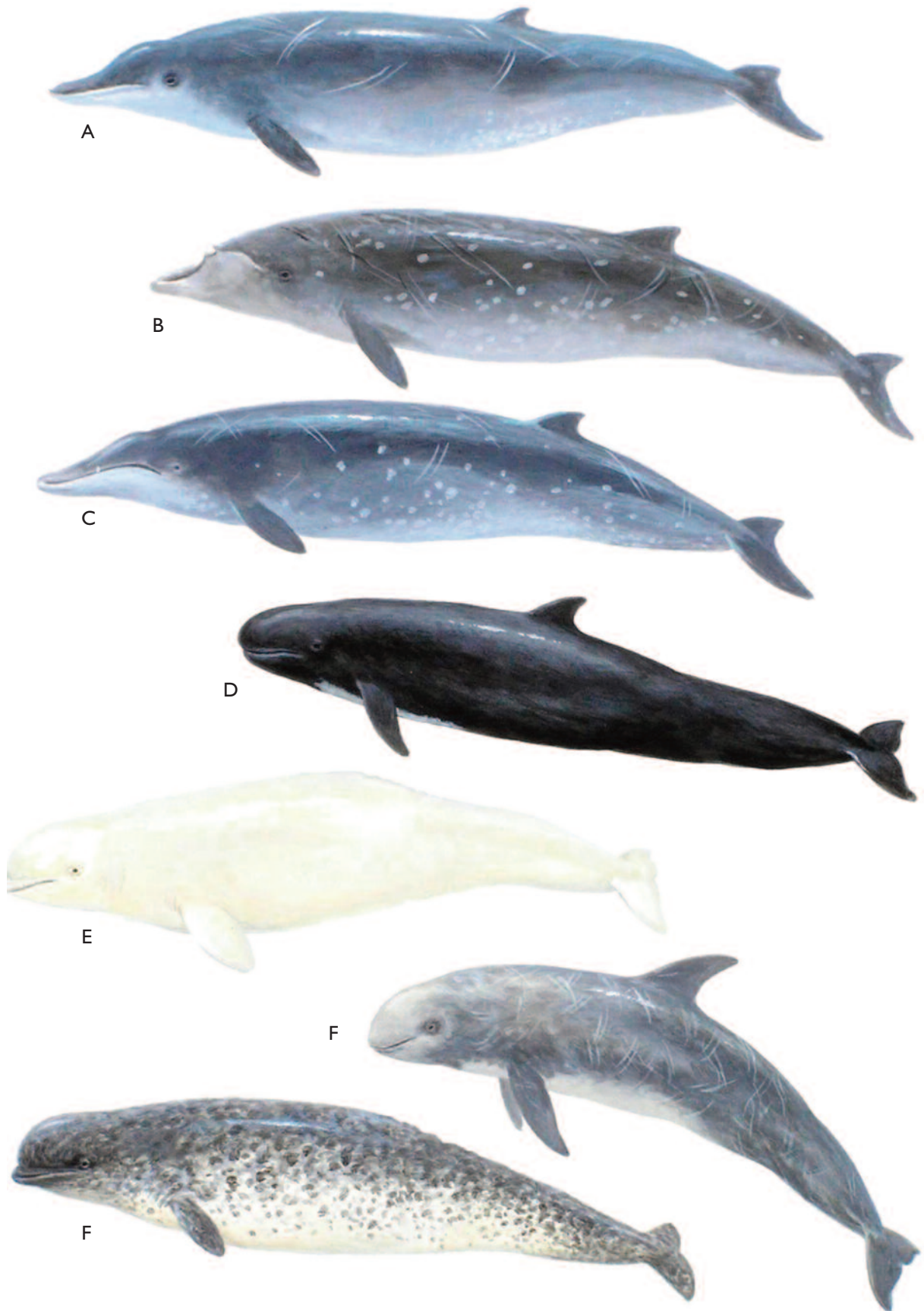
Unusually among cetaceans, has an annual moult; enters sheltered shallow coastal and estuarine waters, actively rubs its skin on gravel substrates [1105, 1115]. Never breaches, but in aggregations may spyhop, tail wave, or tail slap. Facial expression and physical contact, including biting, appear to be important forms of communication within herd [176].

Swims slowly, typically 1–3 km/h but up to 6 km/h during prolonged migration [1104, 1133], which may extend 1100 km from shore and penetrate 700 km into dense polar ice cap with 90% ice cover [1133]. Contrary to expectations, now known to be a capable diver; routinely submerges to seabed, maximum recorded depth >1100 m for up to 25 min [746, 749, 752, 754, 991].

Forages individually, between bouts of resting, beginning with slow directed movement combined with passive acoustic localisation, followed by short sprints and rapid changes of direction using echolocation for orientation and prey capture [108a].

Vocalisations: Known as the ‘sea canary’, the

Plate 15: Cetaceans



A True's beaked whale *Mesoplodon mirus* B Blainville's beaked whale *M. densirostris*
C Sowerby's beaked whale *M. bidens* D False killer whale *Pseudorca crassidens* E Beluga *Delphinapterus leucas* (adult)
F Risso's dolphin *Grampus griseus* G Narwal *Monodon monoceros* (female)

12 Whales, porpoises and Cetacea: Order Cetacea

beluga is very vocal during periods of socialisation, a great variety of whistles, chirps and grunts being clearly heard both above and below water, with as many as 50 call types recognised [1093]. Communicative and emotive calls broadly divided into whistles and pulsed calls typically at frequencies of 0.1–12 kHz. Excellent echolocation system, well adapted to ice-covered waters, and capable of detecting targets at some distance and in high levels of ambient noise and backscatter [69, 70].

FEEDING

Diet: Catholic. Mainly fish, both benthic and pelagic, depending upon seasonal habitat (including arctic cod *Arctogadus glacialis*, polar cod *Boreogadus saida*, salmon *Oncorhynchus* spp., herring *Clupea harengus*, capelin *Mallotus villosus*, smelt *Osmerus nordax* and saffron cod *Eleginus gracilis*), with squid and invertebrates also taken in various parts of range [505, 635, 1054, 1186].

Feeding methods: Feeds both near surface and on seabed, in depths up to 550 m [754].

BREEDING

Single calf born in late spring–early summer, at time of entry to warmer coastal waters or before. Gestation period uncertain, but most likely 13–15 months. Lactation period 2 or more years. Modal calving interval probably 3 years. Mating believed to occur mainly in late winter–early spring, whilst still on wintering grounds or during spring migration.

On assumption of 2 pairs of tooth laminae deposited per year (cf. 1 pair in other odontocetes), both sexes reach sexual maturity around 5–8 years of age, males probably a year or two later than females in same population.

POPULATION

Possibly 30 different stocks around the Arctic [556], though estimate will change with better information on movements and genetics. Population sizes range from a few tens in stocks that have been subjected to over-hunting, to tens of thousands. Total world population probably c. 150 000 [556, 830].

Longevity difficult to establish because tooth wear affects age estimation, but probably few animals reach 30 years, and a 40-year-old is exceptional.

MORTALITY

Due to difficulties in determining age and biases in harvest data, no reliable estimates of mortality rates.

Killer whale, walrus and polar bear are natural

predators [635]. Belugas also prone to ice entrapment; may starve, suffocate and become easy prey to humans and polar bears [176, 1078].

RELATIONS WITH HUMANS

Most populations have been hunted; native harvests continue in several areas, sometimes unsustainably. Maintained in many captive facilities; trained by U.S. and Soviet navies for submarine warfare roles. One in Brighton aquarium, 1878, was one of the first cetaceans in captivity. Legally protected in European, British and Irish waters (Table 12.1).

Increasing human activities in areas that are occupied seasonally by belugas (e.g. St Lawrence R., Canada) have caused habitat destruction, disturbance from vessel traffic, incidental capture in fishing gear and pollution [176, 624, 625, 690, 781].

LITERATURE

Popular introduction to the species [745]. Most detailed academic review available is [176], now somewhat dated. More recent academic reviews [155, 506]; popular account [865].

AUTHORS

A.R. Martin & P.G.H. Evans

GENUS *Monodon*

Narwhal *Monodon monoceros*

Monodon monoceros Linnaeus, 1758; Arctic seas.

RECOGNITION

Body shape similar to beluga: blunt head, no dorsal fin, and pectoral fins which turn up distally with age, especially in males (Plate 15). Age-related change in tail-fluke shape similar to, but even more marked than, beluga. All but youngest males have an unmistakable tusk. Skull similar to beluga, but no erupted teeth in upper jaw (except tusk in males) and none at all in lower.

DESCRIPTION

Stout body with small rounded head, bulbous forehead and very slight beak. One pair of teeth in upper jaw only, left tooth of male greatly extended as spiralled tusk (up to 2.7 m long) pointing forwards and erupting through upper lip. Extremely rarely, both teeth are thus elongated; frequency of this abnormality greatly exaggerated in museum collections. In females, teeth are

embedded in skull and rarely or never erupt. Body mottled grey-green, cream and black; older males look lighter, partly because of accumulation of white scar tissue. Newborn are blotchy slate grey or bluish grey; mottling increases in juveniles. Pectoral fins short, have upturned tip in adults; in very old males, may describe a complete circle, almost touching dorsal surface of fin.

MEASUREMENTS

Length: newborn *c.* 1.6 m; at sexual maturity 3.6 m (females), 4.2 m (males); adult female 4.0 m (max. 4.15 m), male (excluding tusk) 4.2 m (max. 4.75 m). Tusk erupts at body length of 2.6 m, reaches 1.5 m at sexual maturity, and *c.* 2.0 m at physical maturity (max. 2.67 m). Weight: newborn 80 kg, adult 500–1600 kg (males considerably larger than females).

VARIATION

Low genetic (nucleotide and haplotype) diversity revealed by mtDNA, suggests rapid expansion from small founder population after last glaciation [892]. Some genetic differences between populations in Baffin Bay and E Greenland, but also between 2 summering and 1 autumn ground in W Greenland; suggests fidelity to feeding localities [892].

DISTRIBUTION

Discontinuous, (mainly high) Arctic, circumpolar (60–85° N). Rare outside Arctic. Centres of distribution are E Canada/W Greenland and E Greenland/Svalbard/Franz Josef Land. Recorded only 6 times in British waters, presumably involving vagrants from this latter population. Single animals were stranded in 1648, 1800 and 1808, and 2 in Thames estuary, 1949. Only live sighting, 2 off Orkney, also in 1949. No verified records since then [360].

HISTORY

Fossils from Pleistocene, England and Germany, also along Russian Arctic coasts; suggests different range before or during most recent glaciation, as do remains from early Postglacial both N (Ellesmere I.) and S (Gulf of St Lawrence) of present range [503].

HABITAT

Usually in deep offshore waters near or within sea ice. In summer, ventures N into fjords and bays as they become ice-free, occasionally using waters <10 m deep; in autumn, moves S offshore into shelf slope waters of 1000–2000 m depth as coastal areas freeze up. In winter, remains in highly consolidated ice, usually in leads or holes [312, 504].

SOCIAL ORGANISATION AND BEHAVIOUR

Presence of tusk, scarring of adult males, and sexual dimorphism in body size imply polygyny, though not confirmed directly. Social, group-forming species, rarely seen alone; usually small groups, 5–10, migrating together, but sometimes coalesce into larger herds. Vagrants to GB presumably usually aberrant individuals, but multiple records in 1949 show that not always so. Structure of pods similar to those of belugas: small, tightly-knit groups of whales of similar age/sexual status identifiable within often much larger aggregations. These aggregations may cover several km, move as a unit, and can comprise thousands of whales. Adult males usually segregated from groups of females with calves (sometimes accompanied by immature males).

Deep divers, can dive to >1000 m (max. recorded 1164 m) [504], and probably actively chasing prey at these depths [753]. On surface, swim slowly (*c.* 5 km/h) [312].

Vocalisations: Include whistles of 300 Hz–18 kHz, often rising or falling in pitch, lasting 0.5–1 s; pulsed tones of 500 Hz–5 kHz; and echolocating clicks of 500 Hz–48 kHz at 3–10 clicks/s at 48 kHz, and faster click rates (110–150 clicks/s) at 19 kHz [392, 786]. Whistles may be social signals between individuals within groups.

FEEDING

Diet: Mainly squid and fish (both pelagic and demersal), with some invertebrates. Common prey include polar cod *Boreogadus saida*, arctic cod *Arctogadus glacialis*, redfish *Sebastes marinus*, Greenland halibut *Reinhardtius hippoglossoides*, and squid *Gonatus fabricii* [372, 507].

Feeding methods: Little feeding apparently takes place during period in open water (August).

BREEDING

Little known. Calving (single calf) occurs in summer (July–August) in both Greenland and Canada, with mating in early spring, and gestation length *c.* 13–16 months. Modal inter-birth interval is, by inference, probably *c.* 3 years. Lactation *c.* 2 years.

No reliable method for ageing from either protruding tusk or embedded teeth: contain distinctive growth layers in both dentine and cementum, but these merge and become unreadable with age.

POPULATION

Probably 3 main populations – E Canada/ Baffin Bay, Foxe Basin/N Hudson Bay and E

12 Whales, porpoises and Cetacea: Order Cetacea

Greenland/Svalbard/Franz Josef Land. No precise estimates of abundance; aerial surveys suggest low tens of thousands, low thousands and low thousands respectively for these 3 stocks [556, 830].

MORTALITY

Little known. Annual adult mortality probably <10% [623]. Occasional large-scale mortality of whales trapped in savssats (open water in sea ice), which then freeze over (as in Disko Bay, W Greenland [1078]). Like belugas, when entrapped in ice, large numbers may asphyxiate, may then be exploited by Inuit and polar bear.

PARASITES AND COMMENSALS

Whale lice *Cyamus monodontis* and *C. nodosus* found in fold of skin at the base of the tusk, and in any deep wounds. Among endoparasites are *Stenurus alatus*, *Pseudalius alatus*, *Torynurus alatus* and *Pharurus alatus* in middle ear sinuses, *Anisakis simplex* in stomach and intestine, *Ascaris simplex* in the stomach, *Terranova decipiens* and *Porrocaecum decipiens* in the intestine, and *Halocercus monoceris* in the lungs [500].

RELATIONS WITH HUMANS

Hunting for tusks and skin (muktuk) continues in Canada and Greenland. Harvest averaged 550/year in Greenland and 280/year in Canada, 1993–1995 [503]. Some international trade in tusks. No known threats from other human activity, although some have relatively high levels of organochlorines and heavy metals. Legally protected in European, British and Irish waters (Table 12.1).

Mythical horse-like unicorn, with spiralled horn on its forehead, derived from traded narwhal tusks, brought S from Arctic. Long viewed as having healing properties.

LITERATURE

Good academic review [500]; modern ecological study [155]; more recent general account [503].

AUTHORS

A.R. Martin & P.G.H. Evans

FAMILY PHOCOENIDAE (PORPOISES)

A small family of small cetaceans: 3 genera with 6 species of porpoises, only 1 of which occurs in N Atlantic. Distinguished from dolphins by short face, lacking a beak, and by spade-shaped teeth. Possibly closer to Monodontidae than Delphinidae [763].

GENUS *Phocoena*

A small genus of 4–5 species: spectacled porpoise *P. dioptrica* (S hemisphere), vaquita *P. sinus* (Gulf of California), Burmeister's porpoise *P. spinipinnis* (S America) and harbour porpoise *P. phocoena* (N Pacific and N Atlantic), probably also Dall's porpoise *Phocoenoides dalli* (N Pacific).

Harbour porpoise *Phocoena phocoena*

Delphinus phocoena Linnaeus, 1758; Swedish seas. *Llamhidydd* (Welsh); *peileag* (Scottish Gaelic); *neesic*, *pellach* (Shetland); *much mhara* (Irish Gaelic).

RECOGNITION

Smallest British cetacean, <2 m in length (usually c.1.5 m) (Plate 16). Rarely leaps clear of water, as do dolphins. Short blunt head, no beak, and dorsal fin small, triangular, situated in centre of back. Upper and lower jaws contain spade-shaped teeth (conical in all delphinids) (Fig. 12.17).

DESCRIPTION

Small rotund body with small head, no obvious forehead or beak. 19–28 pairs of small spade-shaped teeth in each jaw. Dark grey back with paler grey patch on flanks and white belly, though coloration of back and sides variable. Grey line from flippers to jawline. Short, slightly rounded flippers. Upper and lower jaws, chin, flippers and flukes grey or blackish. Low triangular dorsal fin centrally placed on back (Fig. 12.18). Central notch in tail flukes.

RELATIONSHIPS

No congeners in N Atlantic; closest to Dall's porpoise *Phocaenoides dalli*, N Pacific, which belongs within *Phocoena* [763].

MEASUREMENTS

Length: newborn 65–85 cm (max. c.90 cm); at

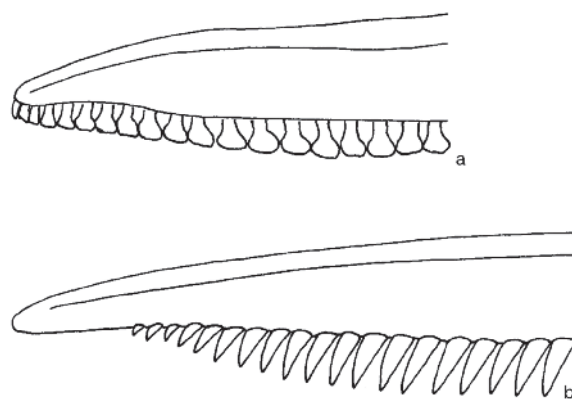


Fig. 12.17 Spade-shaped teeth of harbour porpoise (a) compared with those of common dolphin (b) (drawn by D.W.Yalden).



Fig. 12.18 Harbour porpoise rolling, showing short triangular fin (photo M.E. Baines).

sexual maturity typically 138–147 cm (female), 127–135 cm (male); adult *c.*160 cm (female), *c.*145 cm (male), max. 189 cm (female), 163 cm (male) [708, 711]. Adult weight 50–55 kg (max. 81 kg in females, 54 kg in males).

VARIATION

Using skull material, differences between samples from Denmark and the Netherlands indicate some geographical segregation of Baltic and North Sea populations [627]; Dutch, German and Danish North Sea specimens differ, as do North Sea, Skagerrak, Kattegat and Baltic samples, indicating some degree of separation [628]. Additional studies of tooth ultrastructure [709] and genetics (using mtDNA, nuclear DNA, microsatellites and allozymes) indicate some differentiation in North Sea and adjacent waters, with possible subpopulations occurring in Irish Sea, N vs S North Sea, and E (Danish) vs W (English) North Sea [43, 45, 46, 709, 710, 1151, 1156, 1157, 1196]. Contrarily, extensive microsatellite study of 752 porpoises from locations throughout E North Atlantic range (including Black Sea) imply continuous population structure, with significant isolation only by distance, except in SE part (on a large scale, Black Sea; on a smaller scale, Portuguese waters) where isolation and/or major changes in oceanographic features occur [380].

DISTRIBUTION

Occurs from cool (sub)tropical to subarctic seas of N hemisphere. In E North Atlantic, widely distributed over continental shelf from Barents Sea, S to coasts of Portugal and Spain, and off W Africa from Morocco to Senegal. Isolated population in Black Sea. During 1960s, became scarce in S North Sea, English Channel and Bay of Biscay [6, 346, 1099]. Nevertheless, remained the most frequently observed, and stranded, cetacean around British Isles; most abundant around Scotland, parts of Wales, and off W and S Ireland [340, 346, 360, 481, 857, 973, 1004] (Fig. 12.19). Since late 1980s, particularly late 1990s, sharp increase in sightings and strandings in Dutch and Belgian waters, rising to spectacular peak in 2005/06. This sudden change not well understood; probably reflects a shift in distribution, maybe caused by a decrease in sandeels, a known important prey, further N [210, 211], a recovery in some North Sea herring stocks [344], or a combination of the two. Similar increases in sightings rates off SE England from 1990s [360]. SCANS II survey of NW European shelf waters, July 2005, also indicated a distributional shift with higher densities in S North Sea compared with N North Sea, reversing situation from SCANS I in July 1994 [478].

Occurs year-round in coastal waters of British Isles; distinct seasonal peaks, July–October, in

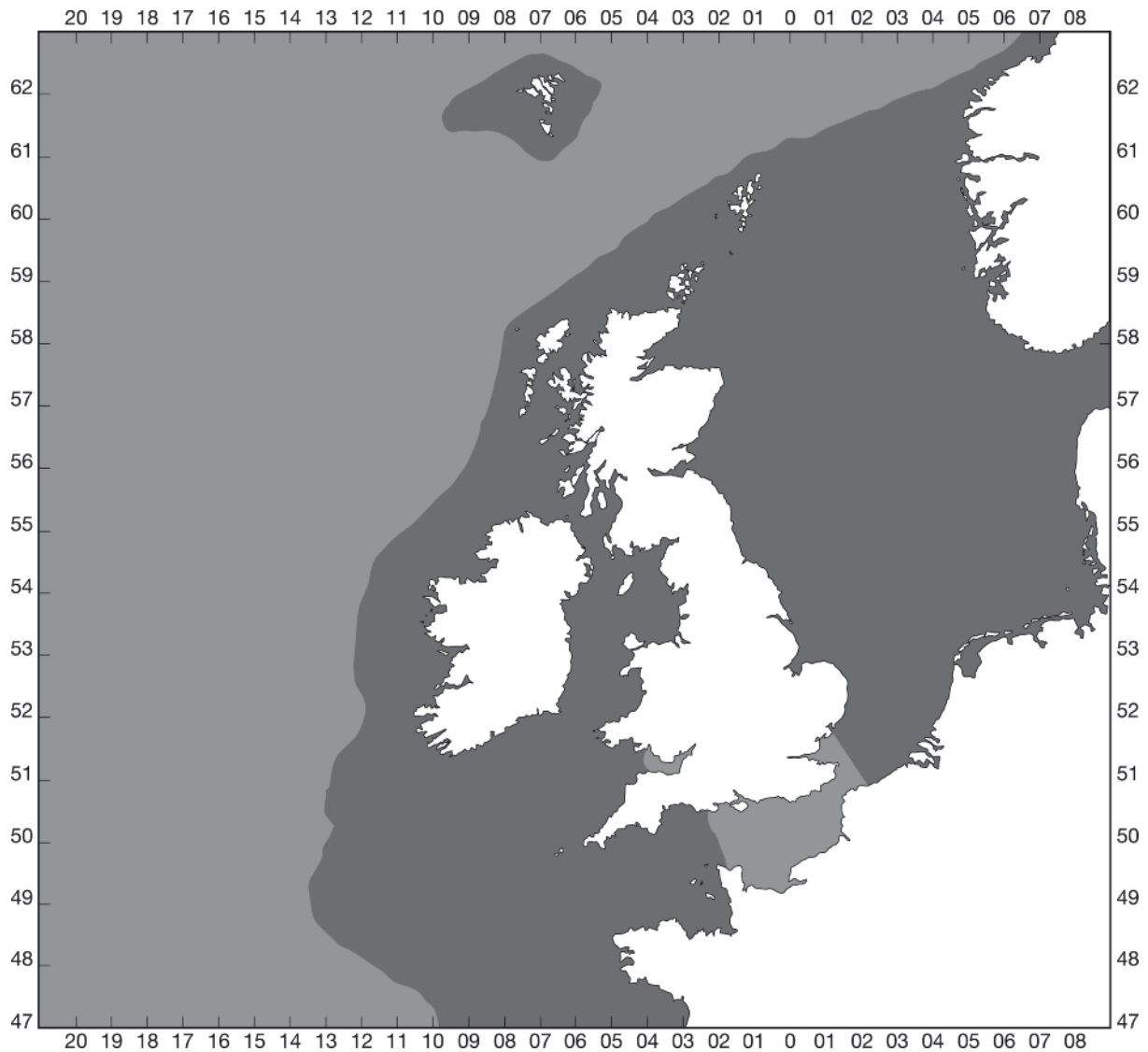


Fig. 12.19 Harbour porpoise *Phocoena phocoena*: distribution around British Isles.

some places [340, 346, 360, 857], but along S English coast and in Dutch waters, is a distinct peak January–April [6, 210, 360]; suggests a seasonal shift in distribution [212].

HISTORY

No fossil or archaeological material known in GB, although there are archaeological finds in the Netherlands and elsewhere in Europe.

HABITAT

Occupies (sub)tropical to cool temperate and subarctic (mainly 11–14 °C) waters, usually (but not exclusively) over the continental shelf at depths of 20–100 m. Consequently is commonly found in coastal bays and estuaries, around headlands, and within tidal channels; in most parts of NW Europe, is the most common cetacean within 10 km of the coast.

SOCIAL ORGANISATION AND BEHAVIOUR

Only a few detailed studies of social organisation or behaviour. Due to their small size and inconspicuous habits, difficult to observe for extended periods. Rarely bow-ride and only in certain circumstances approach moving vessels. Few individuals bear marks that allow recognition of individuals. Most detailed behavioural observations are of captive animals (e.g. [49]), although surface behaviour described for Denmark [1108], Scotland [348], Wales [929] and Germany [1049].

In British waters (as elsewhere), usually solitary or in small loose groups of 2–10 [340, 346, 960]; in most months, median group size is 2, rising to 3 August–October [346]. Larger aggregations of several hundreds observed, but these appear to be temporary coalitions of smaller

groups; off GB, occur primarily in February–April and August–October, either associated with long-distance movements or at feeding concentrations [346, 348, 689]. Group size of Dutch animals from 13 years of observations averaged 1.2–1.6 [1250]. Group composition appears fluid, except for adult females with dependent calves. Patterns of strandings and bycatches suggest segregation by age and sex. Individuals extremely mobile, often travelling >50 km/day [961]; some satellite-tagged in N Danish waters made seasonal movements to winter around Shetland [1139]. Genetic evidence from GB and elsewhere indicates that males disperse more widely than females [45, 709, 1155, 1196].

Surfacing behaviour varies with environmental conditions. In calm weather, rolls slowly at the surface, occasionally resting at or just below the surface for a minute or more, when sexual activity may also be observed [39, 348]. Swims at 6–12 km/h; can reach 22 km/h when pursued. Usually swims unobtrusively, rarely showing more than the upper back. However, in rough seas or in tidal rips, surfaces rapidly, almost clearing the water to breathe. Can remain submerged for up to 5 min and usually takes a series of breaths between long dives. In Bay of Fundy, recorded diving to 226 m [1226]. Off Denmark, 14 with satellite-linked dive recorders averaged 29 dives/h, April–August, and 43 October–November [1142]. Dived day and night, but with peak activity during daylight hours, spending 55% of time in upper 2 m during April–August. Max. dive depths were to sea bottom (30–50 m) in Belt seas and Kattegat, and 132 m in deeper Skagerrak; most frequent depths 14–32 m. Dive durations typically 4–6 min, but possibly up to 10–15 min [1142]. Unlike dolphins, does not bow-ride, but sometimes approaches sterns of slower vessels, particularly in late summer [348].

Does not associate with other species, but may co-occur with minke whale, fin whale or humpback in a restricted area, presumably at food aggregations; seabirds (e.g. shags, gannets, auks and gulls) often aggregate nearby as well [341, 348]. Where bottlenose dolphins and harbour porpoises co-occur (e.g. E Scotland, W Wales), dolphins have been known to kill porpoises [575, 1018], possibly as a result of interspecific competition for food.

Vocalisations: Produces high-frequency sounds for echolocation and communication, but not the frequency-modulated whistles typical of delphinids. High-frequency sounds are comprised entirely of click trains, produced in 2 narrow frequency bands: one weaker and of longer duration (c.0.2 ms) at 1–20 kHz [447, 1048], the

other at 120–160 kHz (peaking around 130 kHz) of shorter duration (c.0.02 ms) [40, 447, 595, 803]. Repetition rates of pulses range between 0.5 and 1000 clicks/s [40]. Maximum source level estimated at 149–177 dB re 1 μ Pa at 1 m [25]. More intense bursts of clicks used during foraging [1175, 1176].

FEEDING

Diet: Can vary both geographically and seasonally. Primarily small (mainly 75–200 mm) schooling fish, found in the water column or on the sea floor. Small cephalopods (mainly Sepiolidae) also consumed, but less frequently than fish. Analyses of tissues from porpoises bycaught at 4 Scan-dinavian localities (from North Sea to Barents Sea), using stable isotopes and trace element cadmium, correlated well with both bathymetry and latitude, indicating a shift in feeding habits from pelagic prey species in deep N waters to more coastal and/or demersal prey in relatively shallow North Sea and Skagerrak [381]. This supports dietary studies from various geographical regions using stomach contents. In France, mainly blue whiting *Micromesistius poutassou*, scad *Trachurus trachurus*, and hake *Merluccius merluccius* [304]. In Germany, mainly sole *Solea solea* and cod *Gadus morhua* [692] or sandeels (Ammodytidae) and sole [112]. Herring *Clupea harengus*, sprat *Clupea sprattus* and gadoids (particularly cod and whiting *Merlangius merlangus*) predominated in large samples (n = 179, n = 145 stomachs) from Denmark and Scandinavia respectively [2, 117, 154, 1039]; gadoids (particularly whiting and *Trisopterus* spp.), sandeel and gobies Gobiidae predominated in large samples (n = 100, n = 58) from GB [746]; gadoids (mainly whiting) and gobies were the main species in a sample of 62 from the Netherlands [1039]. From 188 stomach samples, Scotland (mostly E coast) main prey were whiting and sandeels, although there were differences between regions, seasons and years [1037]. Off Ireland, mainly *Trisopterus* spp., whiting, and herring [119]. Echosounder survey of porpoise–prey associations, Shetland, found significant spatiotemporal associations only with sandeel, despite abundance of gadoid fish (whiting and saithe *Pollachius virens*), which presumably not favoured when sandeels abundant [348].

In much of North Sea, herring became scarcer in the 1970s. Where herring present, frequently major component of diet [2, 423, 698, 950, 951, 963], presumably because fatty and energy rich [344]. In parts of North Sea and in Baltic, stomach contents include gobies as well as cephalopods (Sepiolidae), crustaceans, polychaetes and other molluscs [113, 692, 738, 1039].

Feeding methods: Little is known of how porpoises find and catch their prey in the wild (although several recent captive studies [599, 1176]). Circumstantial evidence that seasonal movements into coastal waters of British Isles, and longer-term status changes in North Sea, related to timing of spawning of herring, sandeels and gadoids [344, 348, 975].

Food requirements: Not well understood; preliminary work with captive animals suggests that adult porpoises require a daily ration of 4–9.5% of body mass, and juveniles up to 15% [599, 645, 717]. Porpoises increase food consumption in the late summer and increase their body weight, reach peak weight with increased fat storage by mid-winter [712, 717]. This aids insulation in the cold months and provides a temporary energy surplus.

BREEDING

Young born mainly May–August though some as early as March; peak in June [6, 375, 598, 708, 711, 805, 1108]. Some evidence for seasonal movements nearshore in various areas around British Isles, may be related to parturition or calf-rearing during summer [346, 348, 357].

Mating season April–September, with a peak in July–August; gestation period *c.*10–11 months; calving interval 1–2 years [375, 598, 708, 713, 1108]. Lactation period may last up to 10 months [711, 713, 805], with calves starting to feed independently after *c.*2–3 months [348]. Age at sexual maturity 3–5 years, little difference between sexes [7, 708, 711, 713].

POPULATION

From line transect surveys (SCANS I) conducted July 1994 [481], population estimated at 341 366 (CV = 0.14; 95% CI 260 000–449 000) from North Sea (*c.*250 000), Baltic (33 000 in Kattegat/Skagerrak), Channel (0) and Celtic Sea (36 000). In Norwegian waters, estimates of 11 000 (95% CI: 4 790–25 200) for Barents Sea and Norwegian waters N of 66° N, and 82 600 (95% CI 52 100–131 000) for S Norway and N North Sea, made during July 1989 [136]. Repeat survey, July 2005 (SCANS II), covering a wider area (continental shelf seas from SW Norway, S to Atlantic Portugal), gave an estimate of 386 000 (CV = 0.20) [478].

Longevity relatively short, usually up to 12 years, but maximum of 24 years in both sexes [708, 711, 713].

MORTALITY

Suffers predation from sharks (including Greenland shark, great white shark and mako) [63, 1144, 1239], and killer whales [340, 547, 573]. In Moray Firth, NE Scotland, and Cardigan Bay, W Wales, also

attacked by bottlenose dolphins [575, 1018].

PARASITES AND PATHOGENS

Whale-lice *Isocyamus delphinii* found on Dutch animals [401]. 22 helminths reported [955]. Internal parasites include the nematodes *Anisakis simplex* (stomach), *Stenurus minor* (cranial sinuses), *Pseudalius inflexus* (bronchi, lung, and heart), *Torynurus convolutus* (bronchi), *Halocercus invaginatus* and *H. tauricus* (in lungs); trematode *Campyla oblonga* (bile and pancreatic ducts); *Crassicauda* sp. (subdermally in blubber); cestode *Diphylobothrium stemmacephalum* (intestine) [48, 89, 92, 93, 304, 441, 442, 487, 713, 955, 1097].

HEALTH STATUS

Some from British waters had morbillivirus infection, although not thought to be cause of death [611, 1222]; antibodies to morbillivirus found in porpoises from Bay of Fundy [334] and British Isles [173] although its significance as a cause of mortality remains uncertain. In a large sample, 32% had positive antibodies to *Brucella* [576], and a Dutch sample gave 27% positive (n = 70) [1]. Lung infections a common cause of death [577]. Frequent pox lesions on skin [88].

RELATIONS WITH HUMANS

Living in Europe mainly on the continental shelf, is exposed to a variety of human activities. Was formerly hunted in drive fisheries in the Baltic and off Faroes. However, major threats currently appear to be fishery conflicts. Incidentally caught in a variety of fishing gear: bottom-set gillnets for hake, cod, turbot and sole; fixed nets or traps for cod or salmon; herring weirs; trawls, drift nets, and purse seines for cod, herring or plaice. Recent independent observer schemes estimate annual bycatches in English and French bottom-set gillnet fisheries of at least 6% of the harbour porpoise population (2237 out of an estimated population of 36 280) in the Celtic Sea W of Cornwall; Danish bottom-set gillnet fishery killed 4% of the population in C and N North Sea (6785 out of an estimated 185 000) [481, 1162, 1182], though have decreased recently [1183]. Bycatches also identified as main cause of mortality (at least 28%) for stranded porpoises in England and Wales [631]. Autopsies similarly showed that bycatch caused at least 50% of stranded porpoises in the Netherlands, 1990s [425], and even higher recently [687]; similar figure for German porpoises [1077].

Examined for pollutants in many areas (reviewed in [16, 1226]). High levels of particular pollutants (notably organohalogen compounds such as DDT and PCBs, heavy metals such as mercury, copper, and zinc) found in small samples

from certain locations (e.g. the Netherlands [644]; Sweden [886]; NW England [672], but levels of some compounds (particularly DDT) have decreased recently in parts of the North Sea and Baltic [16, 460]. Both organochlorine and heavy metal levels generally low in British and Irish waters [671a, 672, 770, 1003, 1218], but PCB levels still high enough to cause concern in some localities, early 1990s [16], including Moray Firth, NE Scotland [1218], and the Netherlands [1045]. Despite slight decrease over the last 20 years, PCB concentrations in many GB-stranded porpoises, 1989–2002 high enough to cause adverse physiological effects in other mammals [580, 928]. Brominated flame-retardants highest in N Irish Sea (median value 2.9 µg/g lipid, Irish and Scottish coasts), and W coast of Scotland (5.1 µg/g lipid) [1264].

Effects of these pollutants not clearly known; PCBs cause immunosuppression as well as reproductive impairment [16, 1136]. Females can transfer organochlorine compounds to their fetuses. Whereas no correlation initially found between PCB levels, body condition and cause of death in GB porpoises [663], nor in organochlorine levels and adrenocortical hyperplasia [662], mortality from infectious diseases considered to be associated with chronic exposure to both PCBs [471, 579] and mercury [114] in a much larger sample.

Often live in the vicinity of vessel traffic, may experience sound disturbance as well as danger of ship strikes. Off Shetland, porpoises showed short-term avoidance of speedboats and large ferries, although reactions varied with group size, social status, and season [348, 349, 359]. Pile-driving activities during windfarm construction shown to result in both short-term and longer-term avoidance by porpoises [227, 1141].

Legally protected in European, British and Irish waters (Table 12.1). Listed by IUCN [971] as 'vulnerable'.

LITERATURE

General review [960]; aspects of biology, diet, management and conservation well covered in special IWC issue [135] and a NAMMCO volume [499]; anatomy and physiology reviewed in [827, 962] and feeding in [1031].

PRINCIPAL AUTHORS

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FAMILY DELPHINIDAE (DOLPHINS)

The most diverse family of cetaceans, with 34–36 species in 17–18 genera [558, 971, 945, 1245]. Relationships within Delphinidae poorly understood [962]. Mostly small, fast-swimming, predators of fish, though largest take other mammals and birds. In British waters, 7 species, each in a different genus, occur regularly, and another 4 occur irregularly.

Bottlenose dolphin *Tursiops truncatus*

Delphinus truncatus Montagu, 1821; R. Dart, Devon. *Dolffin trwyn potel* (Welsh); *muc-bhiorach* (Scottish Gaelic); *deilf bolgshrónach* (Irish Gaelic).

RECOGNITION

Robust dolphin (Plate 16) with short, stout beak. Melon clearly distinct from beak. Coloration generally counter-shaded tones of grey. Some subtle patterning but no strongly contrasting colour patches (cf. other dolphins). Dorsal fin tall, slender, sickle-shaped, placed midway along back. Usually identified by eliminating other species first. Can be confused with harbour porpoise and white-beaked dolphin. Key features are coloration, dorsal fin, blunt beak and demarcated melon.

Behaviour at sea variable. May swim alone or in schools of up to 50 individuals; rarely, schools of hundreds. Often boisterous, with leaps and splashing, readily approach boats and ride pressure waves.

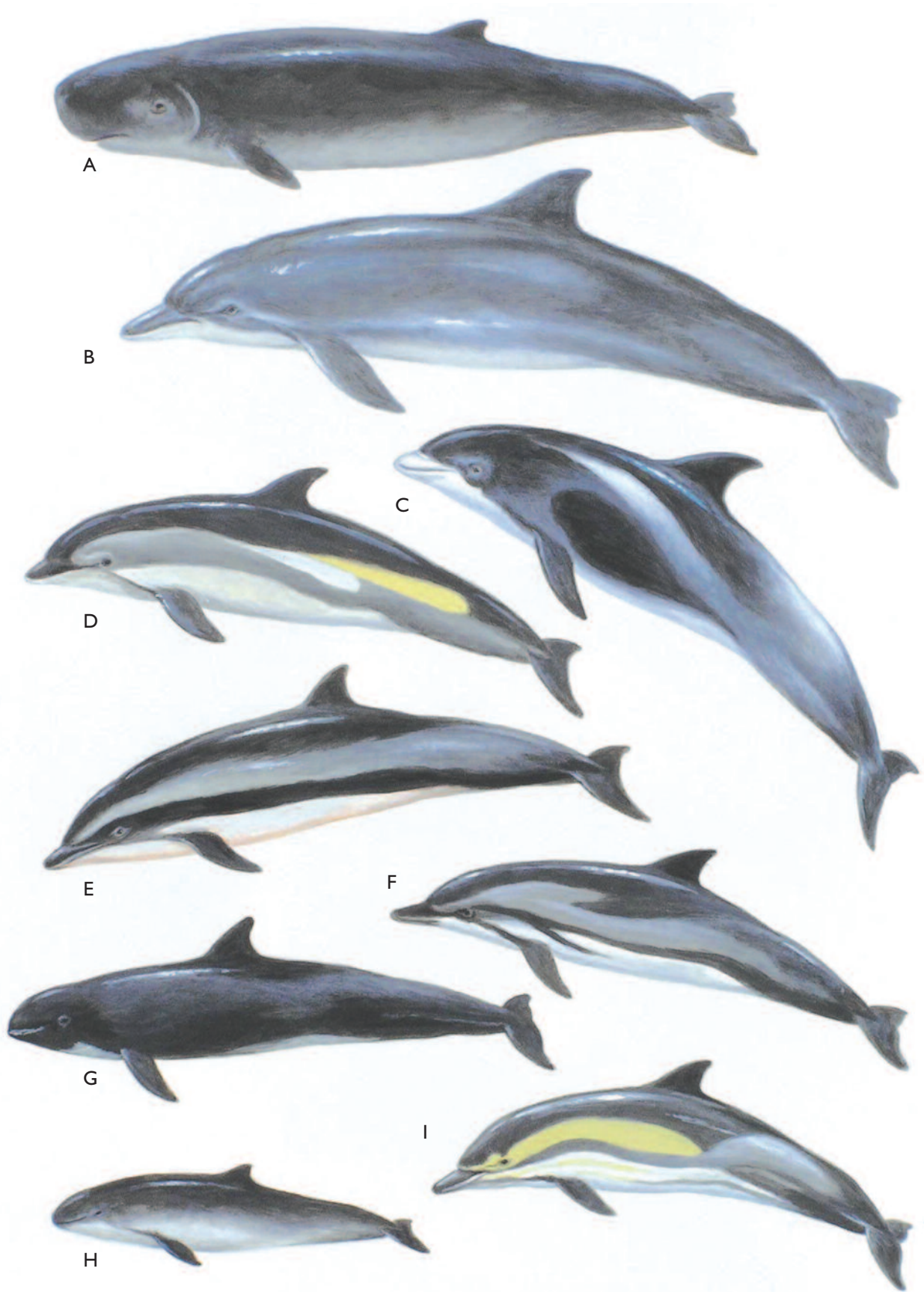
DESCRIPTION

Body: Robust, torpedo-shaped; stout head with blunt bottle-end beak. Abrupt junction between upper jaw and beak. Dorsal fin central on back, tall, generally sickle-shaped, but can be triangular, particularly in young animals. Flippers pointed. Moderately keeled tail stock, tail flukes with deep median notch.

Coloration: Variable. Generally counter-shaded; black, brown or dark grey on back, lighter grey flanks and white or cream on belly. Calves generally paler, often light grey, cream or olive. Neonates marked with several vertical pale bars at intervals along body. Adults may have indistinct cape from apex of melon broadening from blowhole to dorsal fin. Skin frequently marked with pale scars, particularly around jaws. Discoloured skin patches from disease common in British waters.

Skull: Broad with short rostrum. Teeth stout and conical, 19–26 per quadrant (Fig. 12.20). Tooth enamel smooth, tips often worn flat. Morphology

Plate 16: Cetaceans



A Pygmy sperm whale *Kogia breviceps* B Bottlenose dolphin *Tursiops truncatus* C Atlantic white-sided dolphin *Leucopleurus acutus* D White-beaked dolphin *Lagenorhynchus albirostris* E Fraser's dolphin *Lagenodelphis hosei* F Striped dolphin *Stenella coeruleoalba* G Melon-headed whale *Peponocephale electra* H Harbour porpoise *Phocoena phocoena* I Short-beaked common dolphin *Delphinus delphis*

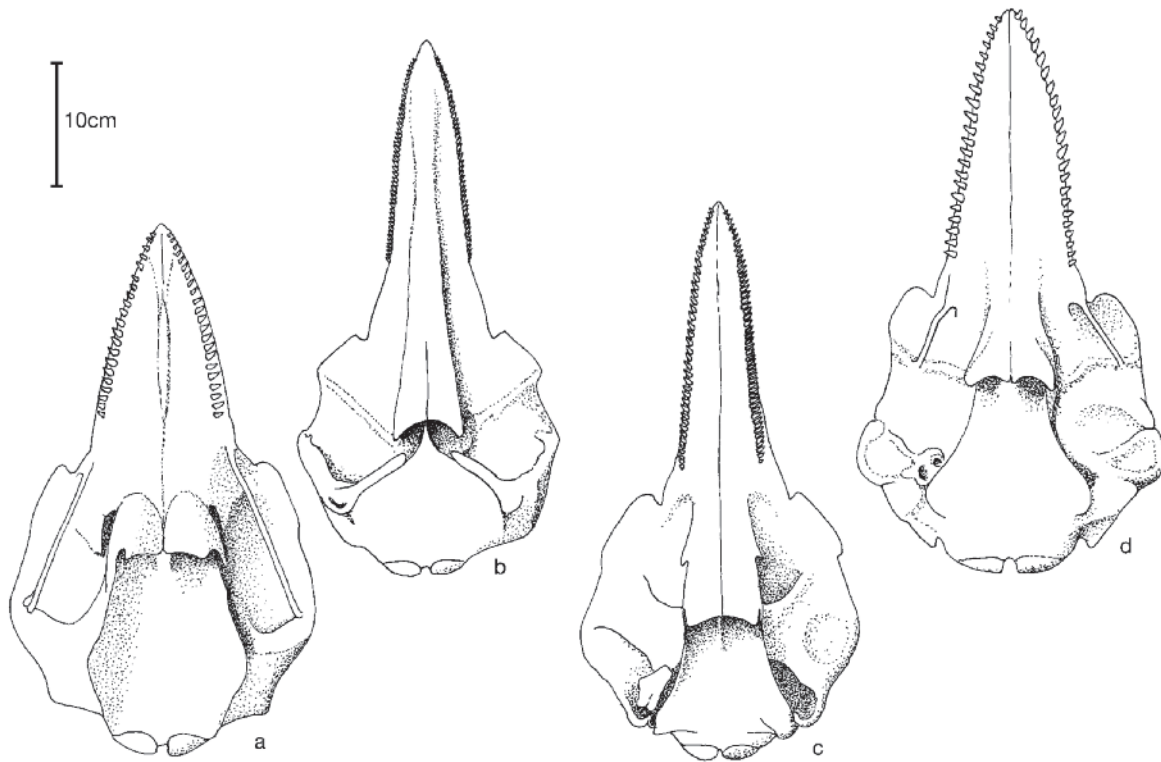


Fig. 12.20 Palates of (a) white-beaked, (b) common, (c) striped and (d) bottle nose dolphins, to show longer beaks with more (c.45) teeth of common and striped dolphins, and the characteristic grooves in the palate of common dolphin (drawn by D.W. Yalden).

variable between regions and habitats, typically larger and more robust in colder climates.

RELATIONSHIPS

Tursiops recently split into 2 species: bottlenose dolphin *T. truncatus* widespread, in tropical and temperate waters worldwide, including around British Isles; Indo-Pacific bottlenose dolphin *T. aduncus*, restricted to coastal waters of warm temperate–tropical Indo-Pacific. Genus remains under review, may be split further in future. Genetically close to *Stenella* and *Delphinus*, though phylogeny within Delphinidae not well resolved [962].

MEASUREMENTS

Highly variable between regions. Animals around British Isles perhaps amongst world's largest. Length: newborn c.1.20–1.30 m, adult c.3.20 m (female), c.3.42 m (male) [1024]. Weight to 365 kg. Age and length at sexual maturity unknown for European populations. Likewise, level of sexual dimorphism unknown, but adult males in W Atlantic 10% longer than females [1154].

VARIATION

Highly variable in morphology, pigmentation and

behaviour across range and habitats. Distinct ecotypes identified in adjacent inshore and offshore areas off E USA and S Africa. Ecotypic and other variation not described for NE Atlantic but other differences include ranging patterns, social organisation and disease [701, 1242, 1251]. Significant genetic variation found in coastal dolphins in British and European waters, boundaries coinciding with transitions in environmental features such as surface salinity, productivity and temperature [832, 901]. Local populations (e.g. off NE Scotland) have lower genetic diversity [901].

DISTRIBUTION

Worldwide in coastal and offshore tropical and temperate waters. In NE Atlantic, locally common from N Africa to N Scotland (Fig. 12.21). Degree of site fidelity in coastal habitats variable: groups apparently resident in Scottish NE coast, Sound of Barra (Scotland), Cardigan Bay (Wales) and Shannon estuary (Ireland) [360], but other groups off Cornwall, Devon (England) and W Isles (Scotland) more mobile. Probably once common in S North Sea [1177]. Current N limit of coastal range, N Scotland. Frequent sightings at or beyond the continental shelf break, offshore distribution extends N at

12 Whales, porpoises and Cetacea: Order Cetacea

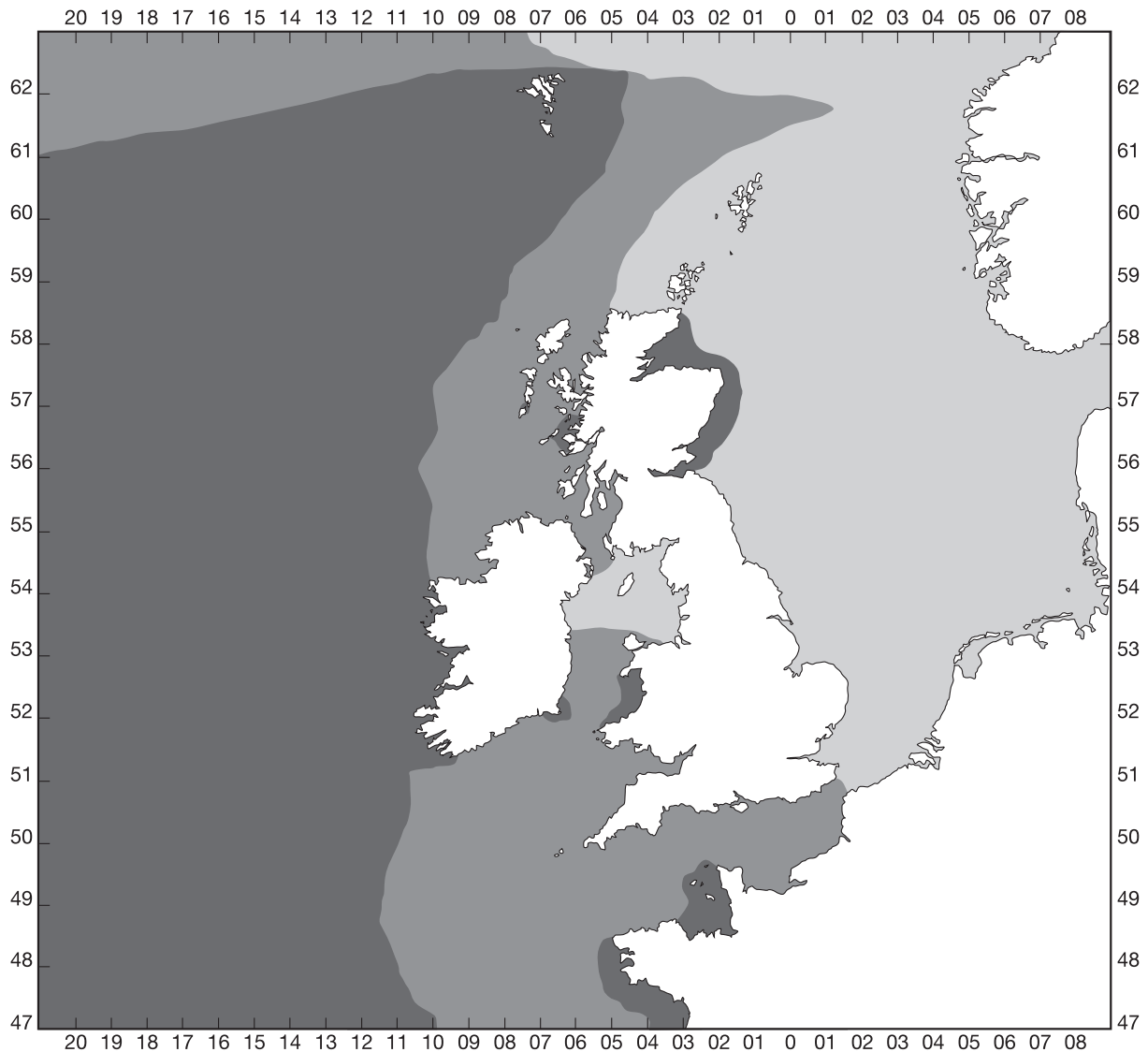


Fig. 12.21 Bottlenose dolphin *Tursiops truncatus*: distribution around British Isles.

least to Faroes [767, 973]. Little known about ecology of offshore animals though often associated with pilot whales *Globicephala melas*. Relationship between offshore and coastal bottlenose dolphins unknown. Local migrations in coastal areas probably driven by prey availability [1251, 1241]. Lone animals occasionally resident in small coastal areas, may associate with humans [707].

HISTORY

Genus *Tursiops* arose *c.*5 mya. *T. truncatus* in fossil record from Pleistocene, recovered from Atlantic and Pacific basins and coastal habitats. Most evidence from area around Mediterranean but specific point of origin unknown [101].

Known in British waters from Anglo-Saxon era (7th–10th centuries AD), when archaeological evidence indicates targeted fishery of population

near the Humber estuary [514]. This population now apparently extinct, other similar changes elsewhere: dolphins in S North Sea became increasingly rare during 20th century, new groups appeared to have settled during the 19th or 20th century (Moray Firth, Scotland; Cornwall, Devon) [342, 1159, 1177, 1240, 1251]. Thus coastal communities can be dynamic and result from extinctions or changes in distribution. Such range shifts may be rapid or gradual, taking a decade or more [1244].

HABITAT

Cosmopolitan in British waters: found offshore, at the shelf break and close inshore. Inshore distribution includes estuaries and harbours; brief forays into fresh water. Areas of strong tidal currents and steep bottom relief particularly favoured [492].

SOCIAL ORGANISATION AND BEHAVIOUR

Most often found in small schools (2–50); sightings of single animals or hundreds comparatively rare. School size generally correlated with habitat; larger schools in more open and offshore environments (Fig. 12.22). School composition best studied in coastal areas where schools dynamic, change composition frequently, forming ‘fission–fusion’ societies. Small groups (20 animals) more stable, typically a mixture of males, females, calves and adults. Seem to show longer-term associations. Studies in N America, Australia suggest that adult females with young preferentially associate with other females and their calves, subadults with other subadults, and adult males form stable alliances with other males of similar age [275, 1107, 1221]. Male alliances thought to influence female movements and mating partners; this not observed in British dolphin communities, males may adopt a different mating strategy [1240].

Cooperation between individuals common, includes baby-sitting and coordinated hunting; with increased defence against predators and infanticide [904], probably main reasons for sociality of this species. Relationships between individuals complex, suggest high degree of individual recognition, long-term memory of previous encounters [275].

Generally slow swimmers (*c.* 4 km/h), can reach 54 km/h [716]. Frequently approach boats to ride pressure waves. Surface behaviour diverse, includes breaches, slapping tails on the surface, side-rolls and a variety of exhalations including rapid loud exhalations and blowing raspberries. Functions of these behaviours poorly understood.

Vocalisations: Diverse. Echolocation clicks (used for orientation and foraging) are intense, short duration, broadband clicks (40–130 kHz) [68]; broadcast in episodic trains, can continue for duration of dive, culminate in buzzes and whines as approach target. Burst pulse vocalisations (barks, yelps and donkey brays, 0.2–16 kHz,) may have a variety of social and feeding-related functions [564]. Whistles, pure-tone frequency-modulated calls ranging from 2–20 kHz, produced in social contexts.

FEEDING

Diet: Generally considered selective opportunistic; includes a wide variety of benthic and pelagic, solitary and schooling, fish and cephalopods. Individuals may specialise on particular prey species or switch as availability changes particularly with area and season. Documented prey in British waters include gadoids (cod, saithe, whiting, haddock), salmon, sprats, sandeels, flatfish and cephalopods [1034].



Fig. 12.22 Cetaceans often form mixed schools, here long-finned pilot whales (foreground) and bottle nose dolphins (photo D. Stroud).

12 Whales, porpoises and Cetacea: Order Cetacea

Feeding methods: Independent and cooperative feeding observed. Local topography, shore line, water surface or tidal interfaces, may be used to herd prey [493, 701, 715]. Exploits human fisheries in several parts of the world, particularly trawling and gillnets. Other than direct competition for prey and accidental capture in fishing nets, few interactions between human fisheries and bottlenose dolphins in British waters are known. Echolocation undoubtedly important for prey detection, may also use passive listening and vision. Probably feeds day and night.

Food requirements: Captive dolphins consume 3–6% of body weight in food per day.

BREEDING

Mating system unclear but violent interactions between males, heavy body scarring, subtle size dimorphism and formation of male–male alliances suggest competition for access to females. In addition, large testis size and high concentrations of spermatozoa in ejaculate imply polygamy. Thus probably a promiscuous system, each sex mating with several partners, but plasticity in behaviour and morphology suggests that mating systems may vary between populations.

Females are spontaneous sporadic ovulators, cycling repeatedly within season. Males may be sexually active throughout the year with prolonged elevation of testosterone during the mating season(s). Single calf (twins exceptionally rare), gestation *c.* 12 months. Extended season for births, though peak May–November in British waters [340, 1240], may be timed to coincide with warmest water temperatures. Sex ratio of births *c.* 1:1. Specifics of female behaviour associated with the birth unclear. Frequent claims of nursery areas, but evidence lacking. Calves dependent on milk for 18–20 months. Weaning gradual, suckling may last several years. Mating and pregnancy occur while previous calf still associating with mother. Calf may leave mother at birth of subsequent calf or remain in association. Interbirth interval variable from 2 to 5 years, generally shorter if calf dies prematurely.

Neonates swim and breathe without aid immediately after birth, gain hydrodynamic advantage from mother by positioning just below and behind her dorsal fin. Breaths taken during awkward lunges through the water surface. Sucking frequent when mother stationary or swimming. Calves gradually become more adept at swimming and gain independence, interacting with males and females from a wide range of age groups. Levels of independence displayed by calf thought to be a compromise between increased social learning and elevated chances of predation

or infanticide. Fathers probably play no part in raising young.

Growth rates greatest during period of suckling, i.e. first 1.5–2 years. Asymptotic size reached around or shortly after puberty. Age at sexual maturity varies regionally, around 5–13 years (females), 10–15 years (males) [1220]. Males may reach >20 years before attaining breeding status [1220]. Females appear to reproduce throughout life, without reproductive senescence. Precise ageing possible by examining tooth sections. Off Florida, females may live to 50 and males to 40–45 years.

POPULATION

Estimates of inshore dolphins around the British Isles total at least 490 individuals [80, 465, 549, 1228, 1243]; at least 85 occur coastally in the English Channel and off W France [702]. Wide-scale SCANS-II survey, 2005, W European continental shelf waters (W Baltic, North Sea and Atlantic margin as far as S Spain) estimated 12 600 bottlenose dolphins in this area (CV=27%), mostly offshore. Numbers W of continental shelf break unknown.

MORTALITY

Causes of death diverse. Disease probably most common cause, killer whale or shark predation less frequent in British waters than elsewhere. Death from attack by other bottlenose dolphins, physical injury, hypothermia, natural poisoning, starvation and mother–calf separation recorded. Eventual mortality often the result of several factors in combination.

PARASITES/COMMENSALS

Of all cetaceans, parasites and diseases of bottlenose dolphins best known due to worldwide distribution, prevalence in captivity and frequency of stranding. Range of organisms diverse [1220]. Ectoparasites including barnacles and remoras generally common, but rare off NW Europe. Endoparasites diverse and common, include trematodes, cestodes and nematodes. Viral, bacterial, protozoan and fungal pathogens frequently described [1220].

RELATIONS WITH HUMANS

The best-known and most widely exhibited of all dolphins in aquaria. Lone wild individuals sometimes associate with bathers and small vessels [707]. Coastal populations increasingly targeted for dolphin-watching activities. Anthropogenic threats diverse. Hunts outlawed but direct physical injury from boat strikes, underwater explosions, and entanglement in fishing equipment occur [147, 856, 993]. Organochlorines,

heavy metals, petrochemicals and other toxins thought to affect immune and reproductive abilities [584]. Habitat alteration and overfishing may reduce prey abundance [905], and noise disturbance may disrupt social communication and foraging [993].

Legally protected in European, British and Irish waters (Table 12.1). Key bottlenose dolphin habitats in the Moray Firth and Cardigan Bay designated as Special Areas of Conservation under EU Habitats Directive (see Chapter 4).

LITERATURE

General review [1220], see also species account in [922].

AUTHOR

B. Wilson

GENUS *Stenella*

Coined by Gray in 1866, *Stenella* considered a subgenus of *Steno* until Oliver raised it to a genus in 1922. Widely distributed, mainly in warm and temperate waters. *Stenella* generally considered to include 5 species of long-beaked slender dolphins [910, 917]: only 1, *S. coeruleoalba* in European waters; pantropical spotted dolphin *S. attenuata*, worldwide in tropical waters; spinner dolphin *S. longirostris*, also worldwide in tropical waters; clymene dolphin *S. clymene*, in tropical and subtropical Atlantic; Atlantic spotted dolphin *S. frontalis*, also in tropical and warm temperate Atlantic. Also a number of poorly differentiated forms; taxonomy has been very confused.

Striped dolphin *Stenella coeruleoalba*

Delphinus coeruleo-albus Meyen, 1833; off Rio del Plata, E coast of S America

Delphinus styx Gray, 1846; S Africa.

Delphinus euphrosyne Gray, 1846 N Pacific.

Euphrosyne or blue-white dolphin; *deilf riabach* (Irish Gaelic).

RECOGNITION

Small, swift dolphin (Plate 16) with slender beak, superficially resembling common dolphin but shorter beak. Always in groups. Frequently breaches clear of water, showing black lateral stripes from eye to flipper and eye to anus that give its name; distinctive light grey blaze on upper flanks, above and behind eye to side of dorsal fin; lacks yellow patches of common dolphin. Skull with similarly numerous teeth but lacking deep palatal grooves of common dolphin (Fig. 12.20).

DESCRIPTION

Slender torpedo-shaped body with elongated beak (to c.10–12 cm). In each jaw, 39–50 pairs of sharp, slightly incurved teeth (c.3 mm in diameter). Distinct groove separates beak from forehead. Coloration variable, dark grey or bluish grey on back, lighter grey flanks, and white belly. 2 distinctive black stripes on flanks, 1 from eye to anus (often doubled by a secondary thinner and lighter stripe originating from this band and turning downwards towards the flippers) and a 2nd thick black stripe from below eye to flippers (Fig. 12.23). Conspicuous light grey blaze originates above and behind eye, narrowing to point below dorsal fin; posterior part of flanks light grey sometimes upwards over dorsal surface of tail stock. Tapering, black flippers inserted in white region, although some individuals show rather pale flippers towards base; slender sickle-shaped, centrally-placed, black dorsal fin. Narrow tail-stock with no obvious keel; dark tail flukes with median notch.

RELATIONSHIPS

Molecular evidence suggests that *S. coeruleoalba* closest to *S. clymene*, then *S. frontalis*; also close to *Delphinus*. Spotted and spinner dolphins *S. attenuata*, *S. longirostris* should probably be in a different genus [763].

MEASUREMENTS

Length: newborn c.0.80–0.95 m; at sexual maturity 1.94–1.97 m (female), 2.01–2.28 m (male); adult female 1.85 m (mean) to 2.25 m (max.), male 2.0 (mean) to 2.4 m (max.) Weight: newborn 7–10 kg, adult mean 70–90 kg, max. c.130 kg [310, 674, 948].

VARIATION

Some intraspecific variation in pigmentation [59, 409, 1169]. Specimens from NE Atlantic longer, heavier than those from Mediterranean [60, 310]; these 2 populations are genetically distinct [167, 426, 1170]. Within Mediterranean population, specimens from S seem to be longer than those from N [208], and inshore and offshore dolphin groups significantly differentiated genetically [430]. No skeletal differences detected between E and W Atlantic populations [60]. Nuclear and mtDNA indicate Atlantic population more genetically diverse than Mediterranean one, the latter having significant heterozygote deficiency [167, 1170]. Bycaught striped dolphins from Celtic Sea showed no significant genetic differentiation (using 13 microsatellite loci) from ones stranded on SW coast of Ireland; both had similar low levels of genetic diversity to Mediterranean population [788].

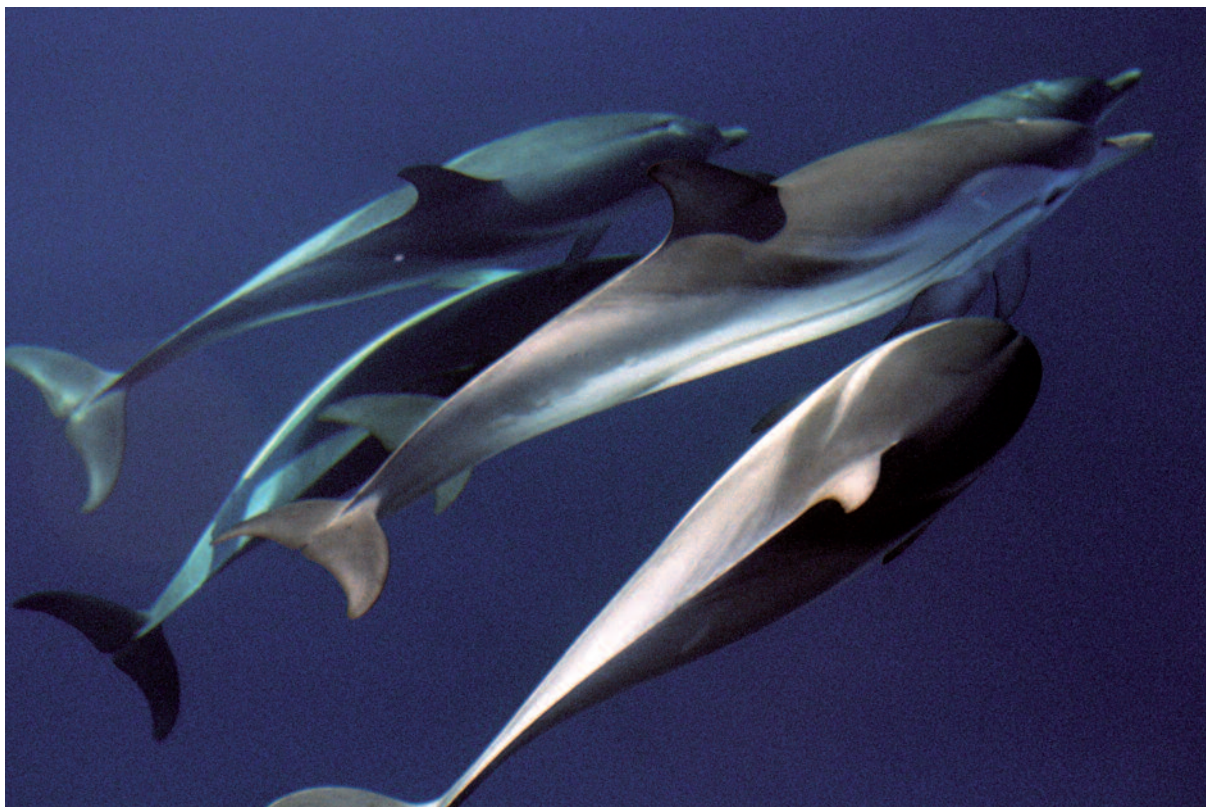


Fig. 12.23 Striped dolphins, showing the eponymous stripes (photo M. Reichelt).

DISTRIBUTION

Worldwide, mainly in tropical and warm temperate waters. In NE Atlantic, occurs mainly offshore from the continental shelf of Spain, Portugal and France (also in W Mediterranean). An occasional visitor around British Isles, recorded mainly from SW [120, 346, 358, 360]; occasionally strays in shelf waters further N to Scotland, where both sightings and live strandings recorded [346, 360, 1074] (Fig. 12.24). Records in mid Atlantic to 62° N suggest that distribution offshore extended northward by Gulf Stream [346, 358, 360].

Only 5 strandings (average 0.09/year) on British and Irish coasts 1913–1969; 9 strandings (average 0.60/year) 1970–1984; sharp increase, to 145 strandings (average 9.67/year), 1985–1999 [120, 188, 408, 816, 1002, 1072, 1074]. Some earlier *Stenella* may have been misidentified as *Delphinus*, as possible also with some Irish specimens [120, 867], but recent increase in both strandings and sightings, including records since mid 1980s from Scotland, indicate that species is ranging further N, possibly reflecting warmer sea temperatures [346, 360]. Has also been recorded recently from Icelandic, Danish, Swedish and Norwegian waters (with sightings up to 66.5° N) [144, 560].

Around British Isles (Fig. 12.24), most sightings July–September, whereas strandings

mainly December–March [120, 346, 360, 864, 1074].

HISTORY

No fossil material found. Often depicted in ancient Greek and Roman art.

HABITAT

An oceanic species of warm and temperate waters (modal SST, NE Atlantic, 19 °C); mainly occurs well beyond continental shelf in depths of >1000 m; occasionally comes on to the shelf, where recorded in waters of 60 m depth or less [360, 384, 386]. From Sea Watch database, 75% of sightings in NW European seas recorded at SSTs of 12.5–16.5 °C (total range including outliers 9.5–18 °C), but upper limits likely to be skewed low since data come from N part of its range [54].

SOCIAL ORGANISATION AND BEHAVIOUR

Sightings in British and Irish waters either single individuals (sometimes in mixed herds with common dolphins) or more usually groups up to 30 individuals [346, 358, 973]. Elsewhere, group size may number hundreds or even low thousands of animals; in European Atlantic waters, groups of 6–60 most common [973], modal group size 30 [384]. May show strong segregation by age, some

Striped dolphin

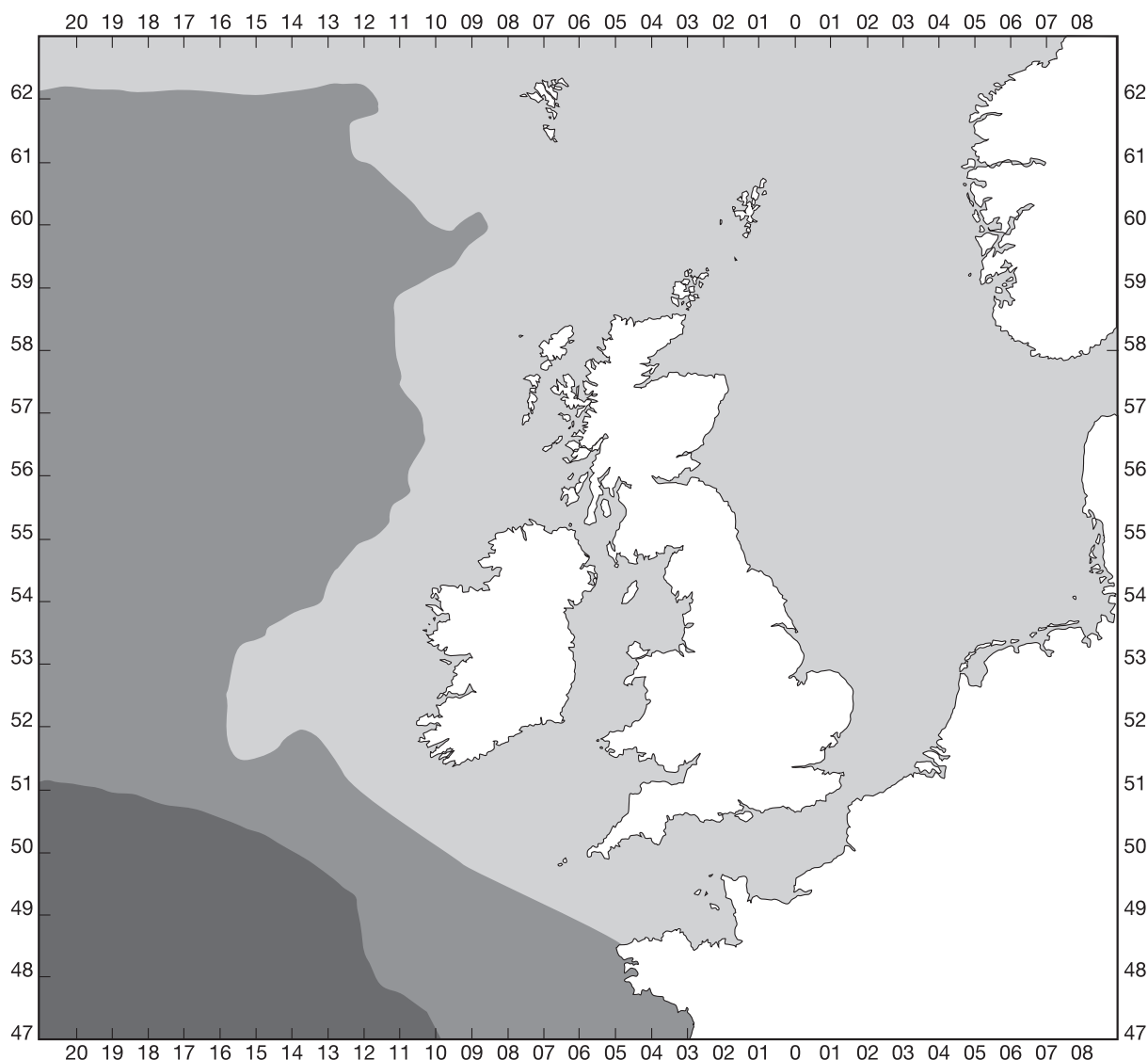


Fig. 12.24 Striped dolphin *Stenella coeruleoalba*: distribution around British Isles.

schools entirely comprising immatures, and others mixed with mature and immature males and females [799]. Some evidence of segregation of sexes outside breeding season, especially around British Isles, where recent strandings predominantly males [120, 834, 1022, 1074]. Fast swimmer (13–25 km/h [665]); frequently breaches clear of water. May also bow-ride, although less inclined than common dolphins to approach vessels.

Vocalisations: Emits clicks from 0.3 to >100 kHz (max. source level 168 dB) at repetition rates of up to 900 clicks/s, and FM whistles from 3.5 to 28.5 kHz (mainly around 10 kHz, max. source level 170 dB) [1204, 1263].

FEEDING

Diet: In E North Atlantic, feeds on a variety of

meso- and benthopelagic fish, including sprat *Sprattus sprattus*, blue whiting *Micromesistius poutassou*, *Trisopterus* spp., *Atherina* spp., silvery pout *Gadiculus argenteus*, whiting *Merlangius merlangus*, hake *Merluccius merluccius*, scad *Trachurus trachurus*, bogue *Boops boops*, anchovy *Engraulis encrasicolus*, *Chauliodus sloanei*, garfish *Belone belone*, myctophids and gobies. Squid are also frequently taken, including *Chirotheutis* spp., *Loligo* spp., *Histioteuthis reversa* and *H. bonnelli*, *Alloteuthis subulata*, *Todarodes sagittatus*, *T. eblanae*, *Ancistroteuthis lichtensteini*, *Illex coindetii*, *Abraliopsis pferrei*, *Onychoteuthis banksii*, *Brachioteuthis riisei*, *Sepietta oweniana*, and *Heteroteuthis dispar* and crustaceans such as *Pasiphaea multidentata*, and *P. sivado*, *Acantheephyra pelagica* and *Sergetes* spp. [119, 138, 304, 675, 945, 996, 1032, 1113, 1253].

Fatty acid profiles from tissues of stranded animals along Scottish, Irish, French and Spanish

12 Whales, porpoises and Cetacea: Order Cetacea

Atlantic coasts show no clear geographical separation, suggesting broadly similar diets [675]. However, stable isotope analysis of stranded animals from French Channel and Irish Atlantic coasts indicates a more oceanic diet for Irish specimens [296]. Stomach contents also differ geographically: haddock/saithe/pollack *Trisopterus* spp. and whiting more than 1/2 estimated prey weight in Scottish strandings; *Trisopterus* spp. and hake most frequently recorded from Irish strandings; in French Atlantic waters, 61% of estimated prey weight comprised a wide variety of fish, whereas squid *Todarodes sagittatus* and gobies together made up c.70% of prey weight in Galician strandings [675], and cephalopods comprised 56% of prey weight in bycaught animals from oceanic waters, Bay of Biscay, with fish (39%), particularly lanternfish, next in importance [996]. Probably change their diet as they move over the shelf [1113].

BREEDING

Reproductive parameters found to vary with exploitation pressure and populations [21, 309, 602]. Gestation period c.12 months, but lactation period between 8 and 20 (probably usually 12–14) months. Calving interval c.2–4 years. Sexual maturity reached at c.12/14 years and 182/180 cm (males/females) in Mediterranean; at 7–14 years, 211–228 cm (males) and 15–18 years, 194–197 cm (females) in E North Atlantic [309, 675]. In sample (n = 60) of Irish strandings and bycaught animals, age at sexual maturity was 15+ years (males) and 6–10 years (females) [621, 948]; asymptotic lengths were 233 cm (males) and 203 cm (females), although males exhibited a slower growth rate than females [1008]. Breeding season extended and probably variable: July–October in Mediterranean, mainly April–May in NE Atlantic [309].

POPULATION

Only population estimate for NE Atlantic covered continental shelf off SW Ireland and NW France (excluding Bay of Biscay) and NW Spain, extending up to 20° W: 73 843 (36 113–150 990) [454]. In NW Mediterranean, population estimated at 50 634 (32 254–79 488) [387], and for whole W Mediterranean basin, 225 000 (131 000–386 000) [385].

In NE Atlantic, sex ratio varied from 1:1.08 male:female in sample from tuna drift net bycatches (n = 406, 1992–1993 seasons), to 1:0.75 in a sample of stranded specimens (n = 761 from 1970 to 1999); both samples possibly unrepresentative because of age/sex segregation [269–271]. No significant variation in sex ratio from Irish strandings [621].

Longevity c.30–35 years, maybe up to 58 years [918]. No mortality rates calculated for European populations.

MORTALITY

Severe die-off due to morbillivirus infection in C and W Mediterranean, 1990–1992. Over 1100 carcasses were collected on Spanish, French and Italian coasts; nevertheless, not possible to evaluate impact on total population [18, 149, 903]. Most significant pathologies were subacute to chronic pneumonia, encephalitis and lymphoid depletion [323]. Did not affect all age classes equally: fully mature dolphins (11–20 years old) most affected [209]. Those that died during initial stages of morbillivirus outbreak (1990–1992) were significantly more inbred than those that died later [1170].

Possible predators are sharks and killer whale [271, 676].

PARASITES

Many parasites recorded, including 10 trematodes, 6 cestodes, 8 nematodes, 2 acanthocephalans and 9 crustaceans [952]. In European waters, frequently infested with nematodes, notably *Anisakis simplex* (which may provoke gastric ulceration [77]), *Stenurus ovatus*, *Skryabinialius guevarai*, and *Crassicauda* spp. Other endoparasites include tapeworms (mainly *Phyllobothrium delphini* and *Monorygma grimaldii*, but also *Strobilocephalus triangularis*, *Scolex pleuronectis* and *Tetrabothrium forsteri*), and trematodes *Pholeter gastrophilus*, *Nasitrema* sp., *Zalophotrema atlanticum*, *Campula rochebruni*, *C. palliata*, *Oschmarinella mascomai* and acanthocephalan *Bolbosoma vasculosum* [4, 304, 308, 370, 442, 739, 869]. Ectoparasitic crustaceans *Conchoderma auritum*, *Isocyamus delphini*, and *Xenobalanus globicipites*, *Lepas* spp., *Syncyamus aequus* and *Penella* spp. [4, 75, 304, 308, 370, 442, 739, 869, 1109]. Oval or circular scars on skin caused by lampreys or remoras.

RELATIONS WITH HUMANS

Occasionally hunted in S Europe (including Mediterranean). Substantial bycatch in French tuna drift net fishery operating in an area from 44–51.5° N, includes Bay of Biscay from 6° to 21° W; annual catches around 1200, representing c.1.6% of estimated population in area [272, 453, 454]. Much smaller GB albacore driftnet fishery, 1995, caused estimated bycatch of 104 striped dolphins [1053]. Irish albacore driftnet fishery, 1996, caused estimated bycatch of 134 striped dolphins, extrapolated to 964 in 1998 due to increased effort [489]; these caught mainly on N edge of Porcupine Seabight, a gently sloping area of relatively high productivity, 500–2000 m in depth [1006]. Overall,

estimated c.12 635 striped dolphins killed incidentally by combined French, Irish and GB tuna driftnet fisheries, 1990–2000 [1005]. With recent ban on driftnets and change to pelagic trawls, number of Irish bycaught striped dolphins has declined (8 striped dolphins out of 145 cetaceans in 1999 [153]).

High pollutant levels (max. 833 $\mu\text{g/g}$ wet weight PCBs and 706 $\mu\text{g/g}$ wet weight total DDT) found in blubber of striped dolphins from French Mediterranean [30]; mean levels much lower, show slight decrease over 1987–1993 [162]. M $\mu\text{g/g}$ dry weight in liver, W Mediterranean specimens [74], up to 42.6 $\mu\text{g/g}$ dry weight of cadmium in kidney [744]. Total PCB concentration may be twice as high in adult males as females, which transfer contaminants to offspring during gestation and lactation; pollutant concentrations therefore decline with age in females [161]. Mediterranean die-off due to morbillivirus infection probably facilitated by known immunosuppressive capacity of PCBs; casualties contained high levels (up to 778 $\mu\text{g/g}$ wet weight in blubber) of PCBs and 440 $\mu\text{g/g}$ wet weight of DDT [14, 15, 160].

Never maintained successfully in captivity. Legally protected in European, British and Irish waters (Table 12.1).

LITERATURE

Worldwide review [918]; recent overview [61].

AUTHORS

P.G.H. Evans & A. Collet

GENUS *Delphinus*

Differs from all other delphinids by the deep lateral grooves in the palate (Fig. 12.20).

Common dolphin *Delphinus delphis*

Delphinus delphis Linnaeus, 1758; European seas. Short-beaked common dolphin; *dolffin cyffredin* (Welsh); *deilf cyffredin* (Scottish Gaelic).

RECOGNITION

Small, swift dolphin with long slender beak (Plate 16). Often attracted to moving vessels; frequently leaps clear of water revealing distinctive hourglass pattern of yellow and light grey intersecting patches on flanks. In stranded specimens, when colour pattern has disappeared, presence of deep palatal grooves in lateral-posterior part of palate distinguishes it from striped dolphin (Fig. 12.20).

DESCRIPTION

Slender torpedo-shaped body, with long (23–

34 cm) dark beak; 41–56 pairs of small, sharp-pointed teeth (diameter c.3 mm) in each jaw. Chevron-shaped groove separates beak from low, receding forehead. Dorsal fin centrally located on back, slender and sickle-shaped to erect. Coloration variable both within and between populations [362, 521, 790, 913]. Species best identified by unique ‘hourglass’ or crisscross colour pattern formed from interaction of dorsal overlay and cape, resulting in distortions of the usual delphinine lateral and ventral fields. Lower margin of dorsal overlay passes high anteriorly and dips to cross ventral margin of low-riding cape, yielding four-part pattern of dark grey to black uppermost portion or spinal field (cape under dorsal overlay); yellow thoracic patch, dirty grey posterior portion or flank patch (undiluted dorsal overlay/lateral field), and white abdominal field [922]. Accessory abdominal stripes more common on animals from N Atlantic; distal flank blaze is either absent or less conspicuous on animals from the N Pacific [31, 521]. Dorsal fin black, but often with large creamy central patch; flipper variable, from black to light grey, particularly in E North Atlantic. Tail flukes dark grey or black, with distinct median notch. Anomalous pigmented forms described in several regions including NE Atlantic [921].

Distinct stripe runs parallel to lower margin of cape, from flipper to anus, passing below corner of gape and fusing with lip patch at >1/2 of gape length in NE Atlantic population [31]. Coloration of area adjacent to genital blaze is sexually dimorphic, males displaying prominent black blaze just above the genital opening, and females a narrower band of black and grey counter-shading [363].

RELATIONSHIPS

Both morphological and genetic data suggest 2 species: short-beaked common dolphin *Delphinus delphis* and long-beaked common dolphin *Delphinus capensis*; latter possibly contains 2 subspecies in Indo-Pacific region, nominate *D. c. capensis* and the extremely long-beaked *D. c. tropicalis* [521, 572, 833, 1012]. Recent research fails to confirm reciprocal monophyly of *D. delphis* vs *D. capensis* [33, 684]; have perhaps only very recently diverged [33, 626]. Overall, *D. delphis* populations, although highly morphologically variable, show low genetic differentiation (with evidence of gene flow across oceans), reflecting high mobility and a fluid social structure (by contrast, *D. capensis* exhibits high differentiation [833]). Closest to some of *Stenella* spp. (see above).

In N Atlantic, anatomical and genetic evidence concur that only short-beaked common dolphin present [33, 824, 833, 1184, 1224].

12 Whales, porpoises and Cetacea: Order Cetacea

MEASUREMENTS

Length: newborn 90–110 cm [268, 821], average 93 cm [1]. *D. delphis* in NE Atlantic among largest documented, with maximum body lengths 250–270 cm [404, 406, 408, 485]. However, since 1980s max. body lengths of 250 cm (males) and 230 cm (females) reported, with most individuals <230 cm [268, 919, 821, 1087]. Weight: newborn 8–10 kg; mature individuals up to 135 kg.

Sexual size dimorphism evident, with ratio of 1.06 (male:female) for body length in NE Atlantic; some cranial and other body measurements also exhibit sexual dimorphism [820, 821]. Mature males have prominent postanal hump [821].

DISTRIBUTION

Occurs worldwide, in both temperate and tropical waters. In NE Atlantic, ranges widely from subtropical waters off Africa to 70° N [217, 345,

360, 363, 496, 1216]. Occurs along mid-Atlantic ridge S of Charlie Gibbs Fracture Zone, in areas of higher SST (14 °C), and from E North Atlantic to 35 °W [217, 1200]. In W North Atlantic mostly reported between the coast and continental shelf; suggests that during summer may be distributed across entire N Atlantic. Majority of on-shelf sightings reported below 60° N latitude, and more northerly incursions offshore likely to be influenced by warm currents of N Atlantic Drift [360, 973]. On GB continental shelf, common in W half of English Channel and S Irish Sea (particularly around Celtic Deep); in smaller numbers N to Sea of Hebrides and S part of Minch [360]. Also common S and W of Ireland [122]. In some years (e.g. since c.2000), occurs further N and E in shelf seas – in N Hebrides, around Shetland and Orkney, and in N North Sea [360, 732], probably due to stronger flow of N Atlantic

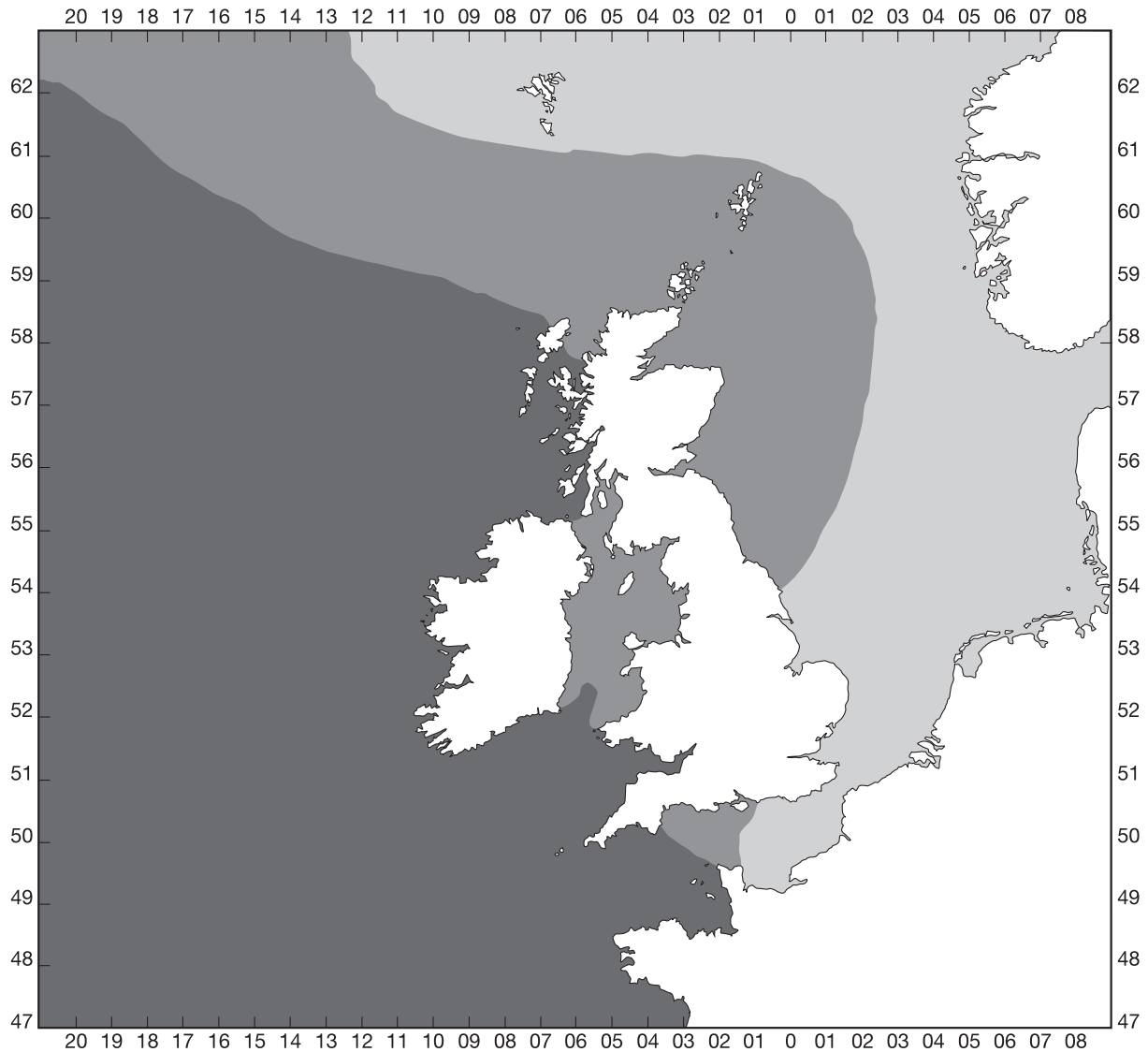


Fig. 12.25 Common dolphin *Delphinus delphis*: distribution around British Isles.

current. Generally rare in C–S North Sea and E English Channel [360, 973] (Fig. 12.25).

Distribution patterns in European seas show long-term changes. During 1930s–1970s, more strandings along Dutch and Danish coasts [91, 629], coinciding with decline along Irish and English coasts; strongly suggests a shift in general distribution [345, 356, 404, 406, 819, 824, 1071]. Decrease in strandings along English coastline appeared to coincide with changes in fish stocks off SW coast of England, and an increase in SST (Russell cycle) between 1920s and 1960s; result was that herring and whiting (along with other fish) became scarcer in English Channel, shifted their distribution northwards, with common dolphins following [356, 404, 824, 1111]. Since 1965, conditions of 1920s have returned, and have been more strandings of common dolphins along SW coast of England [361], S and W coasts of Ireland [819].

In W Scotland, sightings peak in June–July, then decline markedly; in Irish Sea, numbers peak in summer but continue to be present through winter, particularly in S [353, 360]. In W English Channel, S to Bay of Biscay, also occurs year-round, but numbers highest in winter [172, 360, 859].

HABITAT

Distribution correlated with prominent undersea topography such as seamounts and sea escarpments [362, 363], and continental slope

waters [429, 1059]. From Sea Watch database, 75% of sightings in NW European waters occurred at SSTs of 11.5–15 °C (total range including outliers 6–19 °C [54]).

VARIATION

Using genetic (mtDNA and microsatellite) and morphometric analyses of cranial specimens, low genetic differentiation reported between NE and NW Atlantic *D. delphis* populations, suggesting either recent separation or at least some gene flow [833, 1224].

Cranial morphometric analysis reveals population differentiation within E North Atlantic; female Portuguese common dolphins segregated from more northerly regions, may mix with those in the Mediterranean or further S [824]. No significant variation between W Mediterranean and adjacent North Atlantic (Straits of Gibraltar, Portugal), indicating gene flow [831]. Little differentiation between areas within NE Atlantic, suggesting high levels of gene flow [833, 789, 1184], with low or non-significant F_{ST} values and high number of shared haplotypes, although significant F_{ST} values reported using cytochrome *b* gene for both males and females within NE Atlantic [33], but sample sizes small.

Contaminant studies (cadmium levels) suggest 2 ecological stocks, in neritic and oceanic waters, Bay of Biscay, but also based on small sample sizes (from oceanic stock) [667].



Fig. 12.26 Common dolphins leaping (photo P.G.H. Evans).

SOCIAL ORGANISATION AND BEHAVIOUR

In NE Atlantic, usually travel in schools of 6–15 individuals (Fig 12.26); larger concentrations, hundreds or even thousands, sometimes observed, associated with feeding or large-scale movements [217, 340, 453, 721, 973, 1174].

Commonly bow-rides; exhibits a variety of above-surface activities, including forward and side breaches, somersaults, and tail-smacking. One, radio-tagged in NE Pacific, travelled 270 nautical miles (500 km) from capture site in 10 days [362], and even greater movements documented in E tropical Pacific [293]. Generally very agile and active, travelling at 15–20 km/h, sometimes twice as fast. Maximum recorded dive depth 280 m [362].

Evidence of age and sex segregation from sightings, mass live strandings and bycatch observed during both summer [353, 444] and winter [284, 819, 826]. In Portuguese bycatches, spring–summer, sexually mature females found only with young calves; sexually immature males either formed separate groups or joined mature male groups, with complete absence of sexually immature female groups [1087]. Elsewhere in Pacific [371] and off New Zealand [842], nursery groups and male bachelor groups reported, although large mixed groups comprising juveniles, mature males, mature females and their calves also observed [843].

Vocalisations: Include whistles of 1–50 kHz (mainly 5–20 kHz, duration 0.05–2.02 s, max. source level 172 dB); echolocation clicks, not adequately described but may reach 150 kHz (max. source levels 170 dB) at repetition rates of 30–200 clicks/s; pulsed calls, i.e. ‘buzzes’ and ‘barks’ [57, 361, 809, 1132, 1204]. Clicks and whistles may be produced simultaneously [335].

FEEDING

Diet: Includes variety of fish and squid. Reported to be opportunistic feeder [1259], but in NE Atlantic diet predominately comprises a few main species, which vary depending on season and region. Horse mackerel, mackerel, Norway pout and sardines dominant in stomachs of stranded specimens from British Isles, but other species included whiting, herring, scad, sprat and sandeel [119, 280, 451, 663, 902, 1029]. Cephalopods included mainly *Loligo* spp., *Alloteuthis subulata*, *Ancistroteuthis lichtensteini*, *Todarodes sagittatus*, *T. eblane* and *Sepioloa atlantica*, although other squid species, octopus and cuttlefish also consumed. In French inshore waters, 4 taxa contributed to majority of dietary remains: anchovy, sardine, horse mackerel, and *Trisopterus* spp. [780]. Diet

displayed strong inter-annual and seasonal variations, reflecting prey availability in area [780]. In Portuguese waters, sardine, blue whiting, *Atherina* sp., *Trachurus* and scombrid species comprised 84% of total estimated weight, with *Sardina pilchardus* most important [1086]. In Galician waters, blue whiting and sardine together comprised >56% of prey weight consumed; main cephalopods *Loligo vulgaris* and *L. forbesi*; signs of opportunistic feeding, with higher numbers of sardines consumed in years of higher sardine abundance and lower recruitment of blue whiting; other species included scad, sandeels, scaldfish, sole, gobies, garfish, and *Atherina* sp. [1038].

Feeding methods: Food-herding behaviour frequently observed with apparent cooperation between school members [342, 344]. Where preferred prey species are very abundant, tend to be selective for those species. Thus, in inshore areas during winter, mainly prey upon small pelagic fish, whereas beyond continental shelf edge in summer, apparently feed predominantly nocturnally (when deep scattering layer near surface) on squids and mesopelagic fishes, e.g. myctophids [177, 178, 491, 947a].

BREEDING

In NE Atlantic, reproduction seasonal; mating and calving May–September as indicated both by marked seasonal changes in testes mass, cellular activity, in males and by presence of ovulating and recently pregnant females [819, 823]. Newborn calves sighted or stranded in W European waters May–September [268, 340, 360, 864, 928, 1022]. In Irish waters, gestation period c.11.5 months, with annual pregnancy rate (APR) 28.2%, calving interval 42.5 months, lactation period 10.4 months and resting period 20.7 months [819]. Low APR of 25% for NE Atlantic confirmed by data collected for EU BIOCET project, from stranded animals along Irish, French and Galician (N Spain) coasts, over a 2 year period.

Although lactation may last up to 10 months after parturition, dietary studies showed that while calves aged 0–3 months had only milk in their stomachs (n = 8), those aged 3–6 months had both milk and solid food (n = 3) [178, 819].

Average age at sexual maturity (ASM) for males 11.86 years. Mature males ranged from 8 to 28 years, and 195 to 233 cm in length (Irish and French data) [823]. Combined testes mass for mature males 0.45–5 kg – relatively large considering overall size, suggesting sperm competition and promiscuous mating system [823]. Females off Irish coast attained sexual maturity between 9 and 10 years of age. Immatures ranged in body length from 93 to

184 cm, pubertal individuals from 189 to 206 cm and sexually matures from 183 to 216 cm [819]. ASM of 8 years (SE = 0.69) calculated for BIO CET project, but with 89% of mature individuals >10 years [674].

POPULATION

Several surveys using line transect methods have estimated population abundance levels in the NE Atlantic. MICA survey, summer 1993, estimated population of 61 888 (95% CI 35 461–108 010) in area where French tuna driftnet fishery operated (Bay of Biscay, continental shelf W to *c.*20° W, and S to *c.*43° N) [454]. SCANS I survey, July 1994, included the Celtic shelf to *c.*11° W and 48° S, gave estimate of 75 450 (CV = 0.67; 95% CI 23 000–249 000) [481]. Where surveys overlapped in area along shelf edge (11° W–51° N to 8° W–48° N), total summer population estimated at *c.*120 000 [453]. During August 2002, the ATLANTIC aerial survey covered 140 000 km² of continental shelf and shelf break in Bay of Biscay; overlapped with SCANS I survey area in S Celtic Sea, gave estimate of 17 639 (95% CI 11 253–27 652) [994, 1227]. NASS Faroese ship-based survey, 1995, covering 2 large areas to N and W of Ireland (NASS east and NASS west), gave estimate of 273 159 (95% CI 153 392–435 104) for western block [217], whereas SIAR survey estimated only 4496 (95% CI 2414–9320) within area *c.*120 000 km² off W Ireland during 30 July–22 August 2000. Differences may have resulted from survey design and/or precise area covered [864].

MICA and SCANS I did not use a double-platform method, nor correct for animals missed on track line (*g*(0)) and responsive movements; estimates from these surveys may therefore be inaccurate. In 2005, SCANS II surveyed same area as SCANS I, but increased to include Irish Sea, waters off W and N Ireland, W Scotland, and continental shelf waters off France, Spain and Portugal. Total summer abundance for those NE Atlantic shelf waters *c.*63 400 (CV = 0.46) [478].

MORTALITY

Possible predators are sharks, and killer or false killer whales, although no cases reported in European waters [676]. Bottlenose dolphins reported to attack common dolphins in NE Atlantic; carcass of sexually mature lactating female stranded on W coast of Ireland extensively bruised, especially along ventral abdomen between both pectoral fins, and had >25 sets of recent bottlenose dolphin rake marks along body [822].

Maximum age reported in NE Atlantic, 28 years [823]. No mortality rates calculated for this population.

HEALTH STATUS

In British waters, overall increase in numbers stranded since early 1990s, with 3-fold increase since 1999. Most reported in January–March, along SW coast of GB [579]. Increase in strandings attributed to increase in reporting effort, and/or increase in numbers caught in fishing gear, and/or increase in relative density of animals in W English Channel during winter [1023]. During 2000–2004, 61.1% (116/190) of autopsied stranded *D. delphis* diagnosed as incidentally caught in fishing gear, with 15.3% dying as result of a live stranding event, and 3.7% from starvation [1023]. In previous 10 years (1990–1999), data from 212 autopsies found that 56% of individuals died as result of entanglement in fishing gear, 8.9% from a live stranding event, 3.7% from pneumonia, with cause of death in 22.2% of cases undetermined [114, Table 3.3].

In general, common dolphins caught in fishing nets were in good health, and in good nutritional condition. Overall, mortality due to infectious disease rare. A few recent cases of fatal *Brucella* sp. meningoencephalitis in common dolphins in Scottish waters [580]. Overall, low seroprevalence of antibodies to morbilliviruses in common dolphins and other GB-stranded cetaceans examined 1989–1999, and probably therefore only accidental host to cetacean morbillivirus [1023]. [173, 174]. Pathological evidence that common dolphins (and other cetaceans) can suffer *in vivo* gas bubble formation [580]; 5 common dolphins stranded on British coasts 1992–2004 showed acute and chronic systemic gas and fat embolism, which caused acute and chronic lesions in various organs including liver, spleen, kidneys, and lymph nodes [580, 1023].

PARASITES

Often infested with nematodes, including lungworm *Halocerus delphini*, stomach worm *Anisakis simplex*, which may provoke gastric ulceration, and tissue worm *Crassicauda* sp. [77, 488]. Cestodes, e.g. *Phyllobothrium delphini* and *Monorygma* sp., and trematodes, e.g. liver fluke *Campyla* sp. and stomach fluke *Pholeter gastrophilus*, also reported [488]. Whale lice and barnacles *Xenobalanus globicipites* observed only rarely.

RELATIONS WITH HUMANS

Main current cause of concern for NE Atlantic population is large-scale but poorly documented incidental capture in fishing nets [489, 813, 1160, 1161]. In 1990s, extensive bycatch by W European tuna driftnet fisheries [489] led to closure of these fisheries in 2002. Recent PETRACT project estimated total bycatch of common dolphins in GB, Irish, French, Dutch and Danish pelagic trawls, December 2003–May 2005. Incidental

captures reported only in bass and tuna fisheries, with <c.1000 dolphins/year, c.95% identified as common dolphins [859]. Also reported bycaught in following fisheries in NE Atlantic: French, Irish and GB hake fisheries [813, 1161]; Dutch horse-mackerel fishery [279]; and also in Spanish trawls, gillnets and seine nets [720]; and Portuguese gill, beach seine and trawl nets [1087]; consequent bycatch mortality rates not determined.

Numerous contaminants investigated in NE Atlantic, including mercury [533], cadmium [295, 667], lead [232], hexabromocyclododecane [1264], DDT and PCBs [10, 30, 163, 164, 663]. A Σ -PCB level of 17 $\mu\text{g/g}$ lipid reported as threshold level for effects on reproduction in bottlenose dolphin [1051]. However, in W European waters, 40% of the *D. delphis* sample exceeded this threshold value [928]. Highest PCB concentrations in blubber were generally in resting mature females with high numbers of corpora albicantia on their ovaries; unclear whether high contaminant burdens prevented them from reproducing, and inhibited ovulation, or females not reproducing for some other reason, either physical or social, and therefore accumulated high contaminant levels, as unable to pass burdens on to their offspring via placenta or through lactation.

Legally protected in European, British and Irish waters (Table 12.1).

LITERATURE

Worldwide review [363]; overview [913].

AUTHORS

S. Murphy, P.G.H. Evans & A. Collet

GENUS *Lagenorhynchus*

Conventionally a genus of about 6 species of slender dolphins with fewer, larger teeth than *Delphinus* or *Stenella*. However, taxonomy uncertain, molecular data suggest that may not be monophyletic on current taxonomy [962], and *L. acutus* certainly belongs in a different genus from *L. albirostris* (see below).

White-beaked dolphin *Lagenorhynchus albirostris*

Lagenorhynchus albirostris Gray, 1846; Great Yarmouth, England.

Deilf-gheal-ghobach (Scottish Gaelic); *deilf na ngoba bána* (Irish Gaelic).

RECOGNITION

Large, very stout dolphin (Plate 16) with short (5–8 cm) beak (often white in colour), black back except behind dorsal fin, where pale grey to whitish area extends from flanks, forming a distinctive pale ‘saddle’; also grey to whitish blaze on flanks forward of dorsal fin. Black and whitish pattern very distinctive in the field, less obvious in dead animals. Large, often erect, sickle-shaped dorsal fin, centrally placed. Flippers larger, less clearly sickle-shaped than in white-sided dolphin, with fairly straight front margin. Adult skull distinguished from that of white-sided dolphin by being larger and broader, with wider and clearly tapering rostrum and with fewer and larger teeth.

DESCRIPTION

Very stout torpedo-shaped body, rounded snout



Fig. 12.27 Dorsal view of a white-beaked dolphin, showing both the beak and the characteristic black/white pattern on the flanks (photo D. Burn).

White-beaked dolphin

with short, fairly stubby beak and 22–28 pairs of small (*c.*7 mm diameter), sharp-pointed teeth in each jaw. Dark grey or black on back, tail and top of head; dark flank patch of varying extent below dorsal fin, separated from dark back by paler grey coloration of flanks. Pale grey to whitish area extending from flanks over dorsal surface behind fin and back to tail stock ('saddle': less distinct in young animals); pale grey to whitish blaze extending from below dorsal fin forward, sometimes forming pale 'chevron' over head or back (and sometimes passing over the blowhole) (Fig. 12.27). Beak generally white (not always easy to see in the field), but often blotched or spotted with dark grey; sometimes nearly all grey, always paler and contrasting with blackish dorsal surface. Pale eye ring, sometimes connected to beak by thin, white line. Flippers and tail blackish; front edge of flippers near base and lower surface of tail

often freckled with white. Ventral surface white; on central part of abdomen restricted to narrow band between greyish flank patches. Centrally placed, tall (*c.*15% body length), sickle-shaped dorsal fin. Thick tail stock, gradually tapering towards the slightly notched tail flukes, with concave trailing edges.

Adult skull larger, broader, than Atlantic white-sided dolphin, with wider, clearly tapering rostrum, fewer and larger teeth (Fig. 12.20). Lachrymal short and thick, not extending backward below frontal; ramus of lower jaw high, upper margin ascending behind tooth row, ending in a prominent coronoid process. Scapula much wider than high, more or less mushroom-shaped, with clearly concave hind margin. Upper process (acromion) directed nearly horizontally forward; ventral margin of lower process (coracoid) clearly projecting downward below glenoid fossa. Front

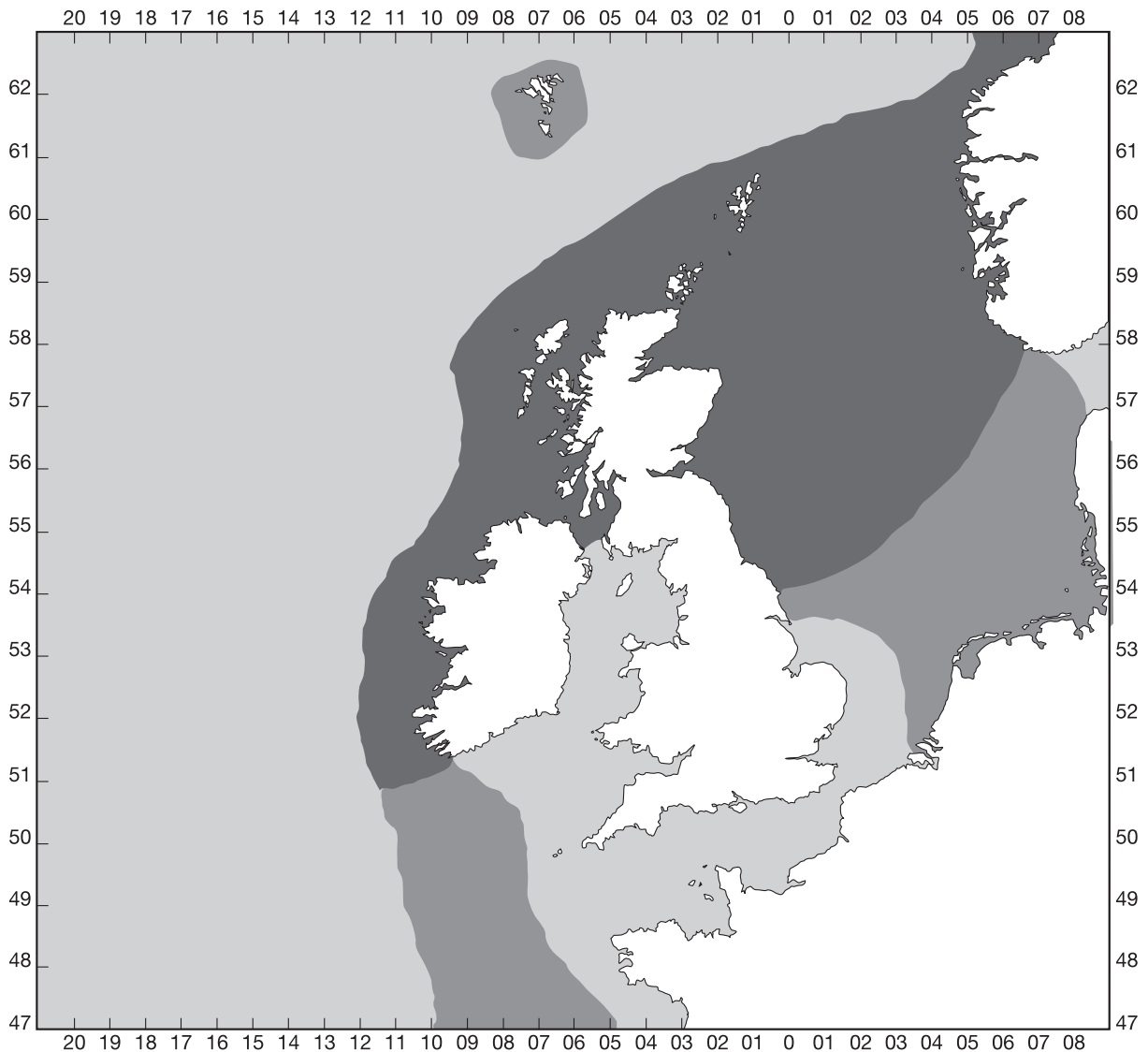


Fig. 12.28 White-beaked dolphin *Lagenorhynchus albirostris*: distribution around British Isles.

12 Whales, porpoises and Cetacea: Order Cetacea

margin of flipper skeleton nearly straight, particularly the radius; combined width of radius/ulna at their distal end about equal to length of radius. These skeletal characters more similar to bottlenose dolphin than to Atlantic white-sided dolphin [1, 112, 800, 969].

RELATIONSHIPS

Analysis of cytochrome *b* [684], osteological characters including skeletal pathology (see below) and occurrence of apparently unique ectoparasite (see below) evidence that white-beaked dolphin not closely related to Atlantic white-sided dolphin, best placed in different genus. Generic name *Lagenorhynchus* thereby restricted to *L. albirostris*, type species for the genus.

MEASUREMENTS

Length: newborn 110–120 cm; at sexual maturity 230–250 cm (female), 250–260 cm (male); adults generally 240–270 cm (female), 250–280 cm (male); max. *c.*3.0 m (female), 3.1 m (male). Weight: newborn *c.*40 kg, adult max. 306 kg (female) (although one pregnant female, Netherlands, weighed 387 kg), 354 kg (male) [413, 630, 970].

VARIATION

Specimens from E and W Atlantic differ in skull characters [783]. Animals in British waters and North Sea may be partially separated from other populations [857, 858]; see also [876].

DISTRIBUTION

Restricted to northern N Atlantic, from SW and CE Greenland, Svalbard and Barents Sea, S to about Cape Cod (USA) and Bay of Biscay. Occurs over much of N European continental shelf; common in British and Irish waters, most abundantly in C and N North Sea across to W Scotland and Ireland; occasional off S Ireland, in the Irish Sea, W Channel, and N Bay of Biscay [97, 340, 345, 346, 360, 481, 857, 858, 973, 1236] (Fig 12.28). Similar distribution to the Atlantic white-sided dolphin, though less pelagic, generally more abundant on the continental shelf [340, 346, 360, 481, 857, 858, 973].

General decline (numbers sighted per unit effort), NW Scotland, since early 1980s; may reflect distributional change [346, 360]. Strandings significantly increased in S North Sea since 1960s, now regularly occur in S Bight [91, 630]. Other important concentrations occur off N Norway [876].

Recorded throughout the year in British waters, but largest numbers seen in late summer, July–September. May move offshore in winter, though poorer coverage may explain lower numbers seen

then in nearshore waters [340, 341, 360, 857, 858].

HISTORY

No fossil or archaeological material known.

HABITAT

Found in cool and subarctic waters, usually over the continental shelf in waters 50–100 m deep. From Sea Watch database, 75% of sightings in NW European waters occurred at SSTs of 11–13 °C (total range including outliers 3–17 °C) [54].

SOCIAL ORGANISATION AND BEHAVIOUR

Most groups <10 individuals, but herds up to 50 not uncommon off NW Scotland, and a few sightings of groups numbering 100–500. Some segregation by age and sex, and, within larger aggregations, subgroups of 2–5 individuals commonly observed. Strandings of small groups (2–7 animals) not uncommon [970]. Otherwise, social structure poorly known. Groups of juveniles may be separated from groups of adults with calves [970]. Apparently adult males generally stay further offshore: of white-beaked dolphins stranded in the Netherlands, juveniles (<2.2 m) show a sex ratio of 1:1, but larger animals predominantly females. Predominance of females among stranded animals also found Denmark, Germany [630].

Moderately fast swimmer, usually travels at 6–12 km/h, attains bursts of 30 km/h [353]. Frequently approaches boats and bow-rides. Often breaches clear of the surface, leaping vertically, falling back into the water usually on its back or side, sometimes directly on to belly [97, 353]. Sometimes associates with fin, sei, and humpback whales, as well as with long-finned pilot and killer whales. Sometimes mixed herds with Atlantic white-sided dolphins, occasionally also with bottlenose dolphin, Risso's dolphin or common dolphin [148, 213, 340, 353, 467, 586, 970].

Vocalisations: Poorly known. Include whistles of 6.5–15 kHz (often *c.*8 kHz), with average source levels (SL) of 180 dB re 1 μ Pa @ 1 m. Echolocation clicks up to at least 325 kHz, with click bursts of 100–750 pulses/s, and maximum SL of 214 dB re 1 μ Pa @ 1 m (mean SL = 204 dB, mean inter-click interval = 51 ms) [795, 796, 957, 970, 1204].

FEEDING

Diet: Great variety of fish (including *Clupea*, *Mallotus*, *Gadus*, *Merlangius*, *Melanogrammus*, *Trisopterus*, *Eleginus*, *Merluccius*, *Trachurus*, *Scomber*, various species of *Ammodytidae*, *Gobiidae*, *Soleidae*, *Pleuronectidae* and *Bothidae*), snow crab *Chionoecetes opilio* and octopus *Eledone cirrhosa*.

Analyses of stomach contents, North Sea and Newfoundland, reveal cod *Gadus morhua*, whiting *Merlangius merlangus* and hake *Merluccius merluccius* as dominant prey [1, 340, 630, 970, 1032] [324, 428, 1101].

Feeding methods: Herds fish cooperatively. Groups seen hunting in a broad front, dolphins swimming parallel to each other at regular distances; fish shoals then encircled and trapped near the surface. Seabirds, particularly northern gannet, kittiwake, and other gull species often closely associate with feeding white-beaked dolphin groups [1, 341, 342].

BREEDING

Data limited. Births mainly in late spring-summer (May–August), with some in September–October [340, 346, 360, 408, 630, 970]. Gestation period c. 10–11 months. Lactation period, calving interval and age at sexual maturity unknown. 3 pregnant animals, Newfoundland, at least 7 years old [324].

POPULATION

SCANS I survey, North Sea and adjacent waters, June–July 1994, gave estimate of 7856 (95% CI 4032–13 301) white-beaked dolphins, or of 11 760 (95% CI 5587–18 528) combining white-beaked and unidentified *Lagenorhynchus* (great majority probably white-beaked). All records were from North Sea and directly NW of Scotland, between c. 54–60° N, 6° W–7° E [481]. Repeat survey (SCANS II), July 2005, covering a wider area (continental shelf seas from SW Norway, S to Atlantic Portugal), gave estimate of 22 700 (CV = 0.42) [478].

MORTALITY

Observed fleeing from pod of killer whales; frequently have scars thought to be caused by sharks and killer whales, but direct evidence of predation lacking [340, 970, 353]. Longevity at least 32 years (males) and 39 years (females) [413]. No information on mortality rates.

PARASITES AND PATHOGENS

2 whale-lice recorded: *Scutocyamus parvus* found on animals from North Sea; unknown from other dolphin species; a few records of *Isocyamus delphinii*, also from North Sea [1, 401].

Endoparasites: Nematodes *Anisakis simplex* (digestive tract) and *Halocercus lagenorhynchi* (bronchi) [170, 324, 441, 1065]; also *Pseudoterranova* sp. (stomach) [64], with trematode *Pholeter gastrophilus* also found [442].

Dystocia (birth trauma in mother, rather uncommon in other dolphins) found several times

[424, 631]. Pneumonia occasional [424, 631]; in 1 animal stranded on Dutch coast, dystocia was associated with morbillivirus, in another with rhabdovirus [630, 885]; morbilli- and rhabdovirus also found in other animals from Dutch coast; 1 stranded in Suffolk had antibodies to morbillivirus [173]. Poxvirus in the skin reported [88]. Diseased jaws and teeth frequent in older animals [646, 970]. Discarthrosis (spondylosis deformans) and spondyloarthritis (spondyloarthropathy: reactive arthritis of the vertebrae) much more common in white-beaked dolphins than in other cetaceans; in one study, discarthrosis reported in 54% of 22 adult females and in 42% of 7 males [646–648]. A few animals found with kyphosis (S-shaped vertebral column) [646, 970]

RELATIONS WITH HUMANS

Organochlorine levels in blubber, kidney and muscle of 27 white-beaked dolphins from Newfoundland were high, considering that all <7 years old; also high levels of lead in kidney, liver and muscle. May have been overwintering in highly polluted Gulf of St. Lawrence [817]. Organochlorine levels in animals from GB generally low [770], as also in Denmark [50], E USA [619], although sample sizes small. Except for lead, heavy metals examined in an adult female, Liverpool Bay, also low [671a, 672]; same true for 7 stranded along Belgian and N French coasts [294].

Other threats poorly known, although small numbers reported bycaught from midwater trawls and driftnets set mainly for cod, mackerel, salmon or herring [347, 855].

Legally protected in European, British and Irish waters (Table 12.1).

LITERATURE

Most recent scientific review [970].

AUTHORS

P.G.H. Evans & C.S. Smeenk

GENUS *Leucopleurus*

Included in *Lagenorhynchus* by most authors, but molecular and genetic evidence argue for separation (see below). Since *L. albirostris* is type species for *Lagenorhynchus*, the generic name *Leucopleurus* (Gray 1866) is applicable to *L. acutus*.

Atlantic white-sided dolphin *Leucopleurus acutus*

Delphinus (Grampus) acutus Gray, 1828; type locality probably North Sea.

Deilf-chliathaich-ghil (Scottish Gaelic); *deilf le cliathán bán* (Irish Gaelic).

12 Whales, porpoises and Cetacea: Order Cetacea

RECOGNITION

Similar to white-beaked dolphin but somewhat smaller. Large, robust dolphin (Plate 16) with short beak, black back; distinctive long, white patch on flanks; narrow, yellow-ochre band extending backwards on tail stock. Large, sickle-shaped dorsal fin, centrally placed. Flippers smaller, much more clearly sickle-shaped than in white-beaked dolphin, with strongly curved front margin. Skull smaller, narrower, with more but smaller teeth.

DESCRIPTION

Stout, torpedo-shaped body, rounded snout with short (*c.* 5 cm) beak. Black on back including tail, top of head and upper jaw; dark grey flanks and side of head; long and narrow, sharply demarcated white patch on flanks from below front edge of dorsal fin to about halfway between dorsal fin and tail (Fig. 12.29), but not extending over back (as often in white-beaked dolphin). Sharply demarcated, long, narrow yellow-ochre band extending on to tail stock, starting as a thin line above the white flank patch and widening towards the tail, set off from grey flanks below by a black line originating from the tail stock. White belly and lower jaw. Flippers pointed and strongly re-curved, black; narrow dark stripe extends from angle of mouth to flipper insertion. Black eye patch, from which a thin black line extends forward to the dark upper jaw, and very thin black line from eye patch to ear opening (not visible in the field). Clearly demarcated black patch around

genital/anal opening. Relatively tall (*c.* 12% body length), centrally placed, sickle-shaped dorsal fin. Very high tail stock, parallel-sided, particularly in adult males, in which it suddenly narrows close to the slightly notched tail flukes, which have a concave trailing edge.

Adult skull smaller and narrower than in white-beaked dolphin, with narrower and only slightly tapering rostrum and with more (29–40) and smaller (*c.* 4 mm diameter) teeth. Lachrymal long and narrow, extending far backward below frontal. Ramus of lower jaw low, upper margin behind tooth row nearly horizontal over about 2/3 of its length, no pronounced coronoid process. Scapula only slightly broader than high, with nearly straight hind margin. Upper process (acromion) directed more or less upward, ventral margin of lower process (coracoid) not or only slightly projecting below glenoid fossa (joint socket). Flipper skeleton strongly curved, particularly the radius; combined width of radius/ulna at the distal end greater than height of radius [1, 112, 800, 969, 970].

RELATIONSHIPS

Previously thought closely related to white-beaked dolphin *Lagenorhynchus albirostris*, and thus placed in same genus. Cytochrome *b* sequences indicate that not closely related, best placed in separate genera [684]. Corroborated by considerable skeletal differences, and occurrence of seemingly unique ectoparasite on white-beaked dolphin (see above).



Fig. 12.29 Atlantic white-sided dolphins rolling, to show distinctive white and yellow-ochre band on flanks. (photo P.H.G. Evans).

MEASUREMENTS

Length: newborn 108–122 cm; at sexual maturity 2.0–2.2 m (female), 2.3–2.4 m (male); adult, generally 210–240 cm (female), 210–260 cm (male); max. *c.*253 cm (female), *c.*274 cm (male). Weight: newborn *c.*25 kg; max 182 kg (female), 234 kg (male) [8, 1007, 1066].

VARIATION

No differences in skull characters between specimens from E and W Atlantic [783].

DISTRIBUTION

Restricted to N North Atlantic, mainly in offshore waters, from SW Greenland, Iceland and W Barents Sea S to Virginia (USA) and the Bay of Biscay. Less common than white-beaked dolphin on European continental shelf [346, 360, 481, 858, 876, 973]. Off British Isles, concentrated around

Hebrides, N Isles and N North Sea, but extends S along Atlantic seaboard, mainly outside or near the continental shelf (*c.*200 m depth), W and S of Ireland and Bay of Biscay; rare in the Irish Sea, English Channel and S North Sea (Fig. 12.30) [279, 340, 346, 360, 630, 688, 858, 969, 973, 1236].

HISTORY

No fossil or archaeological material known.

HABITAT

More pelagic than white-beaked dolphin, occurring mainly along edges or seaward of continental shelves, over depths of 100–300 m. Sometimes comes on to continental shelf, may enter fjords and inlets with depths <50 m. From Sea Watch database, 75% of sightings in NW European seas recorded at SSTs of 7–13 °C (total range including outliers 6–17.5 °C) [54]. In

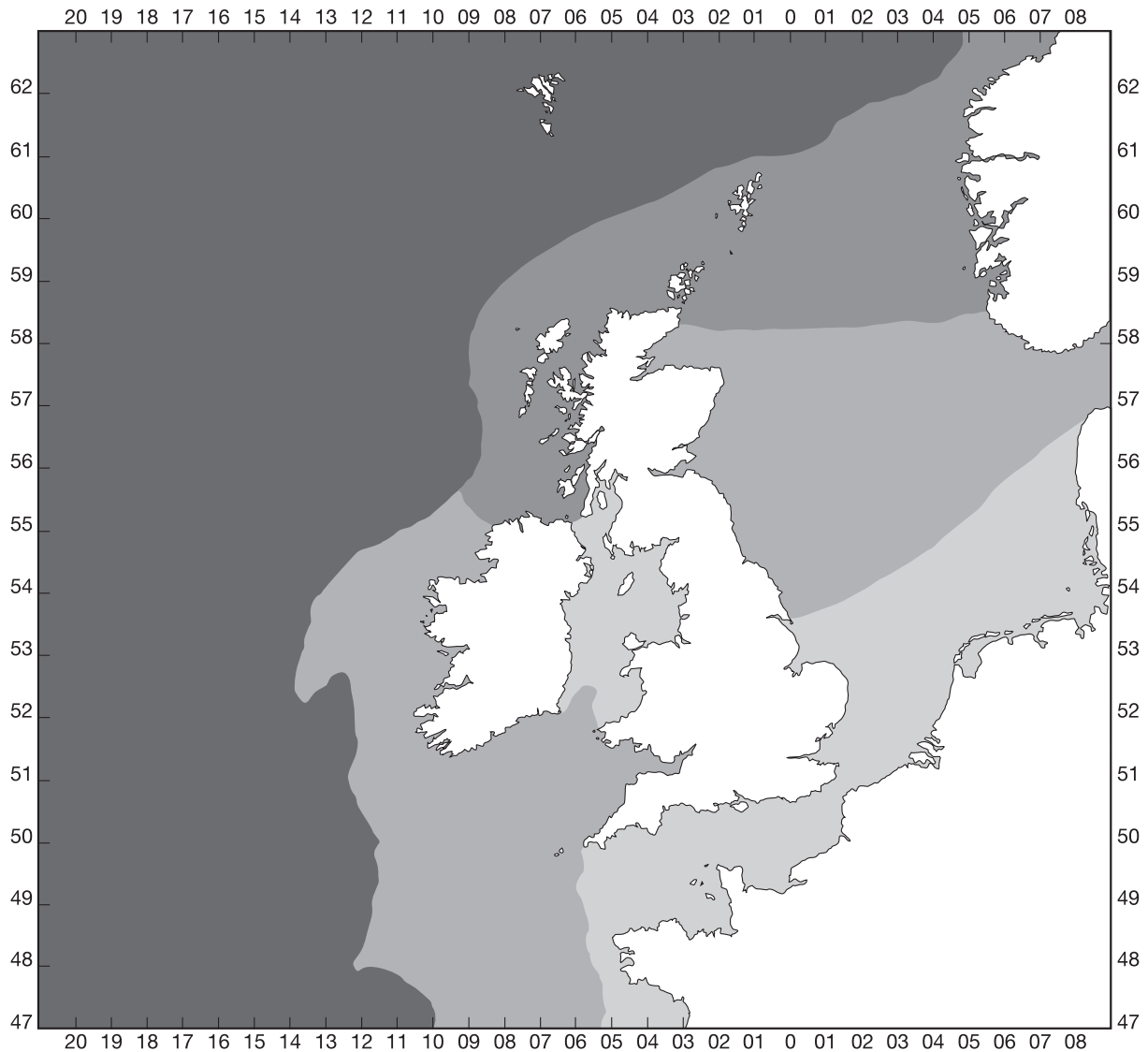


Fig. 12.30 Atlantic white-sided dolphin *Leucopleurus acutus*: distribution around British Isles.

12 Whales, porpoises and Cetacea: Order Cetacea

European seas, occur mainly in SSTs of *c.* 7–12 °C [360]. In E USA, occupies waters of 1–13 °C in spring and autumn, but most occur in waters of *c.* 5–11 °C [1059].

SOCIAL ORGANISATION AND BEHAVIOUR

Very gregarious; groups in E North Atlantic frequently 10s–100s, particularly offshore [340, 346, 360]. Groups up to 1000 recorded on American continental shelf and at shelf edge W and S of Ireland [688, 969]. Within large aggregations, subgroups of 2–15 animals may be distinguished [148, 353, 428, 467, 688]. Groups include both sexes, ages mixed, but possibly with some age segregation, since in 2 mass strandings, immatures aged 3–6 years (assuming 1 dentinal growth layer = 1 year) were absent from breeding groups consisting of adults and calves [1007, 1066]. However, immatures found with adults in bycatches W and S of Ireland [8]. Otherwise, social structure poorly known.

Fast swimmer, travelling over long distances at 14 km/h [760]. Bow-rides occasionally. Frequently breaches, though not as much as white-beaked, bottlenose or common dolphins. Mixed herds frequently formed with white-beaked dolphins, less often with bottlenose and common dolphins; sometimes associate with long-finned pilot whales, northern bottlenose whales, sperm whales, fin whales, and humpback whales [148, 213, 457, 467, 606, 969].

Vocalisations: Include whistles of 7–16 kHz frequency, with mean peak frequencies of 8–12 kHz, and mean duration 0.5 s, and broadband echolocation clicks at 0.2–180 kHz with peak frequencies of 60–80 kHz and single pulse duration of 0.25–1 ms [1204].

FEEDING

Diet: Wide variety of fish (including *Clupea*, *Osmerus*, *Gadus*, *Merlangius*, *Micromesistius*, *Trisopterus*, *Merluccius*, *Scomber* and Salmonidae), squid (*Illex*, *Loligo*) and shrimps [1, 304, 340, 427, 969, 1066, 1101, 1195].

Stomachs of 17 animals in a mass stranding, Co. Mayo, Ireland, September 1994, contained otoliths of gadoid fishes including *Trisopterus* sp., herring *Clupea harengus*, horse mackerel (scad) *Trachurus trachurus*, as well as an argentine *Argentina sphyraena* and a squid beak [1007]. Stomachs of 50 white-sided dolphins from bycatch of Dutch mesopelagic trawl fishery for mackerel and horse-mackerel, 1992–1994, at shelf edge (near 200 m depth contour) W and S of Ireland, revealed mainly mackerel *Scomber scombrus* (67% prey weight) and Gadidae (mainly silvery pout

Gadiculus argenteus: 9% prey weight), various other fish including lantern fish *Notoscopelus kroeyerii*, and cephalopods (13% prey weight, at least 12 species). Nearly all collected in February–March, when mackerel arrive in the area on southward migration, probably attracting white-sided dolphins from deeper waters. One animal, same area, September, showed Gadidae (45% prey weight: mainly silvery pout and blue whiting *Micromesistius poutassou*) and cephalopods (52% prey weight: nearly all Ommastrephidae). In all cases, horse-mackerel was conspicuously absent from stomachs, despite being important target of Dutch fisheries [279, 280].

Feeding methods: Small groups frequently seen herding fish by surface-rushing in a crescent-shaped configuration [353, 688].

BREEDING

Data limited. Births mainly late spring–summer (May–August) [340, 358, 408, 969, 1066], sometimes as early as February and as late as September [8, 1007]. Gestation period *c.* 11 months [1007, 1066]. Lactation period *c.* 18 months [1066]. Calving interval 2–3 years, some animals being both lactating and pregnant [1007, 1114]. Age at sexual maturity 7–11 years (males) and 6–12 years (females), assuming 1 dentine layer/year [8, 1066].

POPULATION

No comprehensive population estimates; estimate of 5587–18 528 *Lagenorhynchus* includes an unknown proportion of white-sided dolphins [481]. Most commonly observed over GB continental shelf July–September; apparently concentrated in deep waters off shelf edge November–May [340, 346, 360, 688, 857, 858, 973].

Greatest number of dentine layers reported so far is 27 in a female, implying age of at least 27 years, and 22 in a male [1066]. Population structure unknown.

MORTALITY

Sharks and killer whales are likely predators, but no attacks reported.

PARASITES AND PATHOGENS

Internal parasites (with body locations where known) found in stranded specimens [79, 131, 438, 441, 442, 1007, 1195] include:

Trematodes: *Pholeter gastrophilus* (stomach and duodenum), *Oschmarinella laevicaecum* (bile ducts and hepatopancreatic ducts).

Cestodes: *Tetrabothrius forsteri* (upper intestine),

Phyllobothrium delphini (blubber), *Strobilocephalus triangularis*, *Monorygma grimaldii* (abdomen, peritoneum and testes).

Nematodes: *Anisakis simplex* (trachea and stomach), *Stenurus globicephalae* (stomach and cranial sinuses), *Crassicauda grampicola* (subcutaneous tissue, mammary glands, see below), *Crassicauda* sp. (subcutaneous tissue; frequently observed, with over 50% of the animals affected in some studies [424, 437, 438, 1007]), *Pseudalius inflexus* (bronchi and lungs), *Torynurus convolutus* (head sinuses), and *Bolbosoma* sp. (intestine).

In 2 mass strandings, Maine (USA), September 1974 and Ireland, September 1994, high incidence of parasitic mastitis caused by the nematode *Crassicauda grampicola* [437, 438, 1007]: 14/30 females in Maine, 5/7 adult females in Ireland, also recorded in bycatch victims [424]. Can severely damage the mammary glands and thus affect milk production [438]. From Irish stranding, neoplasia found in 3/19 animals; 2 cases of benign intestinal leiomyomas and 1 of intestinal fibroma [1007]. In Maine, 4/41 animals had various papillomas, 5 had intestinal leiomyomas. Adrenal lesions such as nodular hyperplasia and cyst formation were found in 20/23 females (and in 1 male) of Maine sample [437]. 2 cases of adrenal adenoma [438]. *Brucella* sp. isolated from a male stranded, Scotland [399].

RELATIONS WITH HUMANS

Not hunted commercially, though taken opportunistically by drive fisheries for small whales in Faroes, up to 500 taken some years [141], formerly also in Norway and Canada. Probably hunted in small numbers off SW Greenland [502]. Incidental mortality in fishing gear reported from British Isles, Ireland and Canada [279, 347, 969]. Numerous in bycatches from former Dutch trawl fishery for mackerel and horse-mackerel near the shelf edge W and S of Ireland. About 90% of this mortality in February–March [279].

Few examined for pollutants, and few details given (e.g. [158, 294]). 17 animals from mass stranding, Ireland, and 5 stranded, Scotland, analysed for chlorobiphenyls (CBs) and organochlorine pesticides [660, 770]. Levels generally low, but 2 adult males had CB levels of >40 and >60 µg/g in blubber. Similar concentrations in 2 bycaught males (1 adult) from Canada. Some of Irish animals also had relatively high levels of pesticides, particularly *p,p'*-DDE, dieldrin and HCB, as had the 2 males from Canada [660, 770]. Juvenile stranded, NW Ireland, had a high concentration (44 µg/g wet weight) of mercury in the liver [672], much higher than in

adult male from Canada [660]. High levels of cadmium in the kidneys of 2 stranded, Belgium, perhaps related to diet [294].

Legally protected in European, British and Irish waters (Table 12.1).

LITERATURE

Good review [969], brief popular overview [245].

AUTHORS

P.G.H. Evans & C.S. Smeenk

GENUS *Lagenodelphis*

Described by Fraser in 1956 from a skeleton brought back from Sarawak over 50 years previously, holotype in NHM, London; external morphology and colour pattern not described until early 1970s [916]; a monospecific genus, intermediate between *Lagenorhynchus* and *Delphinus* in characters.

Fraser's dolphin *Lagenodelphis hosei*

Lagenodelphis hosei Fraser, 1956; mouth of Lutong R., Baram, Borneo.

RECOGNITION

Small, stocky dolphin with a short but distinct beak, small flippers and dorsal fin (Plate 16). Deep palatal grooves; 34–44 teeth in each jaw. Usually in groups, frequently leaps clear of water, showing dark grey to black back, grey flanks and white to pink belly with broad darker stripes from beak to flipper and from eye to genital area. At a distance, eye-to-anus stripe may resemble striped dolphin, and not always visible, but body shape distinctive.

DESCRIPTION

Small dolphin with very short beak (3–6 cm), general shape not as slender as *Delphinus* sp. but not as stocky as *Lagenorhynchus* sp. Forehead slopes gradually to short beak; 34–44 pointed teeth in each jaw; deep palatal grooves. Small flippers; small pointed subtriangular dorsal fin, placed centrally on back. Coloration variable [918]: grey-brown back and appendages, pale grey flanks separated from whitish or pinkish belly by a thick dark stripe running from eye to genital area (although dark stripe sometimes missing on juveniles), giving appearance of 'masked' dolphin (possibly a feature of adult males). Sometimes another dark thick stripe from beak to flipper, but both dark stripes may be faint or absent in some populations. Dorsal fin slightly falcate in calves and females, more erect or canted in adult males. Similarly, postanal hump either absent or slight in females and young, well developed in adult males.

12 Whales, porpoises and Cetacea: Order Cetacea

RELATIONSHIPS

Member of subfamily Delphininae. Cytochrome *b* mtDNA sequences suggest closer to *Stenella*, *Tursiops*, *Delphinus*, and *Sousa* than to *Lagenorhynchus* [684]. Morphologically, skull structure similar to common dolphin *D. delphis* in possessing deep palatal grooves but to *S. longirostris*, *S. coeruleoalba*, and *S. clymene* in several other characteristics.

MEASUREMENTS

Length: newborn *c.*0.9–1.1 m; at sexual maturity *c.*2.1–2.2 m (female), *c.*2.2–2.3 (male) [918]; adult mean 2.2 m, max. 2.64 m (female), mean 2.4 m, max. 2.70 m (male); weight up to 209 kg. Body size may vary over range, Atlantic animals larger than E Pacific [171, 419].

HABITAT

Primarily found in open oceans, particularly warm equatorial waters (between 30° N and 30° S), such as deep waters around oceanic islands where sometimes come very close to coast. Extensions into higher latitudes may be associated with incursion of warm oligotrophic waters. Depth preferences apparently *c.*500–5000 m, although can occur in shallower waters adjacent to continental shelf.

DISTRIBUTION

Poorly known: worldwide in tropical pelagic waters, with rare intrusions into temperate coastal waters (South Australia, Uruguay, British Isles, France). Live sightings in N Atlantic reported from Caribbean (e.g. Dominica, Martinique), Azores and Canaries. First record in European waters, from mass stranding, N Brittany coast, 1984 [171]. Only 1 confirmed record in British waters; a single male stranded on S Uist, Scotland, 1996 [150].

SOCIAL ORGANISATION AND BEHAVIOUR

Most schools 100–1000 individuals but small groups of 4–15 seen. Social structure unknown, groups of mixed sexes and ages reported. Fast, very active swimmers (*c.*20 km/h and more), making low-angle splashy leaps. May approach boats to bow-ride but can also actively avoid boats. Breaches are common. Often associate with other cetaceans, particularly *Peponocephala electra*, but also others (*Globicephala macrorhynchus*, *Pseudorca crassidens*, *Stenella attenuata*, *S. longirostris*, *S. coeruleoalba*, *Grampus griseus*, *Tursiops truncatus* and *Physeter macrocephalus*).

Vocalisations: Information limited, but sounds include at least 2 types of whistles similar in frequency to those produced by *Stenella* (0.5 s and

0.2 s duration), burst pulse vocalisations and echolocation clicks [683, 1211].

FEEDING

Diet: Unknown while in British waters. Specimens stranded on N Brittany coast had fed on blue whiting *Micromesistius poutassou*, *Trisopterus* spp., whiting *Merlangius merlangus* and *Sepia* sp. [171]. In tropical E Pacific and Sulu Sea, feeds on mesopelagic fishes (Myctophidae and Chauliodontidae), shrimps (Oplophoridae), and (in Sulu Sea) squid [319, 1001].

Feeding methods: Takes prey from near surface to depths of at least 500 m; in S Indian Ocean and W Pacific, it may also feed far below the surface [1017, 1153]. In French Polynesia, during daylight hours mainly observed travelling or resting, so possibly feeding largely nocturnally at least in some regions [418]. Myoglobin levels comparable to levels in deepest divers like northern bottlenose whale and sperm whale [321].

BREEDING

Only sparse data available; suggest no strong breeding seasonality. Births may occur year-round, but in Japanese waters peaks in spring and autumn, whereas in S Africa peak in summer. Males reach sexual maturity from 7–10 years of age, and females from 5–8 years. Single testis weight 1–2 kg in mature specimens, which suggests polyandrous or promiscuous breeding strategy [918]. Annual ovulation rate *c.*0.49, gestation period *c.*12.5 months. No information on lactation period. Calving interval *c.*2 years.

POPULATION

Presumably only transient in British waters; no confirmed sightings of live animals despite extensive sighting efforts. Abundance elsewhere in Atlantic unknown; not uncommon in Caribbean, occurs in large groups. Only data on sex ratio and age structure comes from 2 mass strandings, France, Japan [32, 171]. Both schools comprised juveniles and adults of both sexes (aged 5–16 years, France; up to 17.5 years, Japan).

MORTALITY

Probable predators are large sharks, killer whales and false killer whales. Cookie-cutter sharks (*Isistius brasiliensis*) thought to inflict circular wounds.

PARASITES

As many other delphinids, often infested by *Phyllobothrium delphini* and *Monorygma grimaldii*, other cestodes found: *Strobicephalus triangularis* and

Melon-headed whale

Tetrabothrius sp.; trematode *Campula* sp.; nematodes *Anisakis simplex* and *Stenurus ovatus*; acanthocephalan *Bulbosoma* sp. [918]. External parasite, *Xenobalanus* sp. also reported.

RELATIONS WITH HUMANS

Those captured for exhibition died within 14–100 days [476]. Small numbers harpooned in Lesser Antilles and W Pacific, incidental captures in various nets in tropical E Pacific and Philippines, S Africa, Japan and Sri Lanka [265, 318, 679]. Levels of organochlorine pollutants reported for 1 specimen [868].

Legally protected in European, British and Irish waters (Table 12.1).

LITERATURE

General reviews for the species [320, 918].

AUTHOR

P.G.H. Evans

Melon-headed whale *Peponocephala electra*
Lagenorhynchus electra Gray, 1846; N Pacific.

RECOGNITION

Very dark, almost black, with slender form. (Plate 16) Triangular head with rounded forehead but with very indistinct beak, often white lips. Dark mask-like eye patch distinct in good light or under water. Centrally placed sickle-shaped dorsal fin. Flippers have pointed tips (in very similar pygmy killer whale, are usually rounded at tip, more sinuous along rear margin). At close range, and from above, an important distinguishing feature is longer, less-rounded head (in pygmy killer whale, is much shorter and more rounded).

Skull resembles *Lagenorhynchus* but with more rounded cranium, much larger antorbital notches, and much shorter tooth row relative to total length of rostrum. From 20–26 teeth in each half of upper and lower jaw (cf. pygmy killer whale, <15). High tooth count separates skull from other small beakless whales.

DESCRIPTION

Torpedo-shaped body with triangular head and rounded forehead, and slightly underslung jaw presenting a very indistinct beak. In each jaw, 20–26 small, sharply pointed teeth. Mouth terminal to subterminal, angles slightly upward towards eyes. Posterior segment of gape turns slightly downward, ending just below or forward of eye, and thickened at base of lower lips. Body moderately robust in front half, tapering to slender peduncle. Coloration dark grey but with paler belly, particularly around anus and genital region; lips

often white, light grey or pink. Indistinct pale grey anchor-shaped throat patch, and, in some populations, indistinct downward-pointing darker triangle or cape below dorsal fin. Cape is narrow over the head, thorax, and anterior half of tail stock, but dips downward near dorsal fin to form dark triangular region with its apex pointing ventrally, lower limit ill-defined (unlike pygmy killer whale). Dark eye patch broadens as extends from eye to melon, giving appearance of wearing a mask. Long (to 52 cm or more), dark, narrow, tapered flippers, generally pointed at tips, with relatively straight rear edges. Tall (to c.30 cm) centrally placed sickle-shaped dorsal fin, pointed at tip. Slender tail stock, but some males have pronounced ventral keel posterior to anus. Males also have proportionately longer flippers and broader tail flukes than females [129, 802].

Skull typically delphinid in shape but with very broad rostrum and deep antorbital notches; resembles bottlenose dolphin in size, shape and tooth count, but teeth of melon-headed whale much smaller and more delicate looking, distance between antorbital notch and end of tooth row proportionally greater, and premaxillaries do not converge at midlength of rostrum.

RELATIONSHIPS

No congeners. Considered closely allied to false killer whale *Pseudorca crassidens* and pygmy killer whale *Feresa attenuata* [849], but morphological [601] and genetic [1076] evidence indicate the species is most closely related to the pilot whales *Globicephala* spp.; these 4 genera a distinct clade [962].

MEASUREMENTS

Length: newborn c. 1 m [191]; adults c.2.3–2.8 m (males possibly slightly larger than females, asymptotic lengths 2.52 m and 2.43 m). Appears smaller (c.2.0–2.4 m) in French Polynesia and Caribbean [419]. Weight c.160–228 kg.

VARIATION

No information except that dorsal cape clearly visible in E tropical Pacific, Gulf of Mexico, and Philippines, but not around Hawaii [925]. No obvious variation between French Polynesia and Caribbean, however, with cape clearly visible in both regions under suitable light conditions [419].

DISTRIBUTION

Poorly known; occurs around the world in deep offshore tropical and subtropical waters, mainly between 40° N and 35° S. In N Atlantic, most frequently reported from E coast USA (Maryland), Gulf of Mexico (Texas, Louisiana), and Caribbean (St Vincent, Dominica, Puerto Rico). Rather few

12 Whales, porpoises and Cetacea: Order Cetacea

sightings or strandings reported from E North Atlantic: include strandings from Senegal and sightings off Sierra Leone and Cape Verde, Western Africa. Stranding near Charlestown, Cornwall, September 1949, previously identified as *Lagenorhynchus albirostris* [408], found on re-examination to be *Peponocephala electra* [784]; is first record for GB and Europe. Since then, 2 live stranded in France near La Rochelle, August 2003. Such extralimital records may reflect incursions of warmer water further N.

HISTORY

No fossil or archaeological material known.

HABITAT

Occurs mainly in deep warm waters (>1000 m depth), seaward of the edge of continental shelves; can be observed around oceanic islands, where schools may aggregate during daylight hours [419].

SOCIAL ORGANISATION AND BEHAVIOUR

Little information, but groups often very large, 150–1500 individuals [190, 925, 1067, 1191]. Schools tend to be highly packed, travel rapidly with frequent course changes, creating a crescent of water that may obscure clear view of the animals. Is reported to bow-ride slow-moving vessels; sometimes breaches. Relatively inconspicuous at sea, has been recorded swimming just under the surface with dorsal fins exposed, occasionally coming above the surface sufficiently to expose the head and upper body. On diving, tail stock strongly arched. Like pilot whales, sometimes spy-hops with head above the water. During fast porpoising, a pair of 'water moustaches' escape from each side of the head during expiration [419].

Social organisation not known, stranded groups include both sexes and varying ages. Mass strandings reported on several occasions, and one exhibited a female preponderance of 2:1, implies some sexual segregation [718], supported by observation of male-only groups of 10–15 [419, 476]. Associations with Fraser's dolphin frequently reported [298, 682, 801, 925], but may also associate with spinner dolphins and bottlenose dolphins [319]. Scavenging seabirds (e.g. Parkinson's petrels) may associate with herds of melon-headed whales [936].

Vocalisations: Poorly known.

FEEDING

Diet: Small fish, larger ommastrephid squid (e.g. *Dosidicus gigas*), and shrimps [129, 207, 513, 571, 925, 916].

Feeding methods: Has been reported herding and possibly attacking small dolphins (*Stenella* spp.) escaping from tuna seine nets in the tropical Pacific [678], although possibility of confusion with *Feresa*.

BREEDING

Season poorly known, but, in N hemisphere, a neonate was found in July and a near-term (80 cm) fetus collected in October [925], and in S hemisphere, newborn calves also observed during warm season [419]. Gestation period c.12 months [191]. Lactation period and calving interval unknown. Males mature somewhere between 3 and 7 years; females between 4 and 12 years (assuming 1 dentinal/cemental growth layer group = 1 year) [191]. Smallest mature female 230 cm [925]; smallest mature male 248 cm [129].

POPULATION

Only population estimate is 45 000 from a recent survey of E tropical Pacific [1191]; no information on abundance in N Atlantic, but large herds may be seen in E Caribbean [353]. Longevity up to 47 years (on growth layers) [191].

MORTALITY

Mass strandings reported in Australia, Vanuatu, Seychelles, Japan, Brazil, Kwajalein Atoll, Hawaii and Costa Rica [925, 1111], with suggestion that may be caused by panic response in the school when a few members accidentally strand [802], or in case of Hawaii stranding, possibly use of mid-frequency sonar in the vicinity [1111]. No information on predation on this species, but scars thought to be caused by sharks observed, and those of the cookie-cutter shark *Isistius brasiliensis* found on stranded specimen [129].

PARASITES AND PATHOGENS

Remoras observed attached to free-swimming animals in tropical E Pacific [925]. Cyamid whale lice have been found on the exterior [801], and traces of barnacles possibly of the genus *Xenobalanus* on the tail flukes [190].

Internal parasites include trematode *Nastrema gondo* (tympanic cavity); nematodes *Stenurus globicephalae* (tympanic cavity), *Anisakis simplex* and *A. typica* (stomach); and acanthocephalan *Bolbosoma* sp. (rectum); and cestodes *Monorygma* (intestines) and *Halocercus* (host tissue not specified), *Phyllobothrium chamissoni* (blubber, intestines, and between peritoneum and abdominal muscles) [129, 190, 220, 288, 811].

RELATIONS WITH HUMANS

Rarely encountered by humans. Taken opportunistically in various drive fisheries,

particularly off Japan [798]. A herd of *c.*500 animals came into Sturga Bay, Japan, March 1965, half driven ashore and consumed [849]; further 200 animals were trapped in Taiji Bay, Japan, 1980 [797]. Elsewhere, 4 animals landed by small whale fishery on St Vincent, Lesser Antilles [207]; a male calf caught in a tuna net off Guatemala, tropical E Pacific [911]; occasionally harpooned or netted near Sri Lanka and in the Philippines [476, 679, 682]. Specimens from a mass stranding in E Australia, 1973, used as bait in lobster pots [190]. More systematically, melon-headed whales have been taken in the well-established harpoon fishery for sperm whales and various small cetaceans near Lamalera, Indonesia [102, 681]. Focus of opportunistic commercial whale-watching operations in the Marquesas [419].

Sometimes bycaught in various fisheries, including harpoon and drift net fisheries in Philippines [318], Indonesia, Malaysia, and Caribbean; in N Indian Ocean off Sri Lanka [681], and occasionally in E Pacific tuna purse seine fishery [911]. Has been held in captivity in the Philippines, on Hawaii, and in Japan, but generally has not thrived [476, 1067]. In Hawaiian waters, said to have aggressively approached divers [923], but many non-aggressive interactions with divers reported from French Polynesia [419].

Legally protected in European, British and Irish waters (Table 12.1).

LITERATURE

Reviews [923, 925].

AUTHOR

P.G.H. Evans

GENUS *Globicephala*

A genus of 2 closely related species, only 1 of which occurs in NE Atlantic; other has a tropical to warm temperate distribution.

Long-finned pilot whale *Globicephala melas* *Delphinus melas* Traill, 1809; Scapa Bay, Orkney.
Globicephala melaena Thomas, 1898.

Pilot whale, blackfish, caa'ing whale (Shetland), pothead whale; *muc-mhara-chinn-mhoir* (Scottish Gaelic); *miol phiolótach* (Irish Gaelic).

RECOGNITION

Black or dark grey medium-sized whale (Plate 14), with square bulbous head; low dorsal fin, sickle-shaped in subadults and females but more broad-based in adult males, situated slightly forward of centre of back. Long slender flippers. Male larger, with broader dorsal fin and more

bulbous head, than female. Skull similar in shape to killer and false killer but has much smaller teeth.

DESCRIPTION

Long slender body becoming more robust with age, with square bulbous head extending over upper lip, particularly in old males. In each jaw, 8–12 pairs of small (<13 mm diameter) peg-like teeth. Flippers long (usually >15% of body length), pointed and sickle-shaped (in short-finned pilot whales and similar false killer whales, <15% of body length [143, 909, 1063, 1258]). Coloration black or dark grey on back and flanks (young born lighter grey) with 3 areas of lighter pigmentation which are variable in extent and intensity: the throat patch (an anchor-shaped area of greyish white on chin extending to grey on belly, also called the throat chevron), the postdorsal saddle patch (a grey area behind and below the dorsal fin extending down to the midpoint of the body), and the postocular (or postorbital) blaze (a light grey stripe extending backwards from behind the eye, often connecting with the leading edge of the dorsal patch). Fairly low dorsal fin, slightly forwards of midpoint (to the front 1/3 on longer adult males), with long base, sickle-shaped (in adult females and immatures) to broad, with hump on leading edge (in adult males), usually black, but sometimes grey. As changes shape with age, dorsal fin becomes more rounded and less dolphin-like. Thick keel on tail stock, more pronounced on adult males. Tail flukes have concave trailing edge, are deeply notched in centre. Sexual dimorphism of individual features (e.g. dorsal fin, melon overhang) are all related to larger body size in males [143], i.e. there is no indication of allometric growth patterns.

RELATIONSHIPS

2 closely related species of pilot whale: long-finned, *G. melas*, and short-finned, *G. macro-rhynchus*; differ in a few morphological features, principally pectoral fin length, but also skull features. Their primary difference is distributional: short-finned is found in tropical waters (>25° C), while long-finned has antitropical distribution in temperate waters of N and S hemispheres [297]. Relationships to other Globicephalinae uncertain, seem closest to *Peponocephala*, then *Feresa* and *Pseudorca* [962].

MEASUREMENTS

Length: newborn *c.*175–178 cm (weighing 60–80 kg); at sexual maturity *c.*3.0–4.0 m (female), *c.*5.0 m (male); adult *c.*4.0–5.0 (max. 6.0) m (female), *c.*5.5–6.0 (max. 8.5) m (male).

VARIATION

Pigmentation patterns noted to vary between N and S hemisphere populations of long-finned pilot whales in the Atlantic, separated by tropical short-finned pilot whale *G. macrorhynchus*, when they were first proposed as separate species [959]. Later suggested that indicated subspecific variation [297], but even this has been questioned [985]. Morphometric differences have been reported between pilot whales of E and W North Atlantic [142]. Genetic studies showing differences between pilot whales off Greenland and elsewhere in Atlantic suggest SST as an isolating mechanism, perhaps through temperature-dependent distribution of favoured prey [412]. Variability in pigmentation patterns was noted between individual Faroese pilot whales, but this could not be related to school membership [143], and thus was unlikely to be genetic. Variation in isozyme

frequencies suggest that there may be restricted gene flow between certain pods [41, 42]. Analyses of pollutant levels and profiles in Faroese pilot whales showed pod-specific variability, implying 2 subpopulations with 2 different food resources [160, 231]. Genetic analyses of numerous loci have revealed high levels of variation between pods because of the high degrees of relatedness within pods [35, 38].

DISTRIBUTION

Widespread in temperate regions of the world, mainly in offshore waters. Common and widely distributed in NE Atlantic from Iberian peninsula and Bay of Biscay, N to Faroes and Iceland; also common in Mediterranean. (Short-finned pilot whale overlaps this distribution, with strandings in N Spain [446, 854]). Around British Isles, during 1970s–early 1980s, was the most

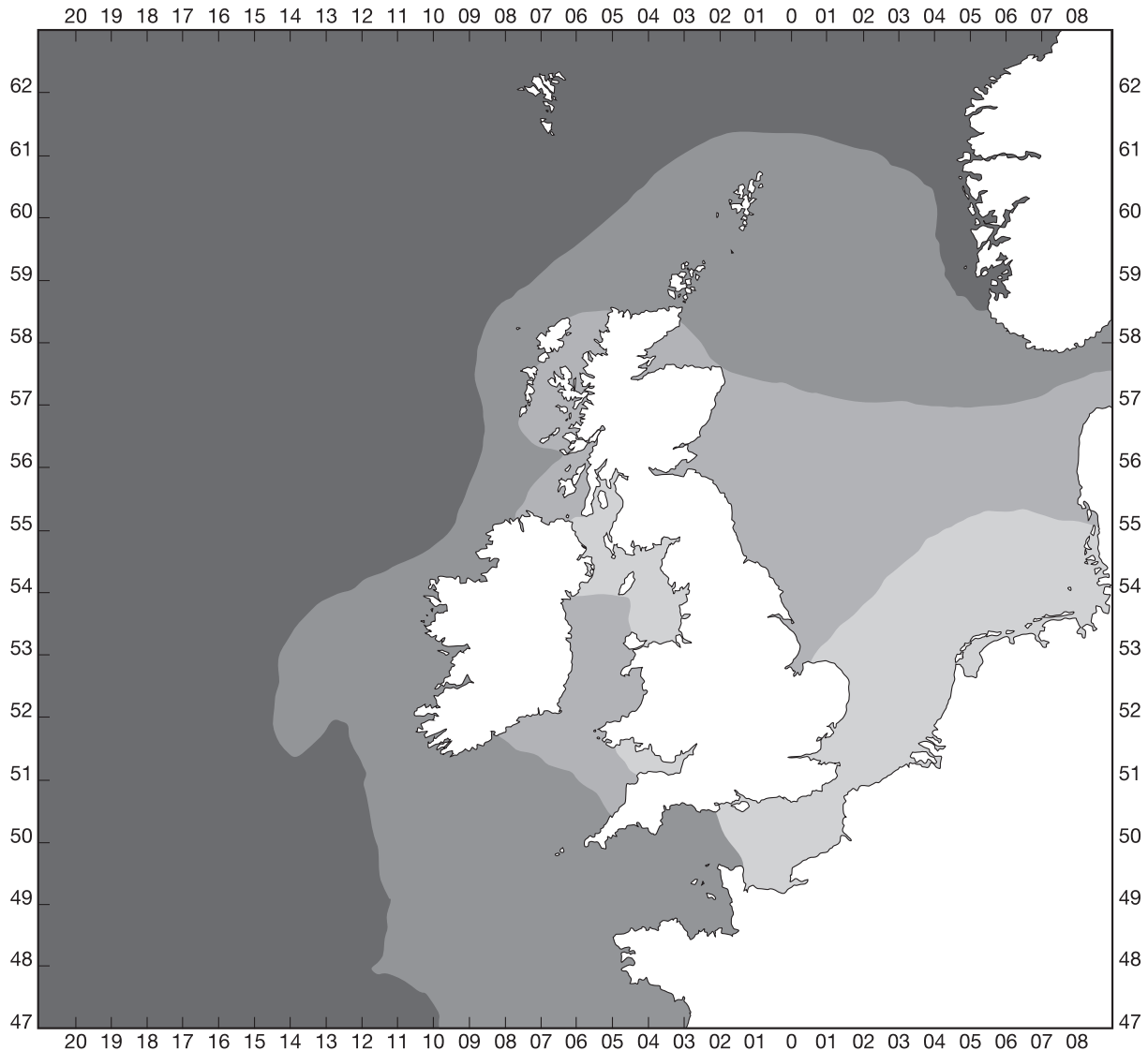


Fig. 12.31 Long-finned pilot whale *Globicephala melas*: distribution around British Isles.

commonly observed whale species [340, 358], but has since become relatively uncommon [346, 358, 360]. Mainly pelagic, seaward of continental shelf edge, with main concentrations occurring in Faroe-Shetland Channel, Rockall Trough, Porcupine Bight and SW approaches to English Channel [360, 973, 1216]. Thus, most sightings over the shelf occur in northern GB (NW and N Scotland), W of Ireland, and in W English Channel [358, 360, 973]. Rare throughout North Sea, except northern-most sector (Fig. 12.31).

Sighted in all months of the year, but numbers in shelf waters highest November–January; possibly associated with an autumn inshore movement following their prey [358, 360]. Sightings offshore from weather ships, 700 km W of Scotland, showed lowest numbers over same period [340, 358].

HABITAT

In E North Atlantic, usually occurs in deep temperate and subpolar waters of 200–3000 m depth (particularly around 1000 m isobath) seaward and along edges of continental shelf where bottom relief is greatest; may occasionally venture into coastal waters, entering fjords and bays [360].

SOCIAL ORGANISATION AND BEHAVIOUR

Gregarious; herds of 20–40 common, sometimes may number hundreds–low thousands (though probably representing temporary coalitions of social groups, particularly during mating/breeding period) [340, 346, 358]. Samples from mass strandings and coastal drive fisheries have revealed herd structure [41, 42, 306, 748, 751, 1062]. Most groups comprise females with calves, immatures and 1 or more adult males. Sex ratio of groups often biased 3:1 in favour of females. All individuals within a pod, including adult males, related [36]; however, males were not the fathers of the calves in their pod, and so mating must be occurring between males and females from different pods [44]. Paternal alleles suggest that fetuses within a cohort may share same father or have related fathers [36], indicating some degree of variability in male mating success. Adult males may serve a defensive role for the pod, often position themselves between a vessel approaching a herd and females with young.

Photo-ID has been attempted with this species [215, 885a, 1214], but use limited by low recognisability of individuals [73].

Relatively slow swimmer, travelling at *c.*5–15 km/h, though may attain *c.*40 km/h. Rarely bow-rides although may allow boats to approach. Usually moves through water in undemonstrative

manner, scarcely ever breaching clear of water (generally only young animals), though may slap surface with tail. Frequently lies vertically in water with head and top of flippers above surface. On occasions, observed resting motionless on surface. Dolphins (mainly bottlenose and Atlantic white-sided) may associate with pilot whale herds (Fig. 12.22).

Tracking studies reveal very variable travel patterns. Off the Faroes, one small group of 4 related individuals averaged 70–111 km/24 h, but the maximum distance travelled was 200 km/24 h [146]. Other studies have tracked pilot whales for 3144 km over 94.5 days in NW Atlantic [761].

Diving behaviour characterised by short, shallow daytime dives (<16 m), with longer (mean *c.*8 min, deep dives occurring at night [85]. Maximum dive durations *c.*26 min [506, 761, 835], and maximum depth 648 m [85].

Vocalisations: Include variety of whistles mainly at 3.4–4.7 kHz lasting 0.65–1.0 s, and echo-location clicks of 0.1–100 kHz [1137], [1214]. Comparisons found vocalisations of long-finned pilot whales to be lower in frequency, longer in duration, and over a narrower frequency range than for short-finned pilot whale [984, 1120, 1137].

FEEDING

Diet: Mainly squid (notably *Todarodes*, but also *Ommastrephes*, *Loligo*, *Gonatus* and *Sepia*), but also variety of fish (*Anguilla*, *Conger*, *Dicentrarchus*, *Gadus*, *Merluccius*, *Molva*, *Pollachius*, *Scomber*, *Solea*, *Trachurus* and *Trisopterus*) [3, 118, 259, 304, 305, 344, 421, 422, 887, 930]. Diet varies with reproductive condition: lactating females ate a greater proportion of fish off the Faroes [305].

Feeding methods: Observations of captive animals show they can use suction feeding [123].

BREEDING

No distinct breeding season, although some evidence for slight peak in births, late winter–early spring (January–March) [340, 346, 751]. Further N, in Faroes, conceptions peak April–July, most births July–September [306, 748], though differences may only reflect variation between pods. Gestation period *c.*14–16 months. Lactation *c.*22 months. Calving interval 3–4 years. Various estimates of age at sexual maturity: 10–12 years (male) and 6–7 years (female) for shore-driven specimens, Newfoundland [1062]; 9–14 years (male) and *c.*7 years (female) from British mass strandings [751]; and 15–20 years (male) and 9–10 years (female) for shore-driven specimens from Faroes [306, 307, 748].

12 Whales, porpoises and Cetacea: Order Cetacea

POPULATION

Surveys across the N Atlantic estimated 778 000 (CV 0.295) long-finned pilot whales in 1989, but coverage did not extend fully into British waters, accuracy of estimates limited by difficulty of estimating group size and distance to centre of group [194]. Longevity at least 20 years (male) and 25 years (female), possibly higher due to difficulty in reading dentine layers in teeth of older animals [751]. Lifespan estimated elsewhere at 40–50 years [1063]. Although segregation of sexes in herds may occur, skewed sex ratios (c.60% females) suggest higher mortality rates for males than females.

PARASITES AND COMMENSALS

Studied intensively in 125 Faroese specimens [953]; 15 species were recorded: whale louse *Isocyamus delphini* common around natural openings and wounds; barnacle *Xenobalanus globicipitis* rare, around natural openings or on edge of dorsal fin and flukes; 3 trematodes, mainly *Pholeter gastrophilus*, also *Leucasiella* sp., and rarely *Odhneriella* sp., in stomach and intestine; 4 cestodes *Trigonocotyle* sp., *Phyllobothrium delphini*, *Diphyllobothrium* sp., *Monorygma grimaldii*, either within blubber or in intestine; 5 nematodes, mainly *Anisakis simplex* and 3 *Sternus* spp., also *Crassicauda* sp., in gut (*Anisakis*), lungs, air sinuses, and tympanic bullae (*Sternus* spp.), and within mammary glands (*Crassicauda* sp.); and one acanthocephalan *Bolbosoma* sp. in intestine.

RELATIONS WITH HUMANS

Organised drives have taken place for at least 11 centuries in Faroes, average annual catch of 850 from 1709 to 1992 [1262]; still continue. Other drive fisheries have operated opportunistically, mainly in Shetland and Orkney, but also in Outer Hebrides and W Ireland, until early 20th century. Extensive fishery in Newfoundland, Canada, 1947–1972. Otherwise, small numbers taken by the coastal Norwegian small whale fishery, off W Greenland and Iceland. Legally protected in European, British and Irish waters (Table 12.1).

Accidental capture in fishing nets is also a problem: off France, 50–100/year were estimated killed in nets [912]; off USA, incidentally caught in mackerel trawl fishery and in a variety of squid fisheries [366, 1198]. Bycatch mortality also reported in British waters, mainly in English Channel during 1960s and 1970s [340, 356].

Relatively high levels (up to 95 µg/g wet weight in blubber) of PCBs found in stranded animals in GB [751] and up to 995 µg/g PCBs in an immature from W Mediterranean [30]. PCB levels generally similar between animals in Faroes [1091] and W Atlantic [778, 1152]. High levels of DDT, PBDE,

mercury and cadmium also recorded from Faroes [160, 231, 686, 699, 841, 845]. Pollutant levels in pilot whale meat consumed by Faroese may exceed 'safe' levels of toxicity allowed for human consumption [1091]. Faroese pilot whales have adapted to high cadmium levels by increasing levels of metallothionein, a known aid to detoxification [34].

Pilot whales change vocalisations in vicinity of military sonar [983], increasing number of whistles; significance currently unknown. Exposure to military sonar previously implicated in some cetacean deaths [578]. Ship strikes may also pose a threat, as has been suggested for the related short-finned pilot whale [22].

AUTHORS

J.R. Boran, P.G.H. Evans & A.R. Martin

GENUS *Pseudorca*

A monospecific genus, resembling *Orcinus* in few, robust, teeth (7–12 in each jaw) but these circular in cross-section.

False killer whale *Pseudorca crassidens*

Phocoena crassidens Owen, 1846; Lincolnshire Fens (subfossil).

Blackfish; *cráin dubh bréagach* (Irish Gaelic).

RECOGNITION

Almost all black, form slender (Plate 15). No beak. Small, slender, tapered head with rounded snout projecting beyond extremity of lower jaw. Tall sickle-shaped dorsal fin, centrally placed. Skull with large teeth, proportionately somewhat smaller than those of killer whale and circular (not oval) in cross-section.

DESCRIPTION

Long slender body with small, tapered head; underslung jaw contains 7–12 pairs of large (25 mm diameter) teeth, circular in cross-section [1116]; slightly fewer (6–10) similar teeth in upper jaw. Melon extends further forward on adult males [773]. Coloration all black except for a blaze of grey (variable from indistinct to nearly white) known as the throat patch or throat chevron [790] on belly between flippers. Sometimes also a light grey postorbital blaze on sides of face. Black, narrow tapered flippers (1/10 body length) with broad hump on front margin near middle, giving distinctive 'elbowed' appearance. Tall (to 40 cm), sickle-shaped (rounded to sharply pointed) dorsal fin just behind midpoint of back [1116].

RELATIONSHIPS

Most closely related to killer whale *Orcinus*, pygmy killer whale *Feresa* and long- and short-finned pilot whales *Globicephala*, often grouped as subfamily Globicephalinae [846, 847], though other studies have placed these in a subfamily Orcininae [192]. Seems closest to *Feresa*, then *Globicephala* [962], placement of *Orcinus* less certain.

MEASUREMENTS

Length: newborn *c.* 160–190 cm; at sexual maturity *c.* 3.3–4.3 m (female), *c.* 3.7–4.6 m (male); adult *c.* 4.5 m (max. 5.1) (female), *c.* 5.4 m (max. 6.1) (male). Weight *c.* 1200–2000 kg.

VARIATION

Morphological comparisons of false killer whales stranded in Australia, S Africa and Scotland [634] showed the 3 groups to be distinct in various features (e.g. overall width and length of the skull, rostrum and mandible). Skulls larger in Scottish animals; differences also noted in growth rates and extent of sexual dimorphism; greatest differences between Scotland and the 2 southern populations, which were more similar. All 3 populations distinct, should be managed as separate stocks [634].

DISTRIBUTION

Worldwide, but mainly in tropical and warm temperate offshore waters. In NE Atlantic, only occasionally N of the British Isles, and records here confined to a few mass strandings: in 1927 (*c.* 150 at Dornoch Firth, NE Scotland) [522]; 1934 (*c.* 25 in S Wales); 1935 (*c.* 75 in S Wales and 41 in SE Scotland) [343, 360, 909]. No strandings since 1935 [408, 1072]. Pelagic, usually occurring in deep waters off the continental shelf edge, so rarely observed at sea; 5 sightings since 1976, variously between 5 and 54 km from land: 2 off W Scotland, 1 S of Cornwall towards the French coast, and 2 off NE Scotland [358, 360]. The first 3 involve single individuals, but the 2 sightings in N North Sea were herds of 10–20 and 100–150 animals. 4 sightings were in July and August [360].

HISTORY

Known from subfossil material from the upper Pleistocene [742, 888]

HABITAT

Found primarily in deep offshore waters, although populations off Hawaii, Costa Rica and Japan reported in waters of *c.* 200 m depth [5, 600, 871]. Migrations into cooler, northern waters have been reported in the NW Pacific [84, 600].

SOCIAL ORGANISATION AND BEHAVIOUR

Mass strandings and observations at sea indicate that may form large herds up to *c.* 300 animals, though groups of 10–30 more common. Herds are of mixed age and sex.

Very fast swimmer, up to 55 km/h, and very manoeuvrable. Captive speed tests found a maximum 8.0 m/s [1009]. May breach clear of water; may bow-ride vessels. Often associates with other dolphin species.

Photo-ID of individuals, exploiting naturally occurring marks and scars, conducted off W coast of Costa Rica [5]; 59 identified at 2 sites, and same ones seen over 2 years.

Vocalisations: Comprise whistles ranging 5.3–8.2 kHz (significantly higher than for pilot whales and killer whales [984]) and echolocation clicks with peak frequencies *c.* 100 kHz [71, 175, 197, 586, 825, 1146]. Able to discriminate between complex harmonic whistles and simpler ones, suggesting that can understand complex vocalisations [1261]. Characteristics of echolocation signals from wild animals suggest that *Pseudorca* should be able to detect fish prey up to 210 m and small squid up to 80 m [735]. Hearing sensitivity is best around 16–64 kHz [1147].

In captivity, false killer whales reported to be as ‘trainable’ as bottlenose dolphins, although also considered the most aggressive species [300]. Can recognise themselves in mirrors, indicating a high degree of self-awareness [301].

FEEDING

Diet: Primarily squid (e.g. *Beryteuthis* and *Gonatopsis* in NE Pacific [84]; *Ommastrephes* in SW Atlantic [28, 1042]; *Thysanoteuthis*, *Argonauta* in central E Atlantic [516] and large fish (e.g. *Seriola*, *Thunnus*, *Sarda*) [1116]. Has been known to prey on dolphins (*Stenella*, *Delphinus*), for example during tropical E Pacific tuna purse seine fishery [924] and has also been reported attacking sperm whales [890].

BREEDING

Females are spontaneous ovulators and seasonally polyestrous, but with no obvious calving peak [65]. Gestation period 15.5 months (but possibly down to 11). 1 captive birth documented at 14 months gestation, using urine and blood serum hormone analyses [871]. 1 birth observed, central E Atlantic, in May [862]. Lactation period 18–24 months [603, 947]. Calving interval reported in one population at almost 7 years [82]. Sexual maturity at *c.* 8–14 years (both sexes) [946, 947]. Hybrids reported with bottlenose dolphins [851].

POPULATION

No estimates of population size in the Atlantic. Sex ratio in Scottish mass strandings around 0.8:1 (male:female). Longevity averages 30–40 years [946, 947], with the oldest female reported at 63 years (measured by dentinal growth layer groups) and the oldest male 58 years [604].

Recent study of genetic variability and population structure suggests at least ‘ocean-basin-scale population structure’ between the NE Atlantic and the Indian Ocean, but additional samples needed to refine this definition [238]. Better sampling in the tropical and subtropical Pacific between 15° S and 40° N found at least 2 distinct populations around Hawaii: one small island-associated population (100–200 animals) and a much larger pelagic one, suggesting local adaptations to specific island habitats via a matrilineal social structure [238].

MORTALITY

No detailed information on mortality rates, but age structure suggests fairly high immature mortality.

PARASITES AND PATHOGENS

Known parasites collected from stranded animals include trematodes *Nasitrema* sp., nematodes *Stenurus*, *Anisakis* and the acanthocephalan *Bolbosoma* [871]. Trematode infestation has been suggested as the cause for at least one mass stranding via damage to the 8th cranial nerve [812]. Scars caused by shark-suckers *Remora*, a commensal fish, are frequently found on the body.

Morbillivirus has been found in false killer whales stranded along E coast of America [334].

RELATIONS WITH HUMANS

Has been actively hunted off Japan [603], and from St Vincent, W Indies, in the 1970s [202]. Caught live off Florida for display as performing animals in many dolphinariums [792]. Accidental bycatch reported from gill net fishery off Australia [490]. Legally protected in European, British and Irish waters (Table 12.1).

Pollutant levels of 728 µg/g wet weight of mercury in liver and 1400 µg/g wet weight DDE in blubber reported from stranded animals off British Columbia [84], where high levels of PCB and DDT also reported [567].

AUTHORS

J.R. Boran & P.G.H. Evans

Risso's dolphin *Grampus griseus*

Delphinus griseus Cuvier, 1812; Brest, France.

Grampus; *Dolffin risso* (Welsh); *deilf-risso* (Scottish Gaelic); *deilf liath* (Irish Gaelic).

RECOGNITION

Large, robust dolphin (Plate 15) with blunt rounded head, slight melon but no beak; greyish (whitening with age), often with numerous white scars on flanks; tall sickle-shaped dorsal fin in midpoint of back. Few teeth, all in lower jaw.

DESCRIPTION

Stout torpedo-shaped body narrowing behind dorsal fin to quite narrow tail stock, blunt snout, rounded with slight melon and no beak. Deep V-shaped crease down middle and front of head from blowhole to top lip, seen only at close range. Has 2–7 (usually 4) peglike teeth at tip of each lower jaw, often badly worn and sometimes lost; no upper teeth. Coloration dark to light grey on back and flanks (Fig. 12.32), palest in older individuals so that head and anterior portion of dorsal surface may be pure white; many conspicuous white scars on flanks of adults; white belly enlarging to oval or anchor-shaped patch on chest and chin (cf. pilot whale). Newborn young overall light grey, changing to chocolate brown as juveniles. Long (17% body length), narrow, pointed flippers, usually dark. Tall, centrally placed, re-curved dorsal fin (taller, more erect in adult males); dark, but may lighten with age, particularly along leading edge. Dark tail flukes with median notch and concave trailing edge.

RELATIONSHIPS

No congeners. Cytochrome *b* sequences place *Grampus* with *Globicephala*, *Feresa*, *Pseudorca*, and *Peponocephala* in distinct subfamily Globicephalinae, supporting earlier inferences from anatomy and blood proteins [684, 763], but relationships between these 5 uncertain.

MEASUREMENTS

Length: newborn *c.*1.35 m; at physical maturity *c.*2.31 m [949]; at sexual maturity 2.60–2.84 m (females), 2.62–2.97 m (males) [915]; adult *c.*3.3–3.8 m. Male slightly larger than female: maxima 3.83 m (male) and 3.66 m (female). Weight 350–400 kg.

VARIATION

Both morphometric [60] and genetic variation demonstrated between regions and ocean basins. Strong significant genetic differentiation found between animals sampled in British waters and those from the Mediterranean, using both microsatellite and mtDNA analysis [433]. The British sample also showed lower genetic diversity.

DISTRIBUTION

Worldwide in tropical and temperate seas in both

Risso's dolphin



Fig. 12.32 Risso's dolphins, showing the grey colour (paler in older dolphins) and taller fin that distinguishes them from the similarly blunt-headed pilot whale (photo P.G.H. Evans).

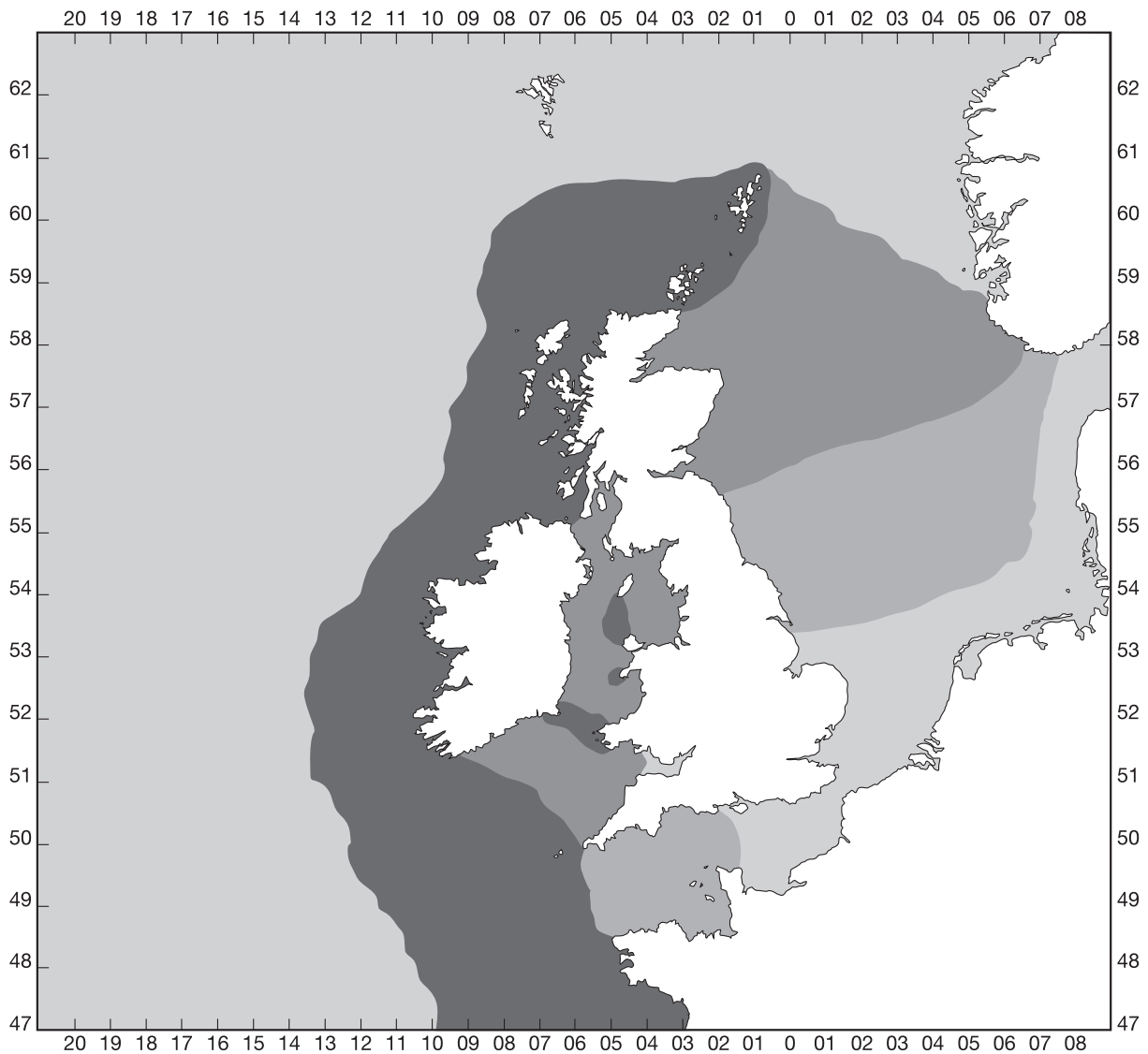


Fig. 12.33 Risso's dolphin *Grampus griseus*: distribution around British Isles.

12 Whales, porpoises and Cetacea: Order Cetacea

hemispheres. In W North Atlantic, occurs from Newfoundland to Lesser Antilles. In E North Atlantic, reaches N limits of its regular range in Northern Isles of Scotland (though has been recorded off Norway), S to Iberia and Mediterranean. Also occurs around oceanic islands like the Azores, Canaries and Cape Verde.

Widely distributed in coastal waters of British Isles, primarily on Atlantic seaboard but also in N North Sea [340, 346, 358, 360, 973]. Major British/Irish populations around Hebrides, but regular also off Northern Isles, in Irish Sea (particularly St George's Channel and around N Wales and Isle of Man), and off W Ireland [346, 360, 973]. Elsewhere, rare in C and S North Sea, and all but W end of English Channel (Fig. 12.33). Regular again in W France, Bay of Biscay, around Iberian Peninsula, and in Mediterranean. On occasions (as in recent years), ranges further into C North Sea, apparently following cephalopod prey. Occurs in much of Mediterranean, most frequently in NW in deep pelagic waters, particularly over steep shelf slopes and submarine canyons [76, 216]. However, estimates of abundance are available only for few regions, and information on their distribution is generally lacking.

Around British Isles, nowhere common; seen most frequently May–September, peaking in July–September [360].

HISTORY

No fossil or archaeological material known.

HABITAT

A widespread pelagic species, preferring warm water (range 7.5–28 °C, but mainly 5–20 °C, and rarely <10 °C [83, 659]), generally favouring continental slope waters. In E Pacific, typically occurs seaward of 180 m isobath, seen in coastal areas only where continental shelf relatively close to shore [657, 680]; depth averaged 1000 m. Steep sections along edge of continental shelf also identified as high-use areas in E USA and Gulf of Mexico [105, 468, 613, 614].

Over continental shelf around British Isles, seen mainly over slopes of 50–100 m depth [66, 67, 358, 360]. In Mediterranean, recorded mainly from 500–1000 m depth in Ligurian Sea [76, 365, 420], and at depths of 400–1200 m (particularly 800–1000 m) off SE Spain [215, 216].

SOCIAL ORGANISATION AND BEHAVIOUR

Form small to medium-sized pods of 2–50 animals (most commonly 6–12 in British waters, 15–20 in Spain, and 5–20 in Ligurian Sea) (Fig. 12.33), although they may be seen singly or in groups of

several hundreds or even thousands. Photo-ID studies indicate that groups can be stable over the long term, individuals associating from one year to the next [66, 67, 342, 353, 430, 657], although associations mostly weak [430]. Limited evidence on genetic similarity among individuals within and among groups in NW Mediterranean, suggests a fluid social structure [430]. Sex and age composition of groups not well known; segregation by age and sex known to occur, with groups of calfless adults, juveniles, and females with calves [353, 657]. Aggressive behaviour frequently observed, is assumed to cause the intense scarring seen on some older animals [66, 67, 342]. Caring behaviour reported around animal wounded by a harpoon [934].

A relatively slow swimmer. When travelling, swims at c.4–12 km/h, but when frightened can speed up to 20–25 km/h [353, 934a, 940]. Usually slightly wary of vessels; occasionally bow-rides (mainly juveniles), and regularly engages in a variety of surface behaviours including breaching (particularly juveniles), spyhopping, tail-slapping, and communal diving.

In N Atlantic, Risso's dolphins sometimes seen swimming with other cetaceans, including long-finned pilot whales, white-beaked, Atlantic white-sided dolphins, common and bottlenose dolphins [66, 67, 233, 340, 353, 659]; in N Pacific, even observed bow-riding and apparently harassing gray whales [1070], as well as showing aggressive behaviour towards long-finned pilot whales [1068, 1069]. In Mediterranean, occasionally seen swimming with striped dolphins [431].

Vocalisations: Include a variety of clicks, whistles, and pulsed calls. Whistles, rarely heard, range over 2.5–20 kHz, usually 8–12 kHz, average duration 0.67 s, and maximum source level of 170 dB re 1 μ Pa @ 1 m [1204]. Clicks have peak frequency 65 kHz, last 40–100 s [68]. Click frequencies are from 0.2 to >100 kHz, with repetition rates of 4–200/s. Click-bursts last 0.2–1.5 s, maximum source level 175 dB re 1 μ Pa @ 1 m [1204]. 8 different kinds of sounds in 3 main categories recognised in Hebridean Risso's dolphins: clicks in discrete series (echolocation clicks, creaks, grunts) with repetition rates of 37–167 pulses/s; fast sequences of pulses (buzzes, squeaks, squeals, moans) with high repetition rates of 187–3750 pulses/s, resulting in harmonics; and whistles of 9–13.2 kHz [115, 116].

FEEDING

Diet: Mainly cephalopods, particularly octopus *Eledone cirrhosa*, cuttlefish *Sepia officinalis* and squids *Todarodes sagittatus*, *Loligo forbesi* and *L. vulgaris*,

Gonatus spp., *Histioteuthis reversa* and *H. bonnellii*, *Ancistroteuthis lichtensteinii*, *Sepiola oweniana* and various Cranchiidae; occasionally small fish (e.g. cod *Gadus morhua*) [67, 109, 222, 259, 263, 266, 304, 339, 792, 939, 1164, 1254, 1266].

Feeding methods: Limited information on diel patterns of activity; off Santa Catalina, California, feeding mainly nocturnal [1068].

BREEDING

Poorly known. Off British Isles (from records of fetuses and newborn calves), births mainly from early spring to summer (March–July) [340, 346, 353, 408], although suggested elsewhere that occur mainly in winter (December–February) [316, 1157]. Examination of 51 stranded animals, NW Mediterranean, indicated calving between end of winter and early summer [949], but number of calves there peaks in July, despite proportion of adults to calves largely the same throughout year [430]. Possible that calves born in most months of the year [233]. Gestation lasts c.13–14 months (recently estimated at 13.87 months [949]); lactation period and calving interval unknown. Age at sexual maturity 3–4 years [680, 1017]. Suspected hybrids from mating with bottlenose dolphin found on Irish coast [405], and hybrid calf of these species successfully produced in captivity in Japan.

POPULATION

In W North Atlantic, 29 000 estimated off E USA and 2700 in N Gulf of Mexico [1199]. No population estimates for any region in E North Atlantic. Study in N Minches, Scotland, identified at least 142 individuals [66, 67]. Similarly, at least 345 individuals photo-identified in NW Mediterranean, 1990–2004 [432].

Oldest individual (male) examined estimated at >29 years (on basis that 1 tooth growth layer = 1 year [949]). One recognisable individual, 'Pelorus Jack', accompanied vessels over 24 years from 1888 [29, 680].

MORTALITY

No instances of predation known [573], but have been observed fleeing from a pod of killer whales [353]. No information on mortality rates.

PARASITES AND PATHOGENS

External parasites include *Isocyamus delphini* and *Xenobalanus globicipitis* [691, 1017]. Internal parasites include the trematode *Nasitrema* spp., cestodes *Phyllobothrium delphini*, *Monorygma grimaldii*, and *Tetrabothrius*, and nematodes *Stenurus minor* and *Crassicauda grampicola* [304, 659, 954].

RELATIONS WITH HUMANS

Hunted in small numbers in several regions of world [552, 553, 792, 965, 971], and previously including Mediterranean [332] and Lesser Antilles [205]. Widely caught incidentally in fishing gear [792, 659, 919]; killed deliberately in Japan to reduce competition with fisheries; has been observed stealing fish from longlines [603]. Recent annual takes estimated at c.250–500 [971]. Bycatches off Sri Lanka thought to be unsustainable [658].

Pollutant burdens are only poorly known; levels of total PCBs very high (466 and 2061 $\mu\text{g/g}$ wet weight) in blubber of 2 animals stranded on Spanish Mediterranean coast [276]. DDT levels in one of them also high (670 $\mu\text{g/g}$ wet weight), but much lower in a Welsh specimen, which also had low levels of heavy metals (with exception of cadmium and zinc) [671]. One stranded, S Adriatic Sea (Italy), had relatively high levels of total mercury in the liver and cadmium in the kidney [1129]. Effects of disturbance from oil and gas exploration, other industrial activities, and shipping largely unknown [469, 659].

Small numbers live-captured for dolphinarium, particularly in Japan [552, 965]. Legally protected in European, British and Irish waters (Table 12.1).

LITERATURE

General review [659].

AUTHOR

P.G.H. Evans

GENUS *Orcinus*

A monospecific genus, characterised by few (10–12) pairs of robust, oval-sectioned, teeth.

Killer whale *Orcinus orca*

Delphinus orca Linnaeus, 1758; European seas. Orca, grampus, blackfish; swordfish, pied whal' (Shetland); *lleiddiad* (Welsh) *mada-chuain* (Scottish Gaelic); *cráin dubh, orc* (Irish Gaelic).

RECOGNITION

Striking black and white pattern (white patch near eye, large white patch extending from belly to flanks, and less distinct pale grey saddle behind dorsal fin). Tall dorsal fin, triangular or sickle-shaped, centrally placed (Fig. 12.34). Broad rounded flippers. Teeth large, pointed and anterioposteriorly compressed.

DESCRIPTION

Powerfully built, robust torpedo-shaped body with conical head, and indistinct beak (Plate 14). 10–12



Fig. 12.34 Killer whales, showing taller fin of adult male (foreground), as well as characteristic pale saddle and white eye-spot (photo F. Ugarte).

pairs of large conical teeth. Coloration very striking: black on back and sides, white ventrally from chin and underside of flippers narrowing rearward along the belly and expanding as a 3-pointed lobe around the urogenital region and along the sides up the flanks. Distinctive, conspicuous white oval patch above and behind eye ('eye spot'). Lighter grey saddle over back behind dorsal fin often shows individual variation. Large, rounded, paddle-shaped flippers; conspicuous centrally-placed dorsal fin, sickle-shaped in adult females and immatures, but very tall (to 1.8 m) and erect (triangular, sometimes tilted forwards) in adult male. Tail flukes black above, white below, with shallow median notch and concave trailing edge.

RELATIONSHIPS

The largest member of Delphinidae. Often grouped with false killer whale *Pseudorca*, pygmy killer whale *Feresa*, Irrawaddy dolphin *Orcaella* and the 2 pilot whales *Globicephala* in a subfamily Globicephalinae [846, 847] or Orcininae [601, 773]; current view has *Orcinus* outside Globicephalinae, but nearest relatives uncertain [192, 962].

MEASUREMENTS

Length: newborn 208–220 cm; at sexual maturity *c.*4.5–4.9 m (female), *c.*5.7–5.8 m (male); adult 5.6–5.7 m (female), *c.*9.4–9.5 m (male). Weight 2500–3000 kg (female), 4000–5000 kg (male).

VARIATION

Regional variation in E North Pacific attributed to existence of 2 'forms' or 'types', specialising on either fish or marine mammal prey (originally termed 'residents' and 'transients', respectively) based on long-term studies along the coasts of W Canada and NW USA [133, 134, 877]. Variation in genetics, morphology, social organisation, feeding ecology and acoustic behaviour all well documented (e.g. [299, 395, 396, 530, 995, 1217]). Genetic studies indicate ongoing gene flow between 'resident' and 'transient' types in E North Pacific, but at rate low enough to maintain differentiation between all putative populations in that region [531]. Fish-feeding populations similar to 'resident' type have been reported in N Atlantic off Norway [1089, 1090, 1130], but in British waters, same pod observed hunting both fish and marine mammals on same day [1]. Worldwide variability in pigmentation and body size suggest further regional phenotypes [125, 364, 1185], yet worldwide genetic diversity is low [530].

DISTRIBUTION

Worldwide, from tropical to polar seas. In NE Atlantic, apparently most numerous around Iceland, Faroes, and in localised regions off W Norway. Widely distributed in small numbers around British Isles (Fig. 12.35), mainly Atlantic seaboard and in N North Sea [340, 358, 360, 973]. Regularly sighted off Scotland, in N Isles and Hebrides; rare in Irish Sea, C and S North Seas

Killer whale

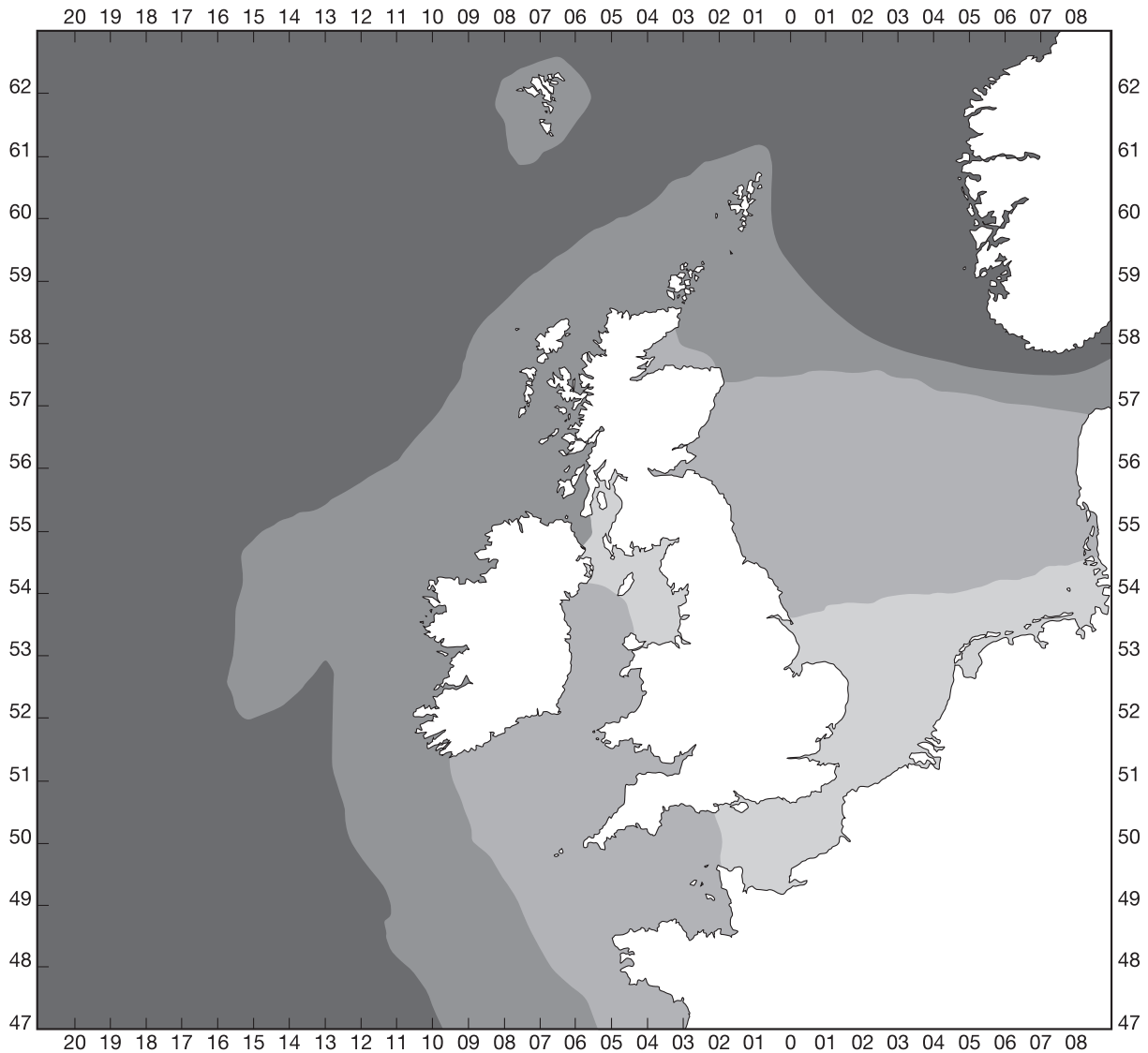


Fig. 12.35 Killer whale *Orcinus orca*: distribution around British Isles.

and English Channel. Recorded in British waters in all months, but most sightings in coastal waters May–September [360]. Offshore, between Shetland and Norway and in N North Sea, regularly occurs November–March, associates with pelagic trawling for mackerel [277, 278, 723]. In April–June, concentrates along continental slope N of Shetland, making onshore movements around N Isles and Caithness coast [343, 360, 1216].

HISTORY

Earliest fossils attributed to *Orcinus* from Pliocene, Italy [220a, 519]. Fossil teeth reported from Suffolk [724].

HABITAT

Found in a wide variety of habitats: common in cold, nearshore waters, but also reported from the

polar ice pack to tropical oceanic islands. Individual populations often develop feeding specialisations which restrict distribution, e.g. on pinnipeds, bringing them near breeding rookeries, or on spawning fish, bringing them to spawning grounds.

SOCIAL ORGANISATION AND BEHAVIOUR

Sightings around British Isles mainly of single individuals or small groups <15, but groups of 100–300 sighted in N North Sea and E of Shetland, generally associated with trawling activities [343, 358, 360, 723]. Elsewhere, groups commonly up to 40, sometimes >100, although these probably represent temporary coalitions. Social structure intensively studied along the Pacific coast of USA and Canada [94, 132]. Groups often matriarchal, basic social unit being mothers with calves,

12 Whales, porpoises and Cetacea: Order Cetacea

including immatures of both sexes and one or more adult males. Single animals are mainly subadults and adult males [132, 343, 511]. 'Resident' groups seem to form extended family units; certainly members remain within the pod for many years [94, 287, 396]. Other evidence that pods remain stable from one generation to the next comes from presence of distinct, pod-specific vocal dialects (even among pods in a localised area), with some shared call-types, but always including predominant calls unique to the pod [169, 389–391, 393, 394, 527, 995, 1130]. The smaller 'transient' pods have a less predictable home range in E North Pacific and smaller vocal repertoire [94, 132]. Some transient individuals photographically identified in California and Alaska, 2300 km apart [445].

'Resident' killer whale pods apparently maintain communal, seasonal territories with large home ranges that may extend for 320–480 km, and even within a single day can range 120–160 km [95]. Fast swimmers, travelling at 14–22 km/h, can attain 50 km/h. No particular diurnal pattern of behaviour has been observed but foraging activities were related to tidal cycle, and amounted to 53% of time spent [368]. Spent 20% of time in percussive foraging; 13% in more obvious play; 12% in rest or sleep; 2% in intermingling behaviour [510, 525, 884].

Average maximum dive depth 140.8 m (max. 264 m, $n = 34$ individuals) in the inland waters of the NE Pacific; max. depth 330 m [86]. No significant differences in diving rates by age or sex, but adult males had higher rates of deep dives than adult females, perhaps due to sex-based differences in feeding patterns. Also, most deep diving occurred during the day, perhaps due to diurnal vertical migrations of favoured salmon prey, vision-dependent feeding or preferences for resting at night with lower levels of vessel noise [86].

Vocalisations: Well studied; include a variety of whistles of variable duration, mainly of 6–12 kHz frequency, a tonal call primarily in the frequency range 1–6 kHz, and very short (41 μ s) broad-band echolocation clicks, some with low- and high-frequency peaks near 29 kHz and 105 kHz [169, 390, 527, 810, 1092]. Source level of clicks made by Norwegian and Icelandic killer whales was 199 dB re 1 μ Pa @ 1 m [1092]. A specific high-intensity call, peak frequency 680 Hz and duration 3.1 s, recorded from foraging killer whales off Iceland but never off Norway [1092]; usually heard just prior to sound of underwater tail slap, thought to be used as an aid to herding herring prey into tight schools before using tail slaps [1092]. Underwater tail slaps produce

broadband, multi-pulsed sounds with source level of 191 dB re 1 μ Pa @ 1 m, which can be heard by other whales at distances of up to 3–4 km [1092]. Mammal-eating killer whales often hunt silently, perhaps adapting to the hearing sensitivity of their mammalian prey [103, 299]. Suggested to be one of the few animals capable of vocal learning [383].

FEEDING

Diet: Highly varied; includes fish, squid, marine mammals and even occasionally turtles and birds, though individuals (or social groups) typically specialise [340, 343, 395, 1157, 1235]. Fish prey include *Salmo*, *Clupea*, *Gadus*, *Scomber*, *Pleurogrammus*, *Hippoglossus*, *Sardinella* and *Sarda*. Marine mammals include minke, humpback and long-finned pilot whales, harbour porpoise, and various seals including grey seal. Auks and kittiwakes have also been taken in Faroese waters. Squid include members of Loliginidae (e.g. *Loligo*).

Feeding methods: Often use tidal rips in which to capture fish such as salmon, cooperatively herding them into tight clusters, at the same time breaching, lobtailing and slapping the water with their flippers [274, 509, 562]. Cooperative feeding on grey seal seen off N Scotland: adult male made the kill, then moved aside for other pod members to feed [340]. Intentional stranding on beach to capture seals (off Argentina and Crozet Is.) suggests a large degree of social learning [151, 524, 722], involved single individuals dominant in provisioning other pod members [524]. Cooperative feeding on schooling herring well documented off Norway [322, 1089, 1090, 1092]; cooperative foraging on salmon in E North Pacific suggested by way subgroups converged [525]. Echolocation studies show that can detect individual large fish at ranges up to 100 m [72], and herring schools within a few km [1092]. Males tend to dive deeper than females; most deep diving occurs during the day [86].

BREEDING

Births probably mainly in late autumn and winter (October–January), may be associated with offshore movement at this time [343, 358, 360]. Fetal lengths from Norwegian specimens suggest that mating peaks around October–November [241, 242]. Precise breeding areas not known. Gestation period *c.* 12 (possibly up to 16) months. Lactation period unknown, but at least 12 months. Calving interval at least 3, maybe sometimes up to 8–9 years. Age at sexual maturity 15–16 years in male, 8–10 years in female [132, 241, 242, 593].

POPULATION

Population estimates incomplete; 1987 survey of N Atlantic from Icelandic and Faroese vessels estimated 6618 animals (95% confidence limits 3500–12 500) [466]. Longevity, based on life history table analysis, was 60 years for males and 90 years for females [877]. Individuals up to 35 years found off Norway [241]. One population had a finite annual rate of increase of 2.92%, relatively high for such a long-lived mammal [877]. Although subject to cropping (for display in oceanaria) and natural population increase, no evidence of density dependence in any life history parameters [877]. However, one population has not recovered from captures for oceanaria, is on list of endangered species, USA [532].

MORTALITY

Has no known predators. Mortality curves U-shaped for both sexes, but narrower for males [877]. Annual mortality estimates in the wild (based on horizontal estimates following individuals over time) low, perhaps 3.9% for mature males and as low as 1.1% for mature females [877]. Mortality in captivity variously estimated at 6.2–8.9%, significantly higher than for wild populations [303, 329, 1098]. Sex differences in mortality for captive animals (males 8.5%, females 5%) not significantly different, possibly due to a small sample size [1098]. Diseases reported from captivity and strandings include pneumonia, systemic mycosis, bacterial infections (of the tooth pulp cavity and of the vestigial hair follicles), atherosclerosis and Chidiak–Higashi syndrome [285, 464, 519]. Depleted populations may be more susceptible to infectious diseases [436].

PARASITES AND PATHOGENS

Endoparasites: Include cestodes *Trigonocotyle spasskyi* and *Phyllobothrium* sp., a nematode *Anasakis simplex* and trematode *Fasciola skrjabini* [288].

Ectoparasites: Rare, but barnacles *Xenobalanus globicipitus* and *Cryptolepas rhachianecti*, remoras Echeleididae and whale-louse *Cyamus antarcticensis* reported [285, 1025].

RELATIONS WITH HUMANS

Has been hunted opportunistically in E Canadian Arctic, W Greenland and Faroes (in latter case using similar driving methods as used on pilot whales). Commercial catches primarily by Norway both in coastal waters and offshore [593]; total catch 1938–1981, 2455 whales [875]. Live capture fishery conducted sporadically off Iceland since 1975, for dolphinarina [1083]. One animal ('Keiko',

star of the film *Free Willy*) returned to Iceland for potential reintroduction to the wild in 1998. In 2002, he 'escaped' during open ocean training, was found 2 months later 1400 km away in Norway. He was held in a Norwegian bay until 2003, when he died of pneumonia.

Sometimes perceived as threat to herring, halibut, tuna and salmon, and bottomfish fisheries, but no evidence for any serious effects on these businesses. For example, in Prince William Sound, Alaska, only a few specific pods developed habits of stealing fish off longlines and this predation amounted to <3% of the overall monetary value of the fishery [1256].

In E North Pacific, various pollutants (PCBs, PBDEs, PBBs and PCNs) collected from known animals; similar high concentrations in fish-eating, southern 'resident' populations that live around the industrialised areas of Seattle and Vancouver and the mammal-eating 'transients' who feed at high trophic levels [958]. Toxicity information non-existent for cetaceans, but levels of PCBs (mean for male transient whales $251.2 \pm 54.7 \mu\text{g}/\text{kg}$) were 3 times those correlated with immunotoxicity in captive harbour seals [1019]. Off Prince William Sound, Alaska, the site of the *Exxon Valdez* oil spill, killer whales had 237.7 $\mu\text{g}/\text{g}$ PCB and 346 $\mu\text{g}/\text{g}$ DDT, levels similar to those found in the belugas of the heavily industrialised St Lawrence River. Of individually identified killer whales, 25 last seen in Prince William Sound swimming through oil slicks from the spill have disappeared, presumed dead [286].

Whale-watching now so popular that some populations may be suffering acoustic threats through masking of natural communication [382, 1238].

Legally protected in European, British and Irish waters (Table 12.1).

LITERATURE

Succinct review [519]; more extensive one [285]; studies of Pacific coast population [81, 396].

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J.R. Boran, A.R. Hoelzel & P.G.H. Evans

12 Whales, porpoises and Cetacea: Order Cetacea

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12 Whales, porpoises and Cetacea: Order Cetacea

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12 Whales, porpoises and Cetacea: Order Cetacea

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12 Whales, porpoises and Cetacea: Order Cetacea

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12 Whales, porpoises and Cetacea: Order Cetacea

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12 Whales, porpoises and Cetacea: Order Cetacea

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12 Whales, porpoises and Cetacea: Order Cetacea

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12 Whales, porpoises and Cetacea: Order Cetacea

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