B

BACULUM

Edward H. Miller

The baculum (os penis) is a bone in the penis of some mammals. It is present in some or all males of small insectivorous placentals (orders Afrosoricida, Erinaceomorpha, and Soricomorpha), Chiroptera, Primates, Lagomorpha, Rodentia, and Carnivora (Burt, 1960; Schultz et al., 2016). The structure has evolved multiple times in mammals (Schultz et al., 2016). Among marine mammals, it is present in all males of Ursidae (polar bear, *Ursus maritimus*), Mustelidae (marine otter, *Lontra felina*, and sea otter, *Enhydra lutris*), and Pinnipedia. The baculum is absent in Cetacea and Sirenia. The corresponding element in females is the little-studied clitoris bone (os clitoridis), which has been described for polar bears and several pinniped species, but presumably is present in all pinnipeds, and in marine and sea otters (it is present in northern river otter, *Lontra canadensis*; Mohr, 1963; Fay, 1982).

The urethral groove in the baculum is deep in the dog but is shallow to absent in bacula of marine mammals (Fig. 1A lower, 1B lower), although is likely present terminally in the undescribed baculum of the marine otter, as in the related northern river otter (Baryshnikov et al., 2003). Bacula of polar bears and phocid seals are fairly simple, being more or less straight or slightly curved (arched dorsally) structures, and lacking elaborate apices (Fig. 1). In at least some phocids,

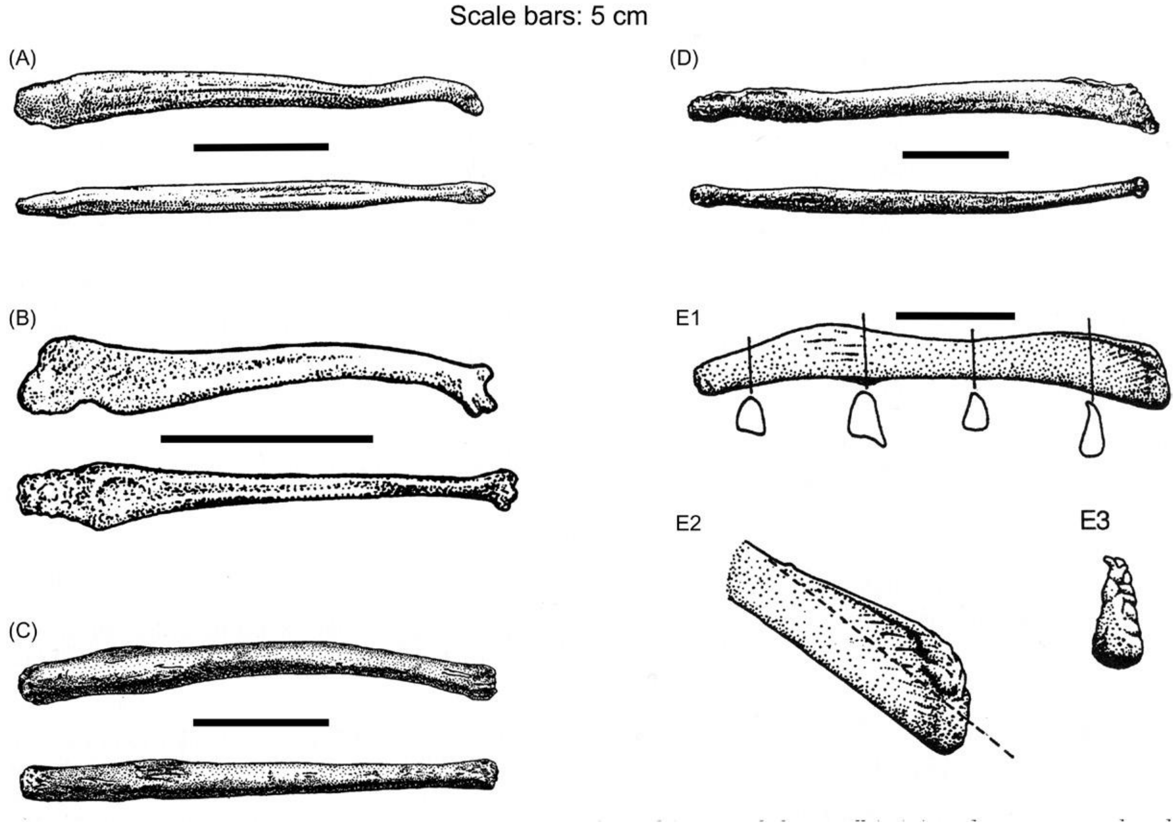

Figure 1 *Bacula of marine mammals are large but most are morphologically simple: (A) polar bear (*Ursus maritimus*); (B) subantarctic fur seal (*Arctocephalus gazella*); (C) Mediterranean monk seal (*Monachus monachus*); (D) crabeater seal (*Lobodon carcinophaga*); (E) Weddell seal (*Leptonychotes weddellii*). Bacula in (A)–(D) are shown in right lateral (upper) and ventral (lower) views. E1: Baculum in right lateral view (note cross-sectional shapes at the indicated points). E2: Oblique view (right side) of the bacular apex (same specimen); dashed line indicates how much growth occurs in the crest (above the line), following sexual maturity. E3: Apical view (dorsal surface above; same specimen). (A) from R. Didier (1950;* Mammalia **14**, *78–94); (B) from R. Didier (1952;* Mammalia **16**, *228–231); (C) from P. J. H. van Bree (1994;* Mammalia **16**, *228–231); (D) from R. Didier (1953;* Mammalia **17**, *21–26); (E) from G. V. Morejohn (2001;* J. Mammal. **81**, *877–881).*

Encyclopedia of Marine Mammals. DOI: http://dx.doi.org/10.1016/B978-0-12-804327-1.00002-9

© 2018 Elsevier Inc. All rights reserved.

Copyright © 2017. Elsevier Science & Technology. All rights reserved.

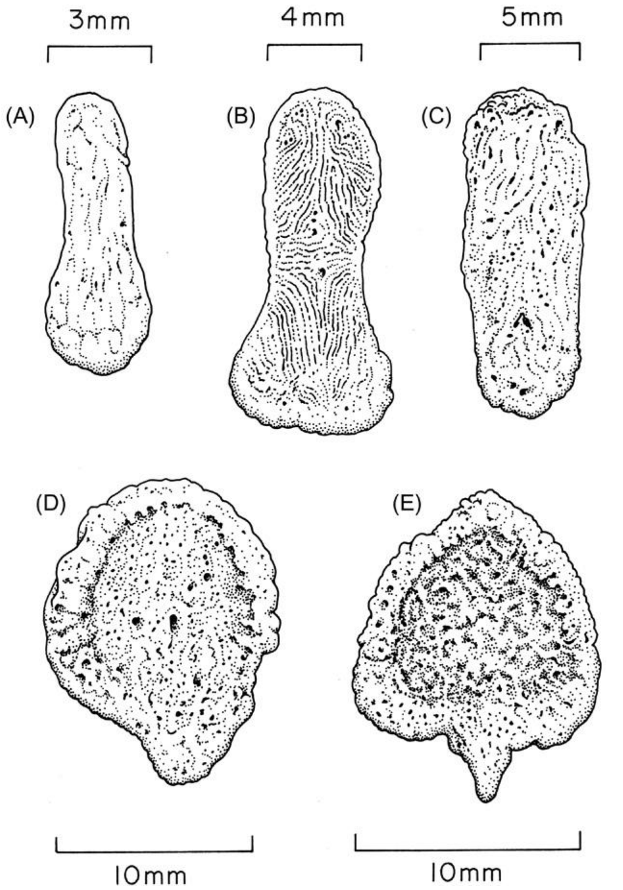

Figure 2 *The bacular apex is morphologically complex and interspecifically diverse in Otariidae. The apex is shown in apical view (dorsal surface up) for: (A) unknown species of* Arctocephalus *fur seal; (B) northern fur seal (*Callorhinus ursinus*); (C) California sea lion (*Zalophus californianus*); (D) Australian sea lion (*Neophoca cinerea*); and (E) Hooker's sea lion (*Phocarctos hookeri*). From G. V. Morejohn (1975;* Rapports et Proces-verbaux des Reunions, Conseil International pour l'Exploration de la Mer **169**, *49–56).*

the bacular apex has a prominent cartilaginous cap (e.g., hooded seal, *Cystophora cristata*). Cross-sectional shapes of phocid bacula vary considerably among species, and a prominent crest develops on the anterior dorsal surface in some Antarctic seals (Fig. 1E). The bacular apex is larger and more elaborate in otariids than phocids, in keeping with the close proximity of the apex to (beneath) the glans penis in otariids, in which apical size and shape may be functionally important during copulation (Fig. 2). Mustelids possess some of the most diverse and morphologically elaborate bacula within the Caniformia, although the baculum is fairly simple in the sea otter (Fig. 3; Baryshnikov et al., 2003). Within species, bacula are variable in size, shape, cross section, and specific structural features, even among individuals of the same age. For example, a dorsal keel may be present or absent in southern elephant seals (*Mirounga leonina*); processes on the shaft near the apex are variably present in California sea lions (*Zalophus californianus*); and bacula may be bilaterally asymmetrical or slightly twisted (Fig. 1D).

The baculum is a heterotopic bone, like the kneecap (patella), which forms through ossification in connective tissue. In rodents, the bacular shaft is true bone, and includes hemopoietic tissue in the enlarged basal portion. In the caniform Carnivora (a group that includes bears, otters, and pinnipeds), bacular development has been detailed only in dog (*Canis familiaris*) but is probably similar in other Caniformia. The dog baculum develops in the proximal portion of the penis, in association with the fibrous septum between the paired corpora cavernosa penis, or in their fibrous noncavernous portion; centers of ossification on left and right sides fuse early in development. The developing baculum grows dorsally above the urethra, and thickens. The bacular base becomes firmly attached to the corpora cavernosa and to the fibrous tunica albuginea which surrounds them.

Bacular growth has been investigated in furbearers and game animals, because it can be informative about age and time of puberty. In Carnivora, bacula grow throughout life in thickness and mass (particularly at the proximal or basal end), but not in length (Fig. 4). Bacular growth is most rapid around puberty. Differential growth occurs in different parts of the baculum (e.g., bacular apex, shaft, and base, in Steller's sea lion, *Eumetopias jubatus*; Miller et al., 2000).

Bacula of Carnivora are fairly large (Dixson, 1995; Lariviére and Ferguson, 2002; Ramm, 2007). Bacular length is approximately 6% of body length in otariids, but relatively longer in polar bears (8%) and phocids (8% in hooded seals; 10% in harp seals, *Pagophilus*

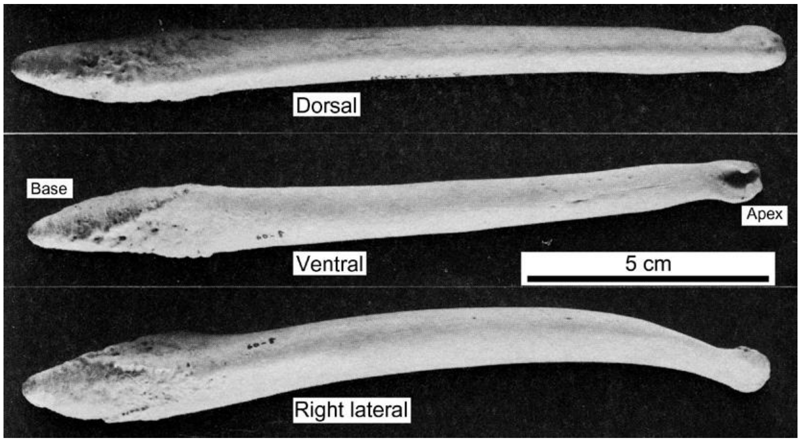

Figure 3 *The baculum of the sea otter (*Enhydra lutris*) is fairly simple, except for the apex. From K. W. Kenyon (1969;* North American Fauna **68**, *1–352).*

Copyright © 2017. Elsevier Science & Technology. All rights reserved.

Figure 4 *Developmental changes in bacular size and shape, illustrated by representative specimens from northern fur seals (*Callorhinus ursinus*), ranging in age from newborn (left) to 8 years of age (right). Specimens are shown in right lateral view, with bacular apex at the top. From V. B. Scheffer (1950; J. Mammal.* **31**, *384–394).*

groenlandicus); the baculum is also much thicker in phocids than otariids (Mohr, 1963; Scheffer and Kenyon, 1963). In pinnipeds, and indeed among all mammals, the walrus (*Odobenus rosmarus*) has the largest baculum both absolutely (to 62.4 cm in length and 1040 g in mass) and relative to body size (18% of body length; Fay, 1982).

Healed fractured bacula have been documented for several species. Fractures result from accidents (e.g., falls in walruses), sudden movements during intromission (e.g., in aquatically mating Caspian seals, *Pusa caspica*), and aggressive social interactions (e.g., fights in adult male sea otters).

Bacula likely serve several functions even within species, for example, in aquatic copulations as a mechanical aid in copulation (especially in the absence of full erection) or to maintain intromission. Interspecific differences in bacular size have been linked to diverse selective pressures: reproductive isolation between species, aquatic vs terrestrial copulation, copulatory duration or pattern, sexual selection and mating system, climate, and risk of fracture (Scheffer and Kenyon, 1963; Eberhard, 1985; Dixson, 1995; Larivière and Ferguson, 2002; Ramm, 2007; Fitzpatrick et al., 2012). The baculum is anatomically complex and species-specific in many groups, though not strikingly so in marine mammals, so has been used extensively in mammalian systematics. Interspecific diversity in size and form likely has evolved largely through postcopulatory sexual selection (internal female choice and male–male competition; Fig. 5). Bacular size may be limited by adverse effects

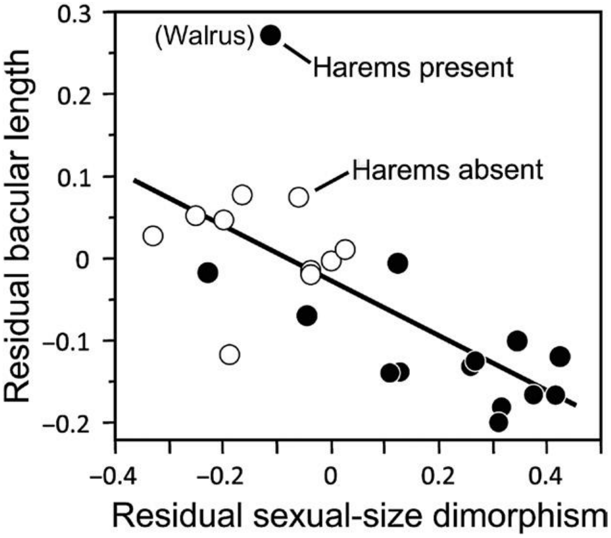

Figure 5 *Phylogenetically controlled analyses reveal that traits important in both precopulatory and postcopulatory sexual selection (e.g., male body size and bacular length, respectively) evolved more quickly and diverged more in pinniped species with harems. One resulting trend is that bacular size (length) is negatively related to sexual-size dimorphism in species with harems (black dots), regardless of whether the outlying walrus (marked) is included in analyses. After J. L. Fitzpatrick et al. (2012; Evolution* **66**, *3595–3604).*

Copyright © 2017. Elsevier Science & Technology. All rights reserved.

on females: a female sea otter and a harbor seal (*Phoca vitulina*) pup died from perforation of the vagina during forced copulations with male sea otters. Understanding interspecific variation in the baculum of marine mammals will require knowledge of morphology and function of female reproductive tracts, and on genital coevolution between the sexes (Kelly and Moore, 2016; Brennan, 2016).

The baculum forms most of the mass of the male genitals that are taken in commercial hunts of African fur seals (*Arctocephalus p. pusillus*) in Namibia, and harp seals in Canada, which may be dried whole, then sold (mainly in Asia) whole or ground, for use as supposed aphrodisiacs or in traditional medicine; genitals are also exported frozen, and served as putatively aphrodisiac-containing food (Miller 2009). Sexual maturation and reproduction may be affected by pollutants, so bacular size and form may also be informative in studies on pollution biology.

See Also the Following Articles

Male Reproductive Systems ■ Mating Systems

References

Baryshnikov, G.F., Bininda-Emonds, O.R.P., and Abramov, A.V. (2003). Morphological variability and evolution of the baculum (os penis) in Mustelidae (Carnivora). *J. Mammal.* **84**, 673–690.

Brennan, P.L.R. (2016). Studying genital coevolution to understand intromittent organ morphology. *Integr. Comp. Biol.* icw018.

Burt, W.H. (1960). Bacula of North American mammals. *Misc. Pub. Mus. Zool. Univ. Michigan* **113** 1–76 + 25 plates.

Dixson, A.F. (1995). Baculum length and copulatory behaviour in carnivores and pinnipeds (Grand Order Ferae). *J. Zool. (Lond.)* **235**, 67–76.

Eberhard, W.G. (1985). *Sexual Selection and Animal Genitalia.* Harvard University Press, Cambridge, MA.

Fay, F.H. (1982). Ecology and biology of the Pacific walrus, *Odobenus rosmarus divergens* Illiger. *N. Am. Fauna* **74**, 1–279.

Fitzpatrick, J.L., Almbro, M., Gonzalez-Voyer, A., Kolm, N., and Simmons, L.W. (2012). Male contest competition and the coevolution of weaponry and testes in pinnipeds. *Evolution* **66**, 3595–3604.

Kelly, D.A., and Moore, B.C. (2016). The morphological diversity of intromittent organs. *Integr. Comp. Biol.* icw103.

Lariviére, S., and Ferguson, S.H. (2002). On the evolution of the mammalian baculum: Vaginal friction, prolonged intromission or induced ovulation? *Mam. Rev.* **32**, 283–294.

Miller, E.H. (2009). Baculum. In "Encyclopedia of Marine Mammals", (W.F. Perrin, B., Würsig, and J.G.M. Thewissen, Eds), 2nd ed., pp. 68–71. Academic Press, Burlington, MA.

Miller, E.H., Pitcher, K.W., and Loughlin, T.W. (2000). Bacular size, growth, and allometry in the largest extant otariid, the Steller sea lion (*Eumetopias jubatus*). *J. Mammal.* **81**, 134–144.

Mohr, E. (1963). Os penis und Os clitoridis der Pinnipedia. *Z. Säugetierkund.* **28**, 19–37.

Ramm, S.A. (2007). Sexual selection and genital evolution in mammals: A phylogenetic analysis of baculum length. *Am. Nat.* **169**, 360–369.

Scheffer, V.B., and Kenyon, K.W. (1963). Baculum size in pinnipeds. *Z. Säugetierkund.* **28**, 38–41.

Schultz, N.G., Lough-Stevens, M., Abreu, E., Orr, T., and Dean, M.D. (2016). The baculum was gained and lost multiple times during mammalian evolution. *Integr. Comp. Biol.* icw034.

Copyright © 2017. Elsevier Science & Technology. All rights reserved.

BAIJI

Lipotes vexillifer

Kaiya Zhou

The baiji or Yangtze River dolphin is endemic to the middle and lower reaches of the Yangtze River in China. It was named Ji early in the ancient dictionary, Erh Ya (200 BC), and Baiji by Kong Wuzhong (AD 1044–1101) in his poem about the porpoise. The baiji was a relict species and the only contemporary representative of the family Lipotidae; it was declared probably extinct in 2007.

I. Characteristics and Taxonomy

The baiji is a graceful animal with a very long, narrow, and slightly upturned beak. It can be easily identified by the rounded melon, longitudinally oval blowhole, very small eyes, low triangular dorsal fin, and broad rounded flippers (Fig. 1). The color is generally bluish gray or gray above and white below. Females are larger than males, with maximum recorded length for females 253 cm and for males 229 cm (Zhou, 1989). Significant differences between the sexes in external proportions were demonstrated in nine characters, and the skull size is also sexually dimorphic (Gao and Zhou, 1992). The mouth is lined with 31–36 teeth in each tooth row. The crown of the tooth is conspicuously inclined labially and is slightly compressed anteroposteriorly. The enamel of the entire crown is ornamented with irregular vertical striae and ridges that present a reticular appearance (Zhou et al., 1979a). The structure of the stomach is unique in cetaceans. The forestomach is lacking, and the main stomach is divided into three compartments (Zhou et al., 1979b). The skull is characterized as having a long slender rostrum and mandible; rostrum length exceeds two-thirds of the condylobasal length. The costal facets of the second to fifth thoracic vertebrae are located on the posterior edge of the centrum. The facet on the posterior edge of the sixth thoracic disappears or is vestigial, and that of the seventh thoracic sits on the anterior edge of the vertebral body. The position of the costal facet on the thoracic vertebrae in baiji is unique and is opposite to that in the boto, *Inia geoffrensis*. This feature is one of the morphological bases for favoring rejection of close relationship between the two taxa.

The largest brain weighed was 590 g. The largest cranial capacity measured was 590 cm (Zhou et al., 1979a), about one-half the size of delphinids of similar body size. Eyes are smaller and placed higher dorsally than those of marine dolphins. The retinal ganglion cell and optic fiber numbers in baiji are about 23,800 and 21,000, respectively (Gao and Zhou, 1987; Gao and Zhou, 1992).

The species was previously classified as either in the family Platanistidae or in the family Iniidae (Brownell and Herald, 1972). Zhou et al. (1978) established the new monotypic family Lipotidae based on osteological studies and anatomy of the stomach. Molecular phylogenetic studies based on mitochondrial and nuclear genes, short interspersed elements (SINEs), and the complete mitochondrial genome have strongly supported the referral of *Lipotes* to a separate family Lipotidae (Hamilton et al., 2001; Nikaido et al., 2001; Yang et al., 2002; Yan et al., 2005; Xiong et al., 2009; Geisler et al., 2011).

The only fossil placed close to *L. vexillifer* is *Prolipotes yujiangensis* (Zhou et al., 1984), roughly of Miocene age.

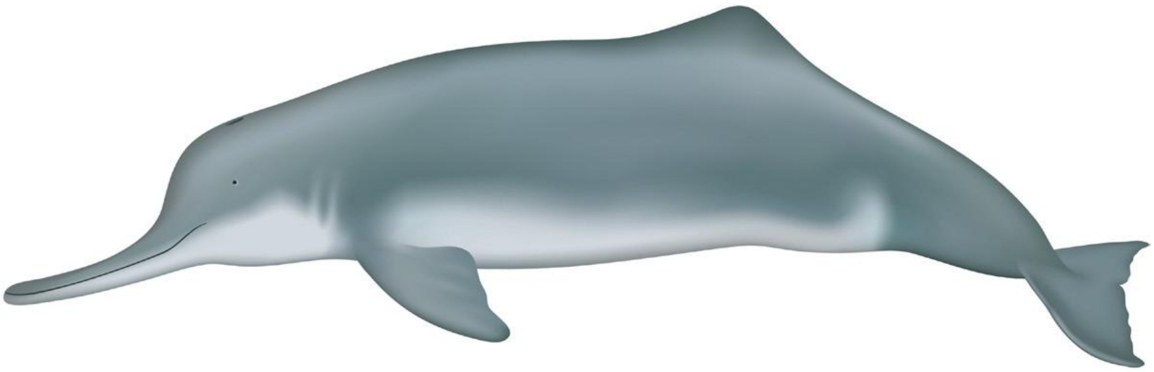

Figure 1 *Baiji,* Lipotes vexillifer *(Illustration by Uko Gorter).*

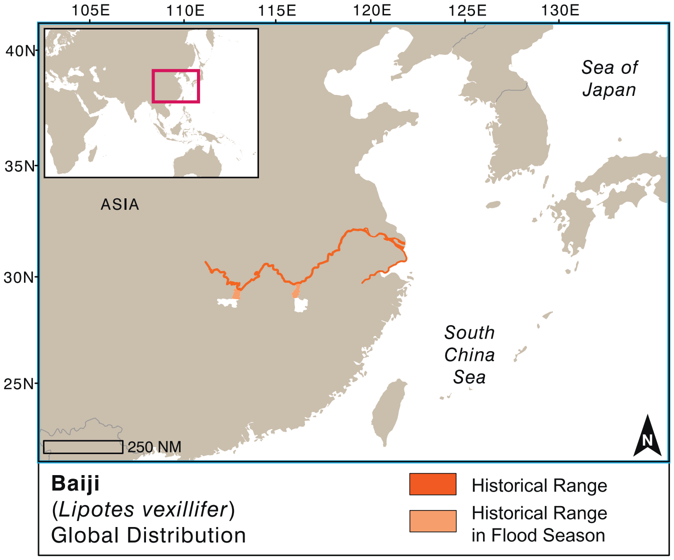

Figure 2 *Baiji distribution. Adapted by Nina Lisowski from Jefferson, T.A., Webber, M.A. and Pitman, R.L. (2015). "Marine Mammals of the World: A Comprehensive Guide to Their Identification," 2^{nd} ed. Elsevier, San Diego.*

II. Distribution and Abundance

Baiji were found mainly in the mainstream of the middle and lower reaches of the Yangtze River (Zhou et al., 1977) (Fig. 2). They occurred historically in Dongting and Poyang Lakes; both were appended water bodies of the Yangtze during intense flooding. About the turn of the 20th century, Hoy and Pope collected specimens separately from Dongting Lake and near its mouth, where the lake joins the Yangtze. The presence of this dolphin in the Yangtze River is noted in documents going back about 2000 years, when it was known only by the ancient name "Ji." While baiji still occurred from the Three Gorges area in the upper Yangtze River to the mouth of the river off Shanghai in the 1940s, there was a progressive diminution of habitat since then, and the last remnants existed not far from the city of Wuhan (Zhou et al., 1977).

The first rough estimate of abundance based on quantitative survey data (1979–81) was only about 400 animals (Zhou, 1982). On the basis of surveys conducted in 1985–86, Chen and Hua (1989) made an educated guess that the total population was around 300. An intensive 6-week multivessel visual and acoustic survey carried out in November–December 2006, covering the entire historical range of the baiji in the main Yangtze channel, failed to find any evidence that the species survives. Although a few undocumented sightings have been reported since 2004, the last authenticated records were that of a stranded pregnant female found in 2001 and a live animal photographed in 2002. The baiji is now thought to be probably extinct (Turvey et al., 2007).

III. Ecology

The river sections inhabited by the baiji were characterized by having one to several sandbars. Baiji were usually sighted immediately upstream or downstream of a sandbar, where a tributary enters the river. They were generally found in eddy counter currents below meanders and channel convergences. These areas of former baiji occurrence are also prime fishing areas, set with nets, traps, and hooks (Zhou and Li, 1989).

The baiji appears to have taken any available species of freshwater fish, the only selection criterion being size. The fish could not be so large that it could not go down the throat (Zhou and Zhang, 1991). Occasionally, baiji and Yangtze finless porpoises (*Neophocaena asiaeorientalis asiaeorientalis*) groups appeared to feed together for short periods (Zhou et al., 1998).

IV. Behavior and Physiology

Baiji lived in small groups. In the 1980s, the most common group size was 2–6 animals; the largest group observed was about 16 individuals in the middle reaches of the Yangtze River. The baiji usually surfaced without causing white water and breathed in a smooth manner (Fig. 3). Photographic identifications and sighting records showed that baiji groups made both local and long-range movements. The largest recorded range of a recognizable baiji was more than 200 km from the initial sighting location (Zhou et al., 1998).

Three kinds of behavior, individual behavior, social behavior, and rhythmic behavior, were observed (Liu and Wang, 1989). The baiji likely had two main kinds of signals, communication signals and echolocation signals (Wang et al., 1989).

V. Life History

Body length at birth was estimated to be 91.5 cm for both males and females. They had about the same growth rate until they were about 4 years old based on estimates of dentinal growth layer groups (GLGs), which was the age at sexual maturity for males. The females attained sexual maturity at about 6 years. The oldest animal that was age-determined was a 242-cm-long female of

Copyright © 2017. Elsevier Science & Technology. All rights reserved.

Figure 3 *Free-ranging baiji in the Yangtze River near Tongling. From Zhou, K., and Zhang, X. (1991).*

24 years of age, and a 21-year-old male was estimated to be about 214cm in body length (Gao and Zhou, 1992).

VI. Interactions With Humans

The baiji was the victim not of active persecution but of incidental mortality resulting from massive-scale human environmental impacts (Turvey et al., 2007). Range contraction and decline in abundance were caused by a combination of factors: possibly some level of direct exploitation historically; incidental mortality from interactions with fisheries; vessel traffic; management of navigation channels, and harbor construction; and loss or degradation of habitat by water development, land use practices, and pollution (Chen and Hua, 1989; Zhou et al., 1998).

The Yangtze River is one of the chief river systems of the world. Nearly one-third of the population of China or almost 10% of the entire world population lives along the Yangtze Valley. It is suffering massive degradation. Waste water volume discharged into the Yangtze is about 15.6 billion cubic meters per year. During the whole-range survey in 2006, a minimum of 19,830 large shipping vessels and 1175 fishing vessels were seen between Yichang and Shanghai (Turvey et al., 2007).

The baiji is classified in the World Conservation Union (IUCN) Red List as critically endangered—possibly extinct. Despite all the efforts made to conserve the baiji since the 1980s, the population declined rapidly in a few decades as the rapid economic development of the Yangtze River Basin led to massive habitat degradation. The baiji is the first cetacean species known to have been driven to extinction by human activity.

References

Brownell Jr., R.L., and Herald, E.S. (1972). Lipotes vexillifer. *Mamm. Species* **10**, 1–4.

Chen, P., and Hua, Y. (1989). Distribution, population size and protection of *Lipotes vexillifer*. In "Biology and Conservation of the River Dolphins. Occasional Papers of the IUCN Species Survival Commission 3", (W.F. Perrin, R.L. Brownell Jr., K. Zhou, and J. Liu, Eds), pp. 81–85. IUCN, Gland.

Gao, A., and Zhou, K. (1987). Studies on the ganglion cells of *Neophocaena* and *Lipotes*. *Acta Zool. Sin.* **33**, 316–322.

Gao, A., and Zhou, K. (1992). Sexual dimorphism in the baiji, *Lipotes vexillifer*. *Can. J. Zool.* **70**, 1484–1493.

Gao, G., and Zhou, K. (1992). Fiber analysis of optic and cochlear nerves of small cetaceans. In "Marine Mammal Sensory Systems", (J.A. Thomas, R. Kastelein, and A. Supin, Eds), pp. 39–52. Plenum Publishing Corporation, New York.

Geisler, J.H., McGowen, M.R., Yang, G., and Gatesy, J. (2011). A supermatrix analysis of genomic, morphological, and paleontological data from crown Cetacea. *BMC Evol. Biol.* **11**, 112.

Hamilton, H., Caballero, S., Collins, A.G., and Browbnell Jr., R.L. (2001). Evolution of river dolphins. *Proc. R. Soc. London B* **268**, 549–558.

Liu, R., and Wang, D. (1989). The behavior of the baiji, *Lipotes vexillifer*, in captivity. In "Biology and Conservation of the River Dolphins. Occasional Papers of the IUCN Species Survival Commission 3", (W.F. Perrin, R.L. Brownell Jr., K. Zhou, and J. Liu, Eds), pp. 141–145. IUCN, Gland.

Nikaido, M., Matsuno, F., Hamilton, H., Brownell Jr., R.L., Ying, C., Wang, D., Zhu, Z., Shedlock, A.M., Fordyce, R., Hasegawa, M., and Okada, N. (2001). Retroposon analysis of major cetacean lineages: the monophyly of the toothed whales and the paraphyly of river dolphins. *Proc. Natl. Acad. Sci. USA* **98**, 7384–7389.

Turvey, S.T., Pitman, R.L., Taylor, B.L., Barlow, J., Akamatsu, T., Barrett, L.A., Zhao, X., Reeves, R.R., Stewart, B.S., Wang, K., Wei, Z., Zhang, X., Pusser, L.T., Richlen, M., Brandon, J.R., and Wang, D. (2007). First human-caused extinction of a cetacean species? *Biol. Lett.* **3**, 537–540.

Wang, D., Liu, W., and Wang, Z. (1989). A preliminary study of the acoustic behavior of the baiji, *Lipotes vexillifer*. In "Biology and Conservation of the River Dolphins". Occasional Papers of the IUCN Species Survival Commission 3", (W.F. Perrin, R.L. Brownell Jr., K. Zhou, and J. Liu, Eds), pp. 137–140. IUCN, Gland.

Xiong, Y., Brandley, M.C., Xu, S., Zhou, K., and Yang, G. (2009). Seven new dolphin mitochondrial genomes and a time-calibrated phylogeny of whales. *BMC Evol. Biol.* **9**, 20.

Yan, J., Zhou, K., and Yang, G. (2005). Molecular phylogenetics of 'river dolphins' and the baiji mitochondrial genome. *Mol. Phylogenet. Evol.* **37**, 743–750.

Yang, G., Zhou, K., Ren, W., Ji, G., Liu, S., Bastida, R., and Rivero, L. (2002). Molecular systematics of river dolphins inferred from complete mitochondrial cytochrome *b* gene sequences. *Mar. Mammal Sci.* **18**, 20–29.

Zhou, K. (1982). On the conservation of the baiji, *Lipotes vexillifer*. *J. Nanjing Normal College (Nat. Sci.)* **4**, 71–74.

Zhou, K. (1989). Review of studies of structure and function of the baiji, *Lipotes vexillifer*. In "Biology and Conservation of the River Dolphins. Occasional Papers of the IUCN Species Survival Commission 3", (W.F. Perrin, R.L. Brownell Jr., K. Zhou, and J. Liu, Eds), pp. 99–113. IUCN, Gland.

Zhou, K., and Li, Y. (1989). Status and aspects of the ecology and behavior of the baiji, *Lipotes vexillifer*. In "Biology and Conservation of the River Dolphins. Occasional Papers of the IUCN Species Survival Commission 3", (W.F. Perrin, R.L. Brownell Jr., K. Zhou, and J. Liu, Eds), pp. 86–91. IUCN, Gland.

Zhou, K., Li, Y., and Qian, W. (1979a). The osteology and the systematic position of the baiji, *Lipotes vexillifer*. *Acta Zool. Sin.* **25**, 58–74.

Zhou, K., Li, Y., and Qian, W. (1979b). The stomach of the baiji, *Lipotes vexillifer*. *Acta Zool. Sin.* **25**, 95–100.

Zhou, K., Qian, W., and Li, Y. (1977). Studies on the distribution of baiji, *Lipotes vexillifer*. *Acta Zool. Sin.* **23**, 72–79.

Zhou, K., Qian, W., and Li, Y. (1978). Recent advances in the study of the baiji, *Lipotes vexillifer*. *J. Nanjing Normal College (Nat. Sci.)* **1978**(1), 8–13.

Zhou, K., Sun, J., Gao, A., and Würsig, B. (1998). Baiji (*Lipotes vexillifer*) in the lower Yangtze River: movements, numbers, threats and conservation needs. *Aquat. Mamm.* **24**, 123–132.

Zhou, K., and Zhang, X. (1991). *Baiji, the Yangtze river dolphin and other endangered animals of China.* Stone Wall Press, Washington, DC.

Zhou, K., Zhou, M., and Zhao, Z. (1984). First discovery of a Tertiary Platanistoid fossil from Asia. *Sci. Rep. Whales Res. Inst.* **35**, 173–181.

Copyright © 2017. Elsevier Science & Technology. All rights reserved.

BAIKAL SEAL

Pusa sibirica

Nobuyuki Miyazaki

Baikal seals (*Pusa sibirica*) are the smallest of the northern true seals (family Phocidae, subfamily Phocinae). The species is endemic to Lake Baikal in Siberia (Russia), from which it derives its common name. It is one of a very few freshwater seal species.

I. Characteristics and Taxonomy

The Baikal seal (*Pusa sibirica*) belongs to the genus *Pusa*, along with the other two species that make up this widely allopatric grouping—the ringed seal (*P. hispida*) and the Caspian seal (*P. caspica*). Baikal seals are uniformly dark silver gray dorsally and light yellowish gray ventrally (Fig. 1). They reach 1.1–1.4 m in length and weight between 50 and 100 kg, with adult males being slightly larger than adult females. Pups weigh 3–3.5 kg at birth and are approximately 70 cm long; their lanugo is grayish-white.

Mitochondrial DNA suggests that the Baikal seal is derived from a ringed seal ancestor in the Arctic Ocean 400 thousand years ago (Sasaki et al., 2003), and is thus not thought to be a Paratethys relict.

II. Distribution and Abundance

The Baikal seal's distribution is restricted to Lake Baikal in northern Russia, southern Siberia (Fig. 2). An outbreak of canine distemper virus is known to have induced a major decline during the 1980s (see below), but population growth and recovery has clearly taken place. The current population size is thought to be at the level of the Lake Baikal ecosystem's carrying capacity at some 80,000–100,000 individuals (see Goodman, 2016 for more detailed temporal coverage).

III. Ecology

Baikal seals are strongly ice associated. In winter, when Lake Baikal is covered with ice, seals are sighted throughout the lake, adjacent to breathing holes in the ice. They give birth to their pups in snow caves (lairs) similar to ringed seals and they also prefer to molt on the ice. In October, they move into bays and lagoons where the ice forms first to occupy areas where reproduction will later take place. Pups are born in February and are nursed by their mothers for 2–3 months. A rather high rate of twinning (4% of annual births) occurs in Baikal seals compared to other seals (Pastukhov, 1968). Mating is thought to take place late in lactation, similar to other phocid seals. Baikal seals molt on the ice at a time when it is breaking up, in late May and early June.

Baikal seals feed primarily on fish, 29 species of which have been recorded in their diet. Their primary prey includes several species of Golomyankas (*Comeophorus* spp.) and sculpins (*Cottocomephorus* spp.) (e.g., Pastukhov, 1993). They are also known to eat gammarid amphipods, such as *Macrohectopus branickii* (Watanabe et al., 2004).

IV. Behavior and Physiology

Diving behavior of Baikal seals has been studied using animal-borne microacceleration loggers and cameras (Watanabe et al., 2004, 2006). In the daytime, dives were characterized by high swimming speeds (mean: 1.2 m/s) and upward-directed acceleration events, while night dives were characterized by lower speeds (0.9 m/s) and undirected deceleration events. Average dive depth is about 70 m, with dives at dusk and dawn being much deeper (150 m). Maximum recorded dive depth for this species is 245 m.

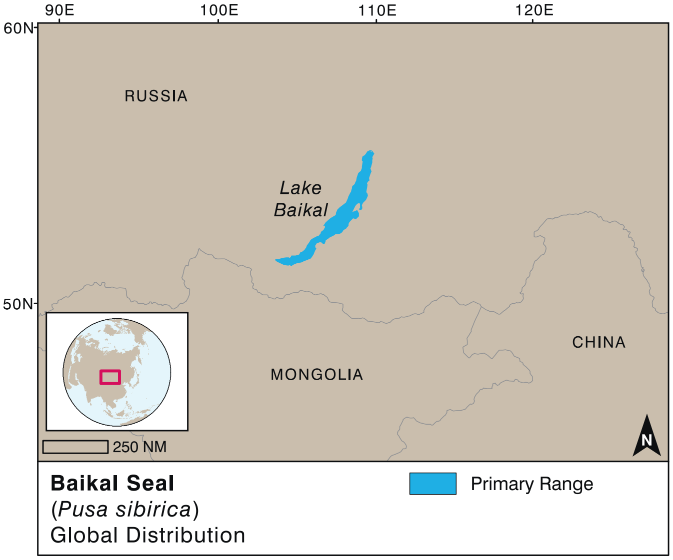

Figure 2 *Baikal seal distribution. From Jefferson, T.A., Webber, M.A. and Pitman, R.L. (2015). "Marine Mammals of the World: A Comprehensive Guide to Their Identification," 2^{nd} ed. Elsevier, San Diego.*

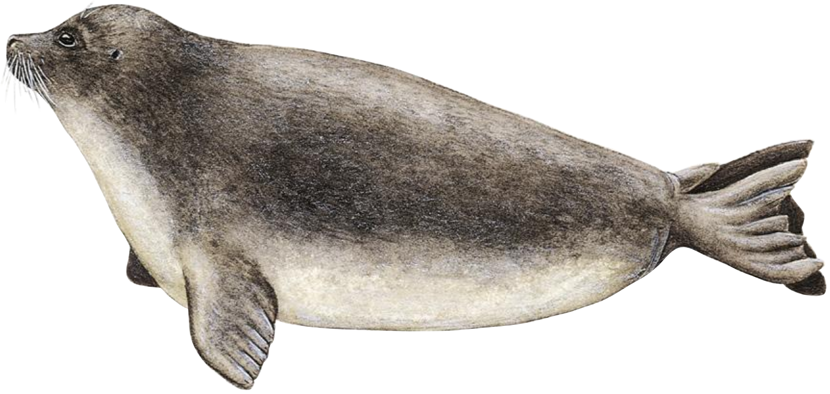

Figure 1 *Baikal seal,* Pusa sibirica *(Illustration by Pieter Folkens).*

Copyright © 2017. Elsevier Science & Technology. All rights reserved.

Figure 3 *A single Baikal seal (*Pusa sibirica*) hauled out on rock in Lake Baikal (Photo by Yuuki Watanabe).*

Figure 4 *Baikal seals (*Pusa sibirica*) sometimes haul out in groups on shore (similar to harbor seals) (Photo by Yuuki Watanabe).*

Dives toward their upper limits of depth and duration (15 min) are followed by prolonged periods at the surface (mean duration, 1.3 h) suggesting that such diving is approaching their physiological limits (Watanabe et al., 2015).

During summer, in the absence of ice, Baikal seals haul out singly (Fig. 3) or in groups (Fig. 4) on rocky island outcrops throughout much of the lake (Stewart et al., 1996). They congregate in the ice-free southeastern part of the lake, with the eastern side of the lake being preferred because it has less human disturbance and greater biological productivity (Pastukhov, 1993).

V. Life History

Males reach sexual maturity at 7–10 years of age while females are mature by the time they are between 3 and 7 years (Pastukhov, 1993). Final body size is reached at approximately 15 years of age (Amano et al., 2000a,b). Approximately 10% of the population is older than 20 years of age, with records of adult females reaching 56 years of age and adult males 52 years of age (Pastukhov, 1993). Females are known to continue to produce pups until they are 43–45 years old.

VI. Interactions With Humans

Subsistence hunting of Baikal seals extends back thousands of years. Commercial hunting of Baikal seals began in the second half of the 18th century and it was an established industry by the early part of the 20th century. Annual harvests have fluctuated between 2000 and 9000 seals (see Goodman, 2016 for details). Harvesting continues today with some desires to expand hunting as skins, meat, and blubber are all valued products.

Baikal seals generally have high contaminant levels because they are top predators with long lives (e.g., Nakata et al., 1995; Miyazaki, 2012). But, viral epidemics are a greater concern at the population level. A mass die off of 8000 Baikal seals occurred in 1987–88, due to a virus (Grachev et al., 1989; Osterhaus et al., 1989), that was likely contracted from feral or domestic dogs.

Besides humans, only the brown bear (*Ursus arctos*) has been reported to kill Baikal seals (Pastukhov, 1993).

References

Amano, M., Koyama, Y., Petrov, E.A., Hayano, A., and Miyazaki, N. (2000a). Morphometric comparison of skulls of seals of the subgenus *Pusa*. In "Lake Baikal" (K. Minoura, Ed.), pp. 315–323. Elsevier, The Netherlands.

Amano, M., Miyazaki, N., and Petrov, E.A. (2000b). Age Determination and growth of Baikal seals (*Phoca sibirica*). In "Advances in Ecological Research, a special thematic volume on Ancient Lakes: biodiversity, ecology and evolution", (A. Rossiter and H. Kawanabe, Eds), pp. 449–462. Academic Press, London.

Goodman, S. (2016). *Pusa sibirica*. The IUCN Red List of Threatened Species 2016: e.T41676A45231738.

Grachev, M.A., Kumarev, V.P., Mamaev, L.V., Zorin, V.L., Baranova, L.V., Denikina, N.N., Belikov, S.I., Petrov, E.A., Kolesnik, V.S., Kolesnik, R.S., Dorofeev, V.M., Beim, A.M., Kudelin, V.N., Nagieva, F.G., and Sidorov, V.N. (1989). Distemper virus in Baikal seals. *Nature* **338**, 209.

Miyazaki, N. (2012). Seal survey in Eurasian waters in collaboration with Russian scientists. *Aquat. Mammal.* **38**(2), 189–203.

Nakata, H., Tanabe, S., Tatsukawa, R., Amano, M., Miyazaki, N., and Petrov, E.A. (1995). Persistent organochlorine residues and their accumulation kinetics in Baikal seal (*Phoca sibirica*) from Lake Baikal, Russia. *Environ. Sci. Technol.* **29**(11), 189–197.

Osterhaus, A.D.M.E., Groen, J., UytdeHaag, F.G.C.M., Visser, I.K.G., van de Bildt, M.W.G., Bergman, A., and Klingeborn, B. (1989). Distemper virus in Baikal seals. *Nature* **338**, 209–210.

Pastukhov, V.D. (1968). On twins in *Pusa sibirica* Gmel. *Zool. Zh.* **47**, 479–482.

Pastukhov, V.D. (1993). *Baikal Seals*. Nauka, Moscow, USSR.269p.

Sasaki, H., Numachi, K., and Grachev, M.A. (2003). The origin and genetic relationship of the Baikal seal, *Phoca sibirica*, by restriction analysis of mitochondrial DNA. *Zool. Sci.* **20**, 1417–1422.

Stewart, B.S., Petrov, E.A., Baranov, E.A., Timonin, A., and Ivanov, M. (1996). Seasonal movements and dive patterns of juvenile Baikal seals, *Phoca sibirica*. *Mar. Mamm. Sci.* **12**, 528–542.

Watanabe, Y., Baranov, E.A., Sato, K., Naito, Y., and Miyazaki, N. (2004). Foraging tactics of Baikal seals differ between day and night. *Mar. Ecol. Prog. Ser.* **279**, 283–289.

Watanabe, Y., Baranov, E.A., Sato, K., Naito, Y., and Miyazaki, N. (2006). Body density affects stroke patterns in Baikal seals. *J. Exp. Biol.* **209**, 3269–3280.

Watanabe, Y.Y., Baranov, E.A., and Miyazaki, N. (2015). Drift dives and prolonged surfacing periods in Baikal seals: resting strategies in open waters? *J. Exp. Biol.* **218**, 2793–2798.

Copyright © 2017. Elsevier Science & Technology. All rights reserved.

BALANCE

Fred Spoor

I. Introduction

The sense organ of balance engages in the perception of movement and spatial orientation and is part of the inner ear, together with the organ of hearing. The mammalian inner ear is housed inside the petrous part of the temporal bone, in a complex-shaped space known as the bony labyrinth. The organ of balance, or vestibular system, consists of two types of motion sensors. The first one is comprised of two otolith organs in the membranous utricle and saccule, and informs the brain about changes in gravitational direction and other forms of linear acceleration of the head. In each organ resides a matrix of gel with embedded dense crystals (a macula with otoliths or otoconia), which deforms by inertia in response to such head movements, and this is detected by an associated bed of hair cells. Little is known of the mammalian otolith system in a comparative context in general, and in relation to life in marine environments in particular. Hence, this part of the organ of balance will not be considered further here (see Spoor and Thewissen, 2007 for details).

The second type of motion sensor concerns the semicircular canal system that perceives rotational (angular) head movements. It comprises three membranous ducts, anterior, posterior, and lateral, that run inside the semicircular canals of the bony labyrinth. Each duct is connected with the membranous utricle inside the vestibule of the bony labyrinth, and thus forms a fluid circuit filled with endolymph. The ampulla, a swollen section at one end of each duct, contains a cupula, a gelatinous structure which seals the duct. Changes in head rotation, acceleration or deceleration, will cause the endolymph to lag behind by inertia, slightly deforming the cupula. This is detected by hair cells with cilia embedded in the cupula, and provides the neural output which encodes the head rotation. Instant mechanical integration by the system makes that the neural output is directly proportional to rotational velocity, rather than acceleration. The three semicircular ducts of each ear are oriented in approximately orthogonal planes, and any head rotation will thus be sensed by at least one duct. Moreover, the output from both ears is integrated to provide comprehensive representation of self-rotation. This information, combined with otolithic, visual, and proprioceptive input, helps coordinate posture and body movements during locomotion, including the reflex stabilization of the head and eyes.

A relationship has been found among mammals between the length of the semicircular ducts of a species and its specific locomotor repertoire (Spoor et al., 2007). Species that are agile and have fast, jerky locomotion have significantly larger-arced, and thus longer ducts relative to body mass than those that move more cautiously. Presumably this is because longer ducts render the canal system more sensitive, and adjusting length is a way of fine-tuning the sensitivity to match the requirements of particular locomotor behaviors. Relatively long, more sensitive ducts that characterize agile animals can instantly resolve small changes in head rotations and this is thought to be important for precise body coordination during fast and highly maneuverable locomotion. It should be noted that other aspects, such as the lumen size (cross section) of the ducts, the relative lengths of the narrower and wider parts of the fluid circuit, and the angles between the duct planes are functionally important as well (David et al., 2016), but these have not yet been studied comprehensively in a comparative context.

II. Comparative Morphology

Differences between aquatic and terrestrial mammals are largely known from studies using computed tomography (CT) to assess the bony semicircular canals rather than the enclosed membranous ducts. Valid functional information can nevertheless be obtained because the length of the duct along its arc is reliably reflected by that of the canal.

All cetacean species examined thus far have fully developed semicircular canals. However, taking into account the species' overall size, they are remarkably small compared with other mammals, and in particular with terrestrial species showing rapid and agile locomotion (Fig. 1). This can be demonstrated by measuring the average arc size of the canals, expressed by their radius of curvature (Fig. 1), and plotting it against body mass (as a measure of overall size). Among cetaceans, the canal arc size varies with body size in the same way as in other mammals (Fig. 2: slopes of regression lines are parallel). However, all cetacean species fall far below other mammals, as their canals are on average three times smaller for their body mass. In broad terms, these differences mean that the canals of the blue whale (*Balaenoptera musculus*) are just smaller than those of humans, and those of the common bottlenose dolphin (*Tursiops truncatus*) are smaller than those of a brown rat (*Rattus norvegicus*).

The semicircular canal arc size in fossil cetaceans that documents the transition from land to water reaches the small, modern proportions in the middle Eocene (Spoor et al., 2002). Only the earliest cetaceans (pakicetids) have canals with the proportions of land mammals.

Sirenian semicircular canals have been studied in the dugong and the manatee (*Dugong dugon*, *Trichechus inunguis*, respectively). They are small in arc size, at the lower end of the range of noncetacean mammals (Fig. 2).

Pinnipeds of which the canal arc sizes have been examined include three phocids, four otariids, and the walrus, *Odobenus rosmarus*. The latter is not significantly different in arc size from terrestrial carnivores (27 species). On the other hand, all three canals are larger in the phocids, whereas the otariids have smaller anterior and posterior canals. See Spoor and Thewissen (2007) for details.

III. Functional Interpretation

The semicircular canal system of cetaceans is distinctly different from that of all other mammals by having strongly reduced arc and lumen sizes. The regular pattern of this reduction suggests a functional adjustment of the system, rather than a vestigial

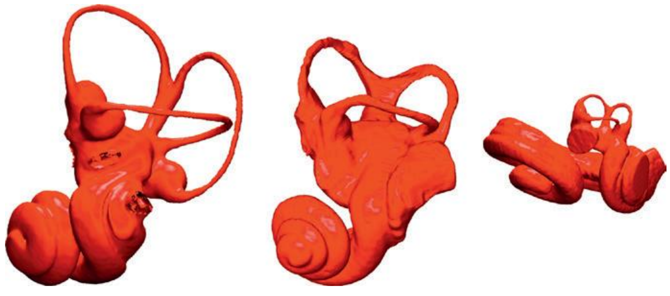

Figure 1 *Inferio-lateral view of the bony labyrinth of (A) a typically agile primate* Galago senegalensis, *(B) the artiodactyl* Hippopotamus amphibius, *a sister taxon of extant cetaceans, and (C) the dolphin* Tursiops truncatus *(Illustrations rendered from CT scans and differently scaled in order to correct for body mass).*

Copyright © 2017. Elsevier Science & Technology. All rights reserved.

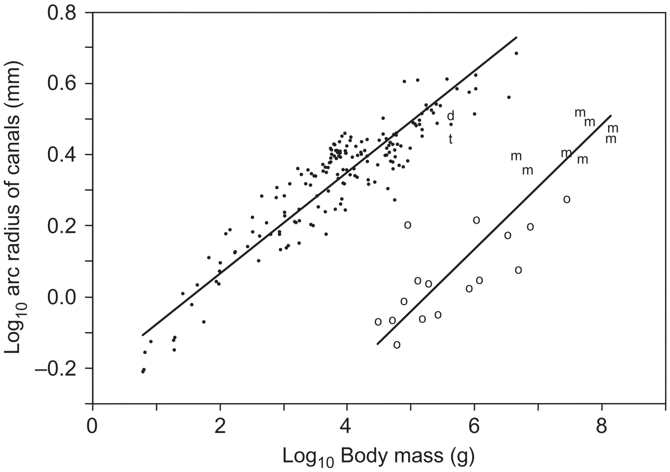

Figure 2 *Average arc size of the three semicircular canals (radius of curvature, indicating duct length) plotted against body mass. Reduced major axis regressions are given for the noncetacean mammal sample (174 species, •) and for the cetaceans (16 odontocetes, o, and 8 mysticetes, m). The dugong (*Dugong dugon*, d) and manatee (*Trichechus inunguis*, t) are labeled individually.*

condition marked by degeneration and redundancy. The hypothesis explaining this phenomenon, proposed in Spoor et al. (2002) and Spoor and Thewissen (2008), is based on two key characteristics of cetaceans. The first one is that extant cetaceans, freed from the restrictions of gravitational pull and the need for substrate contact, are particularly agile and acrobatic when compared with terrestrial animals of similar body size (e.g., compare the killer whale *Orcinus* with the African elephant *Loxodonta*, or the dolphin *Tursiops* with the larger bovid species). The second characteristic is that cetaceans have integrated their head and trunk to streamline the body, and in most species the strongly shortened and frequently fused cervical vertebrae allow little neck motility. This has important implications because a motile neck enables head stabilization during body movements associated with locomotion. It is thus proposed that the acrobatic locomotion of cetaceans, combined with their limited ability to isolate the head from body movements, results in substantially increased rotations perceived by their semicircular canal system compared with terrestrial mammals of similar body size. The small arc size of their canals may therefore reduce the sensitivity, and avoid overstimulation of the canal system. This hypothesis was tested by Kandel and Hullar (2010) by comparing rotational head motions experienced by the bottlenose dolphin and the domestic cow. It was found that cattle head movements always exceeded those of dolphins. Although only a single pair of species was compared, this evidence nevertheless suggests that accentuated head movements of cetaceans are unlikely to explain the reduced size and sensitivity of their semicircular canals.

Sirenians do show reduced neck motility, but not the extreme semicircular canal reduction of cetaceans. However, they are slow and cautious in their swimming, so that fast and effective head stabilization is not a factor of importance. Their canal size is at the lower end of the noncetacean mammalian variation, as are terrestrial species that are slow and cautious in their locomotion.

Among pinnipeds the semicircular canals of phocids and otariids are different in arc size from terrestrial carnivores, but none show the dramatic size reduction seen in cetaceans. This is expected because they all have motile necks enabling effective head stabilization.

Likewise, that phocids have larger canals than terrestrial carnivores is expected, as they are particularly agile in their swimming, and thus follow the normal pattern seen among noncetacean mammals. On the other hand, the smaller anterior and posterior canals of otariids are more difficult to understand. Otariids use a different mode of propulsion than phocids, a bird-like forelimb flight stroke, as opposed to bilateral hind limb undulation, and with a longer neck their center of gravity is located further forward. However, it is not clear how the otariid's smaller canals with reduced mechanical sensitivity relate to either their locomotor pattern or body plan. A better understanding of semicircular canal function in marine mammals will require the use of more complex models (e.g., David et al., 2016) to explore the mechanics of the canal system based on all the relevant morphological aspects, and not just the arc size of the canals.

See Also the Following Articles

Forelimb Anatomy ■ HindLimb Anatomy ■ Locomotion, Terrestrial ■ Swimming

References

David, R., Stoessel, A., Berthoz, A., Spoor, F., and Bennequin, D. (2016). Assessing morphology and function of the semicircular duct system, introducing new in-situ visualization and software toolbox. *Sci. Rep.* **6**, 32772. doi:10.1038/srep32772.

Kandel, B.M., and Hullar, T.E. (2010). The relationship of head movements to semicircular canal size in cetaceans. *J. Exp. Biol.* **213**, 1175–1181.

Spoor, F., and Thewissen, J.G.M. (2008). Balance: Comparative and functional anatomy in aquatic mammals. In "Senses on the Threshold", (J.G.M. Thewissen, and S. Nummela, Eds). University of California Press, Berkeley, CA.

Spoor, F., Bajpai, S., Hussain, S.T., Kumar, K., and Thewissen, J.G.M. (2002). Vestibular evidence for the evolution of aquatic behavior in early cetaceans. *Nature* **417**, 163–166.

Spoor, F., Garland, Th, Krovitz, G., Ryan, T.M., Silcox, M.T., and Walker, A. (2007). The primate semicircular canal system and locomotion. *Proc. Natl. Acad. Sci. USA* **104**, 10808–10812.

BALEEN

ALEXANDER J. WERTH

Baleen is a unique oral tissue that hangs from the roof of the mouth in mysticete whales, where it forms a sieve-like filter to trap food. The word derives from the Latin *balaena* which comes from the Greek φάλαινα meaning "whale." Although it is sometimes called whalebone, baleen is an integumentary specialization made entirely of keratin.

Baleen grows in triangular plates that hang in a pair of comb-like curtains along both sides of the palate from the rostral tip to the esophageal opening, with 140–430 parallel plates in each bilateral "rack" of an adult whale (Fig. 1). Plates are oriented transversely, slightly curved (concave posteriorly), and spaced about 1 cm apart so that filtered water exits the mouth. Plates are 3–8 mm thick but other dimensions differ widely by species. Balaenids have long (up to 3–4 m), narrow (10 cm wide) plates; rorquals have shorter (25–100 cm), wider (30–80 cm) plates. Plates vary in length along a rack. Baleen varies in color from creamy white to gray or black.

Like other keratin, baleen grows throughout life (1–10 cm/year) but the exposed portion comprises dead, cornified cells. Baleen forms

Copyright © 2017. Elsevier Science & Technology. All rights reserved.

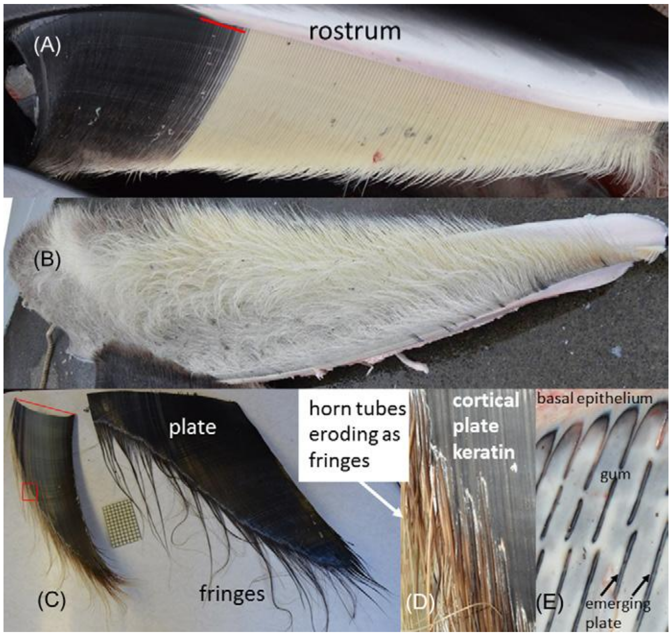

Figure 1 *Baleen structure of fin whale,* Balaenoptera physalus*: (A) right full rack in situ (lateral view, anterior to right) showing dark gray and cream-colored baleen; (B) right full rack in ventral palatal view, showing mesh of overlapping fringes from many plates; (C) anterior face of left plates of fin (left) and blue whale showing fringes on medial side (scale squares = 1 cm*^{2}*); (D) close-up (of red square in (C)) showing horn tubes emerging as fringes from overlapping, eroded cortical plate; (E) section (at red lines in (A) and (C)) showing plate origin in white gum tissue.*

as a sandwich with two thin, flat cortical layers (similar to nails) enclosing a medullary matrix of interstitial cells which bind long, fibrous, cylindrical horn tubes (similar to hair) that grow from papillae in the gums (Fudge et al., 2009; Ekdale et al., 2015). The rubbery gingival tissue called zwischensubstanz firmly anchors plates, enabling them to sway yet form a tough filter withstanding strong forces during the engulfment and water expulsion phases of filter feeding. As plates grow their medial (lingual) sides abrade, wearing away outer layers and exposing the horn tubes, which project ventrally as free fringes, also called bristles, filaments, fibers, or hairs. Fringes vary in length and coarseness by feeding method: short and coarse in gray whales, intermediate in rorquals, and long and delicate in balaenids, where they entangle into a fine, dense mat (150 fringes/cm; Werth, 2013). Both plates and fringes aid in prey capture by direct interception and channeled flow (Werth and Potvin, 2016).

Baleen is a unique tissue with no homologue or functional analogue. Although the oldest fossilized baleen is from the Miocene Epoch 15 million years ago, fossil skulls indicate that baleen likely arose during the Oligocene about 35 million years ago with major oceanographic changes affecting plankton availability (Deméré et al., 2008). All modern mysticetes are edentulous, but the earliest baleen arose in mysticetes with teeth. Ongoing molecular studies (Meredith et al., 2011) suggest potential genetic links between baleen formation and tooth germs, as well as with keratin genes possibly linked to loss of body hair in whales. It has been suggested that baleen relates to transverse palatal ridges of terrestrial carnivorans, though no evidence exists to support this claim.

Baleen appears during fetal growth as transverse ridges in the palate. A 2–5 cm thick layer of basement corium forms pulpy, vascularized papillary processes that grow ventrally to become medullary horn tubes. An overlying layer of dark, 3–8 mm thick epidermis gives rise to flat cortical keratin sheets forming the outside face of each plate (Fig. 1E). These two gum layers and the adjacent rubbery zwischensubstanz bind the growing baleen to the maxillary bones. Baleen displays vertical grooves as well as horizontal ridges that likely indicate annual growth layers (Ruud, 1945). Each whole plate represents 3–5 years of growth in balaenopterids and 10–15 years in balaenids. Isotopic studies of baleen reveal hormonal and dietary changes (Hunt et al., 2014). Plates display scratches and pits and fringes show scuffing, shortening, and bending related to water flow and mechanical damage from tongue movements (Werth et al., 2016). Gray whales exhibit more wear in the right rack due to asymmetric benthic foraging (Young et al., 2015).

Baleen withstands strong compressive, tensile, and shear forces (Werth, 2013). Calcification stiffens baleen into the hardest alpha keratin tissue (Szewciw et al., 2010); it is much more pliable when wet. As a tough yet flexible tissue that does not degrade, baleen has long been used by indigenous cultures for artwork, baskets, implements, armor, and weapons. During the era of industrial whaling it became a highly valuable commodity, peaking in 1853 with over 5.6 million pounds, mostly from right whales, sold in United States ports for almost $2,000,000 (Stevenson, 1907). Brushes were made from fringes; plates were used for corset stays, skirt hoops, umbrella ribs, buggy whips, and many other applications.

References

Deméré, T.A., McGowen, M.R., Berta, A., and Gatesy, J. (2008). Morphological and molecular evidence for a stepwise evolutionary transition from teeth to baleen in mysticete whales. *Syst. Biol.* **57**, 15–37.

Ekdale, E.G., Deméré, T.A., and Berta, A. (2015). Vascularization of the gray whale palate (Cetacea, Mysticeti, *Eschrichtius robustus*): soft tissue evidence for an alveolar source of blood to baleen. *Anat. Rec.* **298**, 691–702.

Fudge, D.S., Szewciw, L.J., and Schwalb, A.N. (2009). Morphology and development of blue whale baleen: an annotated translation of Tycho Tullberg's classic 1883 paper. *Aquat. Mamm.* **35**, 226–252.

Hunt, K.E., Stimmelmayr, R., George, J.C., Hanns, C., Suydam, R., Brower, H., and Rolland, R.M. (2014). Baleen hormones: a novel tool for retrospective assessment of stress and reproduction in bowhead whales (*Balaena mysticetus*). *Conserv. Physiol.* **2**, 1–12.

Meredith, R.W., Gatesy, J., Cheng, J., and Springer, M.S. (2011). Pseudogenization of the tooth gene enamelysin (MMP20) in the common ancestor of extant baleen whales. *Proc. Biol. Sci.* **278**(1708), 993–1002.

Ruud, J.T. (1945). Further studies on the structure of the baleen plates and their application to age determination. *Hvalradets Skr.* **29**, 1–69.

Stevenson, C.H. (1907). Whalebone: its production and utilization. *Bur. Fish. Doc.* **626**, 1–12.

Szewciw, L.J., de Kerkhove, D.G., Grime, G.W., and Fudge, D.S. (2010). Calcification provides mechanical reinforcement to whale baleen alpha keratin. *Proc. R. Soc. B* **277**, 2597–2605.

Werth, A.J. (2013). Flow-dependent porosity and other biomechanical properties of mysticete baleen. *J. Exp. Biol.* **216**, 1152–1159.

Werth, A.J., and Potvin, J. (2016). Baleen hydrodynamics and morphology of crossflow filtration in balaenid whale suspension feeding. *PLoS One.* doi:10.1371/journal.pone.0150106.

Werth, A.J., Straley, J.M., and Shadwick, R.E. (2016). Baleen wear reveals intraoral water flow patterns of mysticete filter feeding. *J. Morphol.* **277**, 453–471.

Young, S., Deméré, T.E., Ekdale, E.G., Berta, A., and Zellmer, N. (2015). Morphometrics and structure of complete baleen racks in gray whales (*Eschrichtius robustus*) from the eastern North Pacific Ocean. *Anat. Rec.* **298**, 703–719.

Copyright © 2017. Elsevier Science & Technology. All rights reserved.

BALEEN WHALES (MYSTICETI)

John L. Bannister

I. Characteristics and Taxonomy

The baleen or whalebone whales (Mysticeti) comprise one of the two recent (nonfossil) cetacean suborders. Modern baleen whales differ from the other suborder (toothed whales, Odontoceti), particularly in their lack of functional teeth. Instead, they feed on relatively very small marine organisms, by means of a highly specialized filter-feeding apparatus made up of baleen plates ("whalebone") attached to the gum of the upper jaw. Other differences from toothed whales include the baleen whales' paired blowhole, symmetrical skull, and absence of ribs articulating with the sternum.

Baleen whales are generally huge (Fig. 1). The blue whale, the largest known animal, grows to more than 30 m long and weighs more than 170 tons. Like all other cetaceans, baleen whales are totally aquatic, and like most of the toothed whales, they are all marine. Many undertake very long migrations, and some are fast swimming. A few species come close to the coast at some part of their life cycle and may be seen from shore; however, much of their lives is spent far from land in the deep oceans. Baleen whale females grow slightly larger than the males. Animals of the same species tend to be larger in the southern than in the Northern Hemisphere.

Within the mysticetes are four families: (1) right whales and bowhead (Balaenidae, balaenids); (2) pygmy right whales (Neobalenidae, neobalaenids); (3) gray whales (Eschrichtiidae, eschrichtiids); and (4) "rorquals" (Balaenopteridae, balaenopterids). Within the suborder, 14 species are now generally recognized. Their relationships, including their relationship to terrestrial ungulates, are indicated in Fig. 2. Many authors now use "rorqual" for all eight balaenopterids (from the Norse "*rørkval*, whale with pleats in its throat"), although strictly speaking the term should probably be applied to the seven *Balaenoptera* species, recognizing the rather different humpback in its separate genus.

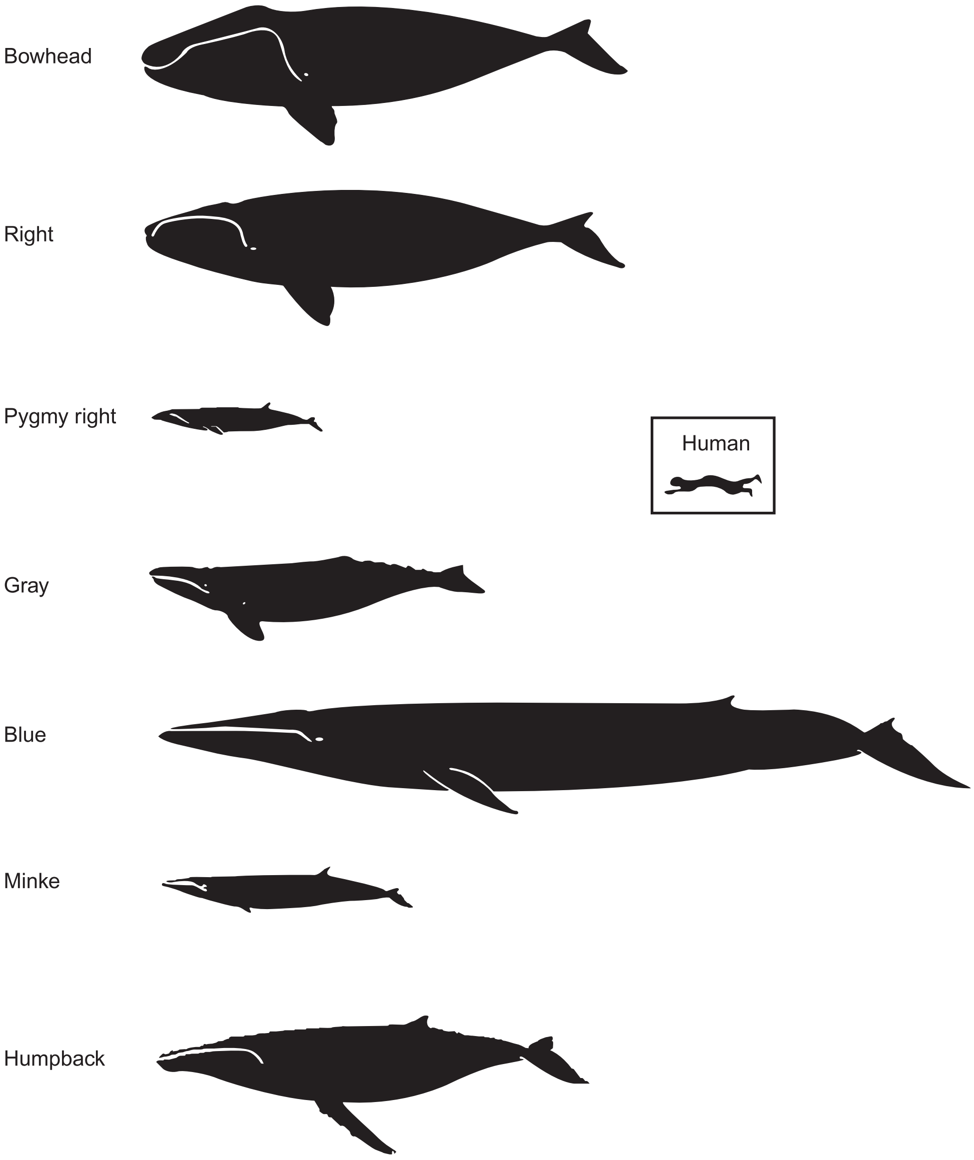

Figure 1 *Lateral profiles of representative baleen whales, with a human figure, to scale.*

Copyright © 2017. Elsevier Science & Technology. All rights reserved.

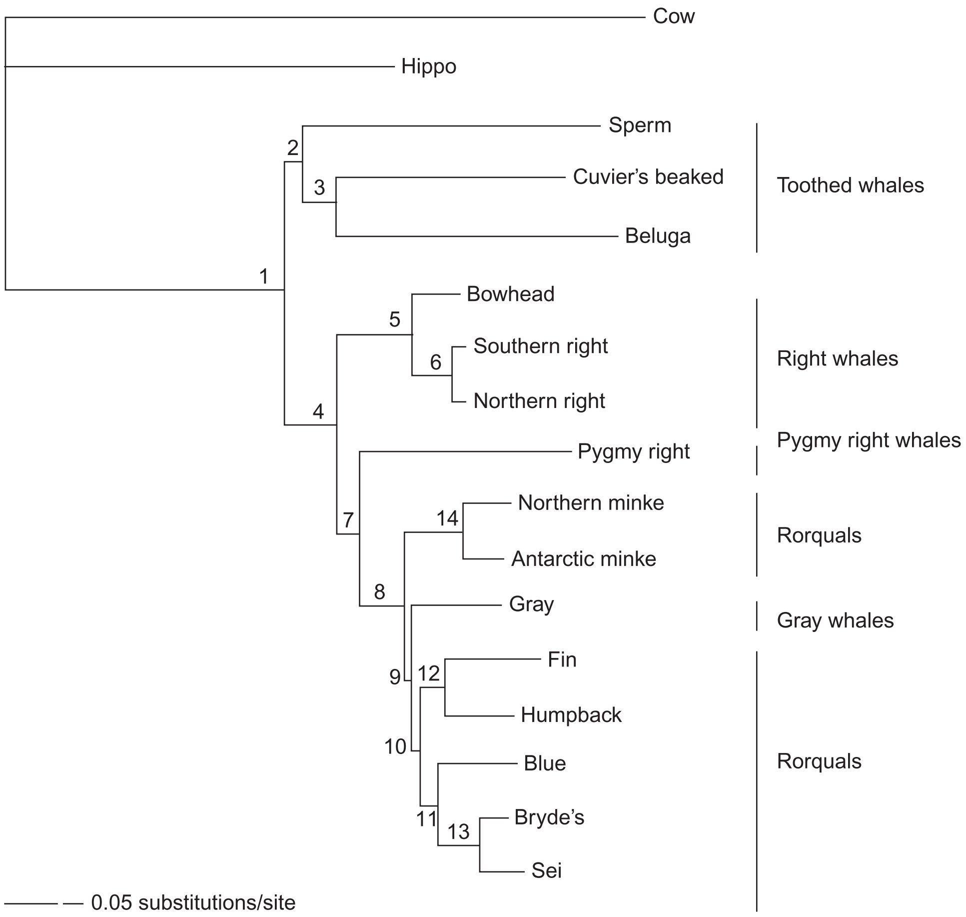

Figure 2 *Phylogenetic tree of baleen whales.* B. omurai, *not included here, lies between the clades for blue, Bryde's, and sei whales and for fin and humpback whales. Also, three species of right whale (North Atlantic, North Pacific and southern) are now generally recognized.*

Right whales (Balaenidae) are distinguished from the other three families by their long and narrow baleen plates and arched upper jaw. Other balaenid features include, externally, a disproportionately large head (approximately one-third of the body length), long thin rostrum, and huge bowed lower lips; they lack multiple ventral grooves. Internally, there is no coronoid process on the lower jaw and the cervical vertebrae are fused together. Within the family are two distinct groups—the bowhead (*Balaena mysticetus*) of northern polar waters (formerly known as the "Greenland" right whale), and the three "black" right whales, *Eubalaena* spp. of more temperate seas, so called to distinguish them from the "Greenland" right whale. All balaenids are robust, unlike the more streamlined balaenopteriids.

Pygmy right whales (*Caperea marginata*) have some features of both right whales and rorquals. The head is short (approximately one-quarter of the body length), although with an arched upper jaw and bowed lower lips, and there is a dorsal fin. The relatively long and narrow baleen plates are yellowish white, with a dark outer border, quite different from the all-black right whale baleen plates. Internally, pygmy right whales have numerous broadened and flattened ribs.

Gray whales (*Eschrichtius robustus*) are also somewhat intermediate in appearance between right whales and rorquals. They have short narrow heads, a slightly arched rostrum, and between two and five deep creases on the throat instead of the rorqual ventral grooves. The body is robust. There is no dorsal fin, but a series of 6–12 small "knuckles" along the tail stock. The yellowish-white baleen plates are relatively small.

Rorquals comprise the seven whales of the genus *Balaenoptera* (blue, *B. musculus*; fin, *B. physalus*; sei, *B. borealis*; Bryde's, *B. edeni*; Omura's, *B. omurai*; common minke, *B. acutorostrata*, Antarctic minke, *B. bonaerensis*), and the humpback whale (*Megaptera novaeangliae*). All have relatively short heads, less than a quarter of the body length. In comparison with right whales, the baleen plates are short and wide. Numerous ventral grooves are present, and there is a dorsal fin, sometimes rather small. Internally, the upper jaw is relatively long and unarched, the mandibles are bowed outward and a coronoid process is present; the cervical vertebrae are generally free.

Baleen whales are sometimes called the "great whales." Despite their generally huge size, some of the species are relatively small, and it seems preferable to restrict the term to the larger mysticetes (blue, fin, sei, Bryde's, Omura's, humpback) together with the largest odontocete (the sperm whale, *Physeter macrocephalus*).

Reviewing the systematics and distribution of the world's marine mammals, Rice (1998) drew attention to the derivation of the Latin word Mysticeti, and clarified the status of a variant, Mystacoceti. He described the former as coming from Aristotle's original Greek *mustoketos*, meaning "the mouse, the whale so-called" or "the mouse-whale" (said to be an ironic reference to the animals' generally vast size). Mystacoceti means "moustache-whales," and although used occasionally in the past (and more obviously appropriate for whales with baleen in their mouths) has been superseded by Mysticeti.

Although Rice believed that all right whales belong with the bowhead in the genus *Balaena*, recent genetic analyses have

Copyright © 2017. Elsevier Science & Technology. All rights reserved.

recognized three separate right whale species, in the genus *Eubalaena*: in the North Atlantic (*E. glacialis*); in the North Pacific (*E. japonica*); and in the Southern Hemisphere (*E. australis*). Indeed, *Eubalaena* is the only mysticete genus where separate species are recognized in each hemisphere.

II. Distribution and Abundance

Baleen whales occupy a wide variety of habitats, from open oceans to continental shelves and coastal waters, from the coldest waters of the Arctic and Antarctic, through waters of both hemispheres and into the tropics. Most specialized is the bowhead, *Balaena*, restricted to the harsh cold and shallow seas of the Arctic and subarctic. The "black" right whales (*Eubalaena*) are more oceanic and prefer generally temperate waters, but come very close to coasts in winter to give birth, particularly in the Southern Hemisphere. Once believed not to penetrate much further south than the Polar Front (Antarctic Convergence, 50–55°S) there have been recent records in the Antarctic proper, south of 60°S. Whether this is a new phenomenon is unclear: a report by Sir James Clark Ross of many "common black" (i.e., right) whales in the Ross Sea (eastern Antarctic) at 63°S in December 1840 was discounted when their presence there later that century could not be confirmed. It has been suggested that the currently greatly reduced population of the western North Atlantic right whale, now wintering off the south eastern United States and summering in coastal waters north to the Bay of Fundy (45°N), may represent the peripheral remnant of a more widely distributed stock, formerly summering north to Labrador and southern Greenland, that is, to at least 60°N.

The taxonomic status of Bryde's whales is complex. Currently one species is provisionally recognized (*B. edeni*) but it has two forms, a larger, more oceanic, and a smaller, coastal, form. Some consider the larger form, described from specimens taken off South Africa, to be a separate species (*B. brydei*) but it is now generally accepted as the same species as *B. edeni*. A further similar but smaller species, Omura's whale, *B. omurai*, was described in 2003; it was previously confounded with Bryde's whale but is now accepted as genetically distinct and not closely related to that species, lying outside the clade formed by blue, sei and Bryde's whales (see Fig. 2).

Subspecies have been described for several mysticete taxa, but only three are at present commonly in use. They are all blue whales, *B. musculus*: the Antarctic, sometimes known as the "true," blue whale, *B. m. intermedia*; the North Atlantic and North Pacific blue whale (*B. m. musculus*); and the Southern Hemisphere, mainly Indian Ocean, pygmy blue whale, *B. m. brevicauda*. A "dwarf" form of the common minke (*B. acutorostrata*) occurs generally in lower latitudes of the Southern Hemisphere; it has yet to be formally described.

The pygmy right whale (*Caperea*) is restricted to Southern Hemisphere temperate waters, mainly between 30°S and 55°S; it can be found coastally in winter in some areas, and year-round in others.

Gray whales (*Eschrichtius*) are the most obviously coastal baleen whales. The long coastal migration of the eastern gray, from Mexico to Alaska, supports a major whale watching industry from November to March. In spring, the animals migrate through the Bering Strait into the more open waters of the Bering Sea, but still favoring more shallow waters.

Among the rorquals, fin and sei whales are probably the most oceanic, the former penetrating more often into colder waters than the latter in summer. Blue whales can be found closer inshore, but often associated with deep coastal canyons, for example, off central and southern California and Western Australia. The Southern Hemisphere pygmy blue whale (subspecies *B. m. brevicauda*) is restricted to more temperate waters than the Antarctic blue whale (*B. m. intermedia*), not often being found much beyond 55°S. The coastal rorqual is the humpback (*Megaptera*), with long migrations between temperate/tropical breeding grounds and cold water feeding grounds. In the Southern Hemisphere, much of its journeys occur along the east and west coasts of the three continents. In the Northern Hemisphere, humpbacks are rather more oceanic, but still coastal at some stage in their migration: in the North Pacific they can be found wintering off the Hawaiian Islands and summering off Alaska; in the western North Atlantic they winter in the Caribbean and summer between New England, the west coast of Greenland, Iceland, and North Norway.

Minke whales are wide ranging, from polar to tropical waters in both hemispheres. In the Southern Hemisphere they can, with blue whales, be found closest to the ice edge in summer. Elsewhere minkes can often occur near shore, in bays and inlets. Their migrations are less well-defined and predictable than the other migratory rorquals; in some regions they may be present year-round.

The most localized rorquals are Bryde's whale and its close relatives. They are the only balaenopterids restricted entirely to tropical/warm temperate waters, and probably do not undertake long migrations. The two forms of *B. edeni*—inshore and offshore, in several areas—can differ in their movements. Off South Africa, for example, the inshore form is thought to be present throughout the year, whereas the offshore form appears and disappears seasonally, presumably in association with movements of its food, krill and shoaling fish.

III. Ecology

Although they include the largest living animals, baleen whales feed mainly on very small organisms, and while strictly carnivorous, on zooplankton or small fish. In "filter-feeding"—sieving the sea—baleen whales are quite different from toothed whales, where the prey is captured individually.

Filter-feeding has been described as requiring, in addition to a supply of food in the water, three basic features: (1) a flow of water to bring prey near the mouth, (2) a filter to collect the food but allow water to pass through, and (3) a means of removing the filtered food and conveying it to the stomach for digestion. Baleen whales meet those requirements by (a) seeking out areas where their food concentrates, (b) either swimming open-mouthed through food or gulping it in, (c) possessing a highly efficient filter formed by the baleen plates, and (d) forcing the water containing the food out through the baleen plates, and then transferring the trapped food back to the gullet and hence to the stomach. In (d) the tongue is presumed to be involved; in balaenopterids the process is aided by the distensible throat and the ability to open the lower jaw to almost 90 degrees.

Although all baleen whales have a filter based on baleen plates, two rather different systems—essentially "skimming" and "gulping"—have evolved to filter a large volume of water containing food. Each relies on the series of triangular baleen plates, borne transversely on each upper jaw. The inner, longer border (hypotenuse) of each plate bears a fringe of fine hairs, forming a kind of filtering "doormat." Quite unrelated to teeth (which appear as early rudiments in the gums of fetal baleen whales), baleen consists of keratin and is close in composition to hair and fingernails. In right whales, filtration is achieved with very long and narrow plates in the very large mouth, in the very large head. The plates, up to 4 m long in bowheads and 2.7 m in other right whales, are accommodated in the mouth by an arched upper jaw, and enclosed in massively enlarged and upwardly bowed lower lips (see Fig. 3). There is a gap between the rows at the front of the mouth, and the whole arrangement allows the whale to scoop up a great quantity of water while swimming slowly forwards. In rorquals, with their much smaller heads, the baleen plates

Copyright © 2017. Elsevier Science & Technology. All rights reserved.

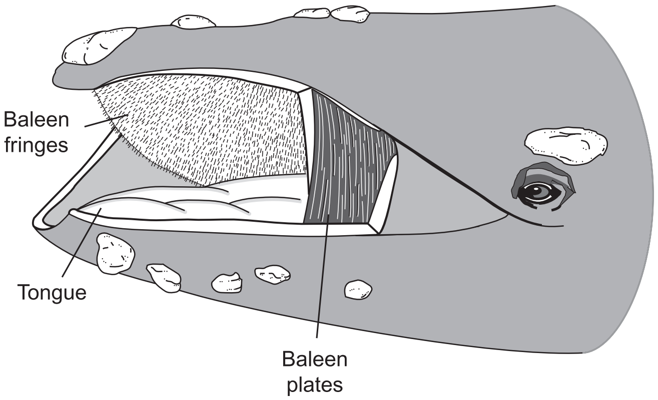

Figure 3 *Head of a right whale, showing the arrangement of the filter-feeding apparatus. The anterior section of the baleen plates on the left side of this whale were removed to show fringes of right baleen plates and tongue. From* Bonner (1980).

are shorter and broader and the rows are continuous at the front. Taking in a large volume of water and food is usually achieved by swimming through a food swarm and gulping, while simultaneously greatly enlarging the capacity of the mouth by extending the ventral grooves, depressing the tongue and widely opening the lower jaw, almost to 90 degrees from the body axis. The two systems allow, on the one hand, the relatively slow-swimming balaenids to concentrate their rather sparse food over a period, and on the other, the faster-swimming rorquals to take in large amounts of their highly concentrated prey over a shorter time.

Typically, baleen whales feed on zooplankton, mainly euphausiids or copepods, swarming in polar or subpolar regions in summer. That is particularly so in the Southern Hemisphere, where the summer distributions of several balaenopterids depend on the presence of *Euphausia superba* (known to whalers by the Norwegian word "krill") in huge concentrations in the Antarctic. In the Northern Hemisphere, with a more variable availability of food, balaenopterids are more catholic in their feeding. Humpbacks and fin whales, for example, while feeding almost exclusively on krill in the south, often take various species of schooling fish in the north.

The variety of organisms taken by the various baleen whale species in different regions is listed in Table 1. Although most feeding occurs in colder waters, baleen whales may feed opportunistically elsewhere. All baleen whales but one, the gray whale, feed in surface waters, generally within 100 m of the surface, and consequently, unlike many toothed whales, do not dive very deep or for long periods. Gray whales feed primarily on bottom-living organisms, almost exclusively benthic crustaceans, in shallow waters.

The baleen plate structure, particularly the inner fringing hairs, to some extent mirrors the food organisms taken, or (in the case of *E. superba*) different size classes. Thus, there is some correlation between decreasing size of prey and fineness of baleen by species, viz., gray, blue, fin, humpback, minke, sei, and right whales. Where food stocks are very dense, for example, around subantarctic South Georgia, blue, fin, and sei whales may all overlap in their feeding on *E. superba*.

Baleen whale food consumption per day has been calculated as some 1.5%–2.0% of body weight, averaged over the year. Given that feeding occurs mainly over about 4 months in the summer in the larger species, the food intake during the feeding season has been calculated at some 4% of body weight per day, approximately 4000 kg/day for a large blue whale. To survive the enormous drain of pregnancy and lactation, it has been calculated that a pregnant female baleen whale needs to increase its body weight by up to 65%. The ability to achieve such increase in only a few months' feeding indicates the great efficiency of the baleen whales' feeding system, as well as the considerable nutritive value of the food.

Apart from humans, the most notable baleen whale predator is the killer whale (*Orcinus orca*). Minke whales have been identified as a major diet item of killer whales in the Antarctic, and off British Columbia, Canada. Killer whale attacks have been reported on blue, sei, bowhead, and gray whales, although their frequency and success are unknown. Humpbacks often have killer whale tooth marks on their bodies and tail flukes. Humpback and right whale calves in warm coastal waters are susceptible to attack by sharks. There are anecdotal reports of calving ground attacks on humpbacks by false killer whales (*Pseudorca*).

A form of harassment occurs on right whales on calving grounds off Peninsula Valdes, Argentina. Kelp gulls have developed the habit of feeding on skin and blubber gouged from adult southern right whales' backs as they lie at the surface. Large white lesions can result. The whales react adversely to such gull-induced disturbance, so much so that the adults may remain at the surface with their backs underwater; young calves are now also being attacked and their development may be affected.

External parasites, particularly "whale lice" (cyamid crustaceans) and barnacles (both sessile and stalked) are common on the slower-swimming more coastal baleen whales such as gray, humpback, and right whales. In the latter, aggregations of light-colored cyamids on warty head callosities have facilitated research using callosity-pattern photographs for individual identification. External parasites are much less common on the faster swimming species, although whale lice have been reported on minke whales (in and around the ventral grooves and umbilicus). The highly modified copepod *Pennella* occurs particularly on fin and sei whales in warmer waters; its presence on those species in colder waters, for example, at South Georgia in the South Atlantic, has been taken to indicate migration from the north. A commensal copepod *Balaenophilus unisetus* often infests baleen plates in warm waters, especially on sei and pygmy blue whales.

A variety of internal parasites has been recorded, although some baleen whales seem less prone to infection than others. They appear, for example, to be less common in blue whales, but prevalent in sei whales. Records include stomach worms (*Anisakis* sp.), cestodes, kidney nematodes, liver flukes, and acanthocephalans ("thorny-headed" worms) of the small intestine.

The cold water diatom *Cocconeis ceticola* often forms a brownish-yellow film on the skin of blue and other baleen whales in the Antarctic. Since the film takes about a month to develop, its extent can be used to judge the length of time an animal has been there. Its presence led to an early common name for the blue whale—"sulfur bottom."

For many years, the origin of small scoop-shaped bites on baleen whale bodies in warmer waters remained a mystery, until they were found to be caused by the small "cookie-cutter" shark, *Isistius brasiliensis*. Some species are highly prone to such attacks. In Southern Hemisphere sei whales, the overlapping healing scars can impart a galvanized-iron sheen to the body.

IV. Behavior and Physiology

A. Sound Production

Unlike toothed whales, baleen whales are not generally believed to use sound for echolocation, although bowheads, for example, are thought to use sound reflected from the undersides of ice floes to navigate through ice fields. However, sound production for communication, for display, establishment of territory or other behavior,

Copyright © 2017. Elsevier Science & Technology. All rights reserved.

TABLE 1 Baleen Whale Food Items

Species	***Subspecies***	***Common name***	***Food items***	
			Northern Hemisphere	***Southern Hemisphere***
B. mysticetus		Bowhead whale	Mainly calanoid copepods; euphausiids; occasional mysids, amphipods, isopods, small fish	
E. glacialis		Northern right whale	Calanoid copepods; euphausiids	
E. australis		Southern right whale		Copepods; post-larval *Munida gregaria* ; *Euphausia superba*
Caperea marginata		Pygmy right whale		Calanoid copepods
E. robustus		Gray whale	Gammarid amphipods; occasional polychaetes, small fish	
M. novaeangliae		Humpback whale	Schooling fish; euphausiids	*Euphausia superba* (Antarctic); euphausiids, post-larval *Munida gregaria* , occasional fish (ex-Antarctic)
B. acutorostrata		Common minke (North Atlantic)	Schooling fish; euphausiids	
		Common minke (North Pacific)	Euphausiids; copepods; schooling fish	
	B. a . ?spp.	Dwarf minke		?Euphausiids, schooling fish
B. bonaerensis		Antarctic minke		*Euphausia superba*, *E. crystallorophias*
B. edeni		Bryde's whale	Pelagic crustaceans including euphausiids	Schooling fish; euphausiids
B. omurai		Omura's whale	?Euphausiids	?Euphausiids
B. borealis		Sei whale	Schooling fish	Copepods incl. *Calanus* ; *Euphausia superba*
B. physalus		Fin whale	Schooling fish; squid; euphausiids; copepods	*Euphausia superba* (Antarctic); other euphausiids (ex Antarctic)
B. musculus	*B. m. musculus*	Blue whale	Euphausiids; calanoid copepods; occasional amphipods, squid	
	B. m. intermedia	Antarctic blue		*Euphausia superba* (Antarctic); other euphausiids (ex Antarctic)
	B. m. brevicauda	Pygmy blue		Euphausiids, incl. *E. vallentini*, *E. recurve*, *Nyctiphanes austra*

is well developed in the suborder. Blue whales produce the loudest sustained sounds of any living animal. At up to nearly 190 decibels, their long (half minute or more), very low-frequency (c. 26 Hz) moans may carry for hundreds of kilometers or more in special conditions. Fin whales produce similarly low-pulsed sounds (20 Hz). Minke whales also produce a variety of loud sounds. Right whales produce long low moans; bowhead sounds, recorded on migration past hydrophone arrays in nearshore leads, have been used in conjunction with sightings to estimate population size off northern Alaska. Southern right whales, at least, seem to use sound to communicate with their calves.

Humpbacks produce the longest, most complex sound sequences in songs (sets of sounds produced in reliably predictive sequences), described as an array of moans, groans, roars, and sighs to high-pitched squeaks and chirps, lasting ten or more minutes before repetition, sometimes over hours. It seems that only the adult males sing, generally only in or close to the breeding season. In any one breeding season, all the males sing the same song, changing progressively over successive seasons. Owing to the constantly changing song pattern within populations, different populations of humpbacks generally have different songs although populations in the same ocean basin often share parts of songs. In the South Pacific, song sharing among neighboring populations is common and has a distinct pattern with songs originating in eastern Australia repeatedly being adopted by whales in New Caledonia and Tonga a year later, and then French Polynesia and other eastern breeding grounds a year or so after that. This "cultural transmission" of behavior over such a large spatial and temporal scale is one of the clearest examples of the phenomenon in a nonhuman species. While the songs of populations in different ocean basins are usually quite different, an example involving humpback songs has been reported where typical Australian east coast humpback song switched to a new, west coast version over a very short period, only 2 years, between 1996 and 1997, probably as a result of the influence of a few male singers from the west coast. "Songs" may also be heard in migrating humpbacks, but less so on the cold water feeding grounds. Simpler songs of repeated sounds also occur in at least bowhead, minke, fin, and blue whales.

Copyright © 2017. Elsevier Science & Technology. All rights reserved.

B. Swimming and Migration

With their streamlined bodies, rorquals include the fastest swimming baleen whales. Sei whales have been recorded at around 35 knots (>60 km/hr) in short bursts; minke and fin whales are also known as fast swimmers, the latter up to 20 knots (37 km/hr). Blue whales are among the most powerful swimmers, able to sustain speeds of over 15 knots (28 km/hr) for several hours. On migration, humpbacks and gray whales average about 3–4 knots (5–7 km/hr), but bowheads only about 2.7 knots (5 km/hr). Migration speeds for southern right whales are not known, but medium range coastal movements off southern Australia indicate 1.5–2.3 knots (2.7–4.2 km/hr) over 24 hr for cow/calf pairs.

Baleen whales undertake some of the longest migrations known. Gray whales may cover some 5000 nautical miles (c. 9000 km) on the round trip between the Baja California breeding grounds and Alaskan feeding grounds. Southern Hemisphere humpbacks may cover as much as 50 degrees of latitude either way between breeding and feeding grounds, a round trip of some 6000 nautical miles (c. 11,000 km); records of humpbacks migrating between the Antarctic Peninsula and Costa Rica involved a single trip of c. 8400 km (4500 nautical miles), the longest recorded migration of any mammal. Not all baleen whale migrations are so well marked. The biannual movements of Bering Sea bowheads are governed by the seasonal advance and retreat of sea ice, which vary from year to year; recent major reductions in multiyear sea ice in the Chukchi Sea and early lead development, possibly associated with climate change, have led to evidence that migration has shifted earlier. Although Southern Hemisphere blue and fin whales all feed extensively in the Antarctic in summer, the locations of their calving grounds are not known. Sei whale migrations are relatively diffuse, and can vary from year to year in response to changing environmental conditions; their name comes from the schooling fish with which they often associate off the northern Norway coast. By comparison, Bryde's whales hardly migrate at all, presumably being able to satisfy both reproductive and nutritional needs in tropical/warm temperate waters. Even among such migratory animals as humpbacks, it may be that not all animals migrate every year: studies off eastern Australia have indicated that a proportion of adult females may not return to the calving grounds each year, and individuals have been reported in summer further north. However, Southern Hemisphere migrating humpbacks show segregation in the migrating stream: immatures and females accompanied by yearling calves are in the van of the northward migration, followed by adult males and nonpregnant mature females; pregnant females bring up the rear. A similar pattern occurs on the southward journey, with cow/calf pairs traveling last. Very similar segregation is recorded among migrating gray whales. However, not only is there segregation within some (possibly all) species, the species themselves may arrive on and leave the feeding grounds at different times. At South Georgia, where they were once common, fin whales tended to leave the feeding grounds after blue whales but before sei whales, the latter having arrived there last.

Baleen whale migrations have generally been regarded as taking place in response to the need to feed in colder waters and reproduce in warmer waters. Explanations for such long-range movements have included direct benefits to the calf (better able to survive in calm, warm waters), evolutionary "tradition" (a leftover from times when continents were closer together), and the possible ability of some species to supplement their food supply from plankton encountered on migration or on the calving grounds. Others have rejected these explanations, suggesting there may be a major advantage to migrating pregnant female baleen whales in reducing the risk of killer whale predation on newborn calves in low latitudes. It has also been suggested that calf development in warm water may lead to larger adult size and greater reproductive success.

C. Social Activity

Large aggregations of baleen whales are generally uncommon. Even on migration, in those species where well-defined migration paths are followed (e.g., gray whales and humpbacks), individual migrating groups are generally small, numbering only a few individuals. It has been stated that predation is a main factor in the formation of large groups of cetaceans, for example, open ocean dolphins. Given the large size of most adult baleen whales, predation pressure is low, and group size can be correspondingly small.

Blue whales are usually solitary or in small groups of two to three. Fin whales can be single or in pairs; on the feeding grounds they may form larger groupings, up to 100 or more. Similarly, sei whales can be found in large feeding concentrations, but in groups of up to only about six elsewhere. The same is true for minke whales, found in concentrations on the feeding grounds, but singly or in groups of two or three elsewhere. Social behavior has been studied intensively in coastal humpbacks, for example, on the calving grounds. Male humpbacks compete for access to females by singing and fighting. The songs seem to act as a kind of courtship display. Males congregate near a single adult female, fighting for position. Such aggression can involve lunging at each other with ventral grooves extended, hitting with the tail flukes, raising the head while swimming, fluke and flipper slapping, and releasing streams of bubbles from the blowhole. As a result of such encounters, individuals can be left with raw and bleeding wounds caused by the sharp barnacles. Among southern right whales, surface active groups (known as SAGs) are often observed on the coastal calving grounds in winter, involving a tight group with a number of males pursuing an adult female, but with less aggression. As for humpbacks, it is not yet certain whether such behavior results in successful mating, although intromission in right whale SAGs is often observed.

Feeding balaenopterids have often been reported as circling on their sides through swarms of plankton or fish. It has been suggested that gray whales feed on their right sides, those baleen plates being more worn down, presumably through contact with the seabed. The most remarkable behavior, however, is reported from humpbacks. In the Southern Hemisphere, on swarms of krill, they may feed in the same "gulping" way as other balaenopterids. In the Northern Hemisphere, two methods are commonly reported—"lunging" and "bubble netting." In the former, individuals emerge almost vertically at the surface with their mouths partly open, closing them to force the enclosed water out through the baleen. In the latter, an animal circles below the food swarm; as it swims upward, it exhales a series of bubbles forming a "net" encircling the prey; the animal then swims upward through the prey with its mouth open, as in lunging. Such behavior has also recently been reported off the Antarctic Peninsula.

V. Life History

Young baleen whales, particularly the fetus and the calf, grow at an extraordinary rate. In the largest species, the blue whale, fetal weight increases at a rate of some 100 kg/day toward the end of pregnancy. The calf's weight increases at a rate of about 80 kg/day during suckling. During that 7-month period of dependence on

Copyright © 2017. Elsevier Science & Technology. All rights reserved.

the cow's milk, the blue whale calf will have increased its weight by some 17 tons, and increased in length from around 7 to 17 m. Blue whales attain sexual maturity at between 5 and 10 years, at a length of around 22 m, and live for about 80–90 years. Adult female blue whales give birth every 2–3 years, pregnancy lasting some 10–11 months.

Other rorquals follow the same general pattern (Fig. 4). Mating takes place in warm waters in winter, birth following some 11 months later. A 7–11 month lactation period may be followed by a year "resting," or almost immediately by another pregnancy. Most adults are able to reproduce from between 5 and 10 years of age, and reach maximum growth after 15 or more years. The smallest balaenopterid, the minke whale, is born after a pregnancy of some 10 months, at a length of just under 3 m. Weaning occurs at just under 6 m, after 3–6 months. The adult female can become pregnant again immediately following birth, but the resulting short calving interval is generally uncommon in baleen whales: 2–3 years is the norm, although humpbacks can achieve a similar birth rate, enabling their stocks to recover rapidly after depletion.

Right whales follow a similar general pattern, but there are some differences. In northern and southern right whales, gestation lasts about 11 months, weaning for about another year. Females are able to reproduce successfully from about 8 years (there are records of successful first pregnancies from 6 years), but the calving interval is usually a relatively regular 3 years. For bowheads, while growth is very rapid during the first year of life (from 4.5 m), it may be followed by a period of several years with little or no growth. Sexual maturity occurs at 13–14 m: at the reduced growth rate that would not be reached until 17–20 years. Similarly, there is evidence of very considerable longevity in this species: harpoon heads and an unexploded bomb-lance found in harvested whales and last known to be used off Alaska in the late 19th or early 20th centuries, together with "chemical ageing" evidence, even suggest a life span of up to 200 years.

VI. Interactions With Humans

For centuries, baleen whales have borne the brunt of human greed, for products and profit. Only the sperm whale, largest of the toothed whales, has rivaled them as a whaling target (Mackintosh, 1965).

In its most recent "Red List" of threatened animals, the World Conservation Union (IUCN-SSC 2015), includes no baleen whale species as either *extinct*, or *critically endangered (CR)*, although five subspecies, populations, or stocks are so listed. Four species are *endangered*; no species are *vulnerable*, although two taxa are. Four species are of *least concern (LC)*; one species is at *lower risk/conservation dependent* (*LR/CD*), and four species and one subspecies are listed as *data deficient* (*DD*).

Those species or stocks under greatest threat (*CR*), are the North Pacific right whale, the Svalbard-Barents Sea bowhead, the western (North Pacific) subpopulation gray whale, the Chile-Peru southern right whale, and the Antarctic blue. Fin and sei whales, together with the Okhotsk Sea bowhead, the North Atlantic right, and the Arabian Sea and Oceania humpbacks, are *Endangered (E)*. The North Atlantic blue and Mediterranean fin are listed as *vulnerable*. Of *least concern (LC)* are the North Atlantic (common) minke, the eastern (North Pacific) gray whale, most southern right whales, and humpbacks apart from the two stocks already mentioned. The taxa for which insufficient information is currently available (*DD*) are the Antarctic minke, Bryde's whale, Omura's whale, and the pygmy blue (Thomas et al., 2016).

The International Whaling Commission's Scientific Committee, responsible for assessments of such stocks' current status, has reported encouraging reversals of stock decline for some stocks of some species. One, the eastern gray whale, has recovered under protection from commercial whaling (but with aboriginal catches up to some 150 per year) to at or near its "original" (prewhaling) state, at about 26,000 animals. Similarly, the Northwest Atlantic humpback and several Southern Hemisphere humpback populations have shown marked increase. The North Atlantic stock, estimated

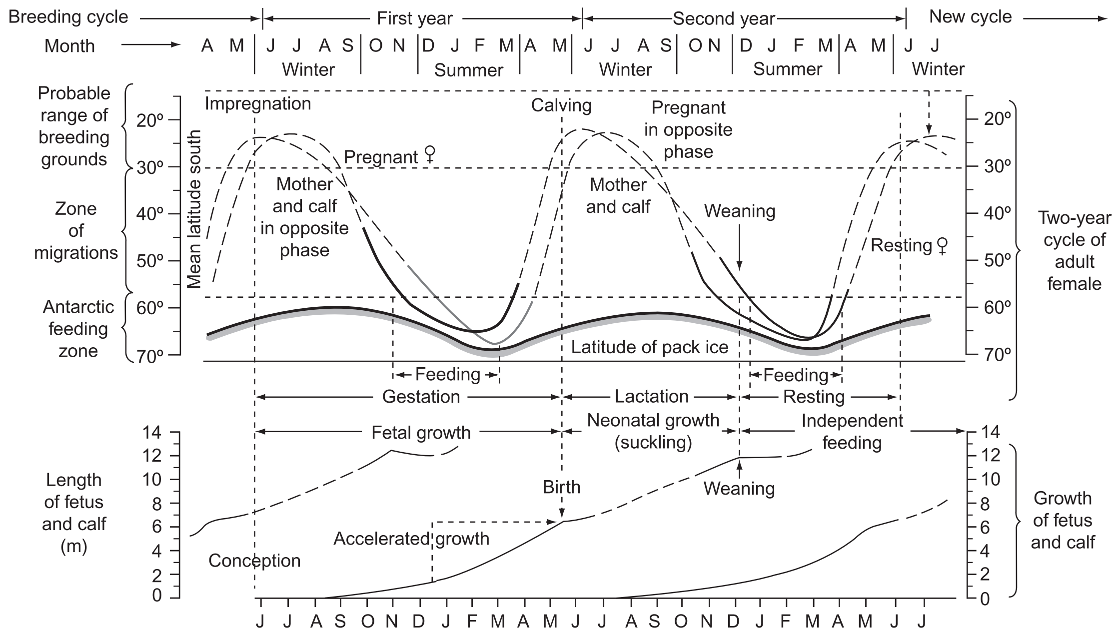

Figure 4 *"Typical" life cycle of a southern baleen whale. As modified by Bonner (1980), from Mackintosh (1965).*

Copyright © 2017. Elsevier Science & Technology. All rights reserved.

at some 11,600 animals in 1992–93 and around 15,000 in 2001, reflects substantial recovery since protection in the 1950s, while several Southern Hemisphere stocks (off southeastern Africa, eastern and Western Australia) have been increasing, off Australia at around 10% per year since the early 1980s. Three southern right whale stocks (off eastern South America, South Africa, and southern Australia) have been increasing since the late 1970s at 6%–7% per year, although all are still well below their "original" stock size. Even the Antarctic blue whale, whose future has been of considerable concern, with estimates for the late 1980s at fewer than 500 animals for the whole Antarctic, has shown recent encouraging signs. Based on a series of Antarctic sightings cruises—mainly for minke whales but including other large whales—calculations give a population size of some 2300 in 1998, increasing at around 7% per year. At that rate, the population size might now be nearing some 8000, although still only a small fraction (around 3%) of its original population size, estimated at some 240,000.

One species or stock for which there is considerable concern is the western North Atlantic right whale. Despite good calving years between 2001 and 2011, absolute abundance (only around 500 known animals in 2012) remains very low, with an annual increase of 2.8%; it is subject to considerable threat from human-induced mortality such as ship strikes and entanglement in fishing gear. Concerns have also been expressed for the northwest Indian Ocean (Arabian Sea) humpback population and for the small population of southern right whales off Chile.

It has been calculated (Laws, 1977) that the great reduction of baleen whales by whaling, for the Antarctic to around one-third of original numbers and one-sixth in biomass, must have left a large surplus of food—some 150 million tons per year—available for other consumers such as seals, penguins, and fish. (In a different way, earlier whaling in the North Atlantic, particularly on right whales, is believed to have influenced the spread of one sea bird—the fulmar—by providing food in the form of discarded whale carcasses.) In response to an increase in available food, there may well have been increases in growth rates, earlier ages at maturity and higher rates of pregnancy in some baleen whale species. However, the evidence is equivocal, as it is for competition between individual whale species. For some, for example, right whales and sei, it has been suggested that an increase in one (right whales) could be inhibited by competition with another (sei whales). In the North Pacific, both sei and right whales can feed on the same prey—copepods—and sei whales can at times be "skimming" feeders, like right whales. However, evidence that they actually compete, on the same prey, in the same area, at the same time, and even on the same prey patch, is lacking. Similarly, there has been much debate and speculation on whether the recovery of the Antarctic blue whale has been inhibited by an apparent increase in minke whales. In that case, there may in fact be very little direct competition for food where the common prey is not limited in abundance (as in the Antarctic) and is available in large patches. The recent increases at substantial annual rates for several stocks of Southern Hemisphere humpbacks and right whales, as well as for the Antarctic blue whale (and possibly even for the fin whale), suggest that such competition is unlikely, at least where, as in the Antarctic, food supplies are abundant (Thomas et al., 2016).

There is, however, increasing concern over the possible effects of climate change, with reductions in sea ice, rise in sea surface temperature and ocean acidification. The first has been considered a factor in reducing the amount of krill available, and the second, for example, has been shown to affect reproductive capacity—elevated sea surface temperature off South Georgia has been found to affect conception and subsequent calving rates in the eastern South American population of southern right whales. Ocean acidification is likely to affect shell-building in a wide range of organisms, some of them baleen whale prey, for example, that of gray whales feeding on benthic crustaceans in the Bering Sea.

Copyright © 2017. Elsevier Science & Technology. All rights reserved.

See Also the Following Articles

Baleen ■ Blue Whale ■ Bowhead Whale ■ Bryde's Whale ■ Fin Whale ■ Gray Whale ■ Krill and other Plankton ■ Minke Whales ■ Omura's Whale ■ Pygmy Right Whale ■ Right Whales ■ Sei Whale ■ Song ■ Sound ■ Species and Subspecies ■ Whaling, Modern ■ Whaling, Aboriginal, and Western Traditional

References

Bonner, W.N. (1980). *Whales.* The Blandford Press, Poole, Dorset.278p.

IUCN-SSC (2015). *Status of the World's Cetaceans.*

Laws, R.M. (1977). Seals and whales of the Southern Ocean. *Phil. Trans. R. Soc. Lond. B* **279**, 81–96.

Mackintosh, N.A. (1965). The Stocks of Whales, 232. Fishing News (Books) Ltd., London.

Rice, D.W. (1998). *Marine mammals of the world: Systematics and distribution.* Special Publication Number 4, the Society for Marine Mammalogy, Lawrence, Kansas. 231.p.

Thomas, P.O., Reeves, R.R., and Brownell, Jr., R.L. (2016). Status of the world's baleen whales. *Mar. Mamm. Sci.* **32**(2), 682–734.

BALEEN WHALES, EVOLUTION

Annalisa Berta and Thomas A. Deméré

I. Introduction

The fossil record of mysticete cetaceans is rapidly improving and providing critical new information about the origin and diversification of this highly specialized mammalian group. Crown mysticetes (i.e., extant baleen whales of the Balaenidae, Neobalaenidae, Balaenopteridae, and Eschrichtiidae clades and their extinct sister taxa the Cetotheriidae) are edentulous as adults, but possess fetal deciduous teeth that are resorbed prior to birth. This ontogenetic pattern reflects an ancestral ontogeny in which fully formed teeth were retained into adulthood. Archaic baleen whales include stem mysticetes, both toothed and toothless, that do not belong to extant lineages. Toothed mysticetes first evolved in the late Eocene or earliest Oligocene, diversified throughout the Oligocene, and appear to have been extinct before the Miocene began. Although contested, it is likely that certain stem toothed mysticetes possessed some form of baleen in the upper jaw. This key filter feeding innovation permitted exploitation of a new niche and heralded the evolution of modern baleen whales, the largest animals on Earth. Stem edentulous mysticetes are first reported from the late Oligocene coincident with the radiation of toothed forms, and underwent their own radiation. The diversification of crown mysticetes and their adaptive radiation as skim suction, and engulfment filter feeders is fairly well-documented in Miocene and Pliocene aged sedimentary rocks.

II. Toothed Mysticetes

As currently understood, toothed mysticetes constitute three distinct lineages: Llanocetidae and Mammalodontidae from the Southern Ocean and Aetiocetidae from the North Pacific. To date no toothed mysticetes are known from the Atlantic region. The presence of a functional adult dentition in toothed mysticetes is the ancestral condition shared with basilosaurid archaeocetes and stem odontocetes. The degree of telescoping of the skull in Oligocene toothed mysticetes is also ancestral and expressed as a limited interdigitation of rostral and cranial elements, with a long intertemporal exposure of the frontal and parietal on the cranial vertex and a relatively small and steeply sloping supraoccipital. In addition, the rostrum is typically akinetic (closed and rigid sutures between premaxilla and maxilla), the supraorbital process of the frontal retains an elevated position on the cranium, and the external narial opening ("blowhole") is only midway between the tip of the rostrum and the orbit. Derived features shared between toothed mysticetes and later-diverging edentulous mysticetes include transverse expansion of the descending process of the maxilla to form an edentulous infraorbital plate and dorsoventral thinning of the lateral margin of the maxilla.

The geologically oldest purported mysticete is *Llanocetus denticrenatus* from the latest Eocene (~34 Ma) of Seymour Island, Antarctica. Although only a portion of the mandible and an endocranial cast have been formally described, the holotype also includes a nearly complete skull and partial skeleton under study by Ewan Fordyce. Despite its antiquity, *Llanocetus* was a large whale with a skull length of about 2 m. The distinctly heterodont dentition of *Llanocetus* consisted of widely spaced molariform postcanine teeth with crowns characterized by roughened enamel and large, palmate denticles. Functional comparisons have been made with the palamate teeth of the modern filter-feeding crabeater seal, *Lobodon carcinophagus*.

The mammalodontids, *Janjucetus hunderi*, *Mammalodon colliveri and M. hakataramea*, from the late Oligocene (~28–24 Ma) of Australia and New Zealand (Fitzgerald, 2006, 2010) Fordyce and Marx, 2016, were smaller, short-faced toothed mysticetes with closely spaced, heterodont dentitions (Fig. 1A). Crown morphology

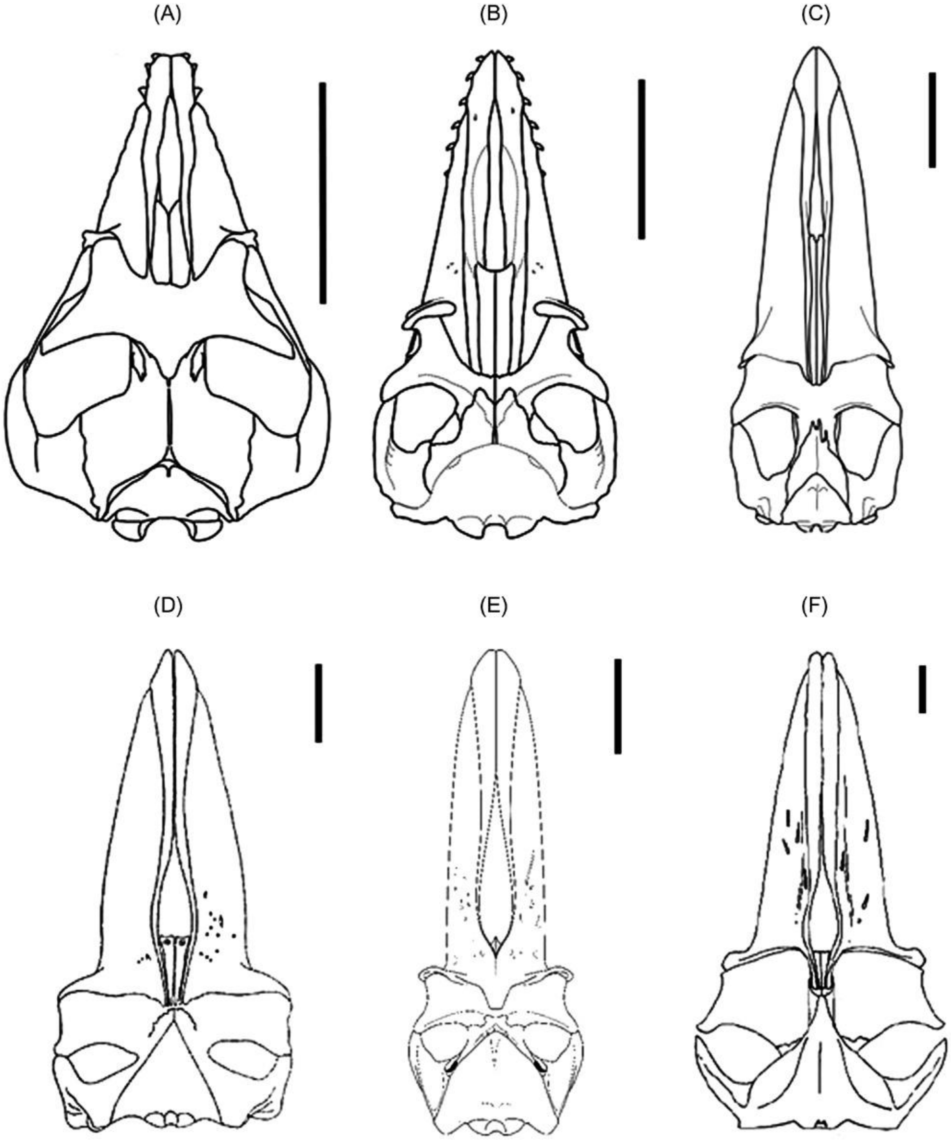

Figure 1 *Stem and crown mysticete skulls. (A)* Janjucetus hunderi *(from Fitzgerald, 2006), (B)* Aetiocetus weltoni *(from Deméré and Berta, 2008), (C)* Yamatocetus canaliculatus *(from Boessenecker and Fordyce, 2016), (D)* A. patulus *(from Kellogg, 1968), (E)* Herpetocetus morrowi *(from El Adli et al., 2014), and (F)* Protororqualus cuvieri *(from Bisconti, 2007). Scale bars equal 20 cm.*

Copyright © 2017. Elsevier Science & Technology. All rights reserved.

of the postcanine teeth is poorly known for *M. colliveri*, but for *J. hunderi* consists of roughened enamel and moderately sized, closely appressed denticles. The orbits of *J. hunderi* are large relative to skull length (~46 cm), suggesting acute vision. In addition, *J. hunderi* possessed an archaeocete-like sutured mandibular symphysis indicating that mammalodontids lacked the mandibular kinesis of later-diverging mysticetes (Fitzgerald, 2011).

Aetiocetids represent the most diverse clade of toothed mysticetes and include eight nominal species grouped into five genera. *Aetiocetus* is the most speciose genus known by four species with monotypic genera *Ashorocetus*, *Chonecetus*, *Fucaia*, and *Morawanocetus*. The oldest reported aetiocetid *Fucaia buelli* was described from the earliest Oligocene (~33–31 Ma) of Washington, USA (Marx et al., 2015). Of particular significance is the fact that this taxon fills a temporal gap between aetiocetids and the oldest known mysticete *Llanocetus*. Overall, most aetiocetids were small-bodied cetaceans with skull lengths of about 60–70 cm and an estimated total body length of 2–3 m. Discovery of a *Morawanocetus*-like earbone from Japan indicates that some aetiocetids were of larger body size as it was estimated to have come from an animal that is nearly twice as large (~8 m) as known aetiocetids. Further, this large aetiocetid was suggested by Tsai and Ando (2015) to indicate niche partitioning of aetiocetids implying different food resources and feeding strategies rather than evidence for sexual dimorphism. Unlike species of *Mammalodon* and *Janjucetus*, aetiocetids had a relatively long rostrum (Fig. 1B). Little is known of their postcranial skeleton except that they had elongated necks and relatively long forelimbs with rigid elbow joints. The aetiocetid skull retained numerous primitive features inherited from their archaeocete ancestors (e.g., anteriorly positioned “blowhole,” elevated supraorbital processes of the frontals, long intertemporal constriction, large mandibular coronoid process, and large mandibular foramen). However, as mosaic stem mysticetes, aetiocetids also possessed important derived features (e.g., broad rostrum, vascularized palate, and outwardly bowed mandible with prominent groove for the elastic, fibrocartilaginous symphysis) that portend the later diversification of fully edentulous baleen whales. Dental morphology varied within the group with *Fucaia* and *Morawanocetus* possessing a distinctly heterodont dentition and postcanine crowns with roughened enamel and numerous accessory denticles. In contrast species of *Aetiocetus* had a nearly homodont dentition consisting of postcanine crowns with lightly roughened enamel and diminutive accessory denticles. The teeth were widely spaced and eastern North Pacific species (*A. cotylaveus* and *A. weltoni*) show a tendency toward polydonty, while one western North Pacific species (*A. polydentatus*) was distinctly polydont. Several genera of aetiocetids (*Fucaia*, *Morawanocetus*, and *Aetiocetus*) possess lateral nutrient foramina and sulci on the palate that suggest the possibility of some form of proto-baleen.

At least two competing hypotheses concerning phylogenetic relationships among stem toothed mysticetes have been proposed, with one promoting a monophyletic toothed grouping consisting of Mammalodontidae + Aetiocetidae (Marx, 2010; Marx and Fordyce, 2016; Tsai and Fordyce, 2016) and the other promoting a monophyletic Mammalodontidae that is sister to a monophyletic Aetiocetidae (Deméré et al., 2008; Fitzgerald, 2011; Boessenecker and Fordyce, 2015c; Bisconti, 2016), which in turn is sister to the Chaeomysticeti clade of edentulous mysticetes. These different tree topologies have important implications for interpreting evolutionary events at the base of the mysticete radiation. A monophyletic Mammalodontidae + Aetiocetidae grouping suggests that an elongate rostrum, elastic mandibular symphysis, and proto-baleen evolved twice—once in a toothed mysticete clade and a second time in an edentulous mysticete clade. In contrast, sequential monophyletic groups (Mammalodontidae, Aetiocetidae, and Chaeomysticeti) suggests that these same features evolved only once in the common ancestor of Aetiocetidae and Chaeomysticeti (Fig. 2).

III. Edentulous Mysticetes

The Oligocene radiation of mysticetes involved not only lineages of archaic toothed species but also a variety of stem edentulous species (Chaeomysticeti). The most speciose of these Oligocene chaeomysticete lineages was the Eomysticetidae known from the early and late Oligocene (~30–24 Ma) of North America (*Eomysticetus* and *Micromysticetus*) and Japan (*Yamatocetus*; Fig. 1C), as well as the late Oligocene (~27–25 Ma) of New Zealand (*Matapa*, *Tohoraata*, *Tokarahia*, and *Waharoa* (Boessenecker and Fordyce, 2015a,b,c). These early functionally edentulous baleen whales were of medium size (skull length 1.5 m and estimated body length of 5–6 m) and possessed a mosaic of ancestral (e.g., elongated intertemporal region with long parietal and frontal exposures on the cranial vertex, anteriorly placed “blowholes,” elongated nasals, large mandibular coronoid processes, and large mandibular foramina) and derived (e.g., loss of adult dentition, flattened rostrum, longitudinal palatal keel, and laterally bowed mandibles) features. Rostral kinesis (unfused joints between maxilla, premaxilla, and nasal) was intermediate between akinetic stem toothed mysticetes (and archaeocetes) and fully kinetic crown chaeomysticetes. Palatal morphology also appears to have been intermediate between toothed and crown mysticetes. Unlike basal toothed mysticetes (e.g., *Janjucetus* and *Mammalodon*) but similar to aetiocetids (e.g., *Aetiocetus* spp.), the palate of eomysticetids had palatal vascular features associated with baleen. These features (lateral palatal foramina and sulci), however, were larger and more numerous than in aetiocetids. Some eomysticetids (e.g., *Yamatocetus* and *Waharoa*) also possessed an alveolar groove on the elongated maxilla and more distinct individual alveoli on the premaxilla and anterior tip of the mandible. Putative adult teeth have been reported in at least one eomysticetid (i.e., *Tokarahia*), but their size and shallow alveoli suggest that the teeth may have been vestigial and not functional. In addition, the mandible of eomysticetids possessed a distinct symphyseal groove and smooth symphyseal surface, features linked with mandibular kinesis (Deméré and Berta, 2008; Fitzgerald, 2011).

Besides eomysticetids, there are several problematic Oligocene edentulous mysticetes that provide a glimpse of the morphological diversity at the base of the radiation of obligate filter-feeding baleen whales. Unfortunately, these archaic species are based on fragmentary fossil remains. *Sitsqwayk cornishorum* from the late Oligocene (~27 Ma) of Washington, USA possessed a relatively short rostrum and edentulous mandible and is suggested to be the most primitive chaeomysticete (Peredo and Uhen, 2016). *Whakakai waipatia* and *Horopeta umarere*, both from the late Oligocene (~27–25 Ma) of New Zealand, lack critical portions of the rostrum, squamosal, and basicranium, but have been placed crownward of eomysticetids and sister to crown Mysticeti (Tsai and Fordyce, 2015, 2016). It has been proposed that *H. umarere* was an engulfment feeder like extant balaenopterids (Tsai and Fordyce, 2015). However, this hypothesis is weakly supported and relies on equivocal mandibular features (a slightly laterally bowed horizontal ramus and a posterolaterally deflected and broken coronoid process) and does not consider other anatomical features that are critical to successful engulfment

Copyright © 2017. Elsevier Science & Technology. All rights reserved.

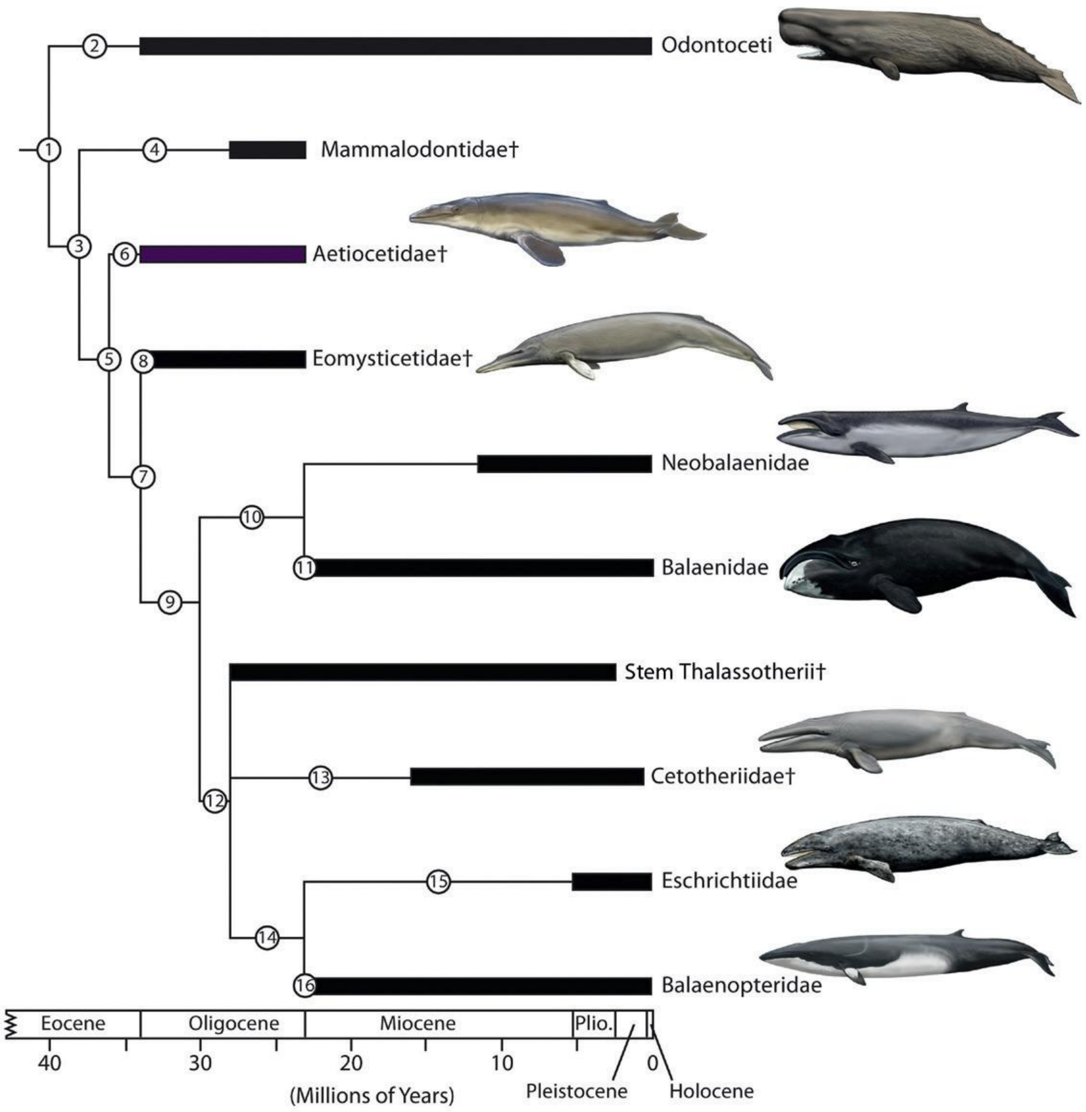

Figure 2 *Phylogenetic relationships and stratigraphic ranges of major mysticete groups (from Berta et al., 2016) (Illustrations of whales by C. Buell). (1) Neoceti, (2) Odontoceti, (3) Mysticeti, (4) Mammalodontidae, (5) Aetiocetidae + Chaeomysticeti, (6) Aetiocetidae, (7) Chaeomysticeti, (8) Eomysticetidae, (9) Crown Mysticeti, (10) Balaenoidea, (11) Balaenidae, (12) Thalassotherii, (13) Cetotheriidae, (14) Balaenopteroidea, (15) Eschrichtiidae, and (16) Balaenopteridae.*

Copyright © 2017. Elsevier Science & Technology. All rights reserved.

feeding, such as a nonsynovial, fibrocartilaginous temporomandibular joint, a medially buttressed mandibular neck, and a robust and posteriorly directed mandibular condyle.

The earliest confirmed fossils of crown mysticetes are known from the early Miocene (~23–20 Ma), and most recent phylogenies (Fig. 2) recognize a fundamental dichotomy within this group between a balaenoid clade (balaenids + neobalaenids) and a thalassotherian clade (Bisconti et al., 2013; Boessenecker and Fordyce, 2016). This taxonomic dichotomy reflects an early divergence event that established the morphological divide between derived skim feeders with narrow, arched rostra (balaenoids) and a more diverse array of generalized and specialized filter feeders with relatively flat and broad rostra (thalassotherians) (Bisconti et al., 2013). Thalassotherians underwent dramatic taxonomic and functional diversification throughout the Miocene and Pliocene (23–2.6 Ma) and Quaternary (2.6 Ma to today), with two discrete thalassotherian lineages consistently recognized in most recent studies—the Cetotheriidae and the Balaenopteroidea (eschrichtiids + balaenopterids). The Cetotheriidae consists of generally diminutive (3–4 m body length) mysticetes (e.g., *Brandtocetus*, *Cetotherium*, *Herentalia*, *Herpetocetus*, *Kurdalogonus*, *Metopocetus*, *Nannocetus*, and *Piscobalaena*) and is characterized by relatively derived telescoping (deep interdigitation of rostral and cranial bones), short exposure of frontal and parietal on cranial vertex, and ascending processes of maxillae that meet or nearly meet posterior to the nasals (Fig. 1E). The earliest cetotheriid fossils are known from the early late Miocene (~12 Ma) of the Paratethys (Gol'din et al., 2014), while the youngest fossils come from the early to middle Pleistocene (2-1 Ma) of the eastern North Pacific (Boessenecker, 2013) (Fig. 2). Although it has recently been suggested that the pygmy right whale, *Caperea marginata*, might be a living cetotheriid (Fordyce and Marx 2012; Marx and Fordyce 2015), this hypothesis is based on an unusual assessment of cranial, petrotympanic, and mandibular morphological characters and glosses over the substantial issue of convergence posed by the many balaenid features of *Caperea* (e.g., dorsally arched rostrum; long, slender, and numerous baleen laminae; extremely telescoped supraoccipital, and reduced coronoid process). The Balaenopteroidea consists of medium to large sized (5–15 + m) fossil taxa and includes eschrichtiids (e.g., *Gricetoides*, *Eschrichtoides*, and *Eschrichtius*) and balaenopterids (e.g., *Archaeobalanoptera*, *Balaenoptera*, *Diunatans*, *Fragilicetus*, *Parabalaenoptera*, *Pleisobalaenoptera*, and *Protororqualus*; Fig. 1F). The clade is characterized by more derived telescoping, abruptly depressed supraoribital process of the frontal, distinct overlap of ascending process of maxilla by anterior wing of parietal, well-developed squamosal cleft, laterally convex mandible, small and dorsally placed mandibular foramen, and relatively large and laterally deflected coronoid process. The earliest balaenopteroids are known from the early late Miocene (~12 Ma) of the eastern North Pacific (Deméré et al., 2005), with relatively derived taxa appearing in the Pliocene (Boessenecker, 2013). A third group of thalassotherians is more problematic, but in general consists of taxa that, depending on the study examined, represent either an unnamed monophyletic group (Boessenecker and Fordyce, 2015a,b,c) (Fig. 2) or a paraphyletic assemblage (Marx and Fordyce 2015; Marx et al., 2016). In either case, this problematic grouping of stem thalassotherians lacks the synapomorphies of cetotheriids and balaenopteroids, and typically consists of the following taxa: *Aglaocetus*, *Cophocetus*, *Diorocetus*, *Halicetus*, *Isanacetus*, *Parietobalaena*, *Pelocetus*, *Thinocetus*, and *Titanocetus* (Fig. 1d).

IV. Tooth Loss, Origin of Baleen, and Bulk Filter Feeding

Baleen is a unique mammalian structure consisting of a serially arranged row of keratinous plates and bristles that grow as a pair of subparallel longitudinal racks from the right and left lateral portions of the palate. The bristles or tubules are the basic filtering medium and occur as single bristles, as bundles of bristles, or, in the plates, as a concentration of bristles enmeshed in an amorphous keratinous, medullary layer sandwiched between cortical layers of amorphous keratin. The frayed tubules on the medial margin of each plate overlap those of adjacent plates to produce a sieve that entraps prey within the oral cavity. Because baleen rarely fossilizes, morphological evidence for its presence (or absence) must rely on correlated osteological features. Extant mysticetes have a highly vascularized palate with distinct lateral nutrient foramina and associated sulci concentrated along the lateral half of each maxilla (Fig. 3). The blood supply and innervation of the developing baleen apparatus pass through these openings (Ekdale et al., 2015). Thus, the presence of lateral palatal foramina and sulci in fossil mysticetes serves as indirect evidence for the presence of baleen. Importantly, such structures have been reported in some toothed mysticetes (Deméré and Berta, 2008; Marx et al., 2016).

Just which group of stem mysticetes were the first to possess baleen is a contested issue that largely hinges on interpretation of the anatomy of aetiocetid toothed mysticetes. One research group proposes that palatal vascular structures (tiny, laterally placed foramina and sulci) found in aetiocetids represent evidence that this group of toothed mysticetes had some form of baleen (Deméré and Berta, 2008; Deméré et al., 2008). The structure of this proto-baleen is unknown and could simply have consisted of exposed keratin bristles or papillae rather than more complexly organized baleen plates. The proto-baleen would have been situated medial to the upper tooth row and functioned as a rudimentary filter, complementing the more traditional suction-assisted raptorial feeding mode (Fig. 4). Under this hypothesis, baleen evolved as a stepwise transition from an ancestor with teeth only, to an intermediate stage with a complete dentition and baleen, to the derived condition with baleen only. Thus, aetiocetids stand apart from other stem toothed mysticetes that lack lateral

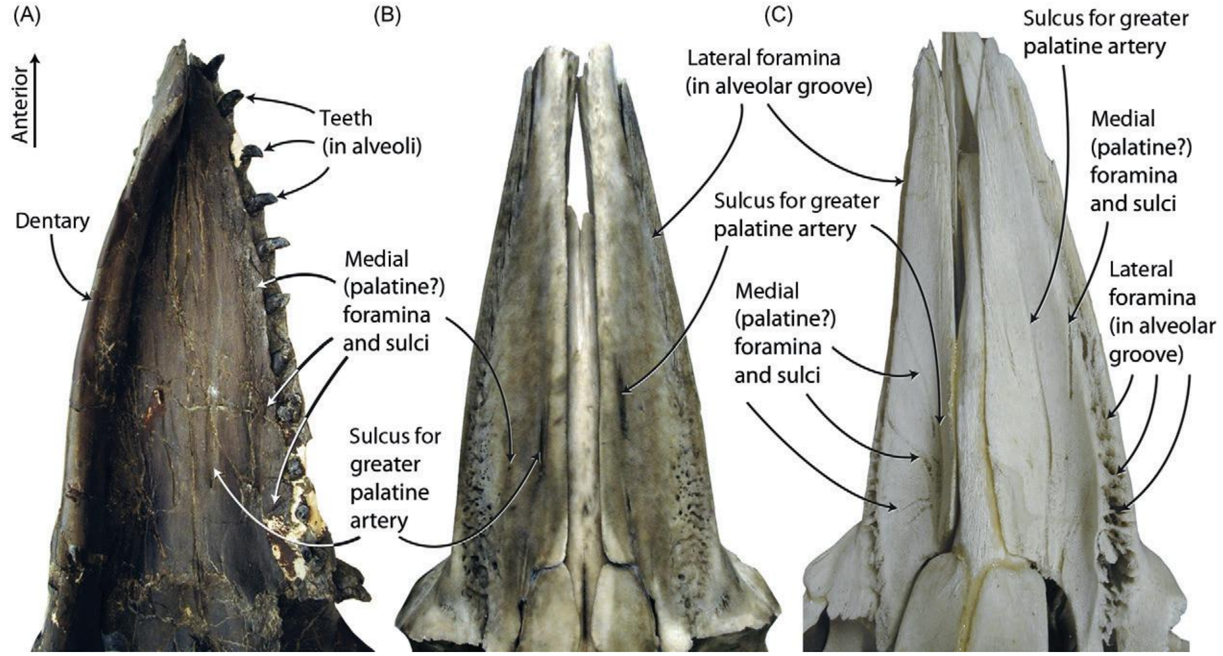

Figure 3 *Ventral view of palates of select mysticetes: (A) Extinct toothed mysticete* Aetiocetus weltoni *UCMP 122900, showing lateral foramina on palate hypothesized as nutrient foramina, (B) juvenile gray whale (*Eschrichtius robustus *SDSU-S-974), and (C) fetal fin whale (*Balaenoptera physalus *USNM 268925) in ventral view. From Ekdale et al. (2015).*

Copyright © 2017. Elsevier Science & Technology. All rights reserved.

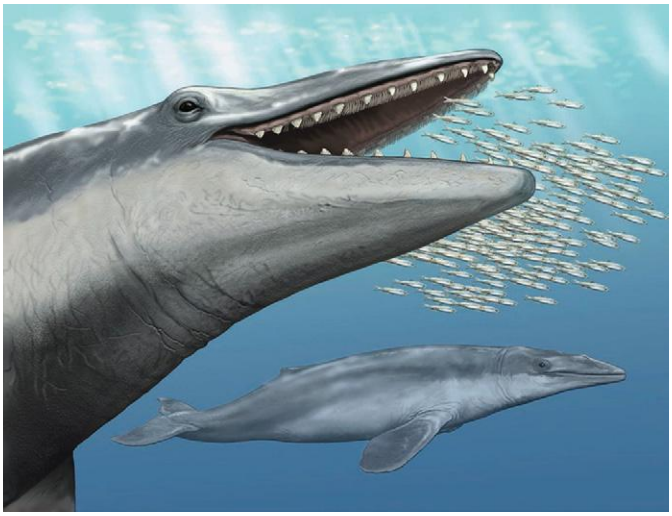

Figure 4 *Original Reconstruction of* Aetiocetus weltoni *illustrated by C. Buell. From Deméré et al. (2008).*

palatal foramina (i.e., mammalodontids) and are sister to the functionally edentulous chaeomysticetes (Fig. 2). This relationship is supported by the shared presence in aetiocetids and chaeomysticetes of an unsutured and elastic mandibular symphysis with attendant symphyseal groove-derived features that are lacking in mammalodontids and that are correlated with mandibular kinesis in extant mysticetes (Deméré and Berta, 2008; Fitzgerald, 2011).

An alternative view of the origin of baleen suggests that the lateral palatal foramina of aetiocetids are not associated with proto-baleen, but instead are likely related to an enlargement of palatal gum tissue that may have helped to partially seal the lateral oral gape during suction feeding (Marx et al., 2016). The complete dentitions of aetiocetids are viewed here as likely interfering with a separate oral filtering apparatus. Under this hypothesis, baleen (and filter-feeding) evolved in stem chaeomysticetes (e.g., eomysticetids), which due to a strong reliance on suction feeding had progressively lost teeth from the posterior part of the palate while retaining a functional anterior dentition. In this scenario, aetiocetids are considered to be more closely related to mammalodontids than to chaeomysticetes, within a monophyletic group of stem toothed mysticetes that all practised suction-assisted raptorial feeding (nonfiltering). This relationship discounts the shared derived features of an unsutured mandibular symphysis and symphyseal groove, suggesting that in spite of the mandibular similarities of aetiocetids and stem chaeomysticetes, the mandibular symphysis in aetiocetids was akinetic and firmly ligamentous.

Whether the transition from teeth to baleen occurred in aetiocetids or not, it is clear that the shift from tooth-aided predation to a filter feeding strategy occurred early in the evolution of mysticetes and was accompanied by numerous anatomical specializations that after 30 million years of evolution have allowed today's baleen whales to process large volumes of water by passing it through a keratinous filter. As discussed, the evolution of these anatomical specializations is archived in the skeletons of fossil and living whales. It is not surprising then that molecules (DNA) present in living mysticetes provide additional evidence of this evolutionary transition. As it turns out, mysticete genomes contain enamel specific genes that are nonfunctional as a result of frameshift mutations (Deméré et al., 2008). Since in a frameshift mutation, one or more bases are inserted or in this case, deleted which disrupts the reading frame of the dental genes, this indicates that these loci are decaying enamel pseudogenes. Thus, the end product in this evolutionary transition from teeth to baleen is the presence of vestigial genes in the mysticete genome that represent "molecular" fossils of the former presence of teeth in mysticetes. A final link in this chain of evidence regarding the toothed ancestry of baleen whales comes from studies of fetal specimens. Embryologically, mysticete fetuses pass through a stage where they have open alveolar grooves on the palate and mandible (Ridewood, 1923). This groove is the site of a developing temporary dentition, which passes through the bud, cap, and bell stages of development before degradation and resorption of the deciduous tooth buds begins (Karlsen, 1962; Ishikawa et al., 1999). At the same time the open alveolar groove starts to fill with bone until finally the distinct lateral nutrient foramina begin to form on the palate while gingival foramina form on the mandible. Dermal papillae of the rudimentary baleen plates start developing on the palate coincident with tooth bud degradation. Thus, extant mysticetes pass through a series of developmental stages including one with teeth only, one with teeth and baleen, and one with baleen only. The first two stages occur *in utero*, while the last phase is seen in neonates and adults. This developmental sequence can be viewed as an ancient evolutionary transformation series that is recapitulated in the ontogeny of extant mysticetes, with mammalodontids, aetiocetids, and eomysticetids representing teeth-only, teeth + baleen, and baleen-only stages, respectively.

References

Boessenecker, R.W. (2013). A new marine vertebrate assemblage from the Late Neogene Purisima Formation in Central California, part II: Pinnipeds and Cetaceans. *Geodiversitas* **35**, 815–940.

Boessenecker, R.W., and Fordyce, R.E. (2015a). A new eomysticetid (Mammalia: Cetacea) from the Late Oligocene of New Zealand and a re- evaluation of *'Mauicetus' waitakiensis*. *Pap. Palaeo* **1**, 107–140.

Boessenecker, R.W., and Fordyce, R.E. (2015b). A new genus and species of eomysticetid (Cetacea: Mysticeti) and a reinterpretation of '*Mauicetus lophocephalus*' Marples, 1956: transitional baleen whales from the upper Oligocene of New Zealand. *Zool. J. Linn. Soc.* **175**, 607–660.

Boessenecker, R.W., and Fordyce, R.E. (2015c). Anatomy, feeding ecology, and ontogeny of a transitional baleen whale: a new genus and species of Eomysticetidae (Mammalia: Cetacea) from the Oligocene of New Zealand. *Peer J.* **3**, e1129. doi:10.7717/peerj.1129.

Boessenecker, R.W., and Fordyce, R.E. (2016). A new eomysticetid from the Oligocene Kokoamu Greensand of New Zealand and a review of the Eomysticetidae (Mammalia, Cetacea). *J. Syst. Palaeo.* doi:10.1080/14772019.2016.1191045.

Bisconti, M. (2007). Taxonomic revision and phylogenetic relationships of the rorqual-like mysticete from the Pliocene of Mount Pulgnasco, northern Italy (Mammalia, Cetacea, Mysticeti). *Palaeo. Italica* **91**, 85–108.

Bisconti, M. (2016). *Fragilicetus velponi*: a new mysticete genus and species and its implication for the origin of Balaenopteridae (Mammalia, Cetacea, Mysticeti). *Zool. J. Linn. Soc.* **177**, 450–474.

Bisconti, M., Lambert, O., and Bosselaers, M. (2013). Taxonomic revision of *Isocetus depawi* (Mammalia, Cetacea, Mysticeti) and phylogenetic relationships of archaic 'cetother' mysticetes. *Palaeo* **56**, 95–127.

Deméré, T.A., and Berta, A. (2008). Skull anatomy of the Oligocene toothed mysticete *Aetiocetus weltoni* (Mammalia: Cetacea): implications for mysticete evolution and functional anatomy. *Zool. J. Linn. Soc.* **154**, 308–352.

Deméré, T.A., Berta, A., and McGowen, M.R. (2005). The taxonomic and evolutionary history of fossil and modern balaenopteroid mysticetes. *J. Mamm. Evol.* **12**, 99–143.

Copyright © 2017. Elsevier Science & Technology. All rights reserved.

Deméré, T.A., McGowen, M.R., Berta, A., and Gatesy, J. (2008). Morphological and molecular evidence for a stepwise evolutionary transition from teeth to baleen in mysticete cetaceans. *Syst. Biol.* **57**, 15–37.

Ekdale, E.G., Deméré, T.A., and Berta, A. (2015). Vascularization of the gray whale plate (Cetacea, Mysticeti, *Eschrichtius robustus*): soft tissue evidence for an alveolar source of blood to baleen. *Anat. Rec.* **298**, 691–702.

Fitzgerald, E.M. (2006). A bizarre new toothed mysticete (Cetacea) from Australia and the early evolution of baleen whales. *Proc. R. Soc. B. Lond.* **273**, 2955–2963.

Fitzgerald, E.M. (2010). The morphology and systematics of *Mammalodon colliveri* (Cetacea: Mysticeti), a toothed mysticete from the Oligocene of Australia. *Zool. J. Linn. Soc.* **158**, 367–476.

Fitzgerald, E.M. (2011). Archaeocete-like jaws in a baleen whale. *Biol. Lett.* **8**, 94–96.

Fordyce, R.E., and Marx, F.G. (2012). The pygmy right whale *Caperea marginata*: the last of the cetotheres. *Proc. R. Soc. B* **280**, 20122645.

Fordyce, R.E., and Marx, F.G. (2016). Mysticetes baring their teeth: a new fossil whale, *Mammalodon hakataramea*, from the Southwest Pacific. *Mem. Mus. Vic* **74**, 107–116.

Gol'din, P., Startsev, D., and Krakhmalnaya, T. (2014). The anatomy of the late Miocene baleen whale *Cetotherium riabinini* from Ukraine. *Acta Palaeontol. Pol.* **59**, 795–814.

Ishikawa, H., Amasaki, H., Dohguchi, H., Furuya, A., and Suzuki, K. (1999). Immunohistological distributions of fibronectin, tenascin, type I, III and IV collagens, and laminin during tooth development and degeneration in fetuses of minke whale, *Balaenoptera acutorostrata*. *J. Vet. Med. Sci.* **61**, 227–232.

Karlsen, K. (1962). Development of tooth germs and adjacent structures in the whalebone whale (Balaenoptera physalus (L.)). *Hval. Skrifter.* **45**, 5–56.

Kellogg, A.R. (1968). Fossil marine mammals from the Miocene Calvert Formation of Maryland and Virginia, Part 7: A sharp-nosed cetothere from the Miocene Calvert. *Bull. US Natl. Mus.* **247**, 163–173.

Marx, F.G. (2010). The more the merrier? A large cladistic analysis of mysticetes, and comments on the transition from tooth to baleen. *J. Mamm. Evol.* **18**, 77–100.

Marx, F.G., and Fordyce, R.E. (2015). Baleen boom and bust: a synthesis of mysticete phylogeny, diversity and disparity. *R. Soc. Open Sci.* **2**, 140434.

Marx, F.G., Tsai, C.-H., and Fordyce, R.E. (2016). A new early Oligocene toothed "baleen" whale (Mysticeti: Aetiocetidae) from western North America: one of the smallest. *R. Soc. Open Sci.* **2**, 150476.

Peredo, C.M., and Uhen, M.D. (2016). A new basal chaeomysticete (Mammalia: Cetacea) from the late Oligocene Pysht Formation of Washington, USA. *Pap. Palaeo* **2**, 1–22.

Ridewood, W.G. (1923). Observations on the skull in foetal specimens of whales of the genera *Megaptera* and *Balaenoptera*. *Philos. Trans. R. Soc. Lond. Ser. B* **211**, 209–272.

Tsai, C.-H., and Ando, T. (2015). Niche partitioning in Oligocene toothed mysticetes. *J. Mamm. Evol.* **23**(1), 33–41.

Tsai, C.-H., and Fordyce, R.E. (2015). The earliest gulp-feeding mysticetes (Cetacea: Mysticeti) from the Oligocene of New Zealand. *J. Mamm. Evol.* **22**(4), 535–560.

Tsai, C.-H., and Fordyce, R.E. (2016). Archaic baleen whale from the Kokoamu Greensand: earbones distinguish a new late Oligocene mysticete (Cetacea: Mysticeti) from New Zealand. *J. R. Soc. N. Zeal.* doi:10.1080/03036758.2016.1156552.

BARNACLES

Dagmar Fertl and William A. Newman

"Barnacle" is the common name for over 1000 marine species of the subclass Cirripedia. Barnacles are unique among crustaceans in being permanently attached as adults to a variety of inanimate and animate objects. Barnacles occur in polar, tropical, and temperate waters, being found from high on the shore to the depths of the ocean. The principal superorder is Thoracica, consisting of stalked (order Pedunculata) and sessile (order Sessilia) barnacles (Newman, 1996). Perhaps as many as 20 living barnacle species have some association with marine mammal species, primarily cetaceans (Ross and Newman, 1967; Newman and Ross, 1976; Hayashi et al., 2013).

Barnacles attached to marine mammals are often referred to as ectoparasites; however, in reality, they do not feed on their hosts, but use them as a moving substratum from which they can strain plankton from the passing water. As a result, "epibiotic" is often considered a more appropriate term describing the barnacle's lifestyle. This has been described as an example of symbiosis, usually commensalism, but barnacles create drag and can cause irritations. Therefore, they are perhaps best termed "semiparasitic," since they survive and perpetuate themselves at the host's expense. On the other hand, some marine mammals eat barnacles and/or their larvae.

I. Life History

Barnacles were described by T. H. Huxley and Louis Agassiz as nothing more than "a little shrimp-like animal, standing on its head in a limestone house and kicking food into its mouth" (Hoover, 2006). Most barnacles are hermaphrodites (i.e., individuals possess the reproductive structures of both sexes). The life cycle usually includes six free-swimming planktonic naupliar stages that feed while progressing by molts to the cypris or cyprid stage, which searches for a place to settle. When settling, to anchor itself, the cyprid secretes cement from its antennules, from glands located in their base, and metamorphoses by molting into a juvenile, which begins to secrete adult cement and the calcareous plates that usually constitute its home.

The cyprid actively selects and explores where it will settle, and those that attach directly to cetacean skin, a chemical cue from the host tissue likely induces larval settlement (Nogata and Matsumura, 2006) and detailed studies of site selection have been made (Carrillo et al., 2015). Through an aperture between the plates, six pairs of feathery thoracic limbs (cirri) can be spread out for passive feeding in currents, or they can be swept through the water like a net to entrap planktonic organisms. The breeding season of barnacles that cling to whales is probably largely synchronous with that of the whales' breeding season.

II. Sessile Barnacles

The Sessilia, or sessile barnacles, are stalkless, the usually well-articulated shell wall being attached directly to the substratum. Because of their superficial resemblance to acorns of oak trees, they are called acorn barnacles. Marine mammals host species of *Amphibalanus*, *Balanus*, *Cetopirus*, *Chelonibia*, *Coronula*, *Cryptolepas*, *Platylepas*, *Tubicinella*, and *Xenobalanus*. *Xenobalanus* superficially resembles a stalked barnacle since it has developed an aberrant pseudo-stalk, but it is nonetheless a sessile barnacle (Fig. 1).

III. Stalked Barnacles

The pedunculate, or stalked, barnacles are more primitive than the sessile barnacles. The terminal sac housing the appendages is called the capitulum. It is supported by a flexible, muscular stalk or peduncle attached to the substratum. While the capitulum is usually protected by shell plates, it is naked in *Conchoderma* spp., the goose barnacles (*Lepas* spp.), and rarely, the leaf barnacles (*Pollicipes* spp.), species of which attach to whales.

Copyright © 2017. Elsevier Science & Technology. All rights reserved.

Figure 1 *The pseudo-stalked sessile barnacle Xenobalanus attached to the dorsal fin of a bottlenose dolphin (Photo by V. Thayer and K. Rittmaster, North Carolina Maritime Museum).*

IV. Barnacles and Marine Mammals

Barnacles appear to settle in greatest numbers on large baleen whales, in contrast to toothed whales. Striped dolphins (*Stenella coeruleoalba*) involved in a mass mortality event in the Mediterranean had an unusual abundance of barnacles likely due to the reduced movement and/or an impaired immune function of the skin of sick individuals (Aznar et al., 2005). Orams and Schuetze (1998) demonstrated that *Xenobalanus* spp. were more prevalent on young than adult bottlenose dolphins (*Tursiops* spp.), presumably because they are less active and/or less resistant.

Cryptolepas rhachianecti, considered to be host-specific to the gray whale (*Eschrichtius robustus*), has been found on a killer whale (*Orcinus orca*) stranded in southern California and on belugas (*Delphinapterus leucas*) housed in San Diego Bay. *Xenobalanus globicipitus*, while worldwide in distribution, are almost always found on the trailing edges of the dorsal and pectoral fins and on the flukes of at least 27 cetacean species (Kane et al., 2006; Fig. 1). What may remain of their wall in the skin of the host after death superficially resembles the wall of platylepas; this likely accounts for a report (Mead and Potter, 1990) of platylepas on a bottlenose dolphin. *Tubicinella major*, which lives within a columnar shell opening at the surface of its host's skin, and usually found among callosities of southern right whale (*Eubalaena australis*), was once collected from the flank of a stranded northern bottlenose whale (*Hyperoodon ampullatus*). *Coronula* spp., the most generalized of the sessile whale barnacles, are large and generally attach to the skin of baleen whales (Scarff, 1986). *C. reginae* and *C. diadema* (Fig. 2) are commonly epizooites of humpback whales (*Megaptera novaeangliae*), attached to flukes, flippers, ventral grooves, genital slit, and the head (Clarke, 1966). *Cetopirus complanatus* closely resembles *C. reginae*, and both occur on the right whale (Scarff, 1986). Humpback males scrape each other with their barnacle-encrusted flippers (analogous to "brass knuckles") on the breeding grounds; one individual caught during whaling operations was reported to have as much as 450 kg of *Coronula* removed from it. On the other hand, various forms of grooming, including flipper-body grooming (Sakai et al., 2006), would likely remove freshly settled larvae and young juveniles; this may account for the lack of barnacles on the bodies of most small toothed whales.

Figure 2 *Humpback whale with the acorn barnacle* Coronula diadema *and a few stalked barnacles* Conchoderma auritum *attached to them. Also visible are whale lice (Photo by Alisa Schulman-Janiger, off California, 2016).*

Figure 3 Conchoderma auritum *attached to the teeth of a Blainville's beaked whale (*Mesoplodon densirostris*) off Hawai'i (Photo by Alice Mackay, courtesy Cascadia Research).*

Of the pelagic pedunculate barnacles, *Conchoderma auritum* and *C. virgatum* are commonly recorded from cetaceans, though *Pollicipes polymerus*, a rocky shore barnacle, was recorded on a humpback whale (Clarke, 1966). *Conchoderma* spp. require a hard surface for attachment. *C. auritum*, identified by its' rabbit ear-like appendages, may be found at a site where teeth are exposed and unprotected (Soto, 2001), such as on erupted teeth of adult male beaked and bottlenose (*Hyperoodon* spp.) whales (Fig. 3), or because of a malformation (including bone injury) in the jaw. *Conchoderma* spp. are less commonly found on baleen plates and were once collected from the penis of a stranded sperm whale (*Physeter macrocephalus*). *C. auritum* is often found attached to *Coronula* spp. (most

Copyright © 2017. Elsevier Science & Technology. All rights reserved.

commonly to *C. diadema*). *C. virgatum*, although sometimes attaching directly to a cetacean, is usually epizootic on other barnacles, and then most often on *Conchoderma auritum*. *C. virgatum* has been found on the parasitic copepods *Pennella* spp. and on the cyamid amphipod, *Neocyamus physeteris*, which crawls about on cetaceans and their barnacles (Clarke, 1966; Oliver and Trilles, 2000). *Lepas* spp. usually occur on floating objects, yet *L. pectinata* and *L. hillii* have been found between the teeth of some Mediterranean striped dolphins.

There are comparatively few published records of barnacles on pinnipeds, yet *L. pacifica*, *L. australis*, and *L. hillii*, as well as *C. auritum* and *C. virgatum*, are recorded from their dorsal body surface, attached to hair or even directly to the skin of various species, including both species of elephant seals (*Mirounga* spp.) (Best, 1971; Setsaas and Bester, 2006; Fig. 4).

Manatees (*Trichechus* spp.) may acquire acorn barnacles when in brackish or seawater, but when they enter fresh water the barnacles die and drop off, leaving temporary scars. The common barnacle found embedded in the skin of West Indian and West African manatees (*Trichechus manatus* and *T. senegalensis*, respectively) is *Chelonibia manati* (Cintrón De Jesús, 2001), a close relative of its congeners on turtles. Moreover, turtle barnacles *Platylepas hexastylos* and *P. decorata* have been found on the dugong (*Dugong dugon*) and West Indian manatee. The brackish water species, *Amphibalanus amphitrite*, *A. eburneus*, *A. reticulatus*, and *A. improvisus*, and the marine species, *Balanus trigonus*, attach to the *Chelonibia* spp. on the manatees, rather than to their skin.

It is not surprising that some baleen whales eat barnacle larvae (Mayo and Marx, 1990) since the experimentally estimated filtering efficiency of 95% for plankton larger than 333 μm for the right whale (Mayo et al., 2001) would include the larvae of pelagic and some coastal barnacles.

Sea otters (*Enhydra lutris*) in California and Alaska will eat the large acorn barnacles *Balanus nubilus* and *Semibalanus cariosus*. Faurot et al. (1986) reported otters feeding on *Pollicipes polymerus*, suggesting that they may be intentionally ingesting it if not simply being incidental to their take of mussels.

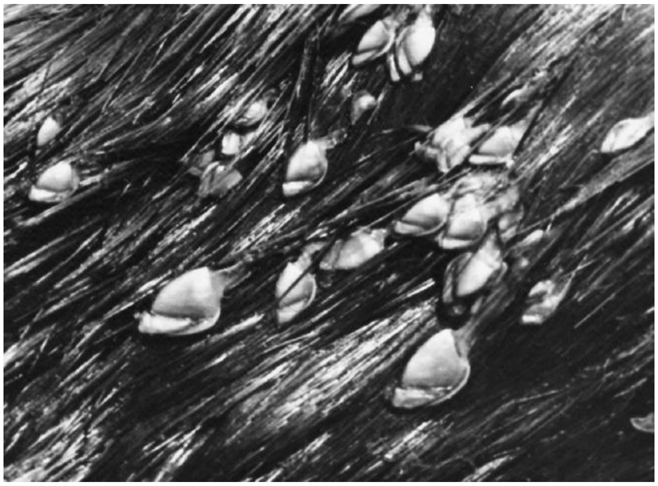

Figure 4 *Goose barnacle (*Lepas australis*) attached among the hairs of a subantarctic fur seal (*Arctocephalus tropicalis*) (Photo by M. N. Bester).*

Copyright © 2017. Elsevier Science & Technology. All rights reserved.

See Also the Following Articles

Callosities ■ Health ■ Krill and other Plankton ■ Parasites

References

Aznar, F.J., Perdiguero, D., Pérez del Olmo, A., Repullés, A., Agusti, C., and Raga, J.A. (2005). Changes in epizoic crustacean infestations during cetacean die-offs: The mass mortality of Mediterranean striped dolphins *Stenella coeruleoalba* revisited. *Dis. Aquat. Org.* **67**, 239–247.

Best, P.B. (1971). Stalked barnacles *Conchoderma auritum* on an elephant seal: Occurrence of elephant seals on South African coast. *Zool. Afr.* **6**, 181–185.

Carrillo, J.M., Overstreet, R.M., Raga, J.A., and Aznar, F.J. (2015). Living on the edge: Settlement patterns by the symbiotic barnacle *Xenobalanus globicipitis* on small cetaceans. *PLoS ONE* **10**, e0127367.

Cintrón de Jesús, J. (2001). *Barnacles associated with marine vertebrates in Puerto Rico and Florida. Master's thesis.* University of Puerto Rico.

Clarke, R. (1966). The stalked barnacle *Conchoderma*, ectoparasitic on whales. *Nor. Hvalfangst.-Tid.* **55**, 153–168.

Faurot, E.R., Ames, J.A., and Costa, D.P. (1986). Analysis of sea otter, *Enhydra lutris*, scats collected from a California haulout site. *Mar. Mamm. Sci.* **2**, 223–227.

Hayashi, R., Chan, B.K.K., Simon-Blecher, N., Watanabe, H., Guy-Haim, T., Yonezawa, T., Levy, Y., Shuto, T., and Achituv, Y. (2013). Phylogenetic position and evolutionary history of the turtle and whale barnacles (Cirripedia: Balanomorpha: Coronuloidea). *Mol. Phylogenet. Evol.* **67**, 9–14.

Hoover, L.P. (2006). *Hawai'i's Sea Creatures*, 3rd ed. Mutual Publishing, Honolulu, Hawai'i.

Kane, E., Olson, P., and Gerrodette, T. (2006). The commensal barnacle *Xenobalanus globicipitis* Steenstrup, 1851 (Crustacea: Cirripedia) and its relationship to cetaceans of the eastern tropical Pacific. NMFS-SWFSC Administrative Report LJ-06-03.

Mayo, C.A., and Marx, M.K. (1990). Surface foraging behavior of the North Atlantic right whale, *Eubalaena glacialis*, and associated zooplankton characteristics. *Can. J. Zool.* **68**, 2214–2220.

Mayo, C.A., Letcher, B.H., and Scott, S. (2001). Zooplankton filtering efficiency of the baleen of a North Atlantic right whale, *Eubalaena glacialis*. *J. Cetacean Res. Manage.* (Spec. Issue 2), 225–230.

Mead, J.G., and Potter, C.W. (1990). Natural history of bottlenose dolphins along the central Atlantic Coast of the United States. In "The Bottlenose Dolphin", (S. Leatnerwood, and R.R. Reeves, Eds), pp. 165–195. Academic Press, San Diego, CA.

Newman, W.A. (1996). Cirripedia; suborders Thoracica and Acrothoracica. In "Traité de Zoologie Tome VII, Crustacés, Fascicule", (J. Forest, Ed.), Vol. 2 (in French), pp. 453–540. Masson, Paris.

Newman, W.A., and Ross, A. (1976). Revision of the balanomorph barnacles; including a catalog of the species. *Mem. San Diego Soc. Nat. Hist.* **9**, 1–108.

Nogata, Y., and Matsumura, K. (2006). Larval development and settlement of a whale barnacle. *Biol. Lett.* **2**, 92–93.

Oliver, G., and Trilles, J-P. (2000). Crustacés parasites et epizoïtes du Cachalot, *Physeter catodon* Linnaeus, 1758 (Cetacea, Odontoceti), dans le golfe du Lion (Méditerranée occidentale). *Parasite* **7**, 311–321.

Orams, M.B., and Schuetze, C. (1998). Seasonal and age/size-related occurrence of a barnacle (*Xenobalanus globicipitis*) on bottlenose dolphins (*Tursiops truncatus*). *Mar. Mamm. Sci.* **14**, 186–189.

Ross, A., and Newman, W.A. (1967). Eocene Balanidae of Florida, including a new genus and species with a unique plan of "turtle-barnacle" organization. *Am. Mus. Novit.* **2288**, 1–21.

Sakai, M., Hishii, T., Takeda, T.S., and Kohsima, S. (2006). Flipper rubbing behaviors in wild bottlenose dolphins (*Tursiops aduncus*). *Mar. Mamm. Sci.* **22**, 966–978.

Scarff, J.E. (1986). Occurrence of the barnacles *Coronula diadema*, *C. reginae* and *Cetopirus complanatus* (Cirripedia) on right whales. *Sci. Rep. Whal. Res. Inst. Tokyo* **37**, 129–153.

Setsaas, T.H., and Bester, M.N. (2006). Goose barnacle (*Lepas australis*) infestation of the Subantarctic fur seal (*Arctocephalus tropicalis*). *Afr. Zool.* **41**, 305–307.

Soto, J.M.R. (2001). First record of a rabbit-eared barnacle, *Conchoderma auritum* (Linnaeus, 1767) (Crustacea, Cirripedia), on the teeth of the La Plata dolphin, *Pontoporia blainvillei* (Gervais & D'Orbigny, 1844) (Cetacea, Platanistoidea). *Mare Magnum* **1**, 172–173.

BASILOSAURIDS AND KEKENODONTIDS

Mark D. Uhen

Basilosaurids are a paraphyletic group of archaeocete cetaceans known from the late middle to early late Eocene of all continents except Antarctica. The family includes 20 species in 12 genera. They range in size from around 4 m (*Saghacetus osiris*) to around 16 m (*Basilosaurus cetoides*). Basilosaurids are the earliest fully aquatic cetaceans (Uhen, 1998) and are thought to have given rise to modern cetaceans (Barnes et al., 1985; Uhen, 1998). Kekenodontids are a small group of basal Neoceti that occur in the Oligocene and are poorly known, mostly from the Southern Hemisphere. Kekenodontidae currently includes two species in two genera.

I. Characteristics

Like all archaeocetes, basilosaurids lack telescoping of the skull like that seen in modern mysticetes or like that seen in modern odontocetes (Fig. 1; Miller, 1923). In addition, basilosaurids are diphyodont (have two tooth generations: milk and adult teeth), lack polydonty (11 or fewer teeth per jaw half), and retain a heterodont dentition, in which incisors, canines, premolars, and molars are easy to distinguish based on their morphologies (Kellogg, 1936; Uhen, 1998).

Basilosaurids also share a number of characteristics that distinguish them from other archaeocetes. All basilosaurids lack upper third molars, and the upper molars lack protocones, trigon basins, and lingual third roots. In addition, the cheek teeth of basilosaurids have well-developed accessory denticles on the cheek teeth (Fig. 1). The hind limbs of basilosaurids are greatly reduced (Fig. 2; Gingerich et al., 1990; Uhen and Gingerich, 2001) and lack a bony connection to the vertebral column. Basilosaurids also lack sacral vertebrae, although vertebrae that are likely to be homologs of sacral vertebrae are identifiable (Kellogg, 1936; Uhen, 1998).

Other characteristics may be found only in basilosaurids (within archaeocetes) but are currently not known from other archaeocetes. For instance, basilosaurid forelimbs had broad, fan-shaped scapulae with the distal humerus, radius, and ulna flattened into a single plane (Fig. 2). In addition, the elbow joint motion was restricted to the same plane, and pronation and supination of the forelimb was not possible based on the articular surfaces of the distal humerus, proximal radius, and proximal ulna. Since forelimbs are poorly known in more derived protocetids, it is unclear whether these features are found only in basilosaurids, or whether they are characteristic of a larger group.

Some of the characteristics of basilosaurids can be seen in some protocetid archaeocetes, like *Georgiacetus*. Although the innominate of *Georgiacetus* is large, it does not appear to have been connected to the vertebral column. None of the vertebrae is fused into a sacrum, yielding a condition similar to that seen in basilosaurids. In addition, the cheek teeth of *Georgiacetus* have small accessory denticles, somewhat different from those in basilosaurids, but certainly larger than any of the serrations seen in other nonbasilosaurid archaeocetes.

Kekenodontidae occur from the early to late Oligocene. Kekenodontids are both heterodont and diphyodont, with many cranial and dental characteristics similar to those of basilosaurids, but they have some cranial features that ally them with Neoceti. Kekenodontids also have larger diastemata between their cheek teeth when compared with basilosaurids (Clementz et al., 2014).

II. Taxonomy

Taxonomy for the family Basilosauridae is after Uhen (2013). The names "zeuglodonts" and "zeuglodons" are often colloquially used to refer to basilosaurids or archaeocetes in general. These common names are derived from the disused generic name *Zeuglodon* (discussed below), and their usage should be avoided. Gingerich and Zouhri (2015) revived some long disused taxonomic

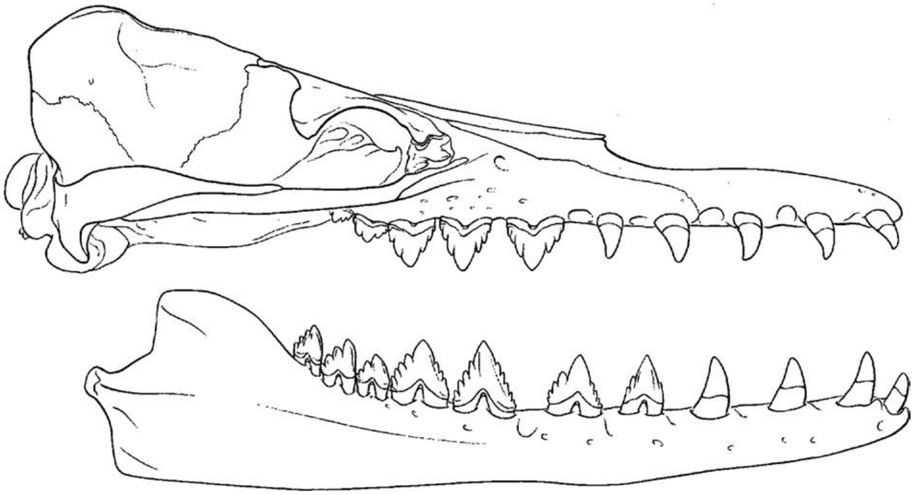

Figure 1 *Skull and lower jaw of* Dorudon atrox, *lateral view. This drawing is a composite drawn from specimens of* D. atrox *at the University of Michigan Museum of Paleontology by Bonnie Miljour.*

Copyright © 2017. Elsevier Science & Technology. All rights reserved.

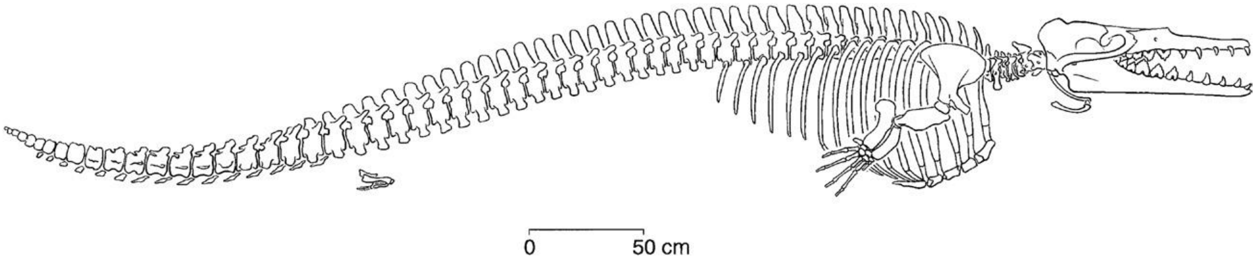

Figure 2 *Skeleton of* Dorudon atrox, *lateral view. This drawing is a composite drawn from specimens of* D. atrox *at the University of Michigan Museum of Paleontology by Bonnie Miljour.*

names for some basilosaurids, but this classification is not followed here, in part because the holotype specimens for the type species of these genera are either nondiagnostic or lost.

Taxa that are currently included in the family Basilosauridae include *Ancalecetus* (Gingerich and Uhen, 1996), including only *A. simonsi*; *Basilosaurus* (Harlan, 1834), including *Basilosaurus cetoides*, *Basilosaurus isis*, and *Basilosaurus drazindai*; *Basiloterus* (Gingerich et al., 1997), including only *Basiloterus hussaini*; *Basilotritus* (Gol'din and Zvonok, 2013), including *Basilotritus uheni*, *Basilotritus wardii*, and the new combination *Basilotritus aithai*; *Chrysocetus* (Uhen and Gingerich, 2001), including *Chrysocetus healyorum* and *Chrysocetus fouadassii*; *Cynthiacetus* (Uhen, 2005), including *Cynthiacetus maxwelli* and *Cynthiacetus peruvianus*; *Dorudon* (Gibbes, 1845), including *D. serratus* and *D. atrox*; *Masracetus* (Gingerich, 2007), including only *Masracetus markgrafi*; *Ocucajea* (Uhen et al., 2011), including only *Ocucajea picklingi*; *Saghacetus* (Gingerich, 1992), including only *Saghacetus osiris*. *Stromerius* (Gingerich, 2007), including only *Stromerius nidensis*; *Supayacetus* (Uhen et al., 2011), including only *Supayacetus muizoni*; and *Zygorhiza* (True, 1908), including only *Z. kochii*.

Currently, the family Kekenodontidae includes two species in two genera: *Kekenodon* (Hector, 1881), including only *K. onamata*; and *Phococetus* (Gervais, 1876), including only *P. vasconum*.

III. Life History

A. Locomotion

Basilosaurids are the earliest cetaceans that are thought to be fully aquatic. Based on the greatly reduced hind limbs that are disconnected from the vertebral column, elongation of the vertebral column by addition of additional posterior thoracic and lumbar vertebrae, and restriction of motion in joints of the forelimb, basilosaurids were incapable of supporting their body weight on land. In addition, they have dorsoventrally flattened posterior caudal vertebrae indicative of soft tissue tail flukes, suggesting locomotion using these flukes like modern cetaceans.

B. Feeding

Based on the size, morphology, and shapes of their teeth, basilosaurids are thought to have acquired individual prey items, chewed those prey and swallowed the fragments of prey. There is neither any indication that basilosaurids used echolocation to find prey nor any indication that they used their teeth for filter feeding. Basilosaurids most likely used their anterior teeth to acquire prey items, and their cheek teeth for prey processing prior to swallowing. Limited stomach contents support a piscivorous diet (Uhen, 2004). The teeth of some kekenodontids are more widely spaced, and it has been suggested that perhaps they used these teeth for filter feeding like modern crabeater seal, *Lobodon carcinophaga* (Clementz et al., 2014).

C. Habitat and Ecology

Most basilosaurids are known from marginal marine tropical to subtropical waters, although some from the Southern Hemisphere may have lived in cooler waters than those known from North African and the southeastern United States. Basilosaurids are all predatory. Some larger basilosaurids like *Basilosaurus* and *Cynthiacetus* may have fed on smaller basilosaurids like *Dorudon*, particularly on juveniles (Fahlke, 2012).

IV. Phylogenetic Relationships

The phylogenetic relationships among basilosaurids, and their relationships to other archaeocetes, mysticetes, and odontocetes are shown in Fig. 3. Many of the character state transformations that occur between basilosaurids and protocetids are associated with the adoption of a fully aquatic existence; such as presence of pterygoid air sinuses, extreme reduction of the hind limb, loss of the sacrum, increase in the number of trunk vertebrae, and the presence of dorsoventrally flattened posterior caudal vertebrae (Uhen, 1998). Others, such as the loss of M3, loss of lingual roots on the upper molars, and the development of accessory denticles on the cheek teeth, have to do with changes in feeding that are not as easy to interpret.

Each genus of basilosaurid is distinguishable from the other genera based on the presence of autapomorphies, but it is difficult to confidently link any of the genera based on any clear synapomorphies. The result is a polytomous relationship among the genera or an imbalanced tree with Neoceti nested well within Dorudontinae. *Chrysocetus* is preferred as the sister taxon to Neoceti based on the interpretation of it and early mysticetes and odontocetes as monophyodont. Hopefully, some of the relationships among basilosaurids will become more secure as more of the anatomy of more of the species becomes known.

Phylogenetic placement of kekenodontids has fluctuated, with some suggesting a sister group relationship with Mysticeti, and others suggesting a sister group relationship with Neoceti (Clementz et al., 2014). Kekenodontids are very similar to derived basilosaurids in much of their cranial architecture and dentition, and the position as sister group to Mysticeti + Odontoceti is supported, pending further description of fossils and analysis. If this phylogenetic position is supported by further analysis, Kekenodontidae should be considered stem Neoceti.

See Also the Following Articles

Archaeocetes, archaic ■ Cetacean Evolution

Copyright © 2017. Elsevier Science & Technology. All rights reserved.

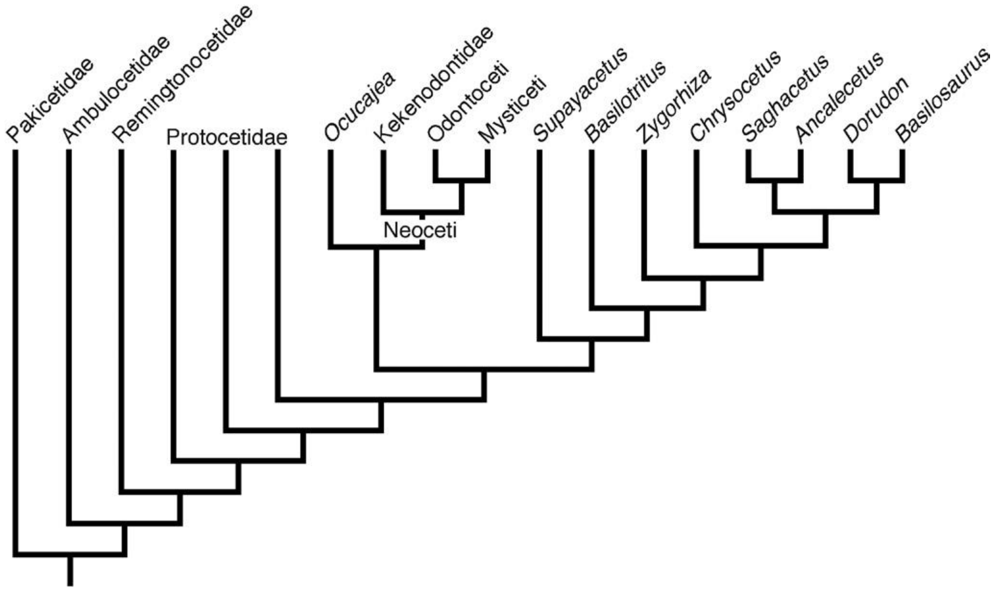

Figure 3 *Cladogram of basilosaurids, selected nonbasilosaurid archaeocetes, mysticetes, and odontocetes. Genera listed in italics are basilosaurids.*

References

Barnes, L.G. (1985). Evolution, taxonomy and antitropical distributions of the porpoises (Phocoenidae, Mammalia). *Mar. Mamm. Sci.* **1**, 149–165.

Clementz, M.T., Fordyce, R.E., Peek, S.L., and Fox, D.L. (2014). Ancient marine isoscapes and isotopic evidence of bulk-feeding by Oligocene cetaceans. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **400**, 28–40.

Fahlke, J.M. (2012). Bite marks revisited – evidence for middle-to-late Eocene *Basilosaurus isis* predation on *Dorudon atrox* (both Cetacea, Basilosauridae). *Palaeontol. Electron.* **15**, 1–16.

Gingerich, P.D., Smith, B.H., and Simons, E.L. (1990). Hind limbs of Eocene *Basilosaurus*: Evidence of feet in whales. *Science* **249**, 154–157.

Gingerich, P.D., and Zouhri, S. (2015). New fauna of archaeocete whales (Mammalia, Cetacea) from the Bartonian middle Eocene of southern Morocco. *J. Afr. Earth Sci.* **111**, 273–286.

Gol'din, P., and Zvonok, E. (2013). *Basilotritus uheni*, a new cetacean (Cetacea, Basilosauridae) from the Late Middle Eocene of Eastern Europe. *J. Paleontol.* **87**, 254–268.

Kellogg, R. (1936). A Review of the Archacoceti, Vol. 482. Carnegie Institution of Washington Special Publication.1–366.

Miller Jr., G.S. (1923). The telescoping of the cetacean skull. *Smiths Misc. Coll.* **76**(5), 1–71.

Uhen, M.D. (1998). Middle to late Eocene Basilosaurines and Dorudontines. In "The Emergence of Whales", (J.G.M. Thewissen, Ed.), pp. 29–61. Plenum Press, New York.

Uhen, M.D. (2004). Form, function, and anatomy of *Dorudon atrox* (Mammalia, Cetacea): An archaeocete from the Middle to Late Eocene of Egypt. *Univ. Mich. Mus. Paleontol. Pap. Paleontol.* **34**, 1–222.

Uhen, M.D. (2013). A review of North American Basilosauridae. *Ala. Mus. Nat. Hist. Bull.* **31**, 1–45.

Uhen, M.D., and Gingerich, P.D. (2001). New genus of dorudontine archaeocete (Cetacea) from the middle-to-late Eocene of South Carolina. *Mar. Mamm. Sci.* **17**(1), 1–34.

BEAKED WHALES, OVERVIEW

Colin D. MacLeod

Beaked whales belong to the odontocete family Ziphiidae. This is the second largest family of cetaceans after the family Delphinidae (the dolphins). They are medium-sized cetaceans with spindle-shaped bodies and a dorsal fin set two-thirds of the way along the body, and adult size ranges from just under 4 m to about 12 m. Adult males of most species have a single pair of tusks that are used in aggressive male–male combat, and in general, juveniles and females are functionally toothless. There are currently 22 recognized species in six different genera. All known species live in waters deeper than 200 m, and they feed on deep water squid, fish, and to a lesser extent, crustaceans.

I. Classification

Family Ziphiidae	
Subfamily Ziphiinae	
Berardius arnuxii	Arnoux's beaked whale
Berardius bairdii	Baird's beaked whale
Tasmacetus shepherdi	Shepherd's beaked whale
Ziphius cavirostris	Cuvier's beaked whale
Subfamily Hyperoodontinae	
Hyperoodon ampullatus	Northern bottlenose whale
Hyperoodon planifrons	Southern bottlenose whale
Indopacetus pacificus	Longman's beaked whale
Mesoplodon bidens	Sowerby's beaked whale
Mesoplodon bowdoini	Andrews' beaked whale
Mesoplodon carlhubbsi	Hubbs' beaked whale
Mesoplodon densirostris	Blainville's beaked whale
Mesoplodon europaeus	Gervais' beaked whale
Mesoplodon ginkgodens	Ginkgo-toothed beaked whale
Mesoplodon grayi	Gray's beaked whale
Mesoplodon hectori	Hector's beaked whale
Mesoplodon hotaula	Deraniyagala's beaked whale
Mesoplodon layardii	Strap-toothed beaked whale
Mesoplodon mirus	True's beaked whale
Mesoplodon perrini	Perrin's beaked whale
Mesoplodon peruvianus	Pygmy beaked whale
Mesoplodon stejnegeri	Stejneger's beaked whale
Mesoplodon traversii	Spade-toothed beaked whale

Copyright © 2017. Elsevier Science & Technology. All rights reserved.

II. Diagnostic Characteristics and Taxonomy

Beaked whales range in length from just under 400 cm in the Pygmy beaked whale (*Mesoplodon peruvianus*) to 1200 cm in Baird's beaked whale (*Berardius bairdii*). In all species, the maximum girth is midway between the tip of the rostrum and the tail, resulting in a spindle-shaped body that is unique to beaked whales (Balcomb, 1989; Heyning, 1989; Mead, 1989a,b,c). The small subtriangular dorsal fin is set two-thirds the distance between the head and the large, relatively wide tail flukes. Unlike most other whales, there is typically no central notch in the tail flukes. The pectoral fins are small and can be folded into pocket-like depressions on either side of the body. This adaptation increases the streamlining of the body, and when they are not being used for maneuvering, the pectoral fins are held tightly against the body (Fig. 1). On the throat, there is a single pair of grooves. These are thought to help expand the throat and allow individuals to capture their prey by suction feeding. There is no strong evidence of sexual dimorphism in body size in the beaked whales, but in species where one sex is larger, females are usually larger than males. The only exception to this is the Northern bottlenose whale (*Hyperoodon ampullatus*), where males appear to be consistently larger.

The main features that distinguish the different species of beaked whales are the profile of the forehead, the length of the beak, and the shape and position of the teeth (Balcomb, 1989; Heyning, 1989; Mead, 1989a,b,c). In general, species with shorter beaks have flatter, less clearly defined foreheads, while those with longer beaks have bulbous or rounded foreheads. The dentition of beaked whales sets them apart from all other cetaceans and is the key feature used to identify them both when stranded and at sea. Typically, dentition is limited to one or two pairs of teeth that only erupt to become functional in adult males in most species, or adults of both sexes in the two members of the genus *Berardius* (Balcomb, 1989; Heyning, 1989; Mead, 1989b). The exception to this is Shepherd's beaked whale (*Tasmacetus shepherdi*) and members of the genus *Hyperoodon*. Shepherd's beaked whale has a full set of functional teeth, as well as a pair of sexually dimorphic tusks similar to those found in other beaked whale species (Mead, 1989c). In contrast, the two members of the genus *Hyperoodon* have a more typical beaked whale dentition, with only a single pair of teeth, but these remain embedded within the gums throughout life, even in adult males (Mead, 1989a).

While the teeth in all other genera are conical, and are set at the tip of the lower jaw, in the genus *Mesoplodon* there is a substantial amount of variation in terms of their shape and position (Mead, 1989b). The single pair of teeth in this genus vary, when fully erupted in adult males, from being conical and set at the tip of the lower jaw in True's beaked whale to being long strap-like structures that cross over the top of the upper jaw in the strap-toothed beaked whale (*M. layardii*). In other species, such as Blainville's beaked whale (*M. densirostris*), the tusks, despite being set in the lower jaw, are raised up on bony support structures above the top of the head. Associated with the development of tusks in adult male beaked whales (or in both sexes in the case of species of *Berardius*) is the ossification of the rostrum. In some species, such as Blainville's beaked whale, this ossification of the rostrum results in the densest bone ever recorded in any vertebrate.

There are currently 22 recognized species of beaked whale, and new species have been discovered on a regular basis over the last century. Two new species were described in the 1990s alone, and a

Figure 1 *Beaked whales have spindle-shaped bodies with small, subtriangular dorsal fins set two-thirds of the way along their bodies. Males, such as this adult male Blainville's beaked whale, typically have a pair of sexually dimorphic teeth that protrude from the closed mouth to form tusks. These tusks are used in male–male combat, resulting in large amounts of scarring on the head and dorsal surface. These scars do not repigment, and instead remain clearly visible as white lines that criss-cross the body.*

Copyright © 2017. Elsevier Science & Technology. All rights reserved.

further two have been resurrected as separate species in their own right since 2000. Extant species of beaked whales are traditionally divided into two subfamilies, Ziphiinae, containing the genera *Berardius* (two species), *Tasmacetus* (one species), and *Ziphius* (one species); and Hyperoodontinae, containing the genera *Hyperoodon* (two species), *Indopacetus* (one species), and *Mesoplodon* (15 species). New molecularly based analyses, however, suggest that this taxonomic view is in need of revision because it does not reflect the evolutionary history of beaked whales. These molecular analyses suggest that the genus *Berardius* was the first to split from the main beaked whale lineage, followed by a second split that divides living species into two distinct groups: one containing the genera *Hyperoodon*, *Tasmacetus*, and *Ziphius*; and a second containing the genera *Indopacetus* and *Mesoplodon*.

There is general agreement that the six currently recognized living genera are true monophyletic groups. Of these genera, two consist of a pair of species with antitropical distributions (*Hyperoodon* and *Berardius*), two contain a single species with a cross-equatorial distribution (*Ziphius* and *Indopacetus*), and one has a circumpolar distribution in the Southern Hemisphere (*Tasmacetus*). In contrast, the genus *Mesoplodon* currently contains 15 extant species with highly variable distributions (MacLeod et al., 2006).

III. Distribution and Ecology

A. Habitat

Beaked whales are generally thought of as oceanic, or offshore, species (Balcomb, 1989; Heyning, 1989; Mead, 1989a,b,c). However, it is their preference for deep waters, usually over 200 m deep, rather than the distance from shore itself that limits their occurrence. Where suitably deep waters are found close to shore, such as around oceanic islands, beaked whales are frequently observed (MacLeod and D'Amico, 2006). In the few locations where habitat preferences have been studied, beaked whales have generally, but not always, been linked to areas of complex seabed topography where deep-water currents interact with the seabed. This can create upwelling or mixing within the water column, resulting in hotspots of primary productivity that presumably attract the type of prey, generally but not always squid, on which beaked whales feed.

B. Behavior

Beaked whales are well known for their diving abilities, and they are among the deepest and longest diving of all marine mammals (MacLeod and D'Amico, 2006). They are capable of diving to depths of at least several thousand meters (Tyack et al., 2006). During such dives, they can remain submerged for well over an hour, and may spend the majority of their lives at such depths. As a result, they can be rightly considered deep-water species that occasionally come to the surface to breathe rather than surface species that dive to great depths to forage.

All individuals in a group of beaked whales tend to dive at the same time and stay close together, even at depth (Tyack et al., 2006). Most dives can be divided into three distinct sections: the vertical descent, the time spent at depth, and the vertical ascent. Beaked whales often tend to forage at or close to the seabed, where they use echolocation to find suitable prey. The prey are then pursued and captured individually, and prey capture is most likely by suction feeding, although this has not been directly observed.

Other than diving behavior, little is known about the behavior of beaked whales because of the difficulties in studying them at sea. In the past, beaked whales generally have been assumed to be boat-shy and to avoid close contact with vessels, but it is probably more appropriate to assume that beaked whales are boat-neutral rather than boat-shy, and for the most part, they ignore vessels rather than actively avoid or approach them.

C. Vocalizations

Beaked whales echolocate, using clicks that are of relatively high frequency for their body size, presumably to aid in navigation and prey capture, but this echolocation generally only occurs during foraging dives and at depths greater than 200 m (MacLeod and D'Amico, 2006; Tyack et al., 2006). Clicks used for navigation are usually in the region of 2–20 kHz and serve to orient an individual in relation to aspects of its surrounding environment, such as the position of the seabed. Clicks used for prey capture tend to occur in rapid sequences known as "click trains," which can have frequencies of up to 200 kHz in some species of beaked whales. There is currently little evidence that beaked whales produce any other types of sound.

D. Diet

Beaked whales are generally thought of as specialist consumers of deep-water squid, but while these squid do make up the majority of prey for the family as a whole, some species, such as Sowerby's beaked whale, seem to almost exclusively eat deep-water fish (MacLeod and D'Amico, 2006). In addition, there may be geographic variations in diet within individual species of beaked whales. For example, Cuvier's beaked whales consume more fish in some parts of their distribution than in others, while in areas such as the Caribbean Sea, deep-water crustaceans seem to form an important part of their diet.

E. Social Organization

Social organization is poorly known in beaked whales, but it appears that species can be divided into at least two basic groups in terms of their social structure (MacLeod and D'Amico, 2006). Most species in the genera *Hyperoodon*, *Mesoplodon*, and *Ziphius* form small groups, typically of one to five individuals, and are very rarely recorded in groups larger than 10. Most of these groups contain a mixture of adult females, any dependent offspring, and one, or sometimes more, adult males. The second type of social structure can be seen in Longman's beaked whale (*Indopacetus pacificus*) and the two members of the genus *Berardius* (Arnoux's beaked whale, *Berardius arnuxii*, and Baird's beaked whale, *Berardius bairdii*). In these species, the group size is typically much larger, with most groups containing 5–20 individuals, and groups of up to 100 individuals are not uncommon. These groups usually contain females, juveniles, and multiple mature males. Why these two types of social structure exist remains unknown.

IV. Life History and Reproduction

Little is known about breeding in beaked whales (Heyning, 1989; MacLeod and D'Amico, 2006; Mead, 1989a,b,c). Gestation is probably about 12 months in almost all species, and female beaked whales bear a single offspring, which is probably about one-third of the mother's body length when born. Offsprings are likely dependent on their mothers for at least the first year, and possibly for several years. It is likely that it takes up to a decade or more to reach maturity, and there is evidence that sexual maturity occurs before physical maturity, particularly in males. In many species, adult males are covered in linear scars that do not repigment, and so accumulate throughout their lives. These scars are caused by the tusks of other males during aggressive male–male interactions, presumably over access to receptive females. The level and severity of

Copyright © 2017. Elsevier Science & Technology. All rights reserved.

scarring varies between species and is related to the size, development, and positioning of the tusks.

V. Status, Conservation, and Interactions With Humans

Of the 22 known species of beaked whale, two (Cuvier's beaked whale and the Southern bottlenose whale) are currently classified as *least concern* by the IUCN, and the remaining 20 species are considered *data deficient*. This reflects the general lack of knowledge of the ecology and biology of beaked whale. Estimates of global population sizes are not available for any species, and where regional population estimates are available, these are often for all beaked whales rather than individual species. Some species, such as Blainville's beaked whale and Cuvier's beaked whale, appear to be relatively common within their respective distributions. Others, such as Shepherd's beaked whale and Longman's beaked whale, appear to be naturally rare.

Only one species, the Northern bottlenose whale, has been the target of a major commercial whaling industry, but many other species are taken either as part of small-scale coastal fisheries or opportunistically by fishermen. Commercial whaling almost certainly depleted numbers of Northern bottlenose whales (Mead, 1989a), but small-scale coastal fisheries and opportunistic takes likely only have a relatively small impact on local populations rather than entire species.

The ingestion of plastic debris, such as plastic bags, appears to be an issue for some species, such as Cuvier's beaked whale, because ingested plastic can become trapped in the stomach and cause death through necrosis of the stomach lining. The impact on individual populations and species of beaked whales remains unclear; however, ingestion of debris could be sufficiently debilitating to have conservation implications for some populations living in areas where plastic debris is particularly common, such as the northeast Atlantic.

Beaked whales are also affected by noise pollution. In particular, mid-frequency military sonar has been associated with a number of mass strandings throughout the world (MacLeod and D'Amico, 2006). Current evidence suggests that normal diving activities are, for some reason, disrupted by such sonar, causing some individuals to suffer symptoms similar to decompression sickness, which can result in disorientation, stranding, and death.

Beaked whales are likely to be affected by the increasing number of fisheries that exploit deep-water ecosystems, through damage to the ecosystem structure and composition and/or prey depletion. These ecosystems seem particularly vulnerable to the impacts of fisheries, but the likely impacts on beaked whales themselves are difficult to assess and quantify, so the full extent of these potential impacts remains unknown. Climate change is also likely to affect many species of beaked whales, resulting in, among other things, changes in distribution. The extent of these changes and their implications for the conservation status of individual species remain unclear and are likely to be complex.

Despite our impacts upon them, few humans will ever encounter a living beaked whale, and most people do not even know this enigmatic family of whales exists. As a result, unlike almost all other families of cetaceans, there is little or no public perception of what a beaked whale is. Even within the scientific community, there is little general awareness of beaked whales, and while beaked whales started to receive scientific scrutiny in the late 18th century, this was primarily limited to identifying species and examining stranded specimens. In fact, it was not until the late 1990s that interest in studying living beaked whales at sea finally started to expand, driven primarily by the association of mass strandings of beaked whales with the use of mid-frequency military sonars. The attempt to understand why these strandings occurred and how to prevent more of them happening in the future has led to a rapid expansion in our knowledge of the ecology and biology of beaked whales, but the exact cause of the strandings remains unclear.

References

Balcomb, K.C. (1989). Baird's beaked whale *Berardius bairdii* Stejneger, 1883: Arnoux's beaked whale *Berardius arnuxii* Duvernoy, 1851. In "Handbook of Marine Mammals", (S.H. Ridgway, and R.J. Harrison, Eds), Vol. 4, pp. 261–288. Academic Press, London, UK.

Heyning, J.E. (1989). Cuvier's beaked whale *Ziphius cavirostris* G Cuvier, 1823. In "Handbook of Marine Mammals", (S.H. Ridgway, and R.J. Harrison, Eds), Vol. 4, pp. 289–308. Academic Press, London, UK.

MacLeod, C.D., and D'Amico, A. (2006). A review of knowledge about behaviour and ecology of beaked whales in relation to assessing and mitigating potential impacts from anthropogenic noise. *J. Cetacean Res. Manage.* **7**, 211–222.

MacLeod, C.D., Perrin, W.F., Pitman, R., Barlow, J., Ballance, L., D'Amico, A., Gerrodette, T., Joyce, G., Mullin, K.D., Palka, D.L., and Waring, G.T. (2006). Known and inferred distributions of beaked whale species (Cetacea: Ziphiidae). *J. Cetacean Res. Manage.* **7**, 271–286.

Mead, J.G. (1989a). Bottlenose whales *Hyperoodon ampullatus* (Forster, 1770) and *Hyperoodon ampullatus* Flower, 1882. In "Handbook of Marine Mammals", (S.H. Ridgway, and R.J. Harrison, Eds), Vol. 4, pp. 321–348. Academic Press, London, UK.

Mead, J.G. (1989b). Beaked whales of the genus *Mesoplodon*. In "Handbook of Marine Mammals", (S.H. Ridgway, and R.J. Harrison, Eds), Vol. 4, pp. 329–430. Academic Press, London, UK.

Mead, J.G. (1989c). Shepherd's beaked whale *Tasmacetus shepherdi* Oliver, 1937. In "Handbook of Marine Mammals", (S.H. Ridgway, and R.J. Harrison, Eds), Vol. 4, pp. 309–320. Acadamic Press, London, UK.

Tyack, P.L., Johnson, M., Aguilar Soto, N., Sturlese, N., and Madsen, P.T. (2006). Extreme diving of beaked whales. *J. Exp. Biol.* **209**, 4238–4253.

BEARDED SEAL

Erignathus barbatus

KIT M. KOVACS

The bearded seal (*Erignatus barbatus*) is the largest northern true seal belonging to the family Phocidae. The genus contains a single species. Their English common name derives from their elaborate facial whiskers. Bearded seals are an ice-associated seal that is found throughout the circumpolar Arctic in shallow areas where ice floes and sufficient benthic prey can be found.

I. Characteristics and Taxonomy

The bearded seal is the largest of the northern true seals (Figs 1 and 2). Adults are 2–2.5 m long and are gray-brown in color; some individuals have irregular light-colored patches. The weight of bearded seals varies dramatically on an annual cycle, but an average weight for adults is 250–300 kg. Females are somewhat larger than males in this species and can weigh in excess of 425 kg in the spring. The sexes are not easily distinguished. Pups are

Copyright © 2017. Elsevier Science & Technology. All rights reserved.

approximately 1.3m long at birth and weigh an average of 37kg. They are born with a partial coat of fuzzy gray-blue fur, but have already commenced molting into a smooth dark-gray coat, with a light belly, that is their complete pelage by the time they are a few weeks old (Kovacs et al., 1996). Their shed fetal hair is formed into disks (similar to hooded seals) that are passed with the placenta. Similar to adults, young animals often have irregular light patches here and there on their bodies. Pups faces have white cheek patches and white eyebrow spots that give them a "teddy-bear" appearance (Fig. 2A). Yearlings look very similar to pups, but the facial patterns are somewhat less distinct and they often have dark spots on their bellies.

Bearded seals have several distinctive physical features; their body shape is rectangular and their heads appear to be small compared to their body size, similar to monk seals. They also have extremely elaborate, smooth, facial whiskers that tend to curl when dry (Fig. 2B). They also have very square-shaped fore flippers (with the longest toe being the middle one), which bear very strong claws (Fig. 2C). Females have four mammary glands (another characteristic shared with the monk seal lineage), unlike the other northern phocids, which have only two. Genetically and morphologically, the bearded seal is an intermediate form, sharing characteristics of the two Phocidae subfamilies (Phocinae and Monachinae).

The dentition of bearded seals is typical for phocid seals: I 3/2 C1/1 PC 5/5 though anomalies in number are common, and often the teeth of older animals are worn down to the gum-line.

II. Distribution and Abundance

Bearded seals have a patchy distribution throughout much of the Arctic and subarctic (Fig. 3; Burns, 1981). Their preferred habitat is drifting pack ice in shallow, coastal areas but they do occupy offshore pack ice in some regions. Bearded seals can maintain holes in relatively thin ice, but avoid heavy ice areas, preferring to use leads and ice edges for haul out. During winter, they concentrate in areas that contain polynyas or in areas where leads in the ice tend to be a regular feature. Juvenile animals wander quite broadly and are sometimes found far south of the normal adult range.

Bearded seals exhibit strong genetic population substructuring across their range (Davis et al., 2008), but the fine-scale geographic limits for the various populations are not known. No abundance estimates are available for any bearded seal population or stock. Because they occur at relatively low densities, and are spread over wide ranges, survey logistics are challenging. Despite the lack of data, it is assumed that this species probably numbers in the low hundreds of thousands globally.

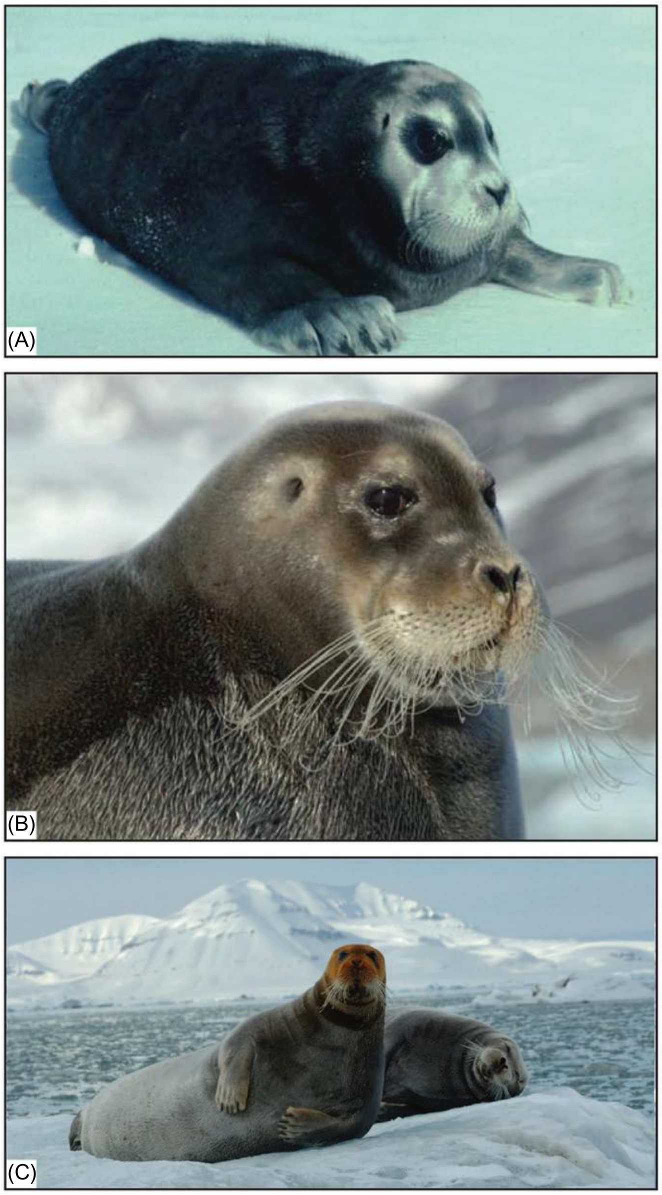

Figure 2 *(A) Bearded seal pup, 2 days old. (B) Adult male bearded seal close-up showing the elaborate vibrissae. (C) Two adult bearded seals hauled out on calved glacier ice; right: newly molted, left: just prior to molt, note the iron oxides on the facial hair (Photos by Kit M. Kovacs & Christian Lydersen, NPI).*

Figure 1 *Bearded seal,* Erignatus barbatus *(Illustration by Pieter Folkens).*

Copyright © 2017. Elsevier Science & Technology. All rights reserved.

III. Ecology

Bearded seals are an ice-associated species. High levels of primary productivity and benthic biomass, as well as the presence of ice floes, have positive influences on abundance in a given area. Bearded seals are somewhat more flexible regarding their haul-out platform than other ice-breeding seals, in some areas they do come ashore to rest, particularly at the time of peak molting in midsummer. Bearded seals are not deep divers; they feed in shallow, often coastal, areas and hence normally do not dive to depths of more than 100 m. Pups dive to much greater depths during their first year (450+ m) while learning where to successfully forage, but older, experienced animals remain in shallow water (Gjertz et al., 2000). Most bearded seal dives are less than 10 min in duration, although they can dive for up to 20–25 min.

Bearded seals eat a wide variety of different types of prey, but they are predominantly benthic feeders, eating clams, shrimps, crabs, squid, fishes, and a variety of other small prey that they find near the bottom or even within soft-bottom substrates. They search for food using their whiskers, and capture it using a combination of water jetting and suction (Marshall et al., 2008). Some bearded seals have rust-colored faces and fore flippers. This coloration is the result of iron compounds from bottom substrates sticking to the hairs while they feed and then chemically reacting with oxygen when the seal comes to the surface. The rust material adheres to the surface of the hair shafts, so newly molted animals are not rust colored (see Fig. 1C).

Polar bears are the main predator of bearded seals, but walruses, killer whales, and Greenland sharks also kill bearded seals, particularly pups and juveniles. Additionally, they are important as traditional food for humans in most parts of their range.

IV. Behavior and Physiology

Bearded seals are largely solitary, although it is not unusual to see them hauled out together in small groups along leads or at holes in the spring or early summer. They are rarely more than a body length from the water, and usually face toward the water. However, they are not wary in a general sense and in areas where they are not heavily hunted they can be approached to within a few meters.

The time of breeding appears to vary somewhat geographically, with peaks occurring between late March and mid-May depending on the locality. Females give birth in a solitary fashion, on small drifting floes in areas of shallow water. Pups are born with a thin layer of subcutaneous blubber, which is thought to be an adaptation to entering the water shortly after birth. Bearded seal pups swim with their mothers when they are only hours old. This precocial entry into the sea has likely evolved as a mechanism to avoid polar bear predation. Neonatal swimming skills develop quickly in this species, and pups can dive to depths >90 m and remain submerged for periods in excess of 5 min when they are only a few weeks old. They spend approximately half of their time in the water during the nursing period, which lasts a total of 18–24 days and commence foraging on solid food while still accompanied by their mother. Female bearded seals spend little time on the surface with their pups, beyond that which is necessary for nursing. Most of the time, they attend the pups from the water next to the floe where the pup is resting at a given time. Females do leave their pups unattended for periods to forage, starting when they are a few days old (Krafft et al., 2000). Pups grow quickly during the nursing period, gaining about 3.3 kg/day, while drinking >7.5 L of milk per day. The fat content of the milk is quite stable through lactation, at about 50%. Bearded seal pups have leaner bodies at the time of weaning than less active phocid pups, but still have significant blubber stores and a body composition that is about one-third fat (Lydersen and Kovacs, 1999). Pups are about 100 kg when they are weaned; weaning is not as abrupt as it is in most phocid species.

Mating takes place around the time that females leave their offspring. Male bearded seals perform vocal displays underwater to attract females and compete with other males. Their beautiful, slightly melancholy, underwater songs are composed of a downward spiraling trill that can be heard for many kilometers in calm conditions. The onset of vocal displays (at least in captivity) is coincident with the onset of sexual maturity (Davies et al., 2006). In the wild, males defend small patches of ocean with elaborate bubble displays, where they sing their songs intensively and repeatedly over a period of some weeks. Bearded seal calls exhibit marked geographic variation in call dialects, while repertoires of calls seem to be quite stable regionally (Risch et al., 2007). Relatively little is known regarding the specifics of mating behavior in this species because pairing takes place in the water, but individual territorial males are known to occupy the same areas from 1 year to the next for at least several years, while transient males roam around in key breeding areas (Van Parijs et al., 2001, 2003). Males do engage in physical combat during the breeding season and some bear scars from battle with other males.

Bearded seals shed their hair much more diffusely than other phocid seals, losing hair most of the year. But, they do have a concentrated period of molting in June when they prefer not to go into the water. At this time of year there is not a lot of ice available in some coastal areas, so bearded seals can be seen in small groups on the available ice or even on shore in some regions. Modestly dense aggregations can occur at this time of year, particularly in years (or areas) with poor ice conditions.

The most notable sensory adaptation of bearded seals beyond their highly developed acoustic system is the extreme development of their facial vibrissae. They have approximately 244 highly sensitive, active-touch receptors within their facial whisker pads, which are among the most sensitive in the animal world with 1300 mylinated axons ("nerve-endings") associated with each whisker (Marshall et al., 2006). The extreme development of the sensitivity of the whiskers of bearded seals is presumably an adaptation to their benthic feeding habit and might also be linked to feeding in low light conditions during the long polar night when the sun does not rise for some months.

V. Life History

Neonatal growth is fast, similar to all phocid seals, but growth over the rest of the first year of life is minimal. Female bearded seals reach sexual maturity when they are about 5 years old, whereas males are a bit older—usually six or seven and they likely do not become part of the breeding population for a few more years. Females are thought to give birth annually, similar to other phocid seals. Bearded seals normally live to an age of 20–25 years.

Bearded seals in some populations are resident throughout the year within small home ranges, while in other populations they show clear seasonal migration patterns that follow the retraction of the pack ice northward during the summer and southward again in the late fall.

VI. Interactions With Humans

Bearded seals are an important subsistence resource for coastal peoples throughout much of the Arctic. They are harvested for use as human food, dog food, and for their thick leather, which is

Copyright © 2017. Elsevier Science & Technology. All rights reserved.

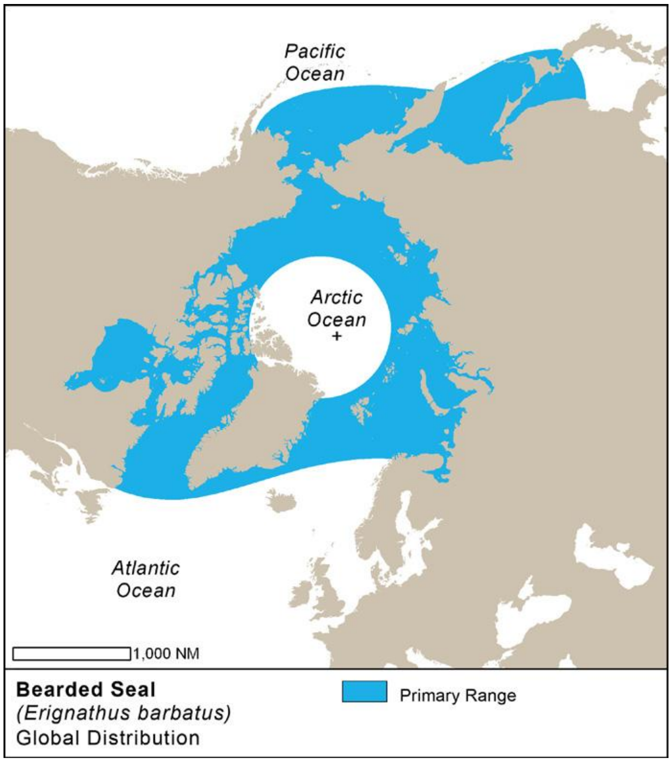

Figure 3 *Bearded seal distribution. Map produced by Anders Skoglund, Norwegian Polar Institute.*

important for various traditional articles of clothing and for making skin boats. Russia is the only country that has had a commercial-scale harvest of bearded seals. Soviet ships took catches that exceeded 10,000 animals in some years during the 1950s and 1960s. Quotas were introduced to limit the harvests of the declining populations in the Okhotsk and Bering seas, and the catch dropped to a few thousand seals annually through the 1970s and 1980s. This hunt provided food for people and dogs in addition to fueling feed production for fur-farm animals. Sinking loses are a serious problem when hunting bearded seals. During much of the year they sink when shot in open water or too close to edges; sinking loss is estimated to be as high as 50%.

Because bearded seals feed low in the food chain, they tend to have low toxic contaminant loads. The most obvious threat to this species, beyond overexploitation at a local level, is climate change (Cameron et al., 2010; Kovacs et al., 2011; Laidre et al., 2015). Sea ice predictions for the coming decades suggest that breeding habitat for bearded seals will decline dramatically.

References

Burns, J.J. (1981). Bearded seal *Erignathus barbatus* Erxleben, 1977. In "Handbook of Marine Mammals", (S.H. Ridgway, and R.J. Harrison, Eds), Vol. A. (Seals), pp. 145–170. Academic Press, London.

Cameron, M.F., Bengtson, J.L., Boveng, P.L., Jansen, J.K., Kelly, B.P., Dahle, S.P., Logerwell, E.A., Overland, J.E., Sabine, C.L., Waring, G.T., and Wilder, J.M. (2010). *Status review of the bearded seal (Erignathus barbatus).* U.S. Department of Commerce, NOAA Technical Memorandum NMFS-AFSC-211.

Davies, C.E., Kovacs, K.M., and Lydersen, C. (2006). Development of display behavior in young captive bearded seals. *Mar. Mamm. Sci.* **22**, 952–965.

Davis, C.S., Stirling, I., Strobeck, C., and Coltman, D.W. (2008). Population structure of ice-breeding seals. *Mol. Biol.* **17**, 3078–3094.

Gjertz, I., Kovacs, K.M., Lydersen, C., and Wiig, Ø. (2000). Movements and diving of bearded seals (*Erignathus barbatus*) mothers and pups during lactation and post-weaning. *Polar Biol.* **23**, 559–566.

Kovacs, K.M., Moore, S., Overland, J.E., and Lydersen, C. (2011). Impacts of changing sea-ice conditions on Arctic marine mammals. *Mar. Biodiv.* **41**, 181–194.

Kovacs, K.M., Lydersen, C., and Gjertz, I. (1996). Birth-site characteristics and prenatal molting in bearded seals (*Erignathus barbatus*). *J. Mammal.* **77**, 1085–1091.

Krafft, B.A., Lydersen, C., Kovacs, K.M., Gjertz, I., and Haug, T. (2000). Diving behaviour of lactating bearded seals (*Erignathus barbatus*) in the Svalbard area. *Can. J. Zool.* **78**, 1408–1418.

Laidre, K.L., Stern, H., Kovacs, K.M., Lowry, L., Moore, S.E., Regehr, E.V., Ferguson, S.H., Wiig, Ø., Boveng, P., Angliss, R.P., Born, E.W., Litovka, D., Quakenbush, L., Lydersen, C., Vongraven, D., and Ugarte, F. (2015). Arctic marine mammal population status, sea ice habitat loss, and conservation recommendations for the 21st century. *Conserv. Biol.* **29**, 724–737.

Lydersen, C., and Kovacs, K.M. (1999). Behaviour and energetics of ice-breeding, North Atlantic phocid seals during the lactation period. *Mar. Ecol. Prog. Ser.* **187**, 265–281.

Marshall, C.D., Amin, H., Kovacs, K.M., and Lydersen, C. (2006). Microstructure and innervation of the mystacial vibrissal follicle-sinus complex in bearded seals, *Erignathus barbatus* (Pinnipedia: Phocidae). *Anat. Rec.* **288A**, 13–25.

Marshall, C.D., Kovacs, K.M., and Lydersen, C. (2008). Feeding kinematics, suction, and hydraulic jetting capabilities in bearded seals (*Erignathus barbatus*). *J. Exp. Biol.* **211**, 699–708.

Risch, D., Clarke, C.W., Cockeron, P.J., Elepfandt, A., Kovacs, K.M., Lydersen, C., Stirling, I., and Van Parijs, S.M. (2007). Vocalizations of male bearded seals, *Erignathus barbatus*: classification and geographical variation. *Anim. Behav.* **73**, 747–762.

Van Parijs, S.M., Kovacs, K.M., and Lydersen, C. (2001). Spatial and temporal distribution of vocalizing male bearded seals – implications for male mating strategies. *Behaviour* **138**, 905–922.

Van Parijs, S.M., Lydersen, C., and Kovacs, K.M. (2003). Vocalizations and movements suggest alternative mating tactics in male bearded seals. *Anim. Behav.* **65**, 273–283.

BEHAVIOR, OVERVIEW

Peter L. Tyack

Marine mammalogists often divide behavioral research into categories defined by mode of study: "behavior" is often informally defined as that which can be seen by an observer watching animals, "acoustics" is studied by recording underwater sounds with a hydrophone, and "diving" is often studied by attaching tags to animals. This method-oriented view of behavior may be convenient for sorting different research traditions, but it obscures the integrated whole of behavior as it has been shaped by evolution. Each method yields its own view of behavior, but no one view alone can provide a complete picture.

Most behavioral ecologists divide behavior along functional lines, that is, what is the problem the behavior has evolved to solve? The following is a short list of such problems:

- Foraging behavior: how to find, select, and process prey
- Predator avoidance or defense: the flip side of foraging from the prey's point of view
- Dispersal and migration
- Competition and agonistic behavior

Copyright © 2017. Elsevier Science & Technology. All rights reserved.

- Sexual behavior: how to find, court, and choose mates
- Parental behavior
- Social behavior and social relationships

This article discusses marine mammal examples for each of these basic problems in the behavioral ecology of all animal species, with special emphasis on how the marine environment may affect adaptations of marine mammals.

I. Foraging Behavior: How to Find, Select, and Process Prey

The earliest studies of foraging in marine mammals focused on the stomach contents of dead animals in order to define what kinds of organisms were in the DIET of marine mammals. The best that observers could do in early field studies of living marine mammals was to identify behavior associated with feeding, where feeding was linked to observation of prey at the surface or chases, and so on. However, these observations do not do justice to the complex process by which animals find, select, and handle their prey. Increased efforts in foraging theory to identify the kinds of decisions faced by a foraging individual have focused attention on a more detailed view of the stages of foraging, and new techniques such as tags that can record behavior (Johnson and Tyack, 2003) have improved our ability to collect the required data. This section discusses the various phases of foraging. Marine mammals that feed at depth face a separation between two critical resources, air at the surface and deep prey. This requires them to plan their dives to make the best use of the oxygen they need to forage.

Marine mammals use every sensory modality available to find and select their prey. The optimal senses for solving a particular foraging problem depend on the setting. For example, mammalian olfaction evolved to detect airborne odors and vision is an excellent distance sense in air but has a limited range underwater. Even though polar bears (*Ursus maritimus*) are classed as marine mammals, they often hunt their prey in air and may use vision and olfaction in air to search for their pinniped prey. Many seals and dolphins chase fish prey close enough to the surface to be able to use down-welling light to see their prey during daytime. Deep-diving seals such as elephant seals (*Mirounga* spp.) have eyes specially adapted to the wavelengths and low light levels of the deep sea. Many deep-sea organisms have light-producing organs, and marine mammals may use vision to find bioluminescent organisms in the dark.

Sound carries much better than light underwater, and some marine mammals have developed sophisticated adaptations to use sound for finding prey. Perhaps the best-known example is the sonar of odontocetes. Dolphins and most toothed whales can produce a directional beam of intense high-frequency pulses of sound and have an auditory system that is specialized for high frequencies. Most toothed whales echolocate by producing a click and then listening for echoes from surrounding targets. When they are in a search mode, they may produce a slow series of clicks, listening for echoes. As the whale approaches to within a few meters of the prey, it changes from slow clicks to a rapid series of clicks with interclick intervals of about 10 ms. Beaked whales, sperm whales (*Physeter macrocephalus*), and narwhals (*Monodon monoceros*) all show a pattern similar to that of foraging bats, where they search for prey with regular slow clicks and then accelerate clicks into a buzz as they capture prey. Many species show a sudden increase in the rate of change of acceleration at the end of the buzz as they maneuver to capture the prey. Together, these results suggest that deep-diving odontocetes use slow series of clicks to monitor several targets at different ranges at the same time. When the whale has selected a prey item, it accelerates the clicks to get more rapid updates on the location of the prey as it maneuvers to capture it.

Although deep-diving toothed whales use echolocation to find prey in the dark depths, dolphins feeding in shallow waters use a combination of senses and cues to detect and select prey. When wild bottlenose dolphins (*Tursiops truncatus*) from inshore waters near Sarasota, Florida, are feeding, they produce echolocation clicks at 0.39 click trains/min while foraging and a rate of 0.10 click trains/min while not foraging. Dolphins appeared to rely more upon echolocation when they were feeding on fish hiding in seagrass. In contrast, when dolphins were feeding in clear water over sand, they seldom clicked and appeared to rely primarily on vision. Dolphins may also listen for the vocalizations of fish to detect or select prey, then use echolocation to pursue and capture them.

Dolphins and toothed whales are hunters that chase down individual prey items. Many species feed on highly mobile prey such as schooling fish. When a dolphin charges into a fish school, the fish usually disperse, and this can make it less efficient to find and chase down the remaining fish. Dolphins (Fig. 1) and killer whales (*Orcinus orca*) have been reported to coordinate their feeding so that some individuals keep the fish in a tight school as other individuals feed (Benoit-Bird and Au, 2003).

Baleen whales have evolved to capture entire patches of prey in one mouthful. Balaenid whales, such as right (*Eubalaena* spp.) and bowhead whales (*Balaena mysticetus*), are specialized to feed on calanoid crustaceans. When balaenid whales feed, they swim through the prey patch with an open mouth. Their baleen is very long and their head has such a large cross-sectional area, that they can catch their prey by engulfing them in the water that flows into the mouth and out through the baleen. The basic problem faced by a feeding balaenid whale is to find a dense enough patch of prey to pay for the time and additional expense of swimming in the open-mouth foraging mode. Feeding bowhead whales swim slowly, <1 m/s, but their open mouth is large enough that they can filter

Figure 1 *Dusky dolphins (*Lagenorhynchus obscurus*) exhibit coordinated feeding in Admiralty Bay, New Zealand. "Clean" headfirst re-entry leaps, shown here, are common during coordinated feeding; these leaps facilitate diving while allowing a dolphin to quickly catch a breath. The splash in the background is from an Australasian gannet (*Sula serrator*), which has just taken a plunge dive; gannets and other seabirds often feed in conjunction with dusky dolphins (Photo by Heidi Pearson).*

Copyright © 2017. Elsevier Science & Technology. All rights reserved.

3 m^3/s, allowing them to filter 2000 tonnes of water and prey per dive (Simon et al., 2009).

Balaenopterid whales, such as fin (*B. physalus*) or humpback whales (*Megaptera novaeangliae*), have evolved a feeding mode that allows them to capture prey that are faster and more evasive than calanoid crustaceans. Balaenopterids feed on schools of euphausiids or baitfish such as capelin, anchovy, sand lance, or even herring. Balaenopterids have accordion-like pleats in the lower jaw, which can expand rapidly. When a balaenopterid feeds, it lunges and opens its mouth, forcing tens of m^3 of prey and water into the mouth as the pleats expand. An adult fin whale can engulf 60-80 m^3, which is greater than the volume of its whole body (Goldbogen et al., 2007). The whale then quickly closes its mouth, trapping the prey. The pleats then slowly contract, forcing the water through the baleen and leaving the prey behind. Measurements of the time interval between lunges and the volume of water engulfed suggest that balaenopterids filter about 2 m^3/s, which is lower than the balaenid rate. However, if the whale can target a dense patch, the amount of prey may be higher. As with toothed whales, when balaenopterids such as humpback whales feed on the most mobile schooling prey, such as herring, they may feed in coordinated groups. Perhaps the most striking reports concern a group of half a dozen or more female humpback whales who associated together each summer for several years in Southeast Alaska. Each individual played a specific role in prey capture, and their movements appeared to be coordinated with a regular series of vocalizations (D'Vincent et al., 1985).

Marine mammals have evolved several different ways to feed on benthic prey that hide submerged in the sediment on the seafloor. Some bottlenose dolphins have been observed to echolocate on small sand dabs buried in the sand. The mustache of the walrus (*Odobenus rosmarus*) is exquisitely sensitive to touch, and walruses use the vibrissae in their mustache to detect and identify their favored prey within the sediment. Gray whales (*Eschrichtius robustus*) feed on benthic organisms by rolling more than 45 degrees (usually to the right side), sucking mud and prey into the right side of their mouth and then straining out the prey with their baleen.

Most marine mammals just swallow their prey whole, but some species face problems in handling their prey. The most impressive prey handling among marine mammals involves the sea otter (*Enhydra lutris*), which feeds on shellfish such as abalone (*Haliotis* spp.) and sea urchins. Because these prey are too large or too strong for the otter to break the shell by biting it, most otters use a stone as a tool. The sea otter rests the stone on its stomach, and smashes the shell open on the stone.

II. Avoiding Predators and Defense From Predators

Many marine mammals are top predators and historically may not have faced heavy predation pressure. The primary predators for pelagic marine mammals over evolutionary time are the killer whale and sharks. However, in the last few centuries, humans have been extremely effective predators of marine mammals, driving some species such as the Steller's sea cow (*Hydrodamalis gigas*) to extinction. Seals on ice face the risk of predation from polar bears, and seals hauled out on beaches, especially pups, are at risk from other pinnipeds and terrestrial predators such as foxes. Seals on land are less mobile than at sea and appear to be at a higher risk of predation, for they will usually respond to the approach of a terrestrial predator by entering the water.

The first step in lowering the risk of predation is to avoid detection. Most seals and small cetaceans have little chance to defend themselves from killer whales, so they must emphasize strategies to avoid detection by these predators. Female Galapagos fur seals (*Arctocephalus galapagoensis*) are less likely to make their normal foraging trips when the moon is full, apparently to reduce the risk that a predator will see them in the moonlight. Dusky dolphins (*Lagenorhynchus obscurus*) mill in the surf zone as killer whales pass by offshore. They will even hide in tidal lagoons and, at times, become stranded in these lagoons until the next tide. Baleen whales also have strategies to avoid detection by killer whales. For example, gray whales that were exposed to experimental playback of the sounds of killer whales fled into shallow water. The surf zone and kelp beds may be particularly good places to hide from an echolocating predator because they absorb and reflect sound, making echolocation more difficult. Killer whales appear to have evolved countermeasures to these predator-avoidance strategies. There are two sympatric populations of killer whales in the inshore waters of the Pacific Northwest. One population, called residents, feeds primarily on fish; the other population, called transients, feeds primarily on marine mammals. When residents feed on salmon, a fish with poor hearing, the killer whales make regular series of loud clicks. When transients feed on acoustically sensitive marine mammals, they have a much stealthier pattern of echolocation (Barrett-Lennard et al., 1996).

Killer whales are more effective when they are in groups hunting for small marine mammals such as seals and porpoises, and they usually hunt in groups for these marine mammal prey. Many cetaceans fall silent when a killer whale is detected nearby. After they have been detected, most small odontocetes appear to rely on speed to escape killer whales, whereas some pinnipeds may hide from them, either on the land or on the seafloor. The catch rate is highest for groups of three killer whales, and the energetic efficiency of foraging is lower for larger groups. Prey appear to be shared among the group, so the larger the group, the smaller the amount of prey for each individual. Killer whales also hunt large whales in groups, often attempting to isolate an individual to attack it. Baleen and sperm whales use their flukes as a weapon during such an attack, lashing them sideways through the water.

Early whalers had a predator's view of their marine mammal prey, and their observations make up an unusual body of data on predator defense in some species. If a predator attacks a group of sperm whales, calves or wounded animals in the group will be surrounded by the rest of the adults. Most adults will face in toward the animal needing protection and will lash their tails facing outward. Pilot whales also rely upon social defense against killer whales. When they hear killer whale sounds, pilot whales form a more cohesive group and approach the source of the sound (Curé et al., 2012). This appears to be a mobbing reaction, and pilot whales have actually been sighted chasing killer whale groups.

Cetaceans are also subject to parasitism from animals that bite tissue without causing serious injury. In the tropics, many dolphins are subject to attack from the cookie cutter shark (*Isistius brasiliensis*), which takes bites of skin and blubber about 3–5 cm in diameter. Right whales (*E. australis*) in coastal bays in Argentina are subject to attack from seagulls, which peck chunks of skin and blubber from the back of a whale floating at the surface. Although this can evoke a strong behavioral reaction from the whale, right whales do not seem to have an effective defense from this attack, which may be made worse by the growth of seagull populations in areas with human settlements.

Evidence in several cetacean species shows that when an animal has been injured, other members of the group may support them for

Copyright © 2017. Elsevier Science & Technology. All rights reserved.

hours or days. Because marine mammals must breathe air, if they cannot surface on their own, they are at great risk of drowning. This caregiving behavior may cost the caregivers but at potentially life-saving benefit to the incapacitated member of the group.

III. Migration and Orientation

Most marine mammals are excellent swimmers, and many species make annual migrations of thousands of kilometers. Most baleen whales have an annual migratory cycle that affects many aspects of their life. These whales are adapted to take advantage of a burst of productivity in polar waters during the summer. Baleen whales store enough energy reserves during their intensive summer feeding season to last for most of the year, and this annual feast/fast cycle helps to select for large size. A humpback whale that is born in the winter in a tropical breeding ground near 20 degrees of latitude will typically migrate in the spring to summer feeding grounds in polar waters near 40–60 degrees of latitude. Humpbacks have traditional feeding grounds and an individual will often visit specific banks or inshore feeding areas of scales of tens of kilometers. Dolphins on both coasts of the United States also show annual migrations of 1000 km or more. Off the east coast of the United States, harbor porpoises (*Phocoena phocoena*) and bottlenose dolphins tend to move north in summer and south in winter. It is not known whether the colder temperatures in the north during winter are more important for this seasonal migration than are seasonal changes in prey distribution. Some pinnipeds also have annual migrations of thousands of kilometers. For example, northern elephant seals (*M. angustirostris*) that breed and calve near San Francisco may migrate as far as the Aleutian Islands to feed. Very little is known about how marine mammals orient and navigate during migration, and even less is known about how they find oceanographic features such as fronts, which can be important cues for good places to forage.

Other species have more limited annual home ranges. Sea otters show strong fidelity to their home ranges, which are limited to <20 km of coastline. When 139 sea otters were flown 200 km to an offshore island as part of a reintroduction program, most of the otters left and at least 31 managed to return to the area where they had been captured. Bottlenose dolphins in the inshore waters of Sarasota, Florida, tend to be sighted within a home range of 125 km^2. "Resident" killer whales in the inshore waters of Puget Sound have seasonal ranges limited to an area several tens of kilometers by about 100 km. Even nonmigratory species can be highly mobile. For example, resident killer whales will often swim 100 km or more in a day. Bottlenose dolphins and sea otters may suddenly leave their home ranges and swim 100 km away from the normal range.

IV. Competition and Agonistic Behavior

When animals are competing for the same resource, they may fight for access. Among animals that exploit a specific substrate, this competition may be for territory. Territorial defense has been well described for many pinnipeds during the breeding season. Female pinnipeds haul out onto beaches or ice to give birth, and some species mate on land. This concentration of females creates a valuable resource for males. Males in many species will defend an area of beach from other males and may attempt to monopolize opportunities to mate with females there. For animals that live in the open ocean, resources are not likely to be as tied to a particular location. Animals in this setting are more likely to defend a particular resource at one time than to defend a patch of real estate. For example, a male humpback whale will not defend a specific location during the breeding season, but a male escorting a female will fight other males to limit their access to the female.

This pattern of males competing for access to females, either by defending a group of females or a territory (Fig. 2), is common among mammals and leads to behavioral and morphological adaptations. Males in these species are often larger than females. Some of the most extreme sexual dimorphism among mammals occurs in marine mammals where a successful male may mate with many females in one breeding season. For example, male elephant seals may be ten times heavier than females (McCann et al., 1989), and mature male sperm whales may be up to three times heavier than females (Connor et al., 1998). Males may have larger weapons such as teeth or tusks than females. This is particularly striking in beaked whales. In most beaked whale species, the teeth may not erupt at all in females, whereas one or two pairs of teeth erupt in the lower jaw of males at about the time of sexual maturity. Males have scarring patterns that suggest these "battle teeth" are used in fights. Males may also have protected areas of toughened skin. Male elephant seals, for example, often strike one another on the chest, and this area has thickened and hardened skin.

Fighting often involves a gradually escalating series of threats and responses. Overstrom (1983) presented data suggesting this kind of escalated display for bottlenose dolphins in captivity. The earliest stages of a threat may involve one dolphin directing pulsed sounds toward another. Many of the agonistic visual displays used by bottlenose dolphins are related to movements used to inflict injury. For example, the open-mouth display, which can be added to the pulsed sounds, looks like the first step in preparing to bite.

Some animals live in situations where they interact repeatedly with the same individuals. In this setting, animals may develop a predictable hierarchy of who wins and loses in agonistic interactions. Male elephant seals establish a dominance hierarchy on the breeding beaches. When males are competing using territory or dominance for access to females, they often sort out their competitive relations before the peak of the mating season. Dominance relations have also been studied in captive bottlenose dolphins. The most obvious competitive behaviors are violent fights in

Figure 2 *A male sea otter (*Enhydra lutris*) patrols his territory in Prince William Sound, Alaska. The function of patrolling is to search for estrous (receptive) females and intruding males. Females (which are 35% smaller than males) may be attracted to resources contained within the territory such as prey, protection from wind and waves, and resting areas (Photo by Heidi Pearson).*

Copyright © 2017. Elsevier Science & Technology. All rights reserved.

which each opponent responds to aggression with an aggressive response. This is not as useful for determining winners or losers as observation of more subtle submissive behaviors. Systematic observations of winners and losers in dyadic agonistic interactions reveal that adult males are dominant over adult females. The rate of agonistic interactions is higher in males than in females. The low rate of female agonism means that dominance is rarely contested among females, and female dominance can be stable over years. Male dominance relations were characterized by periods of relatively low agonism interspersed with periods of high rates of agonism when one male challenged the other, which can lead to reversals of dominance status. Little is known about dominance relations among wild cetaceans, but because individuals in many species interact repeatedly with the same conspecifics and can recognize different individuals, dominance relations are likely to be important. The threats of elephant seal males do not appear to incorporate acoustic features that directly predict fighting ability; rather each seal has an individually distinctive threat. When a seal hears the threat of a familiar competitor, it recognizes that individual and its response is based upon memory of their previous interactions (Casey et al., 2015).

V. Courtship and Sexual Behavior

Charles Darwin distinguished between features selected to improve chances of mating and features selected for survival. Selection that acts on an animal's mating success was defined as sexual selection to discriminate it from natural selection. Darwin defined two kinds of sexual selection: intersexual and intrasexual. Intersexual selection occurs when a member of one sex selects a member of the other sex for mating; intrasexual selection involves competition between conspecifics of the same sex for mating with a member of the opposite sex. More recently a third mode of sexual selection has been added, where a male may attempt to limit the choice of a female by coercing her to mate with him and not to mate with other males.

Differences between male and female mammals alter the costs and benefits of different elements of reproduction. Female mammals all gestate the young internally and are specialized to provide nutrition to the young after birth. In marine mammals, the female provides most of the parental care. Reproduction in most female mammals is limited by the amount of energy and nutrition they can acquire for pregnancy and lactation. Male mammals usually provide much less parental care to their young. This means that reproduction in most male mammals is limited by the number of females with which they can mate. This situation often leads to a polygynous mating system in which there is high variability in the mating success of different males, with some males mating with many different females and other males mating with none. Males in polygynous species often fight other males for access to females. This often leads to the evolution of weapons and larger body sizes in males than females; the intensity of polygyny is sometimes estimated by assessing the difference in size of males versus females. As discussed earlier, some of the most extreme cases of sexual dimorphism in mammals occur in marine mammals.

Most traditional discussions of mating systems emphasize male strategies. For example, polygyny occurs where one male mates with more than one female; the number of males with which a female mates is not included in the definition. While the variance of reproductive success is higher in males than in females for most marine mammal species, female reproductive strategies influence male strategies and impact other areas of social behavior. Areas in which female reproductive strategies vary include the following:

How seasonal and synchronized is estrus among females?
Do females have one (monoestrous) or more (polyestrous) estrous cycles per year?
Do females ovulate spontaneously or do they require the presence of a male to ovulate?
How many males are available during estrus?
Can the female select a mate?
If a female mates with more than one male, can she influence which male fertilizes the egg?

There are different patterns for the reproductive strategies of males and females in different polygynous mating systems. This article describes five different categories of male strategy. The *resource defense strategy* is adopted by males who defend a resource used by females around the time of mating. In this case, females do not select a mate but rather select an area for breeding and mate with the male defending this area. A *lekking strategy* occurs when males aggregate in an area with no resources needed by the female and produce displays to attract the female. In leks, males provide no parental care and females select a male for mating. The *female defense strategy* is used by males who stay with a female and prevent other males from mating with her while she is receptive. The *sequential defense strategy* differs from the female defense strategy in that a male will defend a female through mating, but then leave in search of other mating opportunities. The strategy called by the name "scramble competition" occurs when a male searches for a receptive female, mates with her, and then moves on to search for another female without preventing access for other males. These last three male strategies depend in part on whether the female is mono- or polyestrous and on the degree of synchronization of different females. The last three models lie on a continuum of male strategies between pure guarding and pure roving. Whitehead (1990) suggests that males should rove between groups of females if the duration of estrus is greater than the time it takes males to swim from group to group. At any one time, a male's decision to leave or stay with a group probably includes other factors, such as his assessment of what other males are doing.

Some of these male strategies preempt the ability of a female to select a male for mating. In the resource defense model, the female does not select a particular male, but rather will select a particular place with the resource she needs. She will then be most likely to mate with the male who happens to be defending this location. When a female can and does choose a male for mating, she may select a mate based on several different criteria. A female may select a male for inherent qualities based on indicators such as size, age, or an advertisement display. She may assess competition between males and select one based on this performance. In some species, males may compete for access to a particular location, and a female can select a good competitor by mating with a male in such a preferred spot. In some species, a female may mate with several males and allow competition between their sperm to determine which male fertilizes the egg. The males in this system would be likely to devote more resources to sperm production, sperm swimming speed, and so on than species that compete by fighting. Evidence shows that sperm competition may play a role in some cetaceans. Odontocete cetaceans have larger ratios of testis to body weight than most mammals. This contrast is also seen among mysticetes. Balaenid whales form mating groups with multiple males, but there is little sign of fighting between the males. Male right whales have

Copyright © 2017. Elsevier Science & Technology. All rights reserved.

testes weighing more than 900 kg; their testes weigh more than six times what would be predicted for a typical mammal of their body size. In contrast, humpback whale males, which fight for access to females, have testes weighing less than 2 kg.

Marine mammals are highly mobile, and in the open ocean it seems unlikely that males could defend a resource in a way that would preempt the ability of a female to use the resource yet mate with another male. Resource defense is much easier to envisage on land. Female pinnipeds have specific requirements for a place to give birth, and they often return to traditional areas. The selection by females of specific sites for mating and giving birth creates an opportunity for males to defend these sites in order to increase their chances of mating with the females who are selecting the site. In most otariid seals, males appear to employ resource defense strategies for mating. In many of these species, males will arrive before the females and will fight to establish territories that they defend from other males. In some phocid species that mate at sea, males may establish and defend territories just off the beach where females give birth. Genetic analyses of paternity, however, show that the fathers of some pups are not among the territorial males. This suggests that some males have alternate mating strategies.

In some marine mammal species, males adopt a strategy of attempting to preempt female choice by guarding a receptive female and preventing her from mating with other males. Northern elephant seal males arrive at breeding beaches before females and compete for dominance status and for position on the breeding beach. A dominant male can guard a group of females and prevent access for other males. If an alpha male can maintain his status, he can prevent access to a group of females for the entire breeding season. This pattern of guarding a group of females is less likely for cetaceans, which are highly mobile. Most male cetaceans would take a shorter time to swim between groups than the duration of female estrus, thus favoring a roving strategy. There is some evidence for sequential female defense in bottlenose dolphins. Groups of two or three adult male bottlenose dolphins may form consortships with an adult female (Connor et al., 2000). A coalition of males may start such a consortship by chasing and herding a female away from the group in which they initially find her. Some of these consortships appear to be attempts by the males to limit choice of mate by the female, who may try to escape from the males. Males in these alliances may form consortships with several different females during a breeding season.

Many pinnipeds and some baleen whales produce reproductive advertisement displays that may play a role in mediating competitive interactions between males and may also be used for female choice of a mate. Male humpback whales sing long complex songs during the winter breeding season. Singing males are usually alone and they usually stop singing when joined by another whale. Aggressive behavior is often seen when a male joins a singer; when a female joins, apparent sexual behavior has been observed (Smith et al., 2008). Male humpbacks do not seem to be able to defend any resource needed by females on the breeding grounds, so this mating system has been described as a kind of floating lek. Vocal reproductive advertisement displays have also been reported for bowhead whales and many species of seal, including polar ice-breeding seals and harbor seals (*Phoca vitulina*). Most of the phocid seals known to produce songs mate at sea. These seals breed in conditions that foster the development of leks. Females gather to breed on isolated sites, but they mate after they have weaned their pups, so there are few resources males could defend. Females are so mobile that it would be difficult for males to prevent them from gaining access to other males. The females are already concentrated in hotspots around the places where they give birth. This creates an ideal setting for males to cluster near the females, producing advertisement displays to attract females for mating. Some of the songs of whales, of ice-loving seals, and the bell-like sounds of the walrus stand as testimony to the power of sexual selection to fashion complex and fascinating advertisement signals.

VI. Parental Behavior

All mammals have some parental care when the female lactates and suckles the young, but there is enormous variability in the duration of parental care among marine mammals. Some phocid seals give birth to their young on unstable ice floes, where they cannot count on a stable refuge for the young. The hooded seal (*Cystophora cristata*) has responded to this situation by an intense 4-day period of lactation when the young pup doubles in weight. Female phocid seals generally stay with their young pup and fast while suckling, but otariid females leave their young in order to feed at sea and then they return to suckle the pup. This pattern leads to a large difference in duration of lactation, from 4 days to 2 months in phocids and from 4 months to 2 years in otariids. Phocoenid porpoises and some baleen whale species also have a strong annual breeding cycle. Some baleen whales, such as the blue whale (*Balaenoptera musculus*), wean their young after about 7 months so that the young can start taking solid food during the summer feeding season. All porpoises and baleen whales wean the young within a year. Toothed whales other than the porpoises have very prolonged periods of parental care when the young are dependent. Bottlenose dolphins only 3 m or so in length often suckle the young for 3–5 years, which is remarkably long considering that the 30-m blue whale can wean the young in 7 months.

The longest periods of parental care known among marine mammals involve sperm whales and short-finned pilot whales (*Globicephala macrorhynchus*). In both species, mothers appear to suckle some calves for up to 13–15 years. The young may start to take some solid food by the first few years of life, but this prolonged suckling indicates a remarkably long period of dependency for the young. Adult female pilot whales typically start having young by 8–10 years, but by the time they are near 30–40, many cease to reproduce (Marsh and Kasuya, 1984). The ovaries become nonfunctional in these nonreproductive females, showing changes similar to those of human females after menopause. Female pilot whales may live into their 50s. If pilot whale females have a life expectancy 15–20 years after becoming nonreproductive, this suggests that females may switch their reproductive effort from having new offspring to parental care of their existing young. The duration of this period suggests either that 15–20 years of parental care are required for the young to succeed or that these older females are caring for other kin, perhaps in a grandparental role.

VII. Social Behavior and Social Relationships

Not only do marine mammals show a broad range in the duration of the maternal bond but also there is great diversity in the duration of social bonds in general, and especially in the importance of individual-specific social relationships. Resident killer whales have the most stable social groups known among mammals: no dispersal of either sex has been described. The only way group composition changes among the resident killer whales of the Pacific Northwest is for an animal to die or for a new animal to be born. The best-known vocalizations from killer whales are group-distinctive repertoires of stereotyped pulsed calls. In contrast, bottlenose

Copyright © 2017. Elsevier Science & Technology. All rights reserved.

dolphins have very fluid social groups. In their fission–fusion society, group composition changes on a minute-by-minute basis. However, some individuals may have strong social bonds and be sighted together for years at a time. As was just discussed in the section on parental care, bottlenose dolphin calves suckle for 3–5 years. The adult male bottlenose dolphins that form coalitions with one to two other unrelated males tend to be sighted together 70%–100% of the time, and alliances may last for over a decade. It is thought that males form alliances to improve their chances of mating with females, but lone males are also successful breeders. Males within a coalition often have highly coordinated displays, both when feeding and when escorting a female. Each bottlenose dolphin produces an individually distinctive whistle vocalization called a signature whistle, which is probably used for individual recognition (Janik and Sayigh, 2013).

In sperm whales, males have different life history patterns than females. Calves are born into matrilineal groups of females and young that appear to be the basic social unit of sperm whales, with a primary function of vigilance against predators and social defense of calves (Whitehead, 2003). Each matrilineal unit numbers about 10–12 animals, but often two units associate for days at a time. Males may leave their natal groups when 5–10 years of age, and they then will join all-male groups. As males grow, they move to higher latitudes and associate in smaller groups of larger males. As the males approach social and sexual maturity at 20–25 years of age, they are increasingly likely to associate temporarily with female groups during the breeding season, when they may mate with females. The social relationships of males thus change over their lifetime, and adult males appear to have only temporary associations. Young females may stay with their natal groups or may leave, but once they reach sexual maturity at 8–10 years of age, they will tend to associate with the same adult females for decades at a time. Because the matrilineal groups often join with other groups but segregate into the original groups, the females must recognize group members over periods of decades. Sperm whales make rhythmic patterns of sounds called codas. There are individually distinctive features of codas, but there are also codas that are shared among groups over broad geographic regions. In the South Pacific, there are five vocal clans consisting of thousands of whales that range over thousands of kilometers. When two units join to form a group, they preferentially join with members of the same vocal clan (Rendell and Whitehead, 2003).

Baleen whales may feed in groups as do sperm whales, but female baleen whales appear to differ from sperm whales in the importance of group care of young. On the feeding grounds, baleen whales of all sexes are often seen in groups of varying sizes. For humpback whales, the size of the feeding group correlates with the horizontal extent of the prey patch. However, during the breeding season, when a female humpback has a calf, she is extremely unlikely to associate with another adult female. When one or more adults escort a female during the breeding season, the escorts are usually males. There is much less evidence for long-term social bonds in baleen whales than among most toothed whales. Odontocetes with little evidence for stable bonds include species such as the harbor porpoise and delphinids of the genus *Cephalorhynchus*, which also appear to have fluid groupings with few social bonds more stable than the mother-calf bond, which lasts less than 1 year in the porpoise. However, future research may find social bonds that have not yet been described.

There appears to be a correlation between the social relations of marine mammals and their communication patterns (Tyack, 1986). Baleen whales and pinnipeds with large apparently anonymous breeding aggregations use reproductive advertisement displays to mediate male–male and male–female interactions on the breeding grounds. Killer whales with highly stable groups produce group-specific repertoires of stereotyped calls. Seals and dolphins with strong individual-specific bonds use a variety of different vocalizations for individual recognition, but no such recognition signals are known for porpoises or *Cephalorhynchus*. Sperm whales appear to use deceptively simple clicks to produce a diverse set of signals that mediate interactions forming their diverse social groupings.

VIII. Conclusions

Marine mammals face the same basic problems that have been identified by behavioral ecologists for all animals. However, marine mammals live in an environment that differs in many important ways from the terrestrial environment. Studies since the 1980s have provided ever-growing opportunities for fascinating comparisons between marine mammals and their terrestrial relatives and between the diverse taxa that live in the sea.

See Also the Following Articles

Communication ■ Feeding Strategies and Tactics ■ Group Behavior ■ Migration and Movement ■ Predator–Prey Relationships ■ Sexual Dimorphism ■ Territorial Behavior

References

Barrett-Lennard, L.G., Ford, J.K.B., and Heise, K.A. (1996). The mixed blessing of echolocation: Differences in sonar use by fish-eating and mammal-eating killer whales. *Anim. Behav.* **51**, 553–565.

Benoit-Bird, K.J., and Au, W.W.L. (2003). Prey dynamics affect foraging by a pelagic predator (*Stenella longirostris*) over a range of spatial and temporal scales. *Behav. Ecol. Sociobiol.* **53**, 364–373.

Casey, C., Charrier, I., Mathevon, N., and Reichmuth, C. (2015). Rival assessment among northern elephant seals: evidence of associative learning during male–male contests. *R. Soc. Open Sci.* **2**, 150228. doi:10.1098/rsos.150228.

Connor, R.C., Mann, J., Tyack, P.L., and Whitehead, H. (1998). Social evolution in toothed whales. *Trend. Ecol. Evol.* **13**, 228–232.

Connor, R.C., Wells, R., Mann, J., and Read, A. (2000). The bottlenose dolphin: Social relationships in a fission–fusion society. In “Cetacean Societies: Field Studies of Whales and Dolphins”, (J. Mann, R. Connor, P. Tyack, and H. Whitehead, Eds), pp. 91–126. University of Chicago Press, Chicago.

Curé, C., Antunes, R., Samarra, F., Alves, A.C., Visser, F., Kvadsheim, P.H., and Miller, P.J.O. (2012). Pilot whales attracted to killer whale sounds: acoustically-mediated interspecific interactions in cetaceans. *PLoS One* **7**, e52201. doi:10.1371/journal.pone.0052201.

D’Vincent, C.G., Nilson, R.M., and Hanna, R.E. (1985). Vocalization and coordinated feeding behavior of the humpback whale in southeastern Alaska. *Sci. Rep. Whales Res. Inst., Tokyo* **36**, 41–48.

Goldbogen, J.A., Pyenson, N.D., and Shadwick, R.E. (2007). Big gulps require high drag for fin whale lunge feeding. *Mar. Ecol. Prog. Ser.* **349**, 289–301.

Janik, V.M., and Sayigh, L.S. (2013). Communication in bottlenose dolphins: 50 years of signature whistle research. *J. Comp. Physiol. A* **199**, 479–489.

Johnson, M., and Tyack, P.L. (2003). A digital acoustic recording tag for measuring the response of wild marine mammals to sound. *IEEE J. Oceanic Eng.* **28**, 3–12.

Marsh, H., and Kasuya, T. (1984). Changes in the ovaries of the shortfinned pilot whale, *Globicephala macrorhynchus*, with age and reproductive activity. In “Reports of the International Whaling Commission Special Issue 6: Reproduction of Whales, Dolphins and Porpoises”, (W.F. Perrin, R.L.J. Brownell, and D.P. DeMaster, Eds),

Copyright © 2017. Elsevier Science & Technology. All rights reserved.

Issue 6: Reproduction of Whales, Dolphins and Porpoises, pp. 311–335. International Whaling Commission, Cambridge.

McCann, T.S., Fedak, M.A., and Harwood, J. (1989). Parental investment in southern elephant seals. *Mirounga leonina. Behav. Ecol. Sociobiol.* **25**, 81–87.

Overstrom, N.A. (1983). Association between burst-pulse sounds and aggressive behavior in captive Atlantic bottlenosed dolphins (*Tursiops truncatus*). *Zoo. Biol.* **2**, 93–103.

Rendell, L.E., and Whitehead, H. (2003). Vocal clans in sperm whales (*Physeter macrocephalus*). *Proc. R. Soc. London B* **270**, 225–231.

Simon, M., Johnson, M., Tyack, P., and Madsen, P.T. (2009). Behaviour and kinematics of continuous ram filtration in bowhead whales (*Balaena mysticetus*). *Proc. R. Soc. B* **276**, 3819–3828.

Smith, J.N., Goldizen, A.W., Dunlop, R.A., and Noad, M.J. (2008). Songs of male humpback whales, *Megaptera novaeangliae*, are involved in intersexual interactions. *Anim. Behav.* **76**, 467–477.

Tyack, P.L. (1986). Population biology, social behavior and communication in whales and dolphins. *Trends Ecol. Evol.* **1**, 144–150.

Whitehead, H. (1990). Rules for roving males. *J. Theor. Biol.* **145**, 355–368.

Whitehead, H. (2003). *Sperm Whales: Social Evolution in the Ocean.* University of Chicago Press, Chicago.

BELUGA WHALE

Delphinapterus leucas

Gregory M. O'Corry-Crowe

The beluga whale is a member of the Monodontidae, an odontocete cetacean family in the order Cetartiodactyla. Its name, a derivation of the Russian "beloye," meaning "white," captures the species most distinctive feature, the pure white color of adults (Fig. 1). This whale is often simply referred to as the white whale in many countries, as well as several other aboriginal names across the north including Sisuaq by the Inupiat and Kooyedyee by the Tlingit. The scientific name *Delphinapterus leucas* means "the white dolphin without a wing," which refers to its lack of a dorsal fin.

I. Characteristics and Taxonomy

The beluga whale is one of two extant monodontid whales; the other is the narwhal, *Monodon monoceros*. The earliest fossil record of the monodontids is of an extinct beluga *Denebola brachycephala* from late Miocene deposits in Baja California, Mexico, indicating that this family once occupied temperate ecozones. Recent phylogenetic studies contend that the Monodontidae emerged some 10.4–14.5 million years ago (Hassanin et al., 2012).

The beluga whale is a medium-sized toothed whale, 3.5–5.5 m in length and weighing up to 1500 kg. Males are up to 25% longer than females and have a more robust build. This species lacks a dorsal fin and is unusual among cetaceans in having unfused cervical vertebrae allowing lateral flexibility of the head and neck. They possess a maximum of 40 homodont peg-like teeth, which become worn with age. Recent studies have found that beluga whales live much longer than previously thought. Levels of the radioisotope ^{14}C rose sharply in the marine environment in the late 1950s because of nuclear bomb testing, and researchers were able to detect this increase in growth layers in beluga teeth. Using this increase as a reference point they determined that beluga whales lay down only one growth layer group a year, rather than two (Stewart et al., 2006). As well as doubling the maximum-recorded age from around 40 to 80 years, this discovery has increased the age of first reproduction and necessitated a revision of other life history parameters. Neonates are about 1.6 m in length and are born a creamy-gray color that quickly turns to a dark brown or blue-gray. They become progressively lighter as they grow, changing to gray, light gray, and finally becoming the distinctive pure white by about age 14 in females and 18 in males (Fig. 2) though some females retain shades of gray long into adulthood.

Belugas are adapted to life in cold waters. They possess a thick insulating layer of blubber up to 15-cm thick beneath their skin, and their head, tail, and flippers are relatively small. The absence of a dorsal fin is believed by some to be an adaptation to life in the ice or perhaps this feature was lost as a means to reduce heat loss. In its place, belugas possess a prominent dorsal ridge that is used to break through thin sea ice.

Figure 1 *Beluga whale,* Delphinpaterus leucas *(Illustrations by Uko Gorter).*

Copyright © 2017. Elsevier Science & Technology. All rights reserved.

Figure 2 *Tail waving behavior by a juvenile beluga whale in a summering group of whales congregating in shallow waters near the Arctic coast. Note the gray coloration of younger animals (Photo by Flip Nicklin/Minden Pictures).*

II. Distribution and Abundance

The beluga, or white whale, inhabits the cold waters of the Arctic and subarctic (Fig. 3). Variation in body size across the species range has been taken as evidence of separate populations. Their nonuniform pattern of distribution, and their predictable return to specific coastal areas, further suggests population structure, which has led to summering groups being managed as separate stocks. Resightings of marked or tagged individuals as well as differences in contaminant signatures and geographic variation in vocalizations add support to the independent identification of a number of these stocks.

A number of molecular genetic studies have confirmed that beluga whales tend to return to their natal areas year after year and that dispersal among different summering concentrations is limited, even in cases where there are few geographic barriers (e.g., O'Corry-Crowe et al., 1997) and where interbreeding takes place in their wintering range (Turgeon et al., 2012). These molecular findings reveal that knowledge of migration routes and destinations appears to be passed from mother to offspring, generation after generation.

III. Ecology

The evolutionary history and ecology of belugas are inextricably linked to the extreme seasonal contrasts of the north and the dynamic nature of sea ice. As well as adaptation to the cold, life in this region has necessitated the evolution of discrete calving and possibly mating seasons, annual migrations in some populations, and a unique feature distinguishing it from most other cetaceans, an annual molt. During the molt belugas rub on the bottom to facilitate the shedding and regeneration of the cork and upper layers of skin (Fig. 2).

When sea ice recedes in spring, most populations shift to their summering grounds, often forming dense concentrations at discrete coastal locations, including river estuaries, shallow inlets, and bays (Fig. 2). Several explanations have been proposed as to why belugas return to these traditional summering areas. In some regions, sheltered coastal waters are warmer, which may aid thermoregulation in neonates. The relatively warm, low-salinity coastal waters may also facilitate molting of dead skin and epidermal regrowth.

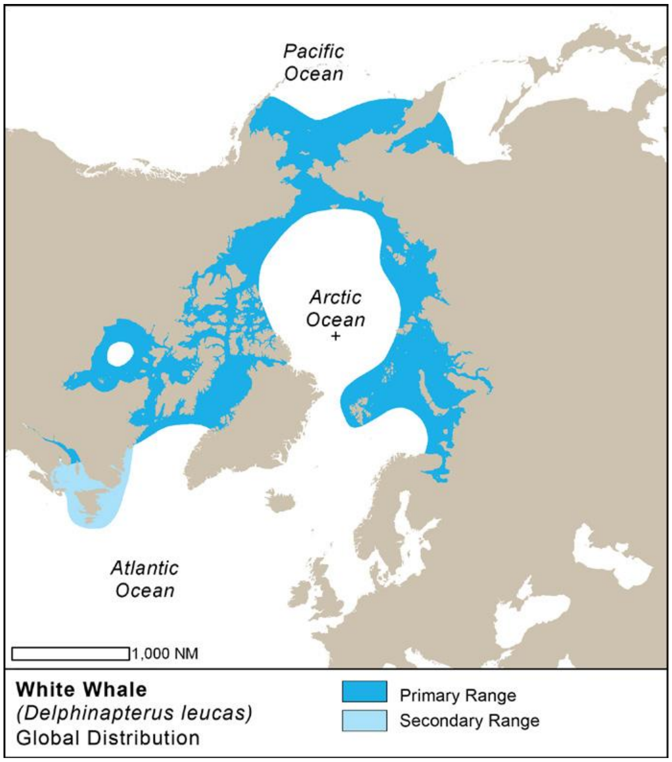

Figure 3 *Beluga whale distribution. Map drawn by Anders Skoglund, Norwegian Polar Institute.*

Belugas feed on a wide variety of invertebrate and vertebrate prey in benthic and pelagic environments, including crangonid shrimps and Arctic cod, *Boreogadus saida*. In some parts of their range belugas feed in nearshore waters on seasonally abundant anadromous and coastal fish such as salmon, *Oncorhynchus* spp.; herring, *Clupea harengus*; capelin, *Mallotus villosus*; smelt, *Osmerus mordax*; and saffron cod, *Eleginus gracilis* (Quakenbush et al., 2015). The relative importance of the above factors in determining coastal distribution patterns may vary among regions depending on environmental and biological characteristics. It is clear, however, that belugas exhibit some degree of dependence on specific coastal areas.

Resident populations in the subarctic display temporal shifts in the use of discrete habitats that have been linked to foraging, calving, and other behaviors including avoidance of anthropogenic disturbance (Lefebvre et al., 2012). In some Arctic populations, such as that in Svalbard, Norway, white whales are not migratory. They live in coastal waters year-round in this archipelago, concentrating a lot of their foraging time in front of tidal glacier fronts (Lydersen et al., 2001). In many areas of the Arctic, however, belugas leave coastal areas in summer to range widely offshore. Satellite tracking has recorded belugas moving up to 1100 km from shore and penetrating 700 km into dense polar ice where ice coverage exceeds 90% (Suydam et al., 2001; Fig. 4). How these animals find breathing holes in this environment is still a mystery. Analysis of dive profiles suggests that beluga whales may use sound at depth to find cracks in the ice ceiling overhead. Diving data also indicate that belugas are probably feeding on deep water benthic prey as well as ice-associated species closer to the surface, and may focus foraging efforts along prey-rich hydrographic fronts between different water masses (Martin et al., 1998; Hauser et al., 2015).

Copyright © 2017. Elsevier Science & Technology. All rights reserved.

Figure 4 *Beluga whales migrating through fractured sea-ice in the Beaufort Sea (Photo by Vicki Beaver/NOAA-NMFS).*

Little is known about the distribution, ecology, or behavior of beluga whales in winter. In most regions, belugas are believed to migrate in the direction of the advancing polar ice front, and recent telemetry studies suggest that different populations may have discrete wintering as well as summering ranges (Citta et al., 2016). However, in some areas belugas may remain behind this front and overwinter in polynyas and ice leads. In the eastern Canadian Arctic, some belugas overwinter in the North Water, a large polynya that remains open throughout the year in northern Baffin Bay, while in the White, Barents, Kara, and Laptev Seas in Russia belugas may occur year-round, remaining in polynyas in deep water during winter.

Killer whales (*Orcinus orca*), polar bears (*Ursus maritimus*), and humans prey on beluga whales. Belugas sometimes become entrapped in the ice, where large numbers may perish or be hunted intensively by humans.

IV. Behavior and Physiology

Belugas can alter the shape of their mouth and melon, enabling them to make an impressive array of facial expressions. The lateral flexibility of the head and neck further enhances visual signaling and enables beluga whales to maneuver in very shallow waters (1–3 m deep) in pursuit of prey, to evade predators, and to generally exploit a habitat rarely used by other cetaceans.

Belugas typically swim in a slow rolling pattern and are rarely given to aerial displays. In nearshore areas, such as Cunningham Inlet on Somerset Island in the Canadian High Arctic, concentrations of belugas sometimes engage in demonstrative behaviors, including spy hopping, tail waving, and tail slapping (Figs 2, 5). When annoyed they can perform quite dramatic jaw-clapping and bubble-blowing displays.

Satellite telemetry studies have confirmed that belugas are capable of covering thousands of kilometers in just a few months, in open water and heavy pack ice alike, while swimming at rates of 2.5–6 km/hr (Lydersen et al., 2001; Suydam et al., 2001). Sensors on satellite transmitters have also recorded belugas regularly diving to depths of 300–600 m, often to the sea floor, and utilizing different oceanographic regimes. In the deep waters beyond the continental shelf, dives can exceed 1000 m, and have durations up to 25 min (Martin et al., 1998).

Belugas are sometimes seen singly, but they usually occur in groups of 2–10 that may aggregate at times to form herds of several hundred to more than a thousand animals. Adult males often form separate pods of 6–20 individuals. Adult females form tight associations with newborns and sometimes a larger juvenile, presumably an older calf. These "triads" may join similar groupings to form large nursery groups. At certain times of the year, age and sex segregation may be more dramatic than at others with males migrating ahead of, or feeding apart from females, young, and immature. In general, group structure appears to be fluid, with individuals readily forming and breaking brief associations with other whales. Apart from cow–calf pairs there appear to be few stable associations, although a recent study found groups of related whales migrating together (Colbeck et al., 2013). However, considering the diverse vocal repertoire of beluga whales including individual signature calls, their wide array of facial expressions, and the variety of interactive behaviors they perform, as well as the numerous accounts of cooperative behavior, this species appears capable of forming complex societies where group members may not always be in close physical proximity to each other.

In areas of open water, beluga whales sometimes divide their days into regular feeding and resting bouts. Belugas appear to hunt individually, even when within a group, but cooperative hunting has also been observed. A typical hunting sequence begins with slow directed movement combined with passive acoustic localization (search mode) followed by short bursts of speed and rapid changes of direction using echolocation for orientation and capture of prey (hunt mode) (Bel'kovitch and Sh'ekotov, 1990).

The beluga possesses one of the most diverse vocal repertoires among marine mammals and has long been called the "sea canary" by mariners awed by the myriad of sounds they make, which can reverberate through the hulls of ships. Communicative and emotive calls are broadly divided into whistles and pulsed calls and are typically made at frequencies from 0.1 to 12 kHz. As many as 50 call types have been recognized; *groans*, *whistles*, *buzzes*, *trills*, and *roars* to name but a few. Belugas are capable of producing individually distinctive calls and can conduct individual exchanges of acoustic signals, or dialogues, over some distance (Bel'kovitch and Sh'ekotov, 1990).

The echolocation system of the beluga whale is well adapted to the icy waters of the Arctic. Its ability to project and receive signals off the surface and to detect targets in high levels of ambient noise and backscatter enables it to navigate through heavy pack ice, locate areas of ice-free water, and possibly even find air pockets under the ice. Geographic variation in aspects of the beluga's vocal repertoire and in echolocation activity have been documented and attributed to evolutionary divergence and habitat differences (i.e., water turbidity, predator presence/absence), respectively.

VI. Life History

Females become sexually mature at age 8–13; males are somewhat older. Gestation lasts 14–14.5 months with a single calf born in late spring-early summer. Mothers produce milk of high caloric content and nurse their young for up to 2 years. The entire reproductive interval averages 3 years. Little is known about the mating behavior or mating season of beluga whales. Mating is believed to occur primarily in late winter-early spring, a period when most belugas are still on their wintering grounds or on spring migration. Mating behavior, however, has also been observed at other times of the year and the question of whether this species has delayed implantation is unresolved.

VII. Interactions With Humans

Beluga whales have long been an important and reliable resource for many coastal peoples throughout the Arctic and subarctic because of their predictable migration routes and return to coastal areas in summer. However, because past commercial harvesting drove a

Copyright © 2017. Elsevier Science & Technology. All rights reserved.

number of populations to the point of economic extinction, current levels of subsistence take from these populations may not be sustainable and comanagement efforts have curtailed subsistence harvest in some populations to maximize recovery (e.g., Cook Inlet, Alaska). Increasing human activity in the beluga's environment brings with it the threat of habitat destruction, disturbance, and pollution. In areas where there are large commercial fishing operations, belugas, particularly neonates, may be incidentally caught in gill nets. In a number of regions of the Arctic, beluga whales exhibit strong avoidance reactions to ship traffic, whereas in some coastal locations they appear to have developed a high tolerance to boat traffic. The potential impacts of emerging whale watching activities (e.g., Churchill, Manitoba; St Lawrence, Quebec; White Sea, Russia) are not yet assessed. In some areas, belugas may also be victims of industrial pollution. A high incidence of various pathologies and immune system dysfunction found in beluga whales in the St Lawrence River, Canada were linked to high levels of heavy metals and organohalogens found in these whales. Recent decades have seen an improvement in water quality in the St Lawrence, though legacy effects of persistent lipophilic contaminants in the long-lived beluga whale will likely continue for some time (Martineau, 2012). Finally, there is concern over the possible downstream effects of hydroelectric dams on estuarine habitats and the environmental and health risks associated with oil and gas development and mining in the Arctic.

Beluga whales were one of the first cetaceans to be held in captivity when in 1861 a whale caught in the St Lawrence River went on display at Barnum's Museum in New York. Today, beluga whales are one of the more common and popular marine mammals in oceanaria across North America, Europe, and Asia including Japan. The majority of these animals were wild-caught, but successful breeding programs at a number of facilities are increasing the number of belugas born in captivity. Russia has become the sole regular supplier of wild-caught beluga whales to zoos and aquaria (Reeves et al., 2011).

The large sizes of some Arctic populations and flexible habitat requirements of beluga whales indicate that this species may not be as sensitive to the environmental consequences of current and future climate change as other arctic marine mammals. Nevertheless, a number of small, isolated populations at the southern margins of the species range are vulnerable to continued climate warming, where habitat loss in concert with the genetic and demographic effects of small population sizes may compromise individual fitness and population viability. Furthermore, it is difficult at present to predict the consequences for beluga whales of increased human activities across the Arctic associated with climate change.

Figure 5 *Aggregations of beluga whales interacting and rubbing on the substrate of a shallow Arctic estuary during the summer molt (Photo by Flip Nicklin/Minden Pictures).*

See Also the Following Articles

Arctic Marine Mammals ■ Climate Change

References

Bel'kovitch, V.M., and Sh'ekotov, M.N. (1990). "The Belukha Whale: Natural Behaviour and Bioacoustics." USSR Academy of Science, Moscow, Translated by Woods Hole Oceanographic Institution, 1993.

Citta, J.J., Richard, P., Lowry, L.F., O'Corry-Crowe, G., Marcoux, M., Suydam, R., Quakenbush, L.T., Hobbs, R.C., Litovka, D.I., Frost, K.J., Gray, T., Orr, J., Tinker, B., Aderman, H., and Drukenmiller, M.L. (2016). Satellite telemetry reveals population specific winter ranges of beluga whales in the Bering Sea. *Mar. Mamm. Sci.* doi:10.1111/mms.12357.

Colbeck, G.J., Duchesne, P., Postma, L.D., Lesage, V., Hammill, M.O., and Turgeon, J. (2013). Groups of related belugas (*Delphinapterus leucas*) travel together during their seasonal migrations in and around Hudson Bay. *Proc. R. Soc. B* **280**, 20122552.

Hassanin, A., Delsuc, F., Ropiquet, A., Hammer, C., Jansen van Vuuren, B., Matthee, C., Ruiz-Garcia, M., Catzeflis, F., Areskoug, V., and Nguyen, T.T. (2012). Pattern and timing of diversification of Cetartiodactyla (Mammalia, Laurasiatheria), as revealed by a comprehensive analysis of mitochondrial genomes. *C. R. Biol.* **335**, 32–50.

Hauser, D.D.W., Laidre, K.L., Parker-Stetter, S.L., Horne, J.K., Suydam, R.S., and Richard, P.R. (2015). Regional diving behavior of Pacific Arctic beluga whales *Delphinapaterus leucas* and possible associations with prey. *Mar. Ecol. Prog. Ser.* **541**, 245–264.

Lefebvre, S.L., Michaud, R., Lesage, V., and Berteaux, D. (2012). Identifying high residency areas of the threatened St. Lawrence beluga whale from fine-scale movements of individuals and coarse-scale movements of herds. *Mar. Ecol. Prog. Ser.* **450**, 243–257.

Lydersen, C., Martin, A.R., Kovacs, K.M., and Gjertz, I. (2001). Summer and autumn movements of white whales *Delphinapterus leucas* in Svalbard, Norway. *Mar. Ecol. Prog. Ser.* **219**, 265–274.

Martin, A.R., Smith, T.G., and Cox, O.P. (1998). Dive form and function in belugas *Delphinapterus leucas* of the eastern Canadian High Arctic. *Polar Biol.* **20**, 218–228.

Martineau, D. (2012). Contaminants and health of beluga whales of the Saint Lawrence Estuary. In "Ecosystem Health and Sustainable Agriculture 2", (L. Norrgren, and J. Levengood, Eds), pp. 139–148. The Baltic University Programme, 2295, Uppsala University.

O'Corry-Crowe, G.M., Suydam, R.S., Rosenberg, A., Frost, K.J., and Dizon, A.E. (1997). Phylogeography, population structure and dispersal patterns of the beluga whale *Delphinapterus leucas* in the western Nearctic revealed by mitochondrial DNA. *Mol. Ecol.* **6**, 955–970.

Quakenbush, L.T., Suydam, R.S., Bryan, A.L., Lowry, L.L., Frost, K.J., and Mahoney, B.A. (2015). Diet of beluga whales, *Delphinpaterus leucas*, in Alaska from stomach contents, March-November. *Mar. Fish. Rev.* **77**, 70–84.

Reeves, R.R., Brownell Jr., R.L., Burkanov, V., Kingsley, M.C.S., Lowry, L.F., and Taylor, B.L. (2011). Sustainability assessment of beluga (*Delphinapterus leucas*) live-capture removals in the Sakhalin–Amur region, Okhotsk Sea, Russia. Report of an independent scientific review panel *Occasional Paper of the Species Survival Commission, No. 44*. IUCN, Gland, Switzerland

Stewart, R.E.A., Campana, S.E., Jones, C.M., and Stewart, B.E. (2006). Bomb radiocarbon dating calibrates beluga (*Delphinapterus leucas*) age estimates. *Can. J. Zool.* **84**, 1840–1852.

Suydam, R.S., Lowry, L.F., Frost, K.J., O'Corry-Crowe, G.M., and Pikok Jr., D. (2001). Satellite tracking of eastern Chukchi Sea beluga whales in the Arctic Ocean. *Arctic* **54**, 237–243.

Turgeon, J., Duchesne, P., Colbeck, G.J., Postma, L.D., and Hammill, M.O. (2012). Spatiotemporal segregation among summer stocks of beluga (*Delphinpaterus leucas*) despite nuclear gene flow: implication for the endangered belugas in eastern Hudson Bay (Canada). *Conserv. Genet.* **13**, 419–433.

Copyright © 2017. Elsevier Science & Technology. All rights reserved.

BERARDIUS BEAKED WHALES

Berardius bairdii and B. arnuxii

J.G.M. Thewissen

The genus *Berardius* contains two species of beaked whales (family Ziphiidae, suborder Odontoceti) that have an antitropical distribution (Figs 1 and 2). Arnoux's beaked whale, *Berardius arnuxii* Duvernoy, 1851, was described based on a skull from New Zealand, and *B. bairdii* Stejneger, 1883, was based on a specimen from the Bering Sea. It has been proposed that Northern Hemisphere individuals actually pertain to two species, and mtDNA haplotypes indicate that one of these is more closely related to Southern Hemisphere *B. arnuxii*, than to the other *B. bairdii* (Morin et al., 2016). *Berardius* is the basal genus of ziphiids (Arnason and Gullberg, 1996; Dalebout et al., 2004).

I. Characteristics and Taxonomy

The skull of ziphiids is asymmetrical, with the nasal opening deviated to the left, and this asymmetry is less pronounced in *Berardius* than in the other genera. Also, unlike other genera, the bone with the greatest extent behind the nasal opening is the nasal bone.

Externally, the two species of *Berardius* are morphologically identical, although Arnoux's beaked whale (8.5–9.75 m) is smaller than Baird's beaked whale (9.1–11.1 m). Dalebout et al. (2004) established the validity of the two species based on mitochondrial DNA. *Berardius* is the least sexually dimorphic species in the Ziphiidae. The entire body is dark brown, but lighter on the ventral side with some irregular white patches. The back of the males (and some females) can be covered with linear scars probably caused by the teeth of conspecifics.

The body is slender with a small head, a low falcate dorsal fin, and small flippers that fit into depressions on the body. One pair of large throat grooves occur on the ventral side between the mandibles, and sometimes additional smaller pairs are also present. These allow the oral cavity to rapidly expand during suction feeding. The blowhole is crescent shaped with the concavity directed anteriorly. The melon is small and its front surface is almost vertical, sharply delineating a slender, projecting rostrum.

Like most ziphiids, there are very few teeth. A single pair of large teeth occurs at the anterior end of the lower jaw. These erupt around sexual maturity and abrade rapidly. The teeth are flat mediolaterally, triangular in lateral view, and less than 10 cm high. Histologically, enamel and a thin layer of dentin are present at eruption but these soon wear off. The pulp cavity of these teeth is filled with massive layers of dentin, and cementum layers are also thick (Kasuya, 2009). Annual layers in the cementum are used to determine the age of *Berardius*. Condylobasal lengths of skulls of adult Arnoux's beaked whales range 1174–1420 mm, and those of Baird's beaked whale are 1343–1524 mm. *Berardius* has between 47 and 52 vertebrae, the vertebral formula is C7, T9–11, L12–14, Cd17–22. The stomach of all beaked whales has many chambers; *Berardius'* stomach lacks an esophageal compartment, but the glandular stomach has up to nine segments.

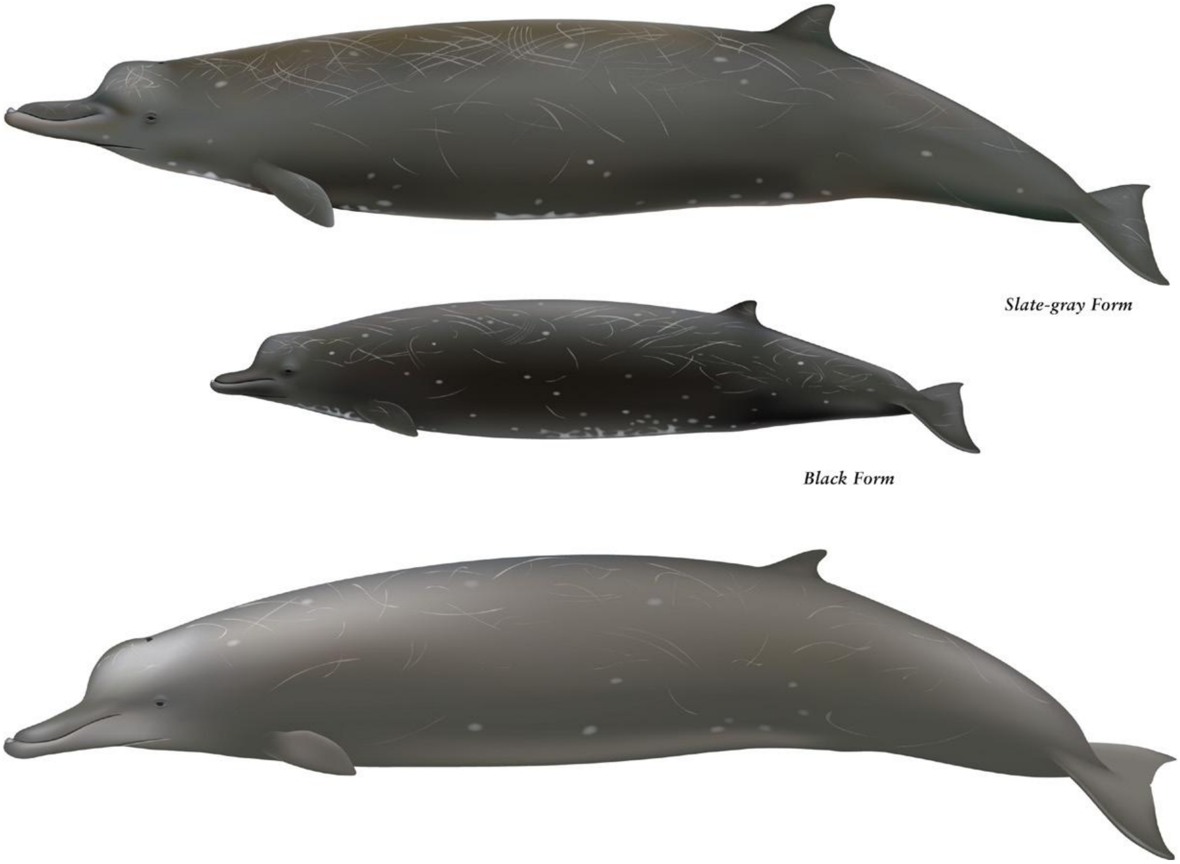

Figure 1 *Baird's beaked whale,* Berardius bairdii *(top two images), Arnoux's beaked whale,* B. arnuxii *(bottom) (Illustrations by Uko Gorter).*

Copyright © 2017. Elsevier Science & Technology. All rights reserved.

II. Distribution and Abundance

Arnoux's beaked whales inhabit vast areas of the Southern Hemisphere, between 24°S and Antarctica (Fig. 2). Baird's beaked whales inhabit the temperate North Pacific, between 30° and 62°N, with occasional records as far south of La Paz (24°) in the southern Gulf of California, and a single record from the Chinese coast (Wang, 1999). They are a deep diving species (3000 m) and Arnoux's beaked whale can be found in areas with much ice cover.

Baird's beaked whales live near the deep waters over the continental slope in the north Pacific. They occur year-round in the Okhotsk Sea and the Sea of Japan, including in areas with drift ice. It is not clear where Baird's beaked whales off Japan spent their winters, but around May they congregate in nearshore waters of 1000–3000 m over the continental slope. Their numbers increase toward summer and then decrease toward October (Kasuya and Miyashita, 1997). Abundance has been estimated only for Japanese waters, 5029 for the Pacific coast, 1260 for the eastern Sea of Japan, and 660 for the southern Okhotsk Sea (International Whaling Commission, 1992, 1994).

III. Ecology

More than 80% of the food of Baird's beaked whales off the Pacific coast of Japan consists of benthopelagic fish (Moridae and Macrouridae) with nearly all of the remainder consisting of cephalopods (Gonatidae and Cranchiidae). However, for Baird's beaked whales in the southern Okhotsk Sea, cephalopods made up nearly 90% of the diet, with the remainder consisting of morid and macrourid fish (Walker et al., 2002). These data are consistent with what is known of the diet of Baird's beaked whales near California, and suggests that they are opportunistic feeders. The stomach of an Arnoux's beaked whale was mostly filled with squid beaks.

The surface of *Berardius* shows a variety of epizoans. Whale lice (cyamid crustaceans) attach on teeth and skin, stalked barnacles attach to the teeth, and diatoms cover the skin. Internally, parasites are common in the stomach, liver, blubber, and kidney, and there may be extensive kidney damage from the nematode *Crassicauda giliakiana*. Evidence of predation includes wounds attributable to the cookie-cutter shark, *Isistius brasiliensis*, in Japanese waters. Scars from killer whale teeth are common on flippers and tail flukes.

IV. Behavior and Physiology

Near Japan, Baird's whales travel in tight schools of up to 30 individuals, but usually in groups from two to nine (Kasuya, 1986; Kasuya and Miyashita, 1997; Kasuya et al., 1997). During surface schooling, individuals blow continuously while swimming slowly and are easily identifiable from vessels. There is some evidence that whales stay together for periods at a time, but not across years (Fedutin et al., 2015).

Mean length of dives is 18 min, but shorter and longer dives are common, with the maximum recorded length 67 min. Between dives, mean time spent at the surface is 4 min, but can be between 1 and 14 min. Time at the surface tends to be greater after a longer dive.

V. Life History

The gestation time of *Berardius* is estimated to be 17 months, and newborns are approximately 4.6 m long (Kasuya, 2009). Females become sexually mature between 10 and 15 years when they are 9.8–10.7 m long, and may reach 54 years. Based on the histology of their testis, males become sexually mature between 6 and 11 years, at body lengths of 9.1–9.8 m. Males can reach 84 years. Length growth of the animal ceases when epiphyses of the

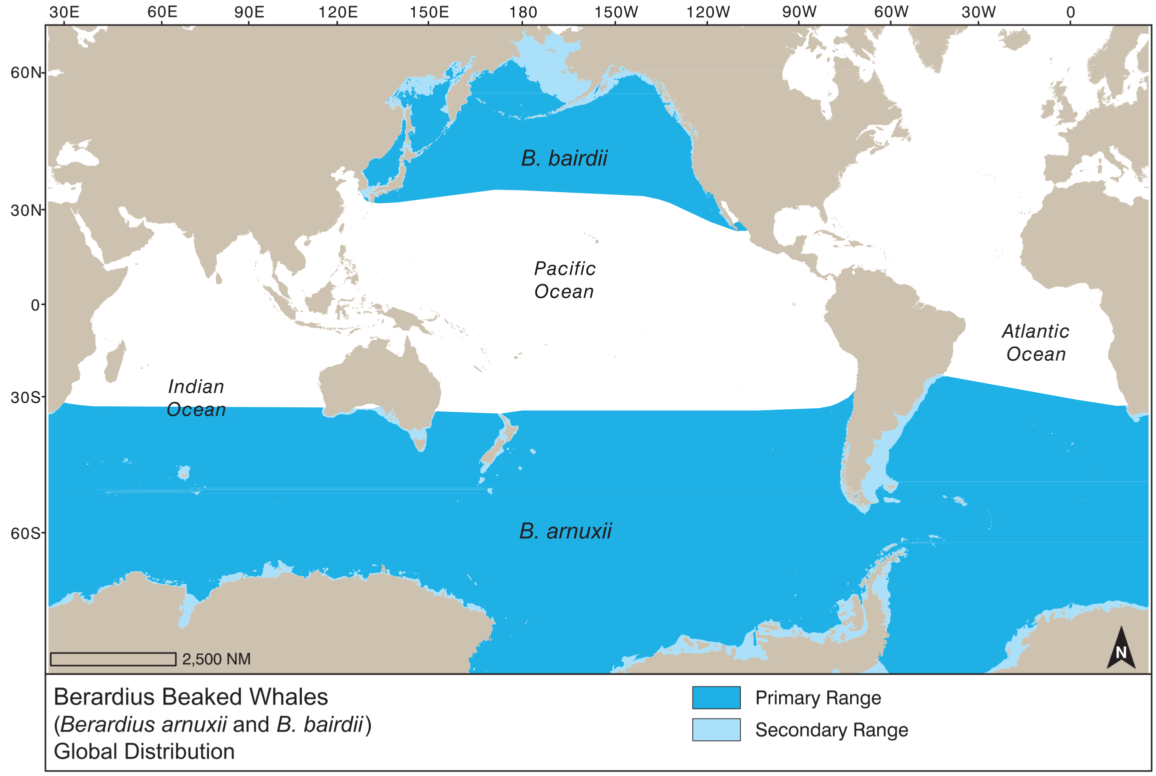

Figure 2 *Arnoux's and Baird's beaked whale distribution. Adapted by Nina Lisowski from Jefferson, T.A. and Pitman, R.L. (2015). "Marine Mammals of the World: A comprehensive Guide to Their Identification," 2nd ed. Elsevier, San Diego, CA.*

Copyright © 2017. Elsevier Science & Technology. All rights reserved.

vertebrae fuse to the vertebral centrum and this is attained less than 5 years after sexual maturity. Mean body length of physically mature *Berardius bairdi* is 10.45 m for females and 10.10 m in males.

Before sexual maturity, there are equal numbers of males and females in a population, but the percentage of females declines with age, and there are no old females. This implies that mortality rates for females must be much higher than for males. If sexual maturity is assessed using genital histology, then less than a quarter of the sexually mature individuals in the population is female. However, in males, the testis weighs 1.5 kg when histological data indicate sexually maturity, but the testis continues to grow to 3–9 kg until the whale is 30 years old. It is possible that only these older males participate in reproduction. If sexual maturity is defined on the basis of this, females make up around 40% of the population (Kasuya, 2009).

Ovulation occurs throughout life at an approximate rate of once every 2 years. The apparent high fecundity and shorter longevity of females combined with greater male longevity have invited speculations on their social structure including a possible male contribution in rearing calves.

IV. Interactions With Humans

No hunting of Arnoux's beaked whales has been reported. In the past, there were low takes of Baird's beaked whales by the USSR, Canada, and the United States, but Japan is the only country with a significant hunt.

Japanese *Berardius* hunting started in the early 17th century at the entrance of Tokyo Bay. The annual catch was less than 25 before 1840 and then declined. In 1891, whaling cannons were introduced and the operation moved off-shore. After World War II, the fishery expanded to the entire northern Pacific, with a reported maximum annual catch of more than 300, but declining over time. Official Japanese statistics are probably underestimates (Balcomb and Goebel, 1977). The Japanese quota for 2007 was 10 for the Sea of Japan, 4 for the southern Okhotsk Sea, and 52 for the Pacific coasts. Japanese whaling is the main human threat to *Berardius*.

See Also the Following Articles

Age Estimation ■ Barnacles ■ Beaked Whales, Overview ■ Gastrointestinal Tract ■ Parasites ■ Whaling, Japanese

References

Arnason, U., and Gullberg, A. (1996). Cytochrome b nucleotide sequences and the identification of five primary lineages of extant cetaceans. *Mol. Biol. Evol.* **13**, 407–417.

Balcomb, K.C., and Goebel, C.A. (1977). Some information on a *Berardius bairdii* fishery in Japan. *Rep. Int. Whal. Comm.* **27**, 485–486.

Dalebout, M.L., Baker, C.S., Mead, J.G., Cockroft, V.G., and Yamada, T.K. (2004). A comprehensive and validated molecular taxonomy of beaked whales, family Ziphiidae. *J. Hered.* **95**, 459–473.

Fedutin, I.D., Filatova, O.A., Mamaev, E.G., Burdin, A.M., and Hoyt, E. (2015). Occurrence and social structure of Baird's beaked whales, *Berardius bairdii*, in the Commander Islands, Russia. *Mar. Mamm. Sci.* **31**, 853–865.

International Whaling Commission, 1992. Report of the sub-committee on small cetaceans. *Rep. Int. Whal. Comm.* **42**, 108–119.

International Whaling Commission, 1994. Report of the sub-committee on small cetaceans. *Rep. Int. Whal. Comm.* **44**, 178–228.

Kasuya, T. (1986). Distribution and behavior of Baird's beaked whales off the Pacific coast of Japan. *Sci. Rep. Whales Res. Inst., Tokyo* **37**, 61–83.

Kasuya, T. (2009). Giant beaked whales *Berardius bairdii* and *B. arnuxii.* In "Encyclopedia of Marine Mammals", (W.F. Perrin, B. Würsig, and J.G.M. Thewissen, Eds), 2nd ed., pp. 498–500. Elsevier, San Diego, CA.

Kasuya, T., and Miyashita, T. (1997). Distribution of Baird's beaked whales off Japan. *Rep. Int. Whal. Comm.* **47**, 963–968.

Kasuya, T., Brownell Jr., R.L., and Balcomb, K.C. (1997). Life history of Baird's beaked whales off the Pacific coast of Japan. *Rep. Int. Whal. Comm.* **47**, 969–979.

Morin, P.A., Baker, C.S., Brewer, R.S., Burdin, A.M., Dalebout, M.L., Dines, J.P., Fedutin, I., Filatova, O., Hoyt, E., Jung, J.-L., Lauf, M., Potter, C.W., Richard, G., Ridgway, M., Robertson, K.M., and Wade, P.R. (2016). Genetic structure of the beaked whale genus *Berardius* in the North Pacific, with genetic evidence for a new species. *Mar. Mamm. Sci.* doi:10.1111/mms.12345.

Walker, W.A., Mead, J.G., and Brownell, R.L. (2002). Diet of Baird's beaked whales, *Berardius bairdii*, in the southern Sea of Okhotsk and off the Pacific coast of Honshu, Japan. *Mar. Mamm. Sci.* **18**, 902–919.

Wang, P. (1999). *Chinese Cetaceans.* Ocean Enterprises, Hong Kong

Copyright © 2017. Elsevier Science & Technology. All rights reserved.

BIOGEOGRAPHY

Rick LeDuc

Biogeography is the study of the patterns of geographic distribution of organisms and the factors that determine those patterns (Brown and Gibson, 1983; Cox and Moore, 1985). This discipline plays a critical role in our understanding of marine mammal evolution and adaptation (Berta et al., 2015).

Although marine mammals are mobile, and there is an apparent lack of physical barriers in the world ocean, only killer whales, (*Orcinus orca*), sperm whales (*Physeter macrocephalus*), and perhaps some few of the balaenopterids are considered to have cosmopolitan distributions. Some Antarctic killer whales make rapid forays to subtropical waters and back to the Antarctic, thus undergoing tremendous water temperature and other ecological transitions in a short space of time (Durban and Pitman, 2011), as opposed to the generally longer-lasting migrations of baleen and sperm whales (Whitehead, 2003; Geijer et al., 2016). Other species have restricted distributions (e.g., coastal South America, Indo-West Pacific), reflecting their ecological requirements and their geographic centers of origin (Jefferson et al., 2015).

Because related species tend to have similar ecological requirements and dispersal abilities, the distribution of higher taxa can also show distinct tendencies and restrictions, which reflect the cumulative distributions of their included species. For example, while delphinids, river dolphins, and sirenians have their highest diversity in tropical latitudes, most pinniped, ziphiid, and phocoenid species occur in temperate and polar regions. From a geographic perspective, specific regions can thus be characterized as centers of diversity for these higher taxa, and past global changes in the environment will have influenced their evolutionary history. For example, cooling of the world climates in several past episodes may have contributed to the radiation of cold-water adapted pinnipeds and mysticetes (See Churchill et al., 2014, for otariid distribution to the Southern Hemisphere).

I. Types of Distributions

There has been considerable effort in recent years to better document what is known about marine mammal distributions (Rice, 1998; Read et al., 2007; Jefferson et al., 2015). Individual species are usually limited to certain latitudinal zones such as tropical, subtropical, temperate, cold-temperate, or polar regions. For example, the Clymene dolphin (*Stenella clymene*) occurs only in the tropical Atlantic, the Steller sea lion (*Eumetopias jubatus*) in the cold temperate North Pacific, and dugongs (*Dugong dugon*) in the tropical Indian Ocean and West Pacific. Species may also be associated with specific physical features, such as nearshore coastal areas (e.g., humpback dolphins, *Sousa* spp.) or the continental slope (e.g., Baird's beaked whale, *Berardius bairdii*), or with oceanographic features, such as specific water masses or bodies of freshwater (e.g., baiji of China, *Lipotes vexillifer*, and the Baikal seal of Lake Baikal, *Pusa sibirica*).

A few species, notably some of the baleen whales, are highly migratory, summering at high latitudes and spending the winter breeding season at lower latitudes. Some of the migrating rorqual species occupy (at least seasonally) a wide range of latitudes in both hemispheres, although the movements of the Northern and Southern Hemisphere populations are seasonally offset such that they do not normally cooccur in the tropics (Davies, 1963). At the other end of the spectrum, there are some species (e.g., the vaquita, *Phocoena sinus*, and Hawaiian monk seal, *Neomonachus schauinslandi*) that have highly restricted ranges.

There are marine mammal distributions that are described as pantropical (or pantropical/temperate), which are exhibited by many delphinids, ziphiids (e.g., Blainville's beaked whale, *M. densirostris*), kogiids (e.g., the pygmy sperm whale, *Kogia breviceps*), and balaenopterids (e.g., Bryde's whale, *Balaenoptera edeni*). There are a few species and species pairs that occur at higher latitudes in both hemispheres but are absent from tropical waters, the so-called antitropical species and species pairs. These are seen in the families delphinidae (e.g., right whale dolphins, *Lissodelphis* spp.), ziphiidae (e.g., the bottlenose whales, *Hyperoodon* spp.), phocoenidae (e.g., some porpoises, *Phocoena phocoena*/*P. spinipinnis*), phocidae (e.g., elephant seals, *Mirounga* spp.), and otariidae (e.g., various fur seals, *Arctocephalus townsendi*/*A. philippii*).

II. Ecology and History Determine Distribution

Beyond descriptive aspects of biogeography, there are distinct factors that determine a given species' distribution. In some cases, distribution is limited because a species may not be adapted for living in certain environments. For example, tropical delphinids may not range into higher latitudes due to limitations on their abilities to thermoregulate in colder water or find food in different habitats. But competition may also be a factor. Throughout most of its range, the West Indian manatee (*Trichechus manatus*) occurs in both coastal and riverine habitats. However, it does not range into the Amazon River, where the exclusively freshwater Amazon manatee (*T. inunguis*) occurs, although it occupies the coastal areas on either side of the river mouth. Here, the two species are parapatric, and competitive exclusion is likely at work (Marsh et al., 2011).

The dispersal abilities of organisms may partly explain why species occur in some areas and not in others. For example, the lack of otariids in the North Atlantic is probably not due to the lack of suitable habitat, but rather lies in the inability of North Pacific or South Atlantic species to get there. Of course, one could also tie this into their ecological requirements, in that dispersal to the North Atlantic would be more likely if North Pacific species ranged far enough north for animals to disperse via the Arctic Ocean across northern North America or Eurasia. For some species that have widely separated allopatric populations (e.g., Commerson's dolphin, *Cephalorhynchus commersonii*), dispersal from one region to the other is a likely explanation for their distribution. In other cases, vicariance events can explain allopatric distributions (Nelson and Rosen, 1981; Wiley, 1998). For example, the two subspecies of Indian River dolphin (*Platanista gangetica*) occur in different river systems, the Indus and Ganges–Brahmaputra River systems. But these rivers used to be connected, and therefore the geographic separation of the populations is from a rather recent vicariance event.

Large-scale changes in the environment can have dramatic influences on species distributions. In times of global cooling, cold boundary currents in the ocean basins extended farther toward the equator. This, in turn, enabled temperate species to disperse across the equator to similar habitats in a different hemisphere, giving rise to antitropical species, such as dusky dolphins (*Lagenorhynchus obscurus*) in the Southern Hemisphere and the closely related Pacific white-sided dolphin (*L. obliquidens*) in the North Pacific (Harlin-Cognato, 2010). Among the antitropical species and species pairs, some tendencies in their distributions are apparent. Although the long-finned pilot whale (*Globicephala melas*), has only been recorded live from the North Atlantic and the Southern Hemisphere, more than 1000-year-old skulls of this species have been unearthed in Japan, and it was probably hunted to extinction (Whaling, Japanese, this volume). For the rest of the seven or so recognized antitropical species and species pairs, all except the bottlenose whale *Hyperoodon* (which also occurs in the North Atlantic) have their northern members limited to the North Pacific. Perhaps the oceanographic and climatic conditions that allow transequatorial dispersal for temperate species occur more frequently or become more developed in the Pacific basin than in the Atlantic. The right whales (*Balaena* spp.) present a slightly different scenario, but one that is consistent with this pattern. Now recognized as three distinct species, molecular analyses indicate that the species in the North Pacific (*B. japonica*) and Southern Ocean (*B. australis*) are more closely related to each other than either is to the North Atlantic species (*B. glacialis*), suggesting a more recent transequatorial dispersal in the Pacific basin, possibly due to collective behavior during the right ecological conditions (Berdahl et al., 2016). The above comparisons do not include the latitudinal migrant species, such as many of the species of balaenopterids. For these, their seasonal occurrence at low latitudes greatly facilitates transequatorial dispersal and would not likely require any significant change in oceanographic or climatic conditions.

Latitudinal migrants do, however, present questions regarding the selective advantage to conducting such extensive movements—sometimes covering thousands of miles (e.g., gray whales, *Eschrichtius robustus* and humpback whales, *Megaptera novaeangliae*). Their occurrence at high latitudes can be explained by the greater abundance of food, but the selective advantage to their seasonal movements to less productive wintering areas is not as apparent. The fact that they occur in high latitudes in the winter season with some regularity means that escape from winter cold may not be a major factor for adults. Calving in warmer climates does make sense, and mating during the same season could lead to wholesale movements of a population. An alternative explanation is that they leave high latitudes in the winter to escape from killer whales, which occur in much higher densities in these areas (Corkeron and Connor, 1999).

Beyond consideration of the underlying mechanisms of a single species' distribution, it is possible to make inferences about the origins of entire ecological communities. One approach is known as vicariance biogeography (Nelson and Rosen, 1981; Wiley, 1988). Vicariance biogeographers look for congruence between the phylogenetic relationships among species and their geographical distributions. Species distributions can be superimposed on phylogenetic

Copyright © 2017. Elsevier Science & Technology. All rights reserved.

trees to create what are called area cladograms (Fig. 1). If the area cladograms of several unrelated but geographically similar higher taxa are congruent, it is good evidence that a specific sequence of vicariance events operated on all of those taxa as speciation mechanisms. Furthermore, it may allow the researcher to make inferences about the centers of origin for the higher taxa being considered (see also Myers and Giller, 1988).

If possible, one should try to incorporate the fossil and geologic record when inferring historical mechanisms in biogeography, especially among distantly related taxa (Thewissen, 2014). A case in point can be seen in the river dolphins. Among the river dolphins, *Inia* and *Pontoporia* appear to be closest relatives among the extant species, the former occupying several South American rivers that flow into the Atlantic, and the latter occurring along the Atlantic coast of South America. However, the closest relative of this pair is probably *Lipotes*, which was found in the Yangtze River in China until its recent probable extinction (Turvey et al., 2007). It is likely that geologic change in river flows (to the Pacific Ocean) and nearshore habitats in especially South America contributed to these relationships.

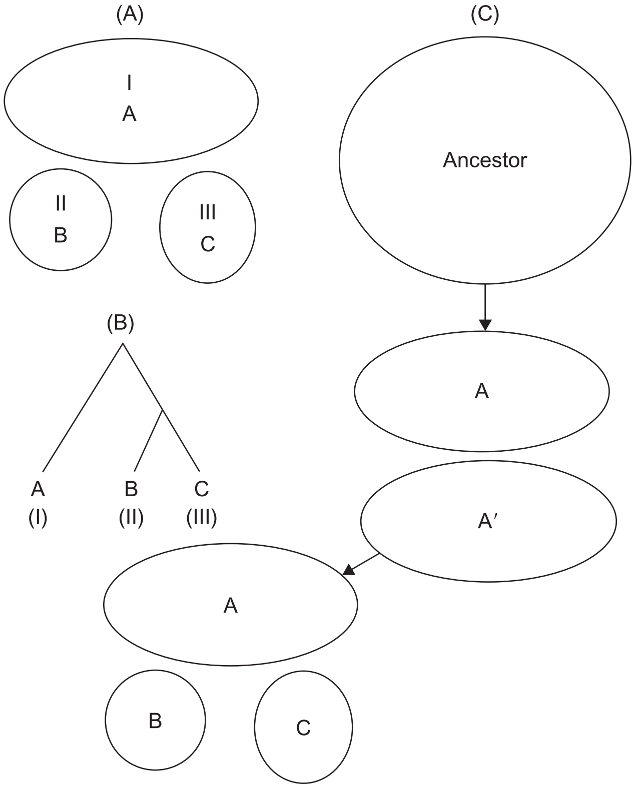

Figure 1 *In vicariance biogeography, the speciation patterns are determined by vicariance events. The analysis attempts to reconstruct the sequence of vicariance events using the pattern of evolutionary relationships within a group of related species with allopatric distributions. (A) Species "A," "B," and "C" occupy ranges I, II, and III, respectively. (B) If a phylogenetic analysis determines that "B" and "C" are sister species to the exclusion of "A," this pattern of relationships is applied to their respective geographic ranges in an area cladogram. (C) Under this scenario, the range of the ancestral species is first divided by a vicariance event into a northern and a southern half. Populations in these two areas speciate into species "A" and "A." Species "A" is the inferred immediate common ancestor to "B" and "C." A later vicariance event divides the range of "A" into eastern and western halves, giving rise to species "B" and "C." If unrelated species groups occupying these areas show congruent area cladograms, the support for this sequence of vicariance events is strengthened.*

In a recent context, human activities have played and are playing a role in altering species distributions, most often in the form of range reduction. For example, hunting may have played some role in the extirpation of gray whales (*Eschrichtius robustus*) from the North Atlantic. More indirect, but just as dramatic, will be the shifts or reductions in species' distributions due to climate change, especially in high latitudes.

III. Taxonomic Patterns

Species within higher taxa share characteristics of their distributions to some degree. It is therefore possible to characterize the distributions of the different groups of marine mammals. The sirenians are primarily a tropical group, with mostly allopatric species occurring in warm coastal waters and some rivers of the Indo-West Pacific and both sides of the Atlantic. The trichechids are represented by two species in the new world (*Trichechus manatus* and *T. inunguis*), and a single congener (*T. senegalensis*) in western Africa, indicating the occurrence of a past trans-Atlantic dispersal event within that lineage. The family Dugongidae, formerly more diverse and widespread, now has only one extant species (*Dugong dugon*) that occurs in the Indian and west Pacific Oceans. One recently extinct species of dugongid (*Hydrodamalis gigas*) had a restricted range in the Commander Islands of the North Pacific, an anomalously cool habitat for a sirenian (see Marsh et al., 2011, for details).

The majority of phocid species inhabit cold temperate and polar regions. Although no species occurs in both the Northern and Southern Hemisphere, there are numerous species that are circumpolar either in the Arctic (e.g., bearded seals, *Erignathus barbatus*) or in the Antarctic (e.g., crabeater seals, *Lobodon carcinophagus*). In fact, all of the southern phocid species have very broad distributions, their range expansions probably assisted by the oceanic currents that traverse the Southern Ocean. In the Northern Hemisphere, however, the habitats and ocean currents are more fragmented by continental landmasses. In addition to the circumpolar species, there are northern species that have more restricted ranges, either endemic to a single ocean basin (e.g., gray seals, *Halichoerus grypus*) or limited to landlocked bodies of water (e.g., Caspian seals, *Pusa caspica*). In contrast to the rest of the family, the three recent (two extant) species of monk seals inhabit(ed) warmer waters of the Mediterranean and eastern Atlantic, Caribbean, and Hawai'i. The spread of monk seals to Hawai'i must have occurred prior to the rising of the Isthmus of Panama, which has separated the Caribbean and Pacific basins for the past 3 million years.

As a group, the otariids are similar to the phocids in their distribution, although they are less well represented at very high latitudes (near the pack ice) and do not occur in the North Atlantic at all. In addition, individual species tend to have more restricted ranges that are widely allopatric from their congeners. For example, the fur seal genus *Arctocephalus* is widespread in the Southern Hemisphere, represented by six species (with an additional species endemic to the Galapagos Islands and another to the eastern North Pacific). However, there are only a handful of localities where more than one species occurs together; for the most part the species are allopatric. It appears then that the dispersal abilities of fur seals have allowed them to colonize many areas in the Southern Hemisphere but have not prevented the resulting disjunct populations from speciating. The odobenids are represented by a single circumpolar Arctic species, the walrus (*Odobenus rosmarus*).

Copyright © 2017. Elsevier Science & Technology. All rights reserved.

Cetacean species exhibit a wide range of distribution patterns. The family Balaenidae includes one antitropical species group (the right whales, *Balaena* spp.) and one circumpolar Arctic species (the bowhead whale, *B. mysticetus*). The gray whale and the various species of balaenopterids are mostly latitudinal migrants in both hemispheres, although the Bryde's-like whales (*Balaenoptera brydei*, *B. omurai*, and *B. edeni*) are restricted to tropical and warm temperate waters, and some primarily migratory species include isolated populations that may be nonmigratory (e.g., humpback whales in the northern Indian Ocean). In addition to the widespread common minke whale (*Balaenoptera acutorostrata*), the Southern Hemisphere also contains an endemic species of minke whale (*B. bonaerensis*). Similarly, the Southern Hemisphere is also home to two distinct forms (considered subspecies at present) of blue whale (*B. musculus*). In both these cases, it is not known if the two southern forms represent divergent lineages that arose within the Southern Ocean or if they were the result of independent dispersal events across the equator.

Sperm whales are virtually cosmopolitan, and the kogiids (*Kogia sima* and *K. breviceps*) are worldwide in tropical and warm temperate waters. Beaked whales show a variety of distribution patterns, including pantropical species (e.g., Blainville's beaked whale), antitropical species pairs (*Berardius* spp.), and ocean basin endemics (e.g., Sowerby's beaked whale, *M. bidens*). Some (e.g., the Peruvian beaked whale, *M. peruvianus*) are only known from a few strandings within limited geographic areas.

Three of the four species of river dolphins (the boto, *Inia geoffrensis*, baiji, and Indian River dolphin) occur only in freshwater in specific tropical river systems, with the fourth species (the Franciscana, *Pontoporia blainvillei*) having a restricted marine coastal range. The two species of monodontids (narwhal, *Monodon monoceros* and beluga, *Delphinapterus leucas*) are restricted to Arctic waters for the most part, and are among the few resident polar cetaceans, although fossil species of this family occurred as far south as San Diego, CA.

Apart from a single Indo-West Pacific coastal species that also ranges into freshwater (the finless porpoise, *Neophocaena phocaenoides*), the phocoenids are strictly marine and cold temperate to warm temperate in distribution, some with very restricted ranges (e.g., the vaquita). Only one phocoenid, the common porpoise (*P. phocoena*), has invaded the North Atlantic, becoming very widespread in both oceans of the Northern Hemisphere and even establishing isolated populations in the Black Sea and off West Africa.

The most speciose family of marine mammals, the delphinids, shows a wide variety of distributions, from pantropical species (e.g., pantropical spotted dolphins, *Stenella attenuata*) to ocean basin endemics (e.g., white-beaked dolphins, *Lagenorhynchus albirostris*) to species with wide-ranging but disjunct populations (e.g., the common dolphin, *Delphinus delphis*). Many delphinids are pelagic, although some inhabit coastal waters (e.g., the *Cephalorhynchus* spp.) and some even invade freshwater (e.g., the tucuxi, *Sotalia fluviatilis*). Only one, the killer whale, seems to regularly range to the pack ice in the far north and south. For the many pantropical/warm temperate species, the continental landmasses effectively separate the populations inhabiting the Indian and Pacific Oceans from those inhabiting the Atlantic Ocean, raising the question of how they came to inhabit all the ocean basins. It has been hypothesized that during warm climatic periods, warm water extended far enough south to allow interchange and range expansion around the Cape of Good Hope. This would enable some species to become pantropical in their distribution, and the subsequent retreat of the warm water and isolation of populations could provide a speciation mechanism for the establishment of the tropical species endemic to the Atlantic Ocean (e.g., Atlantic spotted and Clymene dolphins, *S. frontalis* and *S. clymene*, respectively).

Copyright © 2017. Elsevier Science & Technology. All rights reserved.

IV. Conclusion

Why do species live where they do? Answering such a simple question requires the examination of clues from the past as well as the present. Biogeography involves such diverse disciplines as geology, paleontology, ecology, physiology, behavior, and systematics. For marine mammals, studying biogeographical patterns presents real challenges. There is a paucity of information about past distributions and habitats, gaps in our knowledge of contemporary and recent distributions, uncertainties about evolutionary relationships, and a tremendous amount to learn about the basic ecology and physiology of many marine mammals.

See Also the Following Articles

Cetacean Ecology ■ Climate Change ■ Migration and Movement ■ Pinniped Ecology ■ Systematics

References

Berdahl, A., van Leeuwen, A., Levin, S., and Torney, C.J. (2016). Collective behaviour as a driver of critical transitions in migratory populations. *Mov. Ecol.* **4**, (No. 18). doi:10.1186/s40462-016-0083-8.

Berta, A., Sumich, J., and Kovacs, K.M. (2015). *Marine Mammals—Evolutionary Biology*, 3rd ed. Elsevier/Academic Press, San Diego, CA.

Brown, J.H., and Gibson, A.C. (1983). *Biogeography*, Mosby, St. Louis, MO.

Churchill, M., Boessenecker, R.W., and Clementz, M.T. (2014). The late Miocene colonization of the Southern Hemisphere by fur seals and sea lions (Carnivora: Otariidae). *Zool. J. Linn. Soc.* **172**, 200–225.

Corkeron, P.J., and Connor, R.C. (1999). Why do baleen whales migrate? *Mar. Mamm. Sci.* **15**, 1228–1245.

Cox, C.B., and Moore, P.D. (1985). *Biogeography*, 4th ed. Blackwell Scientific Publications, Cambridge, MA.

Davies, J.L. (1963). The antitropical factor in cetacean speciation. *Evolution* **17**, 107–116.

Durban, J.W., and Pitman, R.L. (2011). Antarctic killer whales make rapid, round-trip movements to subtropical waters: evidence for physiological maintenance migrations? *Biol. Lett.* **8**, 274–277.

Geijer, C.K.A., Notarbartolo di Sciara, G., and Panigada, S. (2016). Mysticete migration revisited: are fin whales an anomaly? *Mamm. Rev.* **46**, 284–296.

Harlin-Cognato, A.D. (2010). The dusky dolphin's place in the delphinid family tree. In "The Dusky Dolphin: Master Acrobat off Different Shores", (B. Würsig, and M. Würsig, Eds), pp. 1–20. Academic/Elsevier Press, San Diego, CA.

Jefferson, T.A., Webber, M.A., and Pitman, R.L. (2015). *Marine Mammals of the World," 2nd ed.* Academic/Elsevier Press, San Diego, CA.

Marsh, H., O-Shea, T.J., and Reynolds, J.E. (2011). *Ecology and Conservation of the Sirenia: Dugongs and Manatees.* University Press, Cambridge, UK.

Myers, A.A., and Giller, P.S. (Eds), 1988. *Analytical Biogeography.* Chapman and Hall, London.

Nelson, G., and Rosen, D.E. (Eds), 1981. *Vicariance Biogeography: A Critique.* Columbia University Press, New York.

Read, A.J., Halpin, P.N., Crowder, L.B., Best, B.D., and Fujioka, E. (Eds), 2007. *OBIS-SEAMAP: Mapping marine mammals, birds and turtles.* World Wide Web electronic publication

Rice, D.W. (1998). Marine Mammals of the World: Systematics and Distribution. Soc. Mar. *Mamm. Spec. Pub.*, 4. Society for Marine Mammalogy, Lawrence, KS.

Thewissen, J.G.M. (2014). *The Walking Whales: From Land to Water in Eight Million Years.* University of California Press, Oakland, CA.

Turvey, S.T., Pitman, R.L., Taylor, B.L., Barlow, J., Akamatsu, T., Barrett, L.A., et al. (2007). First human-caused extinction of a cetacean species? *Biol. Lett.* **3**, 537–540.

Whitehead, H. (2003). *Sperm Whales: Social Evolution in the Ocean.* The University of Chicago Press, Chicago, IL.

Wiley, E.O. (1988). Vicariance biogeography. *Ann. Rev. Ecol. Syst.* **19**, 513–542.

BIOTELEMETRY

Andrew J. Read

Recent advances in computing power, microprocessors, and global telecommunication systems have led to extraordinary insights into the behavior, ecology, and physiology of many marine animals including mammals (Block, 2005). It is now possible to follow the fine-scale behavior of marine mammals for months at a time and from the most remote regions of the world's oceans, from the comfort of one's office. It is also possible to visualize and listen to what a marine mammal sees and hears as it swims through the water column. These and other advances allow researchers to investigate how marine mammals use their three-dimensional world, quantify important physical and biological aspects of their environments, and test potential conservation measures designed to mitigate the effects of adverse human activities. The field continues to develop rapidly, fueled by continuing advances in technology, miniaturization, and data processing.

There are two primary approaches to collect data with telemetry systems. In the first approach, an archival data logger is attached to a marine mammal, records data for a predetermined period, and then it is recovered, allowing researchers to download the information stored in the package. In the second approach, information is transmitted from a marine mammal via radio or acoustic signals to a receiver, usually on land or based on an orbiting satellite.

I. Archival Tags

The earliest data loggers were simple time-depth recorders that used smoked glass disks rotating past recording needles attached to pressure transducers. These devices were first employed in 1963 by Gerry Kooyman to study the diving behavior of Weddell seals (*Leptonychotes weddellii*; Kooyman, 2006). To record time in these devices, Kooyman incorporated simple kitchen timers. This ingenuity is typical of the field of marine telemetry, which is too small to support much of its own commercial research and development. Instead, biologists have adopted, modified, and refined technology developed for other purposes and applied it to study a wide variety of marine mammals.

Modern data loggers are sophisticated digital devices that are capable of storing large quantities of information. Data are collected from one or more sensors that measure parameters such as depth, water temperature, light intensity, or swimming velocity. The location of a tagged animal can be determined by several methods, ranging from simply recording light levels and times of dawn and dusk, and back-calculate latitude and longitude after the tag is recovered to recording high-resolution GPS positions. It is also possible to record physiological data, such as heart rate and body temperature. Researchers routinely record feeding events by transmitting temperature changes in the stomach to external data loggers and jaw movement. A small transmitter, equipped with a temperature sensor, is introduced into the stomach of an animal, which transmits data to a data logger mounted on its external surface. Most prey are heterothermic, or cold-blooded, so when the transmitter is swallowed, the temperature of the stomach drops abruptly. Eventually, the transmitter is passed or regurgitated.

One archival tag—the digital acoustic tag (or DTAG)—developed by Mark Johnson and Peter Tyack at the Woods Hole Oceanographic Institution, has provided a lot of new insights into the behavior of marine mammals. The DTAG records the acoustic environment of the tagged animal, as well as depth, temperature, and fine-scale data on its three-dimensional orientation (Johnson and Tyack, 2003). DTAGs have been used to study the acoustic behavior of marine mammals and to examine their response to anthropogenic sounds. For example, attachment of DTAGs to beaked whales (*Ziphius* and *Mesoplodon*) demonstrated that these deep-diving animals are highly vocal, producing high-frequency echolocation clicks, but only when they are at depths greater than 200 m (Johnson et al., 2004). In addition, the DTAGs were able to detect echoes from prey during foraging events. Researchers have also used DTAGs to examine the response of North Atlantic right whales (*Eubalaena glacialis*) to alert signals designed to make the animals aware of approaching ships (Nowacek et al., 2004). The whales reacted strongly to the alerting signal by swimming rapidly to the surface, a response likely to increase rather than decrease the risk of collision. This work made it clear that mitigation measures other than alerting sounds will be required to solve the problem of ship strikes with right whales.

Data loggers have several advantages over other types of telemetry systems. First, data storage requires considerably less power than data transmission, so fewer and/or smaller batteries are required. In turn, this means that recoverable loggers can be smaller than transmitting tags while storing vast amounts of data.

The primary disadvantage of these systems is the need to recover the data loggers to retrieve the stored information. The use of data loggers in studies of some land-breeding pinnipeds is fairly straightforward, because these animals haul out at predictable times and locations. Researchers studying elephant seals (*Mirounga* spp.), for example, are able to recover up to 95% of their loggers because of the strong fidelity of these animals to their rookeries. The use of data loggers with cetaceans or ice-breeding seals is considerably more challenging, as researchers must first attach the package to an animal and then recover the tag after it is jettisoned. One solution used with some cetacean species is to attach the loggers with suction cups using a hand pole or other remote method, and then to recover the buoyant packages after release by homing in on a radio signal emitted by a tag in the package. Several research groups have employed this technique with considerable success, although this is possible for only short deployments, and involves considerable logistics—sometimes including following the tagged animal(s) at sea.

II. Transmitting Systems

Transmitting systems have also undergone an extraordinarily rapid development over the past several decades. The earliest transmitters were omnidirectional radio or acoustic transmitters that allowed researchers to relocate a tagged animal but did not provide information on its behavior or physiology (Fig. 1). These simple systems have evolved into sophisticated systems in which large quantities of data can be recorded, compressed, and transmitted via orbiting satellites.

The earliest tracking devices used with marine mammals were simple radio transmitters shot into the blubber of large whales or

Copyright © 2017. Elsevier Science & Technology. All rights reserved.

Figure 1 *Data loggers can be very small (because power requirements are low), such as this time-depth-recorder (TDR) glued to the fur of this young ringed seal. But, the down side is that such instruments usually need to be recovered to download data. Hence, this pup is also wearing a VHF radio transmitter (with an antenna) to facilitate recovery of the TDR (Photo by Kit M. Kovacs/Christian Lydersen, NPI).*

Figure 2 *Many marine mammal satellite-linked tags, such as this custom-designed walrus tag, report data to the ARGOS satellite system (Photo by Kit M. Kovacs/Christian Lydersen, NPI).*

Figure 3 *Elephant seals are the largest pinnipeds, and hence have been the most common study subject for CTD-SRDL tag deployments. The tags are glued to the hair and thus usually stay in place until the next molting period (Photo by Kit M. Kovacs/Christian Lydersen, NPI).*

attached to the dorsal fins of dolphins and porpoises or glued to the fur of pinnipeds. These tags allow researchers to follow marine mammals at sea and gain insight into their behavior and short-term movements. But, this involved labor-intensive field work using directional receiving antennas to home in on the radio signal produced by the transmitter when the antenna was above the surface.

Acoustic signals were also used to track animals in the early days; these signals propagate for much greater distances underwater, but often overlap with the hearing range of marine mammals, limiting their applicability. Even under ideal circumstances, radio transmitters have effective ranges of only a few tens of kilometers, so researchers were forced to stay in close proximity to tagged animals. Additionally, the large size and cumbersome design of many early radio tags created significant hydrodynamic drag and resulted in the premature detachment of the packages and possible harm to the animals wearing them.

Today, there are a variety of transmitting systems available to researchers. The most significant advance has been the development of satellite-linked radio transmitters that allow biologists to track the movements and behavior of marine mammals without having to physically follow the animals. These transmitters emit unique radio signals to receivers aboard orbiting satellites. ARGOS tags use the Doppler shift to estimation of the position of the transmitter. But, FASTloc GPS systems now provide even more accurate positions, which are collected by the tag and subsequently shipped via satellite links (Dujon et al., 2014). Data are processed and relayed to the user by e-mail or made available over the web (Fig. 2).

Satellite-linked radio transmitters have been coupled with data logging systems, to allow the collection of detailed behavioral or environmental data from marine mammals via satellite. Typical data collected by these systems include depth and swim speed, although in principle any sensor system can be employed. Recent developments in sensor design and data handling have allowed development of a new generation of tags that are deployed as oceanographic sensors on marine mammals—so called CTD-SRDLs (conductivity-temperature-depth satellite relayed data loggers) (see Fig. 3; Fedak, 2004). Thus, marine mammals now collect and transmit large quantities of data on the physical and biological attributes of their environments, greatly facilitating our understanding of their ecology and ocean systems (e.g., Roquet et al., 2013; Hindell

Copyright © 2017. Elsevier Science & Technology. All rights reserved.

et al., 2016). Marine mammals are adept at exploiting fine-scale oceanographic features that concentrate prey, such as frontal systems, and animals instrumented with appropriate sensors provide considerable information about the location and dynamics of such processes.

Satellite-linked data loggers are extremely powerful data acquisition systems, but they do have limitations. Their signals can be received only when the transmitter is above the surface and a satellite receiver is overhead. Energy for signal transmission is a significant limitation with current battery technology, although battery life may be conserved by using a salt-water switch, which suppresses transmissions when the tag is submerged. In addition, the current satellite system limits each transmission to 256 bits, so algorithms are required to compress complex data, such as records of individual dive profiles, prior to transmission. Nevertheless, these tags have revolutionized our understanding of the ecology, behavior, and environments of marine mammals.

III. Biological Insights

While at sea, most marine mammals spend more than 90% of the time submerged, often in remote or harsh environments in which field research is difficult or impossible. Telemetry allows us to peer into the lives of whales, dolphins, sirenians, and pinnipeds as they go about their daily activities of feeding, finding mates, and avoiding predators (Fig. 4). We can ask how a beaked whale hunts for food at a depth of 1000 m, or how an elephant seal is capable of such long, repeated submergences, or where blue whales (*Balaenoptera musculus*) go in the winter months. The insights provided by this technology will continue to challenge our thinking about these animals; particularly, as new technological developments improve our ability to collect data at sea.

Elephant seals have proven to be particularly amenable to study with telemetry. These are large animals that haul out to breed and molt at predictable times and locations, but which spend the majority of the year far from shore. Thus, it is possible to equip individual elephant seals with fairly large telemetry packages and be confident that most packages will be recovered. Researchers in both hemispheres have equipped a large number of elephant seals with recoverable data loggers and, more recently, satellite-linked data loggers (e.g., Hindell et al., 2016). From a host of telemetry studies done on northern elephant seals in the North Pacific we know that these animals make two long-distance feeding migrations each year, one after breeding and the second after the molt. For example, adult male elephant seals travel from central California to the Gulf of Alaska on each migration, a distance of more than 10,000 km in each round trip. Individuals appear to return to the same feeding area each year and, once on the feeding grounds, forage almost continuously. Individual elephant seals dive repeatedly, spending more than 90% of their time at sea submerged, and sometimes diving to depths of more than 1500 m. Such behavior is consistent with what we know about diet of these animals; elephant seals feed primarily on mesopelagic squid found at depths of 200–1000 m. These prolonged and continuous dives have raised many physiological questions, particularly with regard to the oxygen storage capacity of these animals (discussed later), but insights into the relationships between the animals and their environments are developing rapidly (e.g., Codde et al., 2016). The prodigious diving behavior of elephant seal behavior has led some biologists to refer to them as mesopelagic mammals.

Figure 4 *Peering into the lives of cetaceans using telemetry devices is still challenging in terms of means of attachment of tags. Short-term deployments of some hours or at best days can be achieved with suction cups, but longer-term deployments involve some type of skin/blubber piercing. The white whale on the right in this picture bears a satellite-linked tag that is attached via surgical pins through the skin and blubber beneath the dorsal ridge. Such attachments normally result in data records that are approximately 6 months long in this species (Photo by Kit M. Kovacs/Christian Lydersen, NPI).*

Elephant seals are not alone in possessing an impressive diving capacity. Sperm whales (*Physeter macrocephalus*) have been tracked using telemetry to depths of more than 2000 m during dives that may last for more than an hour. Beaked whales are also capable of long, deep dives. Northern bottlenose whales (*Hyperoodon ampullatus*), for example, equipped with time-depth recorders attached with suction cups, have made dives to 1500 m and for over an hour in duration. Studies using satellite-linked data loggers attached to smaller whales, such as belugas (*Delphinapterus leucas*) and narwhals (*Monodon monoceros*), indicate that these species are also capable of prolonged, deep dives under the Arctic ice (e.g., Heide-Jørgensen et al., 2015).

One of the greatest challenges to understanding the diving and foraging behavior of free-ranging marine mammals is observing and tracking them for extended periods at depth. Early studies relied on a small number of spatial and temporal variables (e.g., dive depth and duration, rate of descent and ascent, time at depth, swimming speed, time-depth profile) obtained from a variety of animal-borne instruments to categorize dives based on behaviors that were inferred but not observed. Advances in the miniaturization of video imaging technology now enable researchers to use animal-borne instruments that record the in situ behavior of diving vertebrates and their prey and, in some cases, three-dimensional dive path (dead reckoned based on depth, speed, and compass bearing), locomotor performance (gliding, stroke-and glide, continuous stroking), the physical environment (e.g., temperature, salinity, dissolved oxygen, and light intensity), and physiological variables (body temperature and the partial pressure of oxygen in the blood) (see Andrews and Enstipp, 2016, for a review). Locomotor performance can be used to estimate the energetic cost of foraging, and the animal-borne video enables us to determine prey species, size, and energy consumption. Physiological variables provide sight into the adaptations that enable marine mammals to make prolonged breath-hold dives while maintaining aerobic metabolism.

Recent studies with data recorders equipped with video cameras, or crittercams, have provided dramatic findings regarding the behavior of marine mammals. Weddell seals have been videotaped

Copyright © 2017. Elsevier Science & Technology. All rights reserved.

flushing prey from crevices in the ice by blowing bubbles and researchers have watched Hawaiian monk seals (*Monachus schauinslandi*) sleep and forage on the sea floor. This type of research has particular relevance to conservation because it is believed that monk seals may be endangered, in part, due to conflicts with commercial fisheries. Documenting the availability of prey and the success rate of capture attempts allow us to test such ideas directly for the first time. Backward-mounted crittercams have been used to study the diving behavior of a variety of marine mammals and, in particular, to investigate how whales and seals can make such long dives without exceeding their aerobic capacities. It now appears, for example, that elephant seals and other marine mammals conserve oxygen by gliding extensively during descent; deployment of accelerometers has advanced our understanding of how animals move through the water column. These animals take advantage of the changes in buoyancy brought about by increased pressure at depth and can effectively descend with little extra expenditure of energy or oxygen (also see Gordine et al., 2015).

IV. Challenges and Future Developments

It is difficult to anticipate what surprises the field of telemetry has in hold, but it is clear that these techniques will be an integral component of the toolbox of future marine mammal researchers. In particular, it is likely that more sophisticated sensors will be developed to take advantage of the success of recoverable and satellite-linked data loggers. Such novel sensors will monitor physiological parameters, such as blood oxygen concentration, hormone levels, and blubber thickness (some of these advances have already been tested with other marine vertebrates). Current advances in wireless technology hold great promise for our ability to telemeter data from marine mammals, because many current applications in acoustic and video telemetry are limited by bandwidth—the amount of information that can be transmitted from the animal to a receiver. New telemetry systems based on global system for mobile communications (mobile phone, GSM) technology have been deployed with great success on several species of pinnipeds in Europe and North America. Seals wearing these mobile phone tags send text messages to researchers when they are in areas of GSM coverage, providing information on location and behavior (Cronin et al., 2016).

Despite the great promise of telemetry for our understanding of the biology of marine mammals, some significant challenges lie ahead. As the cost of tags has been reduced, and their availability and sophistication increased, the number of individual animals studied has increased exponentially. It is not uncommon for very large samples (hundreds) of tags to be deployed in some of the largest telemetry programs such as the TOPP (Tagging of Pacific Pelagics; Block, 2005) or MEOP (Hindell et al., 2016). Our ability to analyze such large data sets has not kept up with the availability of information and new analytical methods are required to gain maximum insight from these large (and costly) field projects. Problems continue to exist with uncertainty in position estimates (although a new generation of GPS tags is helping to resolve some of these issues as in ARGOS's new Kalman filter) and incorporating this uncertainty into an appropriate analytical framework. In particular, it is critical to integrate movement and behavioral data obtained via telemetry with observations of the environment conditions available to the animals (Shaffer and Costa, 2006). Making telemetry information available through publicly available data commons, such as the OBIS-SEAMAP project (Halpin et al., 2006), will facilitate innovative approaches to analysis and integration with environmental data.

Finally, readily availability, off-the-shelf electronic tags have greatly increased the number of animals instrumented each year. Despite this rapid growth in the field, there have been few attempts to determine what behavioral or physiological effects are caused by carrying a transmitter or archival data logger. Such effects could include mechanical artifacts of the attachment method used, increased energy expenditure caused by elevated rates of hydrodynamic drag, or changes to the thermal biology due to decreased heat flow across the integument. The maturation of the field will, without doubt, bring an evaluation of such potential effects on a variety of marine mammal species.

See Also the Following Articles

Behavior, Overview ■ Distribution ■ Identification Methods ■ Migration and Movement

References

Andrews, R.D., and Enstipp, M.R. (2016). Diving physiology of seabirds and marine mammals: Relevance, challenges and some solutions for field studies. *Comp. Biochem. Physiol.* **202**, 38–52.

Block, B.A. (2005). Physiological ecology in the 21st century: Advancements in biologging science. *Integr. Comp. Biol.* **45**, 305–320.

Codde, S.A., Allen, S.G., Houser, D.S., and Crocker, D.E. (2016). Effects of environmental variables on surface temperature of breeding adult female northern elephant seals, *Mirounga angustirostris*, and pups. *J. Therm. Biol.* **61**, 98–105.

Cronin, M., Gerritsen, H., Reid, D., and Jessopp, M. (2016). Spatial overlap of grey seals and fisheries in Irish waters, some new insights using telemetry technology and VMS. *PLoS One* **11**(9), e0160564.

Dujon, A.M., Lindstrom, R.T., and Hays, G.C. (2014). The accuracy of Fastloc-GPS locations and implications for animal tracking. *Methods Ecol. Evol.* **5**, 1162–1169.

Fedak, M.A. (2004). Marine mammals as platforms for oceanographic sampling: A "win/win" situation for biology and operational oceanography. *Mem. Natl. Inst. Polar Res. Spec. Iss.* **58**, 133–147.

Gordine, S.A., Fedak, M., and Boehme, L. (2015). Fishing for drifts: detecting buoyancy changes of a top marine predator using a stepwise filtering method. *J. Exp. Biol.* **218**, 3816–3824.

Halpin, P.N., et al. (9 authors) (2006). OBIS-SEAMAP: Developing a biogeographic research data commons for the ecological studies of marine mammals, seabirds, and sea turtles. *Mar. Ecol. Prog. Ser.* **316**, 239–246.

Heide-Jørgensen, M.P., Nielsen, N.H., Hansen, R.G., Schmidt, H.C., Blackwell, S.B., and Jørgensen, O.A. (2015). The predictable narwhal: satellite tracking shows behavioural similarities between isolated subpopulations. *J. Zool.* **297**, 54–65.

Hindell, M.A., McMahon, C.R., Bester, M.N., Boehme, L., Costa, D., Fedak, M.A., et al. (2016). Circumpolar habitat use in the southern elephant seal: implications for foraging success and population trajectories. *Ecosphere* **7**(5), e01213.

Johnson, M.P., and Tyack, P.L. (2003). A digital acoustic recording tag for measuring the response of wild marine mammals to sound. *IEEE J. Oceanic Eng.* **28**, 3–12.

Johnson, M., Madsen, P.T., Zimmer, W.M.X., Aguilar de Soto, N., and Tyack, P.L. (2004). Beaked whales echolocate on prey. *Proc. R. Soc. London B (Suppl.)* **271**, S383–S386.

Kooyman, G.L. (2006). Mysteries of adaptation to hypoxia and pressure in marine mammals. *Mar. Mamm. Sci.* **22**, 507–526.

Nowacek, D.P., Johnson, M.P., and Tyack, P.L. (2004). North Atlantic right whales (*Eubalaena glacialis*) ignore ships but respond to alerting stimuli. *Proc. R. Soc. London B* **271**, 227–231.

Roquet, F., Wunsch, C., Forget, C., Heimbach, P., Guinet, C., Reverdin, G., et al. (2013). Hydrographic data collected by seals significantly reduce the observational gap in the Southern Ocean. *Geophys. Res. Lett.* **40**, 6176–6180.

Shaffer, S.A., and Costa, D.P. (2006). A database for the study of marine mammal behavior: Gap analysis, data standardization, and future directions. *IEEE J. Oceanic Eng.* **31**, 82–86.

Copyright © 2017. Elsevier Science & Technology. All rights reserved.

BLUBBER

Sara J. Iverson and Heather N. Koopman

Blubber, a dense vascularized layer of fat beneath the skin, is one of the most well-known and universal characteristics of marine mammals. Although, strictly speaking, it is not present in polar bears (*Ursus maritimus*) or sea otters (*Enhydra lutris*), all cetaceans, sirenians, and pinnipeds have blubber and it may comprise up to 50% of the body mass of some species at certain life stages. Blubber is the primary and most important site of fat, and thus also energy, storage in marine mammals. However, it is anatomically and biochemically adapted to also serve as an efficient and adjustable thermal insulator, buoyancy adjuster, and hydrodynamic facilitator. Although blubber is a dynamic tissue, which can reflect both nutritional state and life history stage, the tissue itself has likely evolved to best suit the lifestyles, stresses and constraints of specific marine mammal groups, individual species, and even regional variation in function within an individual.

I. The Structure of Blubber

A. Tissue Characteristics

Blubber is a specialized subcutaneous layer of adipose tissue found only in marine mammals. The blubber layer is almost continuous across the body of marine mammals, lying over but not tightly fixed to the underlying musculature but absent on appendages. The thickness, structure, and biochemical composition of the blubber can vary greatly over the body of an individual, likely associated with localized differences in function. There also usually exists a thermal, as well as biochemical, gradient through the depth of the blubber layer; the outer layer (nearest the epidermis) is usually cooler than the inner layer (nearest the body core). The polar bear also deposits huge quantities of fat subcutaneously, likely providing some degree of insulation. However, this superficial adipose tissue does not differ in structure from the superficial fat depots of other large terrestrial carnivores (Pond, 1998).

Blubber, like other adipose tissue, is composed of numerous fat cells called adipocytes. Adipocytes develop prior to filling with fat and are composed, like other cells, of mostly protein and water. Mature adipocytes are generally large and spherical and packed densely into adipose tissue. Although most other types of adipose tissue contain small-to-moderate amounts of collagen, blubber is distinct in being greatly enriched in collagen and elastic fibers. This gives blubber a firm, tough, and fibrous character from which it derives many of its mechanical and functional properties. The histological structure of blubber in pinnipeds is relatively uniform throughout its depth. However, in some cetaceans, there is a distinct stratification of the tissue into inner, middle, and outer layers based on the size, shape, and metabolic characteristics of adipocytes, as well as on lipid and collagen content (e.g., Fig. 1). Blubber also contains numerous blood vessels and specialized shunts called arterio-venous anastomoses (AVAs), which allow larger and swifter blood flow than would be possible through capillaries alone and are important to thermoregulation. Capillary density itself varies interspecifically by as much as 2-5-fold, suggesting differential relationships between adipocytes and blood supply across species. In manatees, a layer of muscle is imbedded in the middle of the ventral blubber layer, however, a similar arrangement has also been found at certain body sites in some otariids. A possible functional significance for this arrangement is not known.

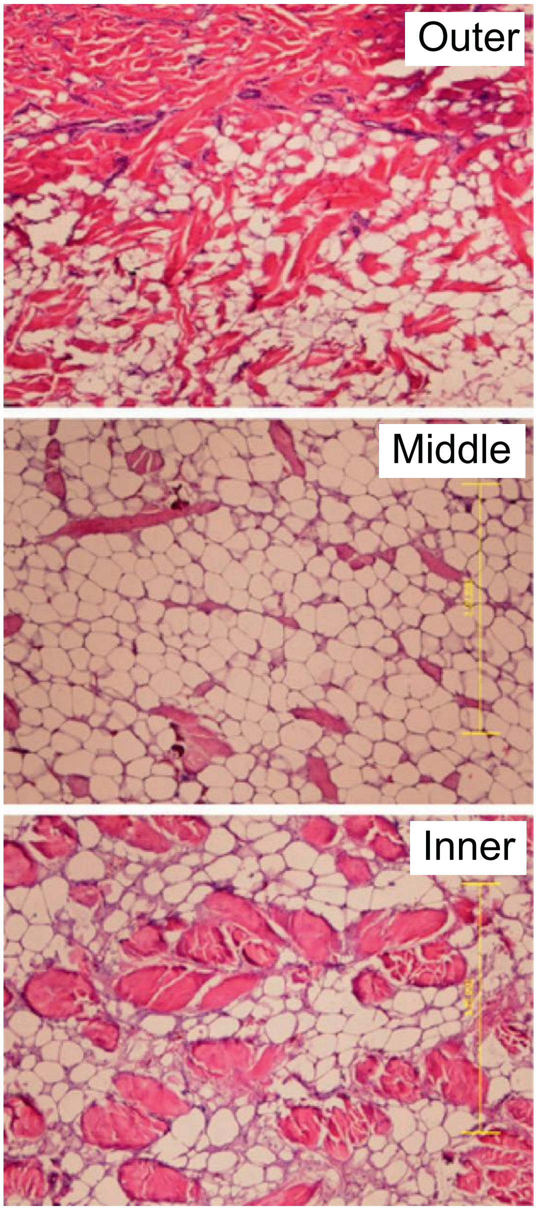

Figure 1 *Microstructure at different depths through the blubber layers of a striped dolphin (*Stenella coeruleoalba*). From Gomez-Campos et al. (2015).*

B. Variation in Thickness and Proximate Composition

The thickness of the blubber layer varies among species. In general, larger species tend to have greater maximum blubber thickness, ranging from a depth of 2.5–3.0 cm in the small harbor porpoise (*Phocoena phocoena*), 7–10 cm in adult pinnipeds, 20–30 cm in fin whales (*Balaenoptera physalus*), and up to 50 cm in bowhead whales (*Balaena mysticetus*, Fig. 2). The adipose tissue of many newborn mammals is empty of lipid, filling quickly after birth during the lactation period; subsequent proliferation of fat depots is due to an increase in both adipocyte numbers and size. However, in adults, changes in the size of fat depots (including blubber) are primarily due to filling or emptying of existing adipocytes. Although baleen whales are born with a blubber layer that is several centimeters

Copyright © 2017. Elsevier Science & Technology. All rights reserved.

Figure 2 *Skin (black near bottom of photo) and blubber as removed from a bowhead whale. Tape measure scale is in centimeters (Photo by J.G.M. Thewissen).*

thick, most pinnipeds are born with very little blubber, at <3 mm in depth in some otariids and accounting for less than 5%–6% of body mass in most phocids. Most newborn pinnipeds rely instead primarily on fur (otariids) or lanugo (downy hair grown by fetuses) and delayed entry into the water until blubber is well formed. In newborn phocid seals, blubber can represent <6% of body mass and contain only 20% lipid; this rapidly changes during a brief (~4–28-day) lactation period, such that the blubber of a newly weaned pup can comprise 50% of body mass and contain >90% lipid. In contrast, lipid can be mobilized rapidly from adipocytes when needed and hence undernourished marine mammals, or those undergoing annual fasting events (e.g., lactation, molting), are characterized by greatly reduced blubber thickness and lipid content. For instance, the sternal blubber of female harbor seals (*Phoca vitulina*) changes during the 24-day lactation period from 3.8 to 1.4 cm in depth and from 92.3% lipid, 2.2% protein, and 5.5% water to 76.9% lipid, 5.9% protein, and 17.2% water: the increases in protein and water content reflect the larger proportion of "emptier" fat cells. Lipid content of adipose tissue in polar bears also changes with nutritional and reproductive status.

C. The Lipids in Blubber

Depot lipid in most animals (including marine mammals) is stored predominantly as triacylglycerols, which consist of three fatty acids (FAs) esterified to glycerol (a three-carbon alcohol). FAs in the marine food web are exceptionally complex and are characterized by high levels of long-chain polyunsaturated FAs (PUFA) produced at the base of the food chain. During digestion of triacylglycerols by monogastric mammals, FAs are released from the glycerol backbone but generally are not degraded and are carried in the bloodstream and taken up by tissues. These FAs are then either used for energy or stored as triacylglycerols in adipose tissue. Thus, FAs travel up the food chain intact, and because the kinds of FAs that can be biosynthesized or modified in mammals are quite limited, most FAs found in blubber arise from the dietary intake of prey lipids. Hence, blubber is usually characterized by high levels of long-chain PUFA as well as unique FAs produced at lower trophic levels.

Marine mammals, like other mammals, can also synthesize some of their own FAs from sources such as dietary amino acids consumed in excess of body needs (glucose would be another source but is scarce in marine mammal diets). These synthesized FAs are usually 16 or 18 carbons long and have, at most, one double bond (i.e., 16:0, 16:1*n*7, 18:0, and 18:1*n*9). Although these FAs are also common in prey of marine mammals, some are undoubtedly deposited in blubber from biosynthesis.

One very unusual FA, isovaleric acid, is also found in the blubber of some species of odontocetes (toothed whales) (Koopman, 2007). Isovaleric acid is short (five carbons), branched, and arises via localized biosynthesis from leucine. When present, it is found in highest concentrations in the outermost layer (nearest the skin) of blubber. Additionally, some marine mammals (primarily some odontocetes) store some or all of their FAs in blubber as wax esters rather than triacylglycerols. A wax ester is a single FA esterified to a long-chain (22–34 carbon) fatty alcohol. The toothed whales are also unique in their deposition of isovaleric and other branched FAs, along with wax esters, in the specialized cranial acoustic tissues (melon and mandibular fats) associated with echolocation and hearing (Koopman et al., 2006). Generally, wax esters are firm, stable, and resistant to degradation, which is why sperm whale (*Physeter macrocephalus*) oil was popular as an illuminant in the last century.

II. Role of Blubber in Temperature Regulation: Heat Conservation and Dissipation

As a whole-body envelope of insulation, blubber is central to thermoregulation in marine mammals, which are homeothermic endotherms and hence need to maintain a stable body core temperature of about 37°C in cooler (usually is ≤25°C) and often much colder (−1 to 5°C) fluid environments. Heat is lost 25 times more rapidly to water than to air. Increasing body size provides less surface area per unit volume over which to lose heat. Even the smallest marine mammals are considered large mammals, being one to two orders of magnitude larger than small terrestrial mammals such as rodents and insectivores. Furthermore, large body size generally allows for thicker insulation (fur or blubber), which further decreases heat conductance.

Fur is a far more effective insulator than blubber in air and is used as the sole means of insulation by sea otters, trapping pockets of air (a poor thermal conductor) among hairs, which then forms the effective insulative layer. However, when fur is wetted or when diving under pressure fur is compressed, expelling the air layer and thus reducing its insulative properties. In contrast, blubber does not compress with depth, offering an advantage while diving.

Adipose tissue is also less metabolically active than other tissues and thus requires less perfusion by blood, which would otherwise tend to cause heat loss at the body surface. Nevertheless, because blubber is vascularized with specialized shunts (arterio-venous anastomoses, AVAs), adjustments of blood flow through the blood vessels and AVAs allow both heat conservation and dissipation as necessary, if surface vessels are either bypassed or utilized.

The effectiveness of blubber as an insulative layer depends on its thickness, lipid content, and lipid composition (Pond, 1998), which may also vary across regions of the body (especially in cetaceans). Many marine mammals, especially those of larger body size, possess a thick blubber layer, allowing them to remain thermoneutral at most of the temperatures of the world's oceans and, for some pinnipeds, even at air temperatures of −10 to −20°C on polar ice. However, smaller species are limited in the depth of blubber they

Copyright © 2017. Elsevier Science & Technology. All rights reserved.

can carry and also have relatively more surface area over which to lose heat. Hence, most of the smallest cetaceans do not occur at high latitudes. The harbor porpoise is the smallest cetacean species to inhabit temperate waters of the Northern Hemisphere. Although its blubber depth is only several centimeters thick, it is generally twice the thickness and contains more lipid than in a similarly sized dolphin inhabiting tropical waters, conferring up to four times greater insulative capacity (Koopman, 2007). Nevertheless, small species such as harbor porpoises must feed nearly continually to maintain metabolism and to preserve blubber's thickness and insulative capacities. In contrast, because of their size, large whales can fast and mobilize blubber reserves for weeks or months, yet remain thermoneutral.

Variation in the lipid composition of blubber may also confer insulative capacities that differ. Unsaturated FAs (of which blubber contains high amounts) have lower melting points than do saturated FAs. Thus, even when the temperatures of the outermost layer of blubber and skin are near that of cold ambient temperatures, blubber can remain fluid and an effective insulator if the melting point of its FAs is low. Saturated and monounsaturated FAs abundant in blubber have melting points of 13–70°C. However, nutritionally important PUFA are usually plentiful in marine mammal diets and thus in blubber, conferring an overall melting point in blubber lipid of <−15°C. Additionally, in some small cold-water odontocetes, high concentrations of isovaleric acid are deposited in blubber. Isovaleric acid has an extremely low melting point of −37.6°C, which clearly provides fluidity, especially to the outer blubber layer and may affect insulation. Increasing blubber's wax content will also enhance its insulative capacity (Bagge et al., 2012). In contrast, while manatees (*Trichechus* sp.) can also store large amounts of blubber, they generally do not tolerate temperatures below 20°C. As plant eaters, manatees must synthesize the majority of their blubber FAs, which would thus be restricted in their degree of unsaturation. However, little is known about the effectiveness of manatee blubber as an insulator in cold temperatures or the role that lipid composition might play in this ability. Finally, recent studies show that blubber may act as a phase-change material, storing heat for later release (Bagge et al., 2012) and that the blubber of some marine mammals may contain brown fat, which would be a source of nonshivering thermogenesis.

III. Role of Blubber in Energy Storage and Water Balance

Blubber, as a rich energy store, is important in the lives of marine mammals because of the critical role that stored lipid plays in their ecology, reproduction, and survival. For many marine mammals, reproduction and especially lactation are often spatially and temporally separated from feeding grounds. For instance, large baleen whales feed in polar regions during the high primary productivity of summers but migrate in winter to warm tropical waters of low food availability to give birth and nurse their young. In phocid and otariid pinnipeds, parturition and lactation occur on land or ice and thus are also separated from the feeding environment of the lactating female. Female polar bears spend the first 3–4 months of lactation in winter dens, without eating or drinking.

In all female mammals, lactation represents the greatest energetic cost of reproduction, requiring large amounts of nutrient transfer, elevated maternal maintenance costs, and hence usually increased maternal food consumption. However, because of large energy reserves that can be stored in blubber, baleen whales and large phocid seals are the only mammals (besides holarctic bears) that can complete much or all of lactation without feeding. Smaller phocids and otariids are able to fast only intermittently during lactation. All species of marine mammals produce high fat milks (~30%–60% fat), maximizing the efficiency of fat transfer from maternal blubber into milk and subsequent neonatal blubber deposition and growth. In species that fast throughout lactation, females switch almost completely to a fat-based metabolism. For instance, during the 16-day lactation period, a gray seal (*Halichoerus grypus*) female draws 97% of the energy required for her own metabolic needs and 90% of the milk energy supplied to her pup solely from her blubber stores (Mellish et al., 1999).

Blubber deposition is equally critical to the suckling neonate, both for thermoregulation and to act as an energy reservoir at weaning. For example, most newly weaned phocid pups fast for several weeks or months and the energy supplied from blubber is critical to survival and continued physiological development of the young while they learn how to forage on their own.

Adult males of many marine mammal species also fast during the breeding season and during annual molting periods, relying on stored blubber lipid as their energy source. Sirenians also use blubber during fasting. For instance in the Amazon, manatees (*Trichechus inunguis*) face dry seasons of up to 6 months at a time, where low waters restrict them to the deep water areas of larger lakes where the aquatic plants they feed upon are unavailable.

Finally, blubber is essential for maintaining water balance during fasting. Each kilogram of lipid oxidized for energy use generates a net production of 1.07 kg metabolic water. In fact, oxidation of blubber yields enough water that individuals usually do not require an additional external source. This is true even of lactating females that are exporting large quantities of water in milk. For instance, a gray seal female exports about 23 kg of water in milk over a 16-day lactation period while fasting and has no external access to water during this time (Iverson et al., 1993).

IV. Role of Blubber in Locomotion

Several forces act on animals swimming in fluids, and blubber plays a significant role in the way marine mammals deal with these forces. Drag is the force that resists the movement of a body through a medium and is much greater in seawater than in air due to seawater's higher density and greater viscosity. The most effective ways to reduce both drag and the power required to move is to have a smooth streamlined shape and to be spindle-shaped to reduce the wake left by a moving animal. Although all marine mammals tend to be somewhat streamlined in body shape as defined by their musculoskeletal system, blubber provides a smooth sculpted contour. Blubber thickness is also often distributed across marine mammals in a nonuniform manner (e.g., thickening and sculpting of hind end or tailstock) to ensure more gradual tapering of the body than would be dictated by the musculoskeleton. This locomotor function may actually constrain the way in which animals utilize their blubber as energy reserves. In large baleen whales as well as the smallest harbor porpoise, blubber may be greatest in depth and fat content, even during nutritional stress, in the posterior dorsal and tail areas of the body, where it serves important locomotory functions by both streamlining and possibly acting as a biomechanical spring, capable of temporarily storing and releasing elastic strain energy (Pabst et al., 1999).

Finally, blubber also plays a role in buoyancy. In most marine mammals (except the sea otter), buoyancy will be determined

Copyright © 2017. Elsevier Science & Technology. All rights reserved.

primarily by the ratio of adipose tissue to lean body tissue and body mass, as fat-filled adipose tissue is less dense than seawater. Consequently, the amount of stored blubber will affect buoyancy and thus energy expended in moving or maintaining position in the water column. Although some newly weaned phocid pups may be positively buoyant at >43% adipose tissue, most adult marine mammals will not be and thus are not likely to require any counteracting of this force when at the bottom of dives or when feeding at the benthos. However, changes in blubber stores will clearly affect the degree of negative buoyancy. For instance, seals descend faster during diving when they are more negatively buoyant, providing evidence that they adjust their diving behavior in relation to seasonal changes in buoyancy.

V. Insights From the Study of Blubber

Blubber is clearly of central importance to the structure and function of marine mammals. Given that blubber has evolved to serve complex functions, and yet the composition and amount carried by an individual can change rapidly, its study can provide unique insights into phylogenetic relationships and environmental adaptations, as well as aspects of feeding habits, foraging ecology, species distribution, and demography that are otherwise difficult to study. For instance, simply the measurement of differences and variation in blubber thickness and proximate composition within populations can provide an important tool for assessing such things as nutritional stress and life history stage of individuals.

Analysis of the structure and composition of blubber at specific body sites can provide clues to regional functions. For instance, in some cetaceans, blubber structure at the thoracic-abdominal area suggests roles in insulation and energy storage, whereas at other sites (e.g., the thick ridge posterior to the dorsal fin or at the caudal peduncle) structure suggests more important roles in maintaining hydrodynamic shape and other locomotory functions (Pabst et al., 1999). Study of how blubber at these various sites is utilized during times of fat mobilization may provide further insight into adaptations of blubber structure.

Studying blubber can also provide insight into phylogenetic relationships and adaptation. For instance, the characteristic of storing primarily wax esters in blubber appears to be confined to beaked whales and sperm whales. These species, although closely related odontocetes, are also all pelagic deep divers. Recent evidence points to an increase in the solubility of nitrogen gas in wax-rich blubber, which may have implications for diving physiology in these species. Likewise, the presence of isovaleric acid is confined to a fairly restricted group of odontocetes, which also may be under special thermal constraints. Thus, the study of isovaleric acid in blubber may provide clues to its function and potential value in insulation.

Finally, since the complex and diverse FAs of blubber arise in large part from dietary intake, the FAs in blubber can provide powerful insights into the foraging ecology and diets of both individuals and populations of marine mammals over time and space. Considered alone, differences in blubber FAs among individuals provide important qualitative insight into spatial and temporal differences in foraging and diets. Even more powerful, it is now possible to use FAs in predators, along with their prey, to quantitatively estimate species composition of predator diets (Iverson et al., 2004). Quantitative fatty acid signature analysis (QFASA) accounts for effects of predator metabolism on FA deposition, and then determines the weighted mixture of prey species FA signatures that most closely resembles that of the predator's FA stores to thereby infer its diet. QFASA has been validated and used to estimate diets in a number of marine mammal (and other) species (Iverson et al., 2004, Iverson 2009). A small blubber or adipose tissue biopsy from a free-ranging animal can provide relatively noninvasive information about diet that is neither dependent on prey with hard parts nor limited to only the last meal, as are analyses of fecal or stomach contents. This approach can be more complicated in some cetaceans with the greater stratification of blubber into distinct layers, but it is still possible. Thus, quantitative studies using blubber FAs can address broad ecosystem-scale processes and provide new insight into foraging patterns and ecology of free-ranging marine mammals that would otherwise not be possible.

See Also the Following Articles

Circulatory System ■ Osmoregulation ■ Pinniped Physiology ■ Skeleton ■ Swimming ■ Thermoregulation

References

Bagge, L.E., Koopman, H.N., Pokorny, A., Rommel, S.A., McLellan, W.A., and Pabst, D.A. (2012). Lipid class and depth-specific thermal properties in the blubber of the short-finned pilot whale and the pygmy sperm whale. *Exp. Biol.* **215**, 4330–4339.

Gómez-Campos, E., Borrell, A., Correas, J., and Aguilar, A. (2015). Topographical variation in lipid content and morphological structure of the blubber in the striped dolphin. *Sci. Mar.* **79**, 189–197.

Iverson, S.J., Bowen, W.D., Boness, D.J., and Oftedal, O.T. (1993). The effect of maternal size and milk output on pup growth in grey seals (*Halichoerus grypus*). *Physiol. Zool.* **66**, 61–88.

Iverson, S.J., Field, C., Bowen, W.D., and Blanchard, W. (2004). Quantitative fatty acid signature analysis: A new method of estimating predator diets. *Ecol. Monogr.* **74**, 211–235.

Iverson, S.J. (2009). Tracing aquatic food webs using fatty acids: from qualitative indicators to quantitative determination. In "Lipids in Aquatic Ecosystems" (M.T. Arts, M.T. Brett, and M. Kainz, Eds), pp. 281–307. Springer-Verlag, New York.

Koopman, H.N. (2007). Phylogenetic, ecological, and ontogenetic factors influencing the biochemical structure of the blubber of odontocetes. *Mar. Biol.* **151**, 277–291.

Koopman, H.N., Budge, S.M., Ketten, D.R., and Iverson, S.J. (2006). The topographical distribution of lipids inside the mandibular fat bodies of odontocetes: Remarkable complexity and consistency. *IEEE J. Oceanic Eng.* **31**, 95–106.

Mellish, J.E., Iverson, S.J., and Bowen, W.D. (1999). Individual variation in maternal energy allocation and milk production in grey seals and consequences for pup growth and weaning characteristics. *Physiol. Biochem. Zool.* **67**, 677–690.

Pabst, D.A., Rommel, S.A., and McLellan, W.A. (1999). The functional morphology of marine mammals. In "Biology of Marine Mammals", (J.E. Reynolds, and S.A. Rommel, Eds), pp. 15–72. Smithsonian Institution Press, Washington, DC.

Pond, C.M. (1998). *The Fats of Life*. Cambridge University Press, Cambridge, UK.

BLUE WHALE

Balaenoptera musculus

Richard Sears and William F. Perrin

Common names are blue whale, sulfur-bottom, Sibbald's rorqual, great blue whale, and great northern rorqual. The largest animal known to have existed on Earth, it is found worldwide, ranging into all oceans (Yochem and Leatherwood, 1985).

Copyright © 2017. Elsevier Science & Technology. All rights reserved.

I. Characteristics and Taxonomy

Southern Hemisphere blue whales are on average larger than those in the Northern Hemisphere. The largest recorded were caught in the Southern Ocean and measured 31.7–32.6 m (104–107 ft) long. The largest recorded for the Northern Hemisphere was a 28.1 m (92 ft) female caught in Davis Strait. In the North Pacific females of 26.8 m (88 ft) and 27.1 m (89 ft) have been recorded. A 190-ton female was reported taken off South Georgia in 1947; however, body weights of adults generally range from 50 to 150 tons.

Blue whales project a tall (10–12 m) spout, denser and broader than that of fin whales (*B. physalus*). When surfacing, the blue whale raises its shoulder and blowhole region out of the water more than other rorquals. The prominent fleshy ridge just forward of the blowhole, or "splash guard," is strikingly large in this species.

Blue whales have a tapered elongated shape, a broad, relatively flat, U-shaped head, adorned by a prominent ridge from the splash-guard to the tip of the rostrum, and massive mandibles (Fig. 1). The black, 1 m long baleen plates found on each side of the upper jaw, number 270–395. There are 60–88 ventral pleats running longitudinally from the tip of the lower jaw to the navel, which enable ventral pouch to distend when feeding.

The dorsal fin, positioned far back on the body, is proportionally smaller than in other balaenopterids and ranges in shape, from a small nubbin to triangular and falcate. The flippers are long and bluntly pointed, slate gray, with a thin white border dorsally and white ventrally; they reach up to 15% of the body length.

Blue whales generally appear paler in coloration than all species of large whale except for the gray whale (*Eschrichtius robustus*), which is much smaller. The characteristic mottled pigmentation is a blend of light and dark shades of gray displayed in patches of varying sizes (Fig. 2). Underwater the color is slate blue on overcast days to silvery/turquoise on bright sunny days (Fig. 3). The mottling is found along the body dorsoventrally, occasionally on the flippers, but not on the head and tail flukes. Two pigmentation configurations are found in blue whales, one where a darker, dominant background is mottled with sparser pale patches of pigmentation, while in the other there is a predominantly pale background mottled with sparser dark patches. Individual blue whale pigmentation can vary from very sparse mottling, to densely mottled individuals. The mottling is unique to each whale, and is the basis for photoidentification studies. Distinct chevrons curving back from behind the blowholes can be found on some individuals. The tail flukes are predominantly gray above and below; however, some individuals have white ventral pigmentation patches that are used for individual identification (Sears et al., 1990). A yellow-green to brown cast, caused by the presence of a diatom (*Cocconeis ceticola*) film, can cover all or part of the body of blue whales found in cold waters. The yellowish, diatom-induced tint is the reason the "sulfur-bottom" moniker was once used for blue whales.

Three subspecies have been designated: what has been considered the largest, *B. musculus intermedia*, found in Antarctic waters; *B. musculus musculus* in the Northern Hemisphere; and *B. musculus brevicauda*, from the subantarctic zone of the southern Indian Ocean and south western Pacific Ocean, also colloquially known as the "pygmy" blue whale.

Our knowledge of the phylogeny of the baleen whales is still in flux. In recent molecular studies, the blue whale has been variously suggested to be the sister taxon of a clade including the Bryde's (*B. edeni*) and sei (*B. borealis*) whales, in combination with a sister clade of the fin and humpback (*Megaptera novaeangliae*) whales, with gray whales (*E. robustus*) the next up the tree (Rychel et al., 2004); in the same arrangement, but with the minke whales (*B. acutorostrata* and *B. bonaerensis*) coming in before the gray whale (Nikaido et al., 2005); again in the same arrangement but with the gray whale not included in the analysis, the balaenids being a sister clade to all the balaenopterids and sister taxon to a clade containing all the other baleen whales except the balaenids (Hatch et al., 2006). Morphological cladistic analyses grouped it with the common minke whale in a clade sister to the humpback. Further work is obviously needed.

II. Distribution and Abundance

Despite having being reduced greatly due to whaling, the blue whale remains a cosmopolitan species separated into populations from the North Atlantic, North Pacific, and Southern Hemisphere (Fig. 4). Photoidentification work from eastern Canadian waters

Figure 1 *Blue whale,* Balaenoptera musculus *(Illustrations by Uko Gorter).*

Copyright © 2017. Elsevier Science & Technology. All rights reserved.

Figure 2 *A blue whale surfaces, showing its striking mottled skin patterns and the small dorsal fin set far back on the body (Photo by Richard Sears).*

Figure 3 *A mother and calf blue whale off southern California, displaying the almost iridescent blue of the species (Photo by Bernd Würsig).*

indicates that blue whales from the St. Lawrence, Newfoundland, Nova Scotia, New England, and West Greenland all belong to the same population, whereas blue whales photoidentified from Northwest Africa, the Azores, Iceland, and Spitsbergen appear to be part of a separate population. The best-known population in the North Atlantic is that found in St. Lawrence from April to January, where 497 individuals have been catalogued photographically (Sears et al., 1990). In the eastern North Atlantic (NEA), where a catalog of 565 individuals exists, most blue whale photoidentification effort has been in Icelandic and Azorian waters. A few photoidentifications also come from Ireland, Jan Mayen, East Greenland, and Spain. It should be noted that considerably less field effort has been carried out in the NEA compared to the NWA. NWA blue whale abundance probably ranges from 600 to 1500 at this time, while blue whales may number from 1500 to 2500 in the NEA; however, more extensive photoidentification surveys are needed for more reliable estimates.

In the North Atlantic, blue whales reach Davis Strait and Baffin Bay in the west and to the east they travel to Jan Mayen and Spitzbergen and to the edge of pack ice during summer months. Though blue whale winter distribution in the NWA is not well defined, some have been observed in the St. Lawrence as late as February, while satellite tagging and acoustic studies confirm distribution out across the North Atlantic basin with presence at offshore seamounts, and as far south as Bermuda, the Carolinas and Florida. The southernmost observations in the NEA are off NW Africa and the Cape Verde Islands.

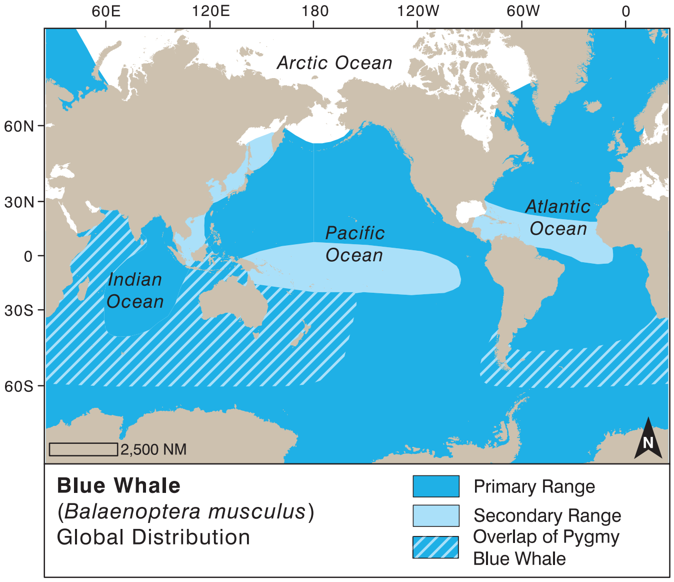

Figure 4 *Blue whale distribution. From Jefferson, T.A., Webber, M.A., and Pitman, R.L. (2015). "Marine Mammals of the World: A Comprehensive Guide to Their Identification," 2nd ed. Elsevier, San Diego, CA.*

In the North Pacific, acoustic analysis of blue whale vocalizations indicates that there are two populations. The best known is that from the eastern North Pacific where blue whales reach as far north as Alaska but are regularly observed from California in summer, south to Mexican and the Costa Rica Dome waters in winter. Abundance estimates of approximately 3000 animals (CV = 0.14) by line-transect methods and 2000 by capture–recapture (photoidentification) have been determined for this extensively studied population (Calambokidis and Barlow, 2004). From the Gulf of California, Mexico (winter/spring), blue whales migrate north (April/June), where a large proportion is found in California waters. From there some reach Canadian waters, and others may disperse north to the Gulf of Alaska.

A few blue whales have been reported recently from the western North Pacific, including the Aleutian Islands, Kamchatka, Kurils, and Japan.

Blue whales are also found in the northern Indian Ocean; however, it is not clear whether these form a distinct population. Recent studies off Sri Lanka have led to the creation of a photoidentification catalog of at least 100 individuals.

In the Southern Ocean, where the blue whale was historically most abundant, it is very rare today, with an abundance estimate at 1700 (95% confidence interval 860–2900) (Branch et al., 2007). A population of 424 (CV = 0.42) has been estimated to frequent the Madagascar Plateau in the austral summer (Best et al., 2003). Although the general population structure in the Southern Ocean is not well understood, evidence shows discrete feeding stocks. A feeding and nursing ground has been identified in southern Chile. Consistent with these feeding areas, the International Whaling Commission has assigned six stock areas for blue whales in the Southern Hemisphere.

Copyright © 2017. Elsevier Science & Technology. All rights reserved.

III. Ecology

Food availability probably dictates blue whale distribution for most of the year. Although they can be found in coastal waters of the St. Lawrence, Gulf of California, Mexico, and California, they are found predominantly offshore. They appear to feed almost exclusively on euphausiids (krill) worldwide in areas of cold current upwellings. When they locate suitably high concentrations of euphausiids, they feed by lunging and gulping large mouthfuls of prey. The mouth is then almost completely closed and the water is expelled by muscular action of the distended ventral pouch and tongue through the still exposed baleen plates. Once the water is expelled, the prey is swallowed. When they feed just a few meters below the surface, they often surface slowly, belly first, exposing the throat grooves of the ventral pouch. If the prey is close to the surface, blue whales lunge vigorously on their sides or lunge up vertically by projecting their cavernous lower jaws 4–6 m up through the surface. Although surface feeding has often been observed during the day, it is more usual for blue whales to dive to at least 100 m into layers of euphausiid concentrations during daylight hours and rise to feed near the surface in the evening, following the ascent of their prey in the water column. In the North Atlantic, blue whales feed on the krill species *Meganyctiphanes norvegica*, *Thysanoessa raschii*, *T. inermis*, and *T. longicaudata*; in the North Pacific, *Euphausia pacifica*, *T. inermis*, *T. longipes*, *T. spinifera*, and *Nyctiphanes symplex*. In Antarctic waters they prey on *E. superba*, *E. crystallorophias*, and *E. vallentini*.

Documentation of natural mortality is rare. The principal predator is the killer whale, *Orcinus orca*, but there is little evidence of attacks on blue whales in the North Atlantic or Southern Hemisphere. However, in the Gulf of California, Mexico, 25% of the blue whales photoidentified carry rake-like killer whale teeth scars on their tails, indicating that attacks occur with some regularity but are probably rarely successful. In the St. Lawrence, ice entrapment, where animals have been crushed, stranded, or suffocated by current and wind-driven ice floes in the late winter-early spring, has been reported.

IV. Behavior and Physiology

Blue whales are observed most commonly alone or in pairs; however, concentrations of 50 or more can be found spread out in areas of high productivity.

Although not noted for raising their flukes when diving, approximately 18% of blue whales observed in the western North Atlantic and Northeast Pacific do so. Studies off Sri Lanka report that 55% of blue whales there fluke up when diving.

When feeding at depth, blue whales will generally dive for 8–15 min; 20-min dives are not uncommon. The longest dive recorded was of 36 min; however, dives of more than 30 min are rare. Swimming at 3–6 km/hr is most common; however, they can attain travel speeds of 7–20 km/hr, and when chased by boats, predators, or interacting with other blue whales, they can reach upward of 35 km/hr.

Blue whales vocalize regularly throughout the year with peaks from midsummer into winter months. The majority of vocalizations are infrasonic sounds of 17–20 Hz, lower than humans can detect. Their sounds, at 188 decibels (re: 1 μPa at 1 m) are one of the loudest and lowest made by any animal. The calls can be heard easily for hundreds even thousands of kilometers under optimal oceanographic conditions, and may cover whole ocean basins. The low frequencies are ideal for communication between individuals of a widely dispersed and nomadic species through water without much loss of information. Geographic variation, seasonality, and diel variation in the sounds have been studied intensively in recent years (Stafford et al., 2004, 2005) and are useful in delineating populations.

Little is known of mating behavior in blue whales. However, female–male pairings have been noted with regularity in the St. Lawrence from summer into fall, some lasting for as long as 5 weeks. When a female/male pair is approached by a third blue whale—usually a male, vigorous surface displays ensue lasting for 7–50 min, where all three animals can be seen racing high out of the water.

Blue whales reach sexual maturity at 8–10 years of age. Length at sexual maturation in females from the Northern Hemisphere is 21–23 and 23–24 m in the Southern Hemisphere. Males reach sexual maturity at 20–21 m in the Northern Hemisphere and at 22 m in the Southern Hemisphere. Mating takes place from late fall and throughout the winter. Females give birth every 2–3 years in winter after a 10–12-month gestation period. The calves, which weigh 2–3 tons and measure 6–7 m at birth, are weaned when approximately 16 m long at 6–8 months. No specific breeding ground has been discovered for blue whales in any ocean, although mothers and calves are sighted regularly in the Gulf of California, Mexico, in late winter and spring, while low numbers of mother calf pairs have been sighted in the Costa Rica Dome region during the same period.

Longevity is thought to be at least 80–90 years and probably longer. Long-term photoidentification studies in the St. Lawrence and northeast Pacific, confirms that they live for at least 45 years.

VI. Interactions With Humans

Because of its great size and commercial value, blue whales were hunted relentlessly beginning in the late 1800s. The greatest number of blue whales was taken from the early 1900s until the late 1930s, with the peak being in the 1930–1931 season when nearly 30,000 were killed. The whaling of blue whales coincided with the advent of explosive harpoons, steam powered vessels, and of factory ships, which could process whale carcasses at sea. Blue whales were severely depleted by whaling, particularly in the Southern Hemisphere, where during the first half of the 20th century 325,000–360,000 were killed in Antarctic waters alone. A further 11,000 were taken in the North Atlantic, primarily in Icelandic waters, and 9500 in the North Pacific. This unbridled hunt for blue whales, which lasted until its worldwide protection in 1966, brought the blue whale to the brink of extinction. Still an endangered species today, there is evidence, however, of population increase in the Antarctic (Branch, 2004).

At least 25% of the blue whales photoidentified in the St. Lawrence carry scars that can be attributed to collisions with ships. Similar scarring has also been reported for Northeast Pacific blue whales and probably have a negative impact at populations.

Though 12% of blue whales found in the NWA carry marks related to contact with fishing gear, few lethal entanglements have been reported.

Persistent contaminants accumulated over time, such as PCBs commonly found in blue whales from eastern Canadian waters, may have an impact on reproduction and limit the recovery of certain populations.

Increasing anthropogenic noise from shipping and oil exploration may also limit recovery of blue whales.

See Also the Following Articles

Baleen Whales ■ Cetacean Life History ■ Noise ■ Pollution ■ Whaling, Modern

Copyright © 2017. Elsevier Science & Technology. All rights reserved.

References

Best, P.B., et al. (2003). The abundance of blue whales on the Madagascar Plateau, December 1996. *J. Cetacean Res. Manage.* **5**, 253–260.

Branch, T.A. (2004). Summary of evidence for increase in Antarctic (true) blue whales. *J. Cetacean Res. Manage.* **6**(Suppl), 256–258.

Branch, T.A., Stafford, K.M., Palacios, D.M., Allison, C., Bannister, J.L., Burton, C.L.K., Cabrera, E., Carlson, C.A., Galletti Vernazzani, B., Gill, P.C., and Hucke-Gaete, R. (2007). Past and present distribution, densities and movements of blue whales Balaenoptera musculus in the Southern Hemisphere and northern Indian Ocean. *Mamm. Rev.* **37.2**, 116–175.

Calambokidis, J., and Barlow, J. (2004). Abundance of blue and humpback whales in the eastern North Pacific estimated by capture-recapture and line-transect methods. *Mar. Mamm. Sci.* **20**, 63–85.

Hatch, L.T., Dopman, E.B., and Harrison, R.G. (2006). Phylogenetic relationships among the baleen whales based on maternally and paternally inherited characters. *Mol. Phylogenet. Evol.* **41**, 12–27.

Nikaido, M., et al. (2005). The baleen whale phylogeny and a past extensive radiation event revealed by SINE insertion analysis. *Mol. Biol. Evol.* **23**, 866–873.

Rychel, A.L., Reeder, T.W., and Berta, A. (2004). Phylogeny of mysticete whales based on mitochondrial and nuclear data. *Mol. Phylogenet. Evol.* **32**, 892–901.

Sears, R., Williamson, J.M., Wenzel, F., Bérubé, M., Gendron, D., and Jones, P.W. (1990). The photographic identification of the blue whale (*Balaenoptera musculus*) in the Gulf of St. Lawrence, Canada. *Rep. Int. Whal. Commun. (Spec. Iss.)* **12**, 335–342.

Stafford, K.M., Bohnenstiehl, D.R., Tolstoy, M., Chapp, E., Mellinger, D.K., and Moore, S.E. (2004). Antarctic-type blue whale calls recorded at low latitudes in the Indian and eastern Pacific Oceans. *Deep-Sea Res. I* **51**, 1337–1346.

Stafford, K.M., Moore, S.E., and Fox, C.G. (2005). Diel variation in blue whale calls recorded in the eastern tropical Pacific. *Anim. Behav.* **69**, 951–958.

Yochem, P.K., and Leatherwood, S. (1985). Blue whale (*Balaenoptera musculus* Linnaeus, 1758). In "Handbook of Marine Mammals", (S.H. Ridgway, and R. Harrison, Eds), Vol. 3, pp. 193–240. Academic Press, London.

BONES AND TEETH, HISTOLOGY OF

Lisa N. Cooper and Mary C. Maas

The bones and teeth of marine mammals, like those of other vertebrates, consist of both organic and mineral components. Because the mineral component (mostly calcium phosphate) predominates, the constituents of bones (bone and calcified cartilage) and teeth (cementum, dentine, and enamel) are referred as "hard tissues." Each of these hard tissues is distinguished by both its composition and microscopic structure. Many of the histological features of marine mammal teeth and bones are typical for mammals, and vertebrates, in general, but others are unique or unusual. Some of these may have evolved in conjunction with their shifts to marine habitats.

I. Bone

A. Bone Structure and Composition

Bone consists of a highly calcified, extracellular bone matrix, and cells (Fig. 1). Bone matrix (also known as osteoid) consists of about 33% organic matter (mostly Type I collagen) and 67% inorganic matter (calcium phosphate, mostly hydroxyapatite crystals). Bone is commonly classified according to its gross appearance as cancellous bone (bone with numerous, macroscopic interconnecting cavities, or trabeculae, also known as spongy or trabecular bone) or compact bone (dense lamellar bone without trabeculae), but both types have the same basic histological structure. In a typical mammalian long bone, the diaphysis (shaft) is composed predominantly of compact bone, with cancellous bone confined to the inner surface around a central medullary cavity while the epiphyses (articular ends) consist mostly of cancellous bone overlain by a thin, smooth layer of compact bone (Fig. 1A, 2A). In short bones, a core of cancellous bone is completely surrounded by compact bone, and in the flat bones of the skull, inner and outer plates of compact bone are separated by the diploë, a layer of cancellous bone.

B. Bone Formation, Growth, and Remodeling

Bone continues to remodel throughout life. Influences on bone remodeling include strain and stress imposed by movement and muscle action, hormones, and growth factors. Modifications of hormonal controls on bone growth and remodeling, in specific parts of the skeleton, are probably responsible for specializations in bone density patterns in some marine mammals (see below).

Because bone growth occurs throughout life, periodic growth marks in skeletal tissue, in particular, periodical deposition of periosteal bone layers, are potentially useful in mammalian age determination. Techniques of skeletal tissue age determination involve the counting of growth layer groups. Growth layer groups are sets of incremental growth lines defined by at least one change in mineral density, such as between more stained and less stained layers or dark and light layers. However, the dynamic nature of bone growth and remodeling limits the accuracy of bone growth layer group counts (Padian and Lamm, 2013).

C. Marine Mammal Bone

Marine mammals show two very different trends in bone architecture and histology, reduced or increased bone thickness, both of which are associated with their aquatic habits (Wall, 1983). Deep-diving marine mammals, especially Recent cetaceans, have bones that are lightweight and lack a thickened cortex unlike homologous elements in terrestrial mammals (Fig. 2A,B). They efficiently overcome buoyancy at depth by the active mechanism of lung collapse, while at surface their lighter bones may enhance buoyancy, allowing them to float with relatively little expenditure of energy. A pattern of reduced bone thickness has been thoroughly documented in small to medium-sized odontocetes, some of the large-bodied cetaceans, and some phocids (notably the elephant seal, *Mirounga*) and is characterized by replacement of cortical bone (the compact bone surrounding medullary cavities) with cancellous bone, which also fills the medullary cavities. This condition is apparently caused by imbalance between bone resorption and redeposition beginning early in ontogeny. Increase in cancellous bone in these mammals does not appear to be pathological—the microscopic architecture of cancellous bone in cetacean limbs is significantly more organized than that of typical osteoporotic bone.

In contrast, shallow-diving marine mammals, such as sirenians, overcome buoyancy while diving in large part by the static mechanism of *increased* bone thickness (Fig. 2C,D). Their bones contain relative more cortical bone compared to a typical mammal's bones. This is achieved in different ways—either by osteosclerosis (reduced size of the medullary cavity), by pachyostosis (swollen bones), or by a combination of both conditions (pachyosteosclerosis) (Domning and Buffrénil, 1991). Sirenians show pronounced

Copyright © 2017. Elsevier Science & Technology. All rights reserved.

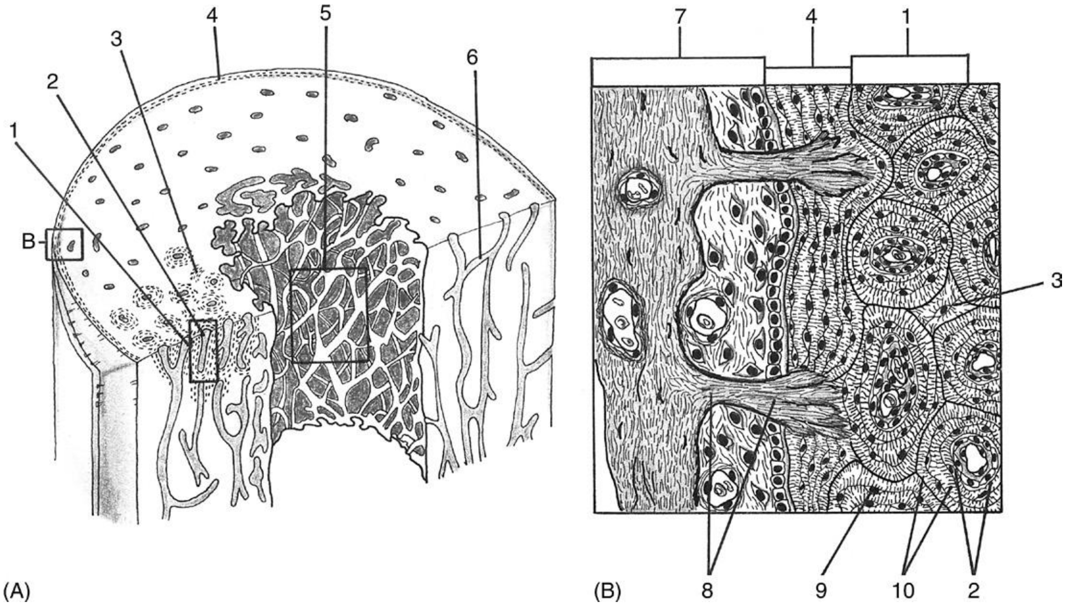

Figure 1 *(A) Schematic model of the wall of a mammalian long-bone diaphysis, consisting of an outer layer of compact bone and an inner layer of cancellous bone, surrounding a central medullary cavity. Periosteum covers the outer bone surface, and endosteum covers the inner bone surface. (B) Enlarged diagram of periosteum and compact bone in (A). 1, osteon; 2, haversian canal; 3, interstitial lamellae; 4, outer circumferential lamellae; 5, cancellous bone; 6, Volkman's canal; 7, periosteum; 8, Sharpey's fibers; 9, lacuna; 10, concentric lamellae. Adapted from Ten Cate (1989).*

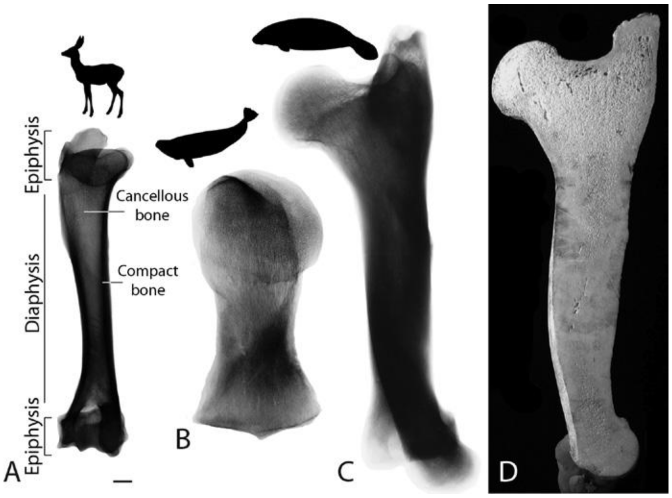

Figure 2 *The long bones of terrestrial mammals have a different organization compared to marine mammals. (A) Most terrestrial mammals have a diaphysis composed predominantly of compact bone, with cancellous bone residing in the medullary cavity. Marine mammals display two long bone phenotypes. (B) The long bones of most deep-diving and fast-swimming cetaceans are composed almost exclusively with cancellous bone, or osteosclerotic. (C, D) Shallow-swimming marine mammals, like manatees, have long bones made almost entirely of thickened compact bone. X-rays of the humerus of (A) deer, (B) beluga, and (C) manatee. (D) Pachyosteosclerotic humerus of a manatee cut in half, to reveal the absence of a medullary cavity and the extent cortical bone has infiltrated the medullary cavity. Scale bar is 1 cm in length.*

pachyosteosclerosis (Fig. 2C,D), especially in the thoracic and occipital regions. Similarly, walruses and some seals have unusually thickened limb bones. Hemopoiesis, the production of blood cells and platelets, typically occurs in the marrow of long bones. Because osteosclerosis reduces or eliminates the medulla, the location of hemopoiesis shifted to the vertebral bodies in sirenians and some cetaceans, and to the spleen in pinnipeds and other cetaceans.

Ongoing research in bone histology of extinct marine mammals indicates extremes of increased or reduced bone thickness evolved independently several times in different groups of marine mammals. Fossil sirenians show pachyosteosclerosis was the result of independent evolution of pachyostosis and osteosclerosis. Likewise, in contrast to recent cetaceans, some bones of extinct Eocene archaeocetes are osteosclerotic. The earliest cetacean, *Pakicetus* (Pakicetidae), shows a pattern of osteosclerosis similar to that seen in extant semiaquatic mammals, probably achieved through osteoclast inhibition (Gray et al., 2007). Later, more fully aquatic archaeocetes, including *Ambulocetus* (Ambulocetidae), *Kutchicetus* (Remingtonocetidae), and *Gaviacetus* (Protocetidae) show histological features associated with pachyostosis as well as osteosclerosis. In *Basilosaurus* (Basilosauridae), osteosclerosis of ribs is very pronounced, with total replacement of medullary trabecular bone by compact bone (Buffrénil et al., 1990). In contrast, long bones of some dorudontine archeocetes show *reduced* thickness of periosteal compact bone, as in modern cetaceans (Madar, 1998). This, along with greater degree of bone remodeling in ribs of *Zyghoriza* (Dorudontinae) than in other archaeocetes suggests that a regional pattern of histological change preceded the systemic osteoporosis of later cetaceans, in conjunction with the functional requirements of the shift from terrestrial to semiaquatic to fully aquatic locomotion (Gray et al., 2007).

Copyright © 2017. Elsevier Science & Technology. All rights reserved.

The ear region of cetaceans is also characterized by histological specializations of the bone. Both periotic and tympanic bones are noteworthy for their density, compactness, and high mineral content, in comparison with other mammals. This pachyosteosclerosis is due to the hypermineralized state of embryonic woven bone, which is maintained throughout life; its occurrence early in development (in the common dolphin, it begins during the fetal stage and is complete by the first year) probably reflects its role in sound transmission (Buffrénil et al., 2004). Some of these dense bones (involucrum of the tympanics of some cetaceans, the ribs of manatees) lack the dense collagen framework seen in terrestrial mammals. Instead, organics of these dense bones are mostly made of nonessential amino acids.

Bone of the toothed whale *Mesoplodon densirostrus* exhibits unique histological features. The rostral bone of this odontocete, which is among the densest bone known among tetrapods, is characterized by hypermineralized secondary osteons. These osteons have unusually well-aligned parallel and platy hydroxyapatite crystals and a tubular network of unusually thin collagen fibrils, and thus differ markedly from the structure of haversian systems of typical mammalian lamellar bone (Zylberberg et al., 1998).

Periodic deposition of periosteal bone layers has been used in studies of age determination in mammals, though limited in use by the fact that mammalian bone undergoes remodeling throughout life (Klevezal, 1996). Bone growth layer groups have been studied in a variety of marine mammals including sirenians, pinnipeds, and odontocetes.

II. Cementum

A. Cementum Structure and Composition

Teeth of marine mammals, like all mammals, consist of a crown, which extends above the gums, and one or more roots, which extend below the gum line and hold the teeth in bony sockets (alveoli). The roots are covered by cementum (also known as cement), which sometimes extends to cover part of the crown, overlapping the cervical enamel. Cementum is similar in composition to bone. Its mineral component (65% by wet weight) consists of crystals of an impure form of hydroxyapatite similar in shape and size to those of bone.

Incremental growth layers known as cementing lines or resting lines are sometimes a prominent histological feature of both cellular and acellular cementum. Cementing lines, like the incremental growth layers found in bone, dentine, and enamel, are distinct layers that parallel the developing surface. Due to periodic variation in mineralization during development, they contrast with adjacent layers. Cementum growth layer groups, like those of bone and dentine, can be empirically defined by at least one change in mineral density, such as between translucent and opaque layers, dark and light layers, ridge and groove, or more stained and less stained layers. Empirical studies have shown that cementum growth layer groups record the periodicity of tissue formation, and thus are useful in age determination.

B. Marine Mammal Cementum

Cementum in marine mammals is for the most part structurally similar to that of other mammals. Cementum growth layer groups are used in conjunction with dentine and bone growth layer groups to estimate age in marine mammals, though their relative clarity varies among species. In some species, cementum formation continues beyond that of dentine, which is an advantage in age determination. In ziphiid whales, where the cementum typically extends over most of the crown and may comprise the bulk of the tooth, cementum growth layer groups are distinguishable without magnification. Ziphiids also have been reported to have an unusual, possibly vascular cementum (Boyde, 1980).

III. Dentine

A. Dentine Structure and Composition

Dentine comprises the bulk of the volume of teeth of most mammals. In the crown, dentine is covered by enamel and in the root it is covered by cementum. Dentine has 75% mineral (hydroxyapatite). Most of the small (2–3 nm in thickness and probably 20–100 nm in length) hydroxyapatite crystals are aligned parallel to each other and to the small collagen fibrils, but others are radially oriented and form spherical or semispherical structures known as calcospherites. Calcospherites are difficult to distinguish histologically because they typically fuse together.

B. Marine Mammal Dentine

The dentine of most marine mammals is structurally similar to that of other mammals, but there are some exceptions. In some, notably the narwhal and sperm whale, the large von Korff fibers are not restricted to the mantle dentine but extend throughout the thickness of dentine, where they are located in the walls of dentine tubules. Denticles have been reported in some odontocetes and sclerotic dentine is found in some marine mammals, especially in seals.

Marine mammal dentine is characterized by prominent incremental growth layers (Fig. 3B) that lie at angles to dentine tubules, and vary in their intensity, both within and among individuals. The finest scale layers are the incremental von Ebner lines, which probably reflect diurnal variation in matrix fiber arrangement. Von Ebner lines appear as alternating dark and light lines in ground sections under polarized light. Other, larger-scale incremental growth layers reflect changes in density due to differences in mineralization. These include the neonatal line, a very prominent growth layer that marks physiological disturbance associated with birth, and other less distinct and consistent growth layers whose physiological bases are uncertain. In some seals, the growth layer groups are accentuated by layers of interglobular dentine. Whatever their origins, there is a regular repetition to growth layer groups that seems to reflect annual or semiannual growth cycles, and counting of dentinal growth layer groups is a primary basis of age determination in pinnipeds, sirenians, and odontocetes.

IV. Enamel

A. Enamel Structure and Composition

Enamel covers the tooth crown in most mammals. It is the most highly mineralized tissue in the body, consisting almost entirely (95% by weight) of highly structured arrangements of hydroxyapatite crystallites. The remaining fraction consists of water and two classes of proteins unique to enamel—enamelins, which predominate in mature (fully mineralized) enamel, and amelogenins, which predominate in developing enamel. The histological structure of enamel reflects the organization of crystallites into units of increasing scale, two of which are enamel prisms and enamel types. This structural organization is determined during enamel development. Unlike bone, cement, and dentine, enamel does not remodel after its initial deposition.

Enamel prisms are cylindrical bundles of largely parallel hydroxyapatite crystals extending outward from the EDJ toward the outer tooth surface. The prism boundaries are defined by differences in orientations prismatic crystallites and those of the

Copyright © 2017. Elsevier Science & Technology. All rights reserved.

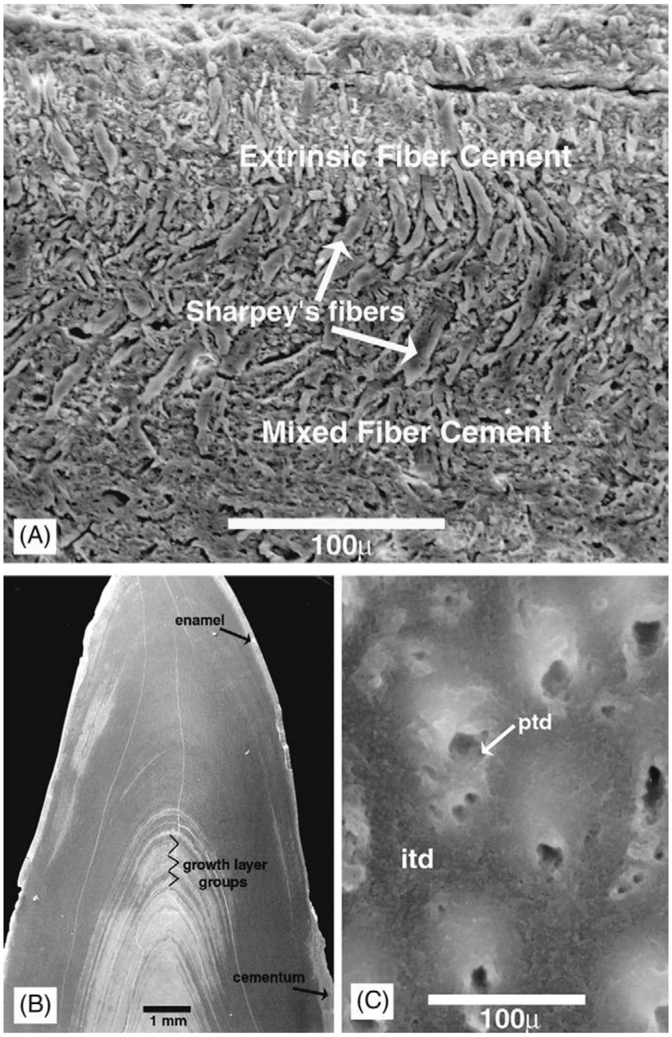

Figure 3 *Scanning electron microscopy images of an isolated tooth of an unidentified delphinoid cetacean (Yorktown Formation, Pliocene, from the Lee Creek Mines, NC). The specimen has been sectioned longitudinally, polished, and etched with dilute HCl. (A) High-magnification view of cementum, which grades from extrinsic fiber cement on the outer periphery (top) to mixed fiber cement closer to the cementum–dentine junction (bottom). Classification of cementum depends on the proportion of Sharpey's fibers contained within the matrix. (B) Thin layers of enamel and cementum lie peripheral to dentine of the crown and root. Dentine growth layer groups appear as pairs of dark/light bands. (C) High-magnification view of dentine. The walls of cross-sectioned dentine tubules contain hypermineralized peritubular dentine (ptd). Less mineralized intertubular dentine (itd) occurs between tubules.*

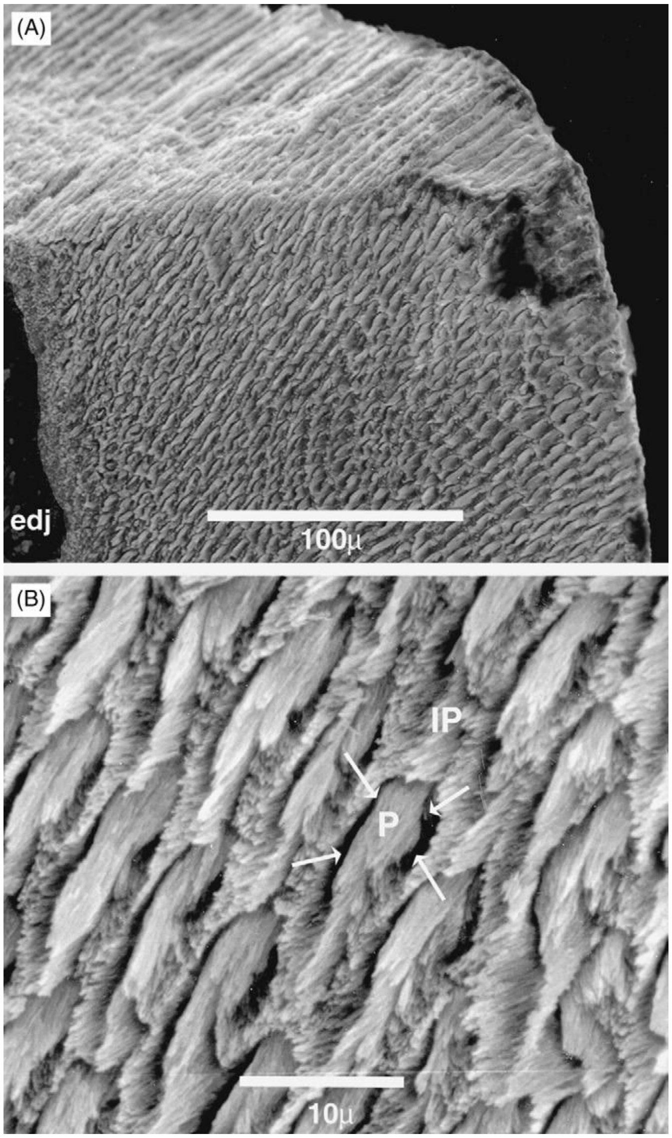

Figure 4 *(A) Scanning electron microscopy image of fractured enamel near tip of tooth (unidentified Pliocene odontocete, Lee Creek Mine, NC). The naturally fractured surface (at top) shows that the prisms take a straight course from the enamel–dentine junction (EDJ) to the outer surface, as is typical in radial enamel. (B) High-magnification view showing enamel prisms (P) sectioned oblique to their long axes. Prism crystallites are parallel to each other, but not to crystallites in adjacent interprismatic enamel (IP). Arrows indicate the position of the prism sheath, which has been artificially enlarged in this acid-etched specimen.*

adjacent enamel that fills the spaces between prisms (Fig. 4). This enamel is called interprismatic enamel. It is compositionally identical to enamel prisms, but differs in crystallite orientation. The submicroscopic gap produced by the change in crystallite orientations at the prism–interprismatic boundary is known as the prism sheath (Fig. 4). Prism sheaths contain slightly greater concentrations of water and protein than the surrounding enamel, and thus are less dense. This allows prism patterns (the cross-sectional shapes and packing arrangement of prisms and interprismatic enamel) to be distinguished in ground sections or in acid-etched scanning electron microscope preparations. Prisms may have closed, circular cross sections or open, arc-shaped cross sections. Prism patterns have been used to distinguish among some mammalian groups, but there is considerable variation within individuals and considerable parallelism among different groups.

Enamel types describe the organization of enamel at a scale greater than individual crystallites or prisms. Common enamel types include parallel crystallite enamel, radial enamel, and decussating enamel. Parallel crystallite enamel, a type of nonprismatic enamel, is a volume of enamel in which hydroxyapatite crystallites

Copyright © 2017. Elsevier Science & Technology. All rights reserved.

are parallel to each other with no discontinuities in orientation and lacking larger-scale structural features, other than incremental lines. Radial enamel refers to a volume of prismatic enamel where prism long axes are parallel to one another and directed radially outward from the EDJ. Decussating enamel is a volume of enamel characterized by layers of parallel prisms, one or more prisms in thickness, whose long axes alternate in orientation with prisms in adjacent layers. Decussating enamel, also known as Hunter–Schreger bands (HSB), includes undulating HSB, where layers of similarly oriented prisms have a gently undulating course from the EDJ to the surface, and zigzag HSB, where the layers undulate with a pronounced vertical amplitude. Differences in enamel types not only have a phylogenetic component but also have different mechanical properties that can be important functionally—parallel crystallite enamel may be harder than prismatic enamel, but prismatic enamel, especially decussating enamel, is more resistant to cracks induced by chewing stress.

B. Marine Mammal Enamel

Although the crowns of most marine mammal teeth are covered with enamel, there is considerable variation in its structural complexity among and within orders. Likewise, prism patterns vary among and within orders, though there is no compelling evidence that prism patterns are diagnostic of particular marine mammal groups.

Most extant cetaceans have thin, structurally simple enamel. In some the enamel consists of a thin layer of radial prismatic enamel with or without an outer layer of nonprismatic parallel crystallite enamel, and in many species the tooth enamel consists entirely of nonprismatic parallel crystallite enamel. In contrast, the most primitive cetacean, the fossil *Pakicetus*, had relatively thick enamel with a more complex structure consisting of parallel crystallite enamel, radial enamel, and a thick inner layer of undulating Hunter–Schreger bands. Later, archaeocetes show the same arrangement of enamel types, but almost all more derived odontocetes have much less complex enamel. This has led some workers to conclude that the enamel of most extant cetaceans is evolutionary degenerate. Only two extant odontocetes, the Indus dolphin *Platanista* and Amazon dolphin *Inia*, have well-developed, undulating HSB. It is unclear whether these were independently acquired in response to functional demands of their diet or a primitive retention from archaeocete ancestors.

Extant sirenians (*Dugong* and *Trichechus*) are reported to have radial enamel with variably circular and arc-shaped prism cross sections. Similar enamel has been reported for some fossil sirenians, and it is likely that this is primitive for the group. Pinniped enamel has not been described in detail, but enamel of some species appears to be more complex than that of sirenians. *Phoca* has undulating HSB, and walrus enamel shows a transition from undulating HSB to zigzag HSB near cusp tips.

Enamel incremental lines generally are not used in age determination of marine mammals. The thin enamel of many species makes resolution of these lines difficult, and, more importantly enamel only records the period of tooth development during which enamel is laid down, which, in most cases, is before birth.

See Also the Following Article

Age Estimation

References

Boyde, A. (1980). Histological studies of dental tissues of odontocetes. *Rep. Int. Whal. Comm. Spec. Iss.* (3), 65–87.

Buffrénil, Vd, Ricqlés, A.D., Ray, C.E., and Domning, D.P. (1990). Bone histology of the ribs of the archaeocetes (Mammalia: Cetacea). *J. Vertebr. Paleontol.* **10**, 455–466.

Buffrénil, Vd, Dabin, W., and Zylerberg, L. (2004). Histology and growth of the cetacean petro-tympanic bone complex. *J. Zool. (Lond.)* **262**, 371–381.

Domning, D.P., and Buffrénil, Vd (1991). Hydrostasis in the Sirenia: Quantitative data and functional interpretations. *Mar. Mamm. Sci.* **7**, 331–368.

Gray, N.-M., Kainec, K., Madar, S., Tomko, L., and Wolfe, S.C. (2007). Sink or swim? Bone density as a mechanism for buoyancy control in early cetaceans. *Anat. Rec.* **290**, 638–653.

Klevezal, G. (1996). "Recording Structures of Mammals, Determination of Age and Reconstruction of Life History." Translated by M.V. Mina and A.V. Oreshkin. A.A. Balkema, Rotterdam.

Madar, S.I. (1998). Structural adaptations of early archaeocete long bones. In "The Emergence of Whales" (J.G.M. Thewissen, Ed.), pp. 353–378. Plenum Press, New York.

Wall, W.P. (1983). The correlation between high limb-bone density and aquatic habits in recent mammals. *J. Paleontol.* **57**, 197–207.

Zylberberg, L., Traub, W., Buffrénil, Vd, Allizard, F., Arad, T., and Weiner, S. (1998). Rostrum of a toothed whale: Ultrastructural study of a very dense bone. *Bone* **23**, 241–247.

BOTTLENOSE DOLPHIN, *TURSIOPS TRUNCATUS*, COMMON BOTTLENOSE DOLPHIN

Randall S. Wells and Michael D. Scott

I. Characters and Taxonomy

Common bottlenose dolphins (*Tursiops truncatus*), usually simply termed "bottlenose dolphins," are arguably the best known of all cetaceans. They figured prominently in the legends of the ancient Greeks and Romans and were described in the writings of Aristotle, Oppian, and Pliny the Elder. Many books and review articles for scientific and public audiences have focused on this species (e.g., Caldwell and Caldwell, 1972; Leatherwood and Reeves, 1982, 1990; Reynolds et al., 2000; Vollmer and Rosel, 2013). The name *Tursiops* can be translated as "dolphin-like," deriving from the Latin *Tursio* ("dolphin") and the Greek suffix *-ops* ("appearance"); *truncatus* derives from the Latin *trunco-* ("truncated"), apparently referring to the worn teeth interpreted by Montagu (1821) as an identifying characteristic.

Fossil records extend back several million years (Barnes, 1990) and the geographical distribution of the fossils falls within the range of the modern animals. Anatomical features suggest that *Tursiops* evolved from some ancestral group of extinct fossil Delphininae, perhaps related to the subfamily Steninae, which might have evolved from the Kentriodontidae. Moura et al. (2013) used mitochondrial genomes and records of past environmental changes to suggest that *Tursiops* originated in Australasian coastal habitats.

Bottlenose dolphins are cosmopolitan in distribution, and demonstrate a great deal of geographical variation in morphology, with a general drawing in Fig. 1. *T. truncatus* is found in most of the world's warm temperate to tropical seas, in coastal as well as

Copyright © 2017. Elsevier Science & Technology. All rights reserved.

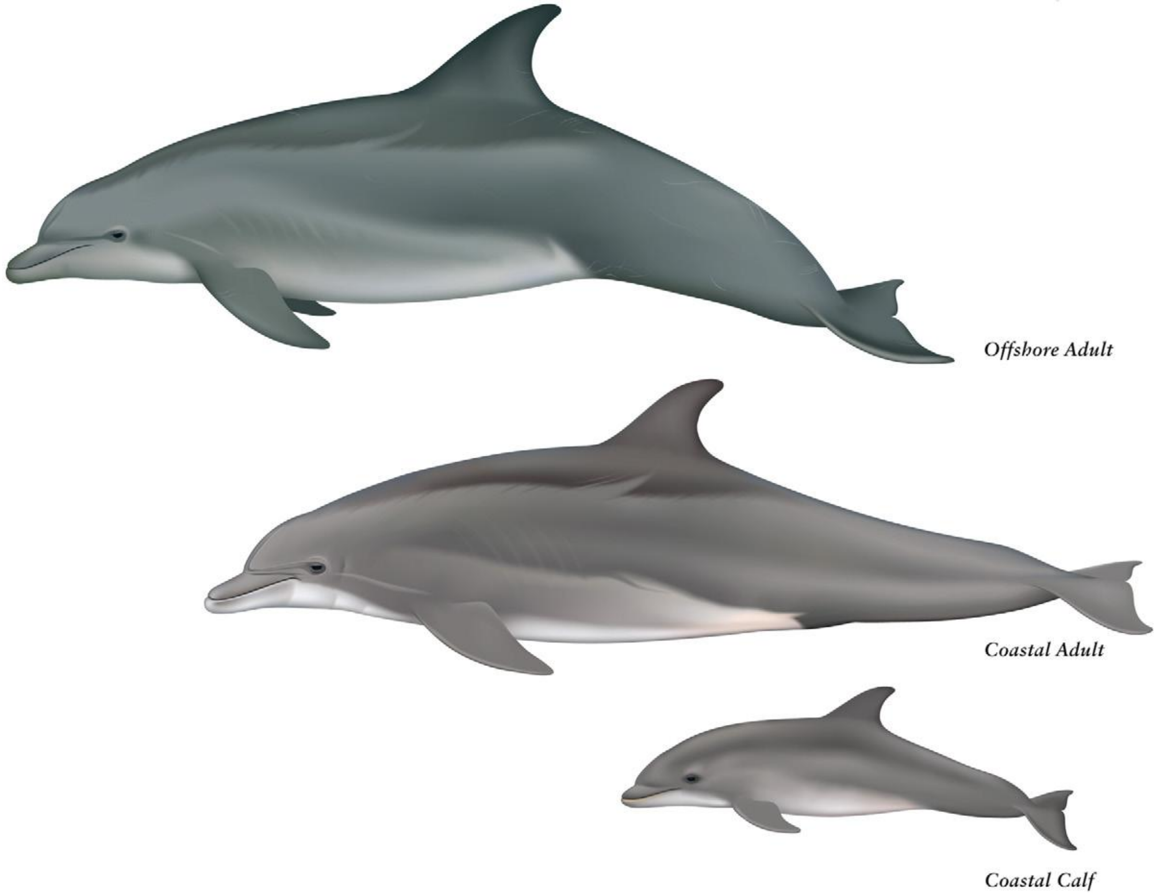

Figure 1 *Generalized body shape and shading of offshore and coastal common bottlenose dolphins (Illustrations by Uko Gorter).*

offshore waters (Fig. 2). They are recognizable by their generalized appearance—a medium-size, robust body, a moderately falcate dorsal fin, and dark coloration, with a sharp demarcation between the melon and the short rostrum (Fig. 3). Adult lengths range from about 2.5 m to about 3.8 m, varying by geography (Mead and Potter, 1990). Bottlenose dolphins are light gray to black dorsally and laterally, with a light belly (Fig. 4), and some show a light blaze or brush marking on their sides. A distinct cape may be visible or may be obscured when the color pattern is very dark.

The taxonomic status of the genus *Tursiops* is problematic. Variations in cranial characteristics associated with feeding, and variations in body size and coloration associated with water temperature, ocean basins, and inshore versus offshore ecotypes have led to descriptions of at least 20 nominal species of *Tursiops* (Hershkovitz, 1966; Rice, 1998). Recognition of the polymorphic nature of *Tursiops* and clinal variation led to general agreement for many years that *Tursiops* was a single-species genus. There are now two recognized species within the genus (*T. aduncus*, "the Indo-Pacific bottlenose dolphin," and *T. truncatus*) and two subspecies (*T.t. ponticus*, "the Black Sea bottlenose dolphin," and *T.t. truncatus*). The two species are not sister species and thus the genus is not a "natural" one; it contains species that are more closely related to species outside the genus than to each other (Perrin et al., 2013). One suggested solution based on taxonomic principles is to place *Tursiops*, along with *Stenella*, *Lagenodelphis*, and *Sousa* within the genus *Delphinus* (LeDuc et al., 1999; Perrin et al., 2013).

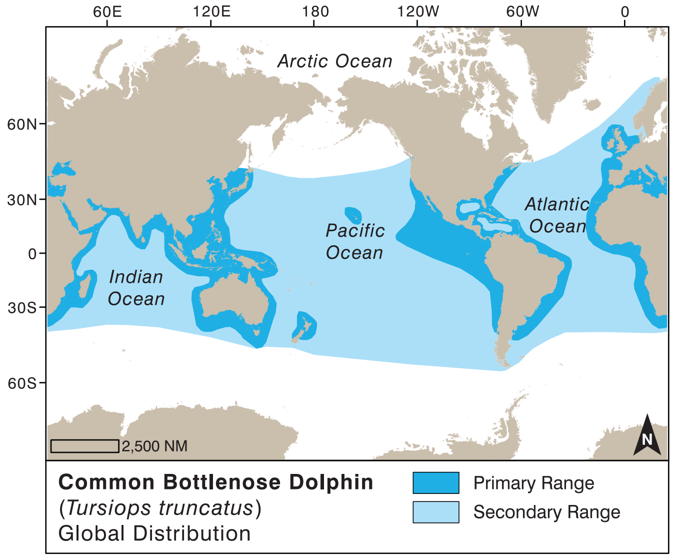

Figure 2 *Common bottlenose distribution. From Jefferson, T.A., Webber, M.A., and Pitman, R.L. (2015). "Marine Mammals of the World: A Comprehensive Guide to Their Identification," 2nd ed. Elsevier, San Diego, CA.*

Copyright © 2017. Elsevier Science & Technology. All rights reserved.

Figure 3 *Lateral view of an adult common bottlenose dolphin,* Tursiops truncatus, *off Sarasota, Florida.*

Figure 4 *Ventral view of a male common bottlenose dolphin,* Tursiops truncatus.

II. Distribution and Abundance

Bottlenose dolphins are found in temperate and tropical marine waters around the world, with an estimated 600,000 animals worldwide (Fig. 3). In the Pacific, they are commonly found as far north as the southern Okhotsk Sea, the Kuril Islands, and central California. In the Atlantic, they are seen inshore during summer months off New England, offshore as far north as Nova Scotia, and they have been recorded off Norway and the Lofoten Islands. Bottlenose dolphins occur as far south as Tierra del Fuego, South Africa, Australia, and southern New Zealand. Limits to the species' range appear to be temperature related, either directly or indirectly, through distribution of prey. Off the coasts of North America they tend to inhabit waters with surface temperatures ranging from about 10°C to 32°C. At the northern limit of the species' range in the western North Atlantic, they are seasonally migratory, with a more southerly distribution in the winter.

III. Ecology

Tursiops inhabits most warm temperate and tropical shorelines, adapting to a variety of marine and estuarine habitats, even ranging into rivers for brief periods. Bottlenose dolphins are primarily coastal, but are also found in pelagic waters, near oceanic islands, and over the continental shelf, especially along the shelf break. In the Indian Ocean, *T. truncatus* tends to inhabit offshore waters, whereas *T. aduncus* is the more-common coastal species.

The diets of bottlenose dolphins have been described from many regions (Barros and Odell, 1990). A large variety of fish and/or squid forms most of the diets, although bottlenose dolphins seem to show a consistent preference for sciaenids, scombrids, and mugilids. Most fish prey are bottom dwellers. Noise-producing fishes make up a large part of the *Tursiops* diet, presumably because sound helps the dolphins to locate prey (Berens McCabe et al., 2010). Differences in diets have been found between inshore and offshore *Tursiops* ecotypes. Across a population, bottlenose dolphins may appear to be generalists with regards to prey, but individuals within the population may show some degree of specialization (Rossman et al., 2015).

Sharks are the most important predators of bottlenose dolphins, although killer whales (*Orcinus orca*) may also occasionally prey on them. Mutual tolerance during encounters between sharks and dolphins is probably typical, but as many as half of all bottlenose dolphins bear shark-bite scars as evidence of occasional encounters, depending on the region. Most wounds and scars from sharks tend to be found on the posterior and ventral regions of the dolphins, suggesting that the dolphins were ambushed from behind and below; some attacks may have been sharks defending a territory. The primary shark predators of bottlenose dolphins are bull (*Carcharhinus leucas*), tiger (*Galeocerdo cuvier*), great white (*Carcharodon carcharias*), and dusky sharks (*Carcharhinus obscurus*) (Wood et al., 1970). Detailed observations suggest that certain species of sharks are recognized as potential threats (McBride and Hebb, 1948; Irvine et al., 1973).

Anecdotal accounts describe bottlenose dolphins attacking sharks by butting them with their rostra or by striking them with their flukes (Wood et al., 1970). Defense may explain the apparently high survival rate indicated by the shark-bite scars on living dolphins. The infrequent occurrence of shark-bite scars on young dolphins indicates either that the calves are well protected by others or that attacks on young dolphins are generally fatal (Wells et al., 1987; Cockcroft et al., 1989a).

Stingrays are an important source of mortality for coastal bottlenose dolphins. Dolphins wounded externally, or internally from ingestion of small rays, may die if the barb migrates and penetrates vital organs or causes infections.

IV. Behavior and Physiology

Coastal bottlenose dolphins exhibit a full spectrum of movements, including seasonal migrations, year-around home ranges, transience, and a combination of occasional long-range movements and repeated local residency (Caldwell, 1955; Wells and Scott, 1999; Toth et al., 2011). Much less is known about the ranging patterns of pelagic bottlenose dolphins. In some places, coastal dolphins living at the high-latitude or cold-water extremes of the species' range may migrate seasonally, as is the case along the Atlantic coast of the United States. Long-term residency has been reported from

Copyright © 2017. Elsevier Science & Technology. All rights reserved.

many parts of the world and may take the form of a relatively permanent home range or repeated occurrence in a given area over many years. For example, the year-round residents of several dolphin communities along Florida's west coast have maintained relatively stable, slightly overlapping home ranges during more than 45 years of observations and through at least five generations; seasonal changes in habitat use may occur within the ranges (Scott et al., 1990; Wells and Scott, 1999). Nearby ranges sometimes can be distinguished by genetic differences (Duffield and Wells, 2002; Sellas et al., 2005; Parsons et al., 2006). Home ranges are often demarcated by physiographic features such as passes or abrupt changes in water depth. Within island chains, populations may associate closely with particular islands or range throughout the archipelago (Baird et al., 2009; Martien et al., 2012; Castilho et al., 2015; Tobeña et al., 2014). Quérouil et al. (2007) suggested that bottlenose dolphins occurring in the pelagic waters of the North Atlantic belong to a large oceanic population.

Longer-distance movements have been reported for coastal bottlenose dolphins, including range shifts of more than 600 km in apparent response to an El Niño warm-water event (Wells et al., 1990), dispersal of more than 1200 km from eastern Scotland to Ireland (Robinson et al., 2012), and a 600-km roundtrip for several identifiable dolphins in Argentina (Würsig and Würsig, 1979). Average daily movements of 33–89 km, monitored through travel distances of as much as 4200 km, have been reported for bottlenose dolphins in offshore waters.

Bottlenose dolphins are typically found in groups of 2–15 individuals, although groups of more than 1000 have been reported (Leatherwood and Reeves, 1982; Shane et al., 1986; Scott and Chivers, 1990). In general, bottlenose dolphins in bays and estuaries tend to form smaller groups than those in offshore waters, but the trend does not continue linearly with increasing distance from shore. Group composition tends to be dynamic, with sex, age, reproductive condition, familial relationships, and affiliation histories appearing to be the most important determining factors (Wells, 2014). Subgroupings may be stable or repeated over periods of years. Basic social units include nursery groups, mixed sex groups of juveniles, and adult males as individuals or strongly bonded pairs (Wells et al., 1987; Owen et al., 2002; Rogers et al., 2004). Females bear calves sired by multiple males over the course of a lifetime; long-term monogamous bonds have not been observed (Duffield and Wells, 2002; Wells, 2014). While social units may be stable over time, large-scale environmental perturbations such as hurricanes can lead to restructuring (Elliser and Herzing, 2011).

Dominance hierarchies have been observed for dolphins under human care, with large adult male bottlenose dolphins dominating all other pool-mates, females forming a less-rigid hierarchy, with the largest females dominant over smaller animals. Aggressive behaviors including contact and posturing are used to establish and maintain hierarchies. Serious agonistic interactions have been noted in the wild between male conspecifics (Parsons et al., 2003) as well as with Atlantic spotted dolphins (Herzing et al., 2003).

Bottlenose dolphins in the wild appear to be active both during the day and at night, interspersing bouts of feeding, traveling, socializing, and resting (Shane et al., 1986; Wells et al., 2013). The duration and frequency of activities are influenced by such environmental factors as season, habitat, time of day, and tidal state, and by physiological factors such as reproductive seasonality. Bottlenose dolphins feed in a large variety of ways and habitats, primarily as individuals, but cooperative herding of schools of prey fish also occurs. Prey capture can involve: (1) high-speed chases with a pin-wheeling capture at the surface, (2) "fishwhacking" in which a fleeing fish is struck with the dolphin's flukes and often knocked clear of the water, (3) strand-feeding in which groups of dolphins send a wave of water that pushes fish onto mudbanks and then partially beach themselves to capture the fish, (4) creating bubble bursts to drive prey to the surface, and (5) herding and perhaps disorienting fish with percussive leaps or tail slaps ("kerplunking"). A particularly intricate cooperative feeding pattern, mud ring feeding, involves one dolphin creating a mud plume in the shape of a ring, and then the dolphin group members lunging in air at the fish jumping out of the ring as it closes (Torres and Read, 2009). Calves apparently learn foraging specializations from their mothers, and patterns may spread through a population from observation, as an indication of cultural transmission of knowledge (Wells, 2003).

Bottlenose dolphins in shallow habitats tend to make relatively brief dives, surfacing on average twice every minute. In deep water habitats, such as the Bermuda Pedestal, dives to more than 1,000 m and for longer than 13 min have been documented, correlating with reported nightly vertical migrations of mesopelagic prey.

Bottlenose dolphins produce three primary categories of sounds: whistles, echolocation clicks, and burst-pulse sounds. Dolphins produce a large variety of whistles, including largely stereotypic "signature whistles" that are individually specific and appear to be used to communicate identity, location, and possibly emotional state (Caldwell et al., 1990; Janik and Sayigh, 2013). Bottlenose dolphins copy the signature whistles of others, addressing the whistle owner, and providing further support of the idea that signature whistles serve as abstract labels or "names" (King and Janik, 2013). They exchange signature whistles when encountering others (Quick and Janik, 2012). Once the signature whistle develops in neonates, it remains stable for many years. Bruck (2013) suggested that bottlenose dolphins have the potential for lifelong memory for each other regardless of relatedness, sex, or duration of association. The signature whistles of many male calves are similar to the whistles of their mothers while those of female calves are not. Recent studies have demonstrated that bottlenose dolphins spread over distances of hundreds of meters to more than 5 km may remain in acoustic contact with one another through whistles (Jensen et al., 2012). Dolphin echolocation involves the production of "clicks," with peak frequencies of about 40–130 kHz (Au, 1993). Echolocation is hypothesized to be used in navigation, foraging, communication, and predator detection (Nowacek, 2005; Quintana-Rizzo et al., 2006). Burst-pulses ("squawks") tend to be produced during social interactions. Low-frequency narrow-band social calls (Simard et al., 2011) and context-specific food-associated calls have also been described (King and Janik, 2015).

Bottlenose dolphins commonly swim with, interact with, and occasionally hybridize with, other species. Aggressive and associative interactions with Atlantic spotted dolphins (*Stenella frontalis*) occur over the Bahama Banks (Elliser and Herzing, 2016). Bottlenose dolphins have been observed to kill harbor porpoises (*Phocoena phocoena*) (Cotter et al., 2012). Interactions with humpback whales (*Megaptera novaeangliae*) described as "play" have been reported. In New Zealand, bottlenose dolphins have been observed regularly associating with and feeding cooperatively with false killer whales (*Pseudorca crassidens*) (Zaechsmar et al., 2013).

V. Life History

Observations and analyses of growth layer groups in teeth have shown that in Sarasota Bay, Florida, female bottlenose dolphins can live up to more than 67 years, and males up to 52 years. Calves

Copyright © 2017. Elsevier Science & Technology. All rights reserved.

achieve most of their growth during the period of suckling, that is, the first 1.5–2 years of life. Females typically reach sexual and physical maturity before males, leading to sexual dimorphism in some regions. Age at sexual maturity varies by region, but in general females usually reach sexual maturity at 5–13 years. In Sarasota Bay, mothers typically first give birth at 9 years of age. Sexual maturity for males tends to occur at 9–14 years; paternity testing of bottlenose dolphins in Sarasota Bay has shown that males 10–40 years of age have sired offspring (Duffield and Wells, 2002).

Although births have been reported from all seasons, calving tends to be diffusely seasonal, with one or more peaks, presumably due to water temperature, prey availability, and predation risk. Hormonal monitoring indicates that females are spontaneous sporadic ovulators, ovulating repeatedly during a given season, while males may be active throughout more of the year with prolonged elevation of testosterone concentrations over the months that different females may be ovulating. The reproductive lifespan is prolonged; females up to 48 years of age have successfully given birth and raised young (Wells and Scott, 1999). Calves are born after a gestation period of about 12.5 months (O'Brien and Robeck, 2012) at lengths of about 84–140 cm, depending on the geographic region.

Lactation is the primary source of nutrition for the first year of life and may continue for several more years. Solid food has been found along with milk in the stomachs of calves as young as 4 months old. Maternal investment for free-ranging calves typically extends for about 3–6 years, with separation often coinciding with the birth of the next calf (Wells and Scott, 1999). Simultaneously pregnant and lactating females have been noted on occasion.

Causes of natural mortality include old age, failure to thrive as a calf, intraspecific agonistic interactions including occasional infanticide, predation, stingray barb wounds, disease (especially respiratory), and biotoxins from harmful algal blooms such as red tides (Wells and Scott, 1999; Twiner et al., 2012; Perrtree et al., 2016). Large-scale mortalities, involving hundreds to thousands of dolphins, have resulted from morbillivirus outbreaks (Rowles et al., 2011). Threats of human origin include entanglement in commercial fishing gear, hooking by, or ingestion of recreational fishing gear, pollution, boat traffic and collisions (Wells et al., 2008; Vollmer and Rosel, 2013), noise from military, shipping, or industrial activities, marine construction/demolition (Buckstaff et al., 2013), and drive or harpoon fisheries. In some cases, the distinction between natural and anthropogenic causes of death becomes blurred, e.g., when it is suspected that exposure to toxic environmental contaminants may increase a dolphin's susceptibility to natural pathogens or biotoxins. In most places, bottlenose dolphins must contend with the cumulative effects of multiple threats.

VI. Interactions With Humans

Bottlenose dolphins take advantage of human activities to facilitate prey capture in a variety of ways. In Mauritania and Brazil, dolphins regularly drive schools of mullet toward fishermen wading with nets in shallow water; in Brazil, this behavior appears to be transmitted through social learning (Daura-Jorge et al., 2012). In many parts of the world bottlenose dolphins collect discarded fish from behind shrimp trawls and small purse seines, or steal fish from various types of fishing gears.

Bottlenose dolphins were publicly displayed first at the Brighton Aquarium in 1883, then at the New York Aquarium in 1914, and have been a regular attraction at Marineland of Florida since 1938. *Tursiops* continues to be the most common dolphin species maintained under human care and displayed throughout the world. According to a June 2016 National Marine Fisheries Service inventory inquiry, 37 US facilities held 487 bottlenose dolphins; in addition, several hundred bottlenose dolphins were held in at least 16 other countries. Within the United States, approximately 70% of the dolphins are held primarily for public display, whereas the remainder are used primarily for research or military purposes. Improved facilities and increased knowledge about the requirements for care of dolphins have led to increasing success in the long-term maintenance of the animals, to the point where birth and survivorship rates at the better facilities approach and, possibly in a few cases, surpass those of wild populations (DeMaster and Drevenak, 1988; Wells and Scott, 1990).

The largest of the historical fisheries for bottlenose dolphins involved several countries surrounding the Black Sea, where dolphins were caught for oil, meat, and leather. Because of declines in dolphin populations, these countries have since outlawed the fishery. Directed takes still occur in other parts of the world, such as Peru, Sri Lanka, Faroe Islands, and Japan for human consumption, to reduce the perceived competition with commercial fisheries, or for bait (Wells and Scott, 1999). Live-capture fisheries for dolphins for public display have existed for more than 100 years. More than 1500 *Tursiops* were removed from the waters of the United States, Mexico, and the Bahamas by 1980 for display, research, or military applications in many parts of the world (Leatherwood and Reeves, 1982). Though no bottlenose dolphins have been collected in US waters since 1989, some live-capture fisheries continued in Cuba, Guyana, Dominican Republic, Haiti, the Solomon Islands, Russia, Turkey, and Japan.

Incidental catches of *T. truncatus* have been reported for a number of fisheries, including purse-seine fisheries for tunas, sardines, and anchovetas, and in shrimp trawls, and gillnets set for a variety of fish (Wells and Scott, 1999). In some cases, dolphins have been killed by fishermen to prevent damage to their fishing gear or stealing of the catch or bait (Leatherwood and Reeves, 1982). Though the impacts of habitat alteration and pollution on dolphins have not been studied systematically, anecdotal accounts suggest that human-caused degradation may have led to declines in some dolphin populations (Wells and Scott, 1999). Extremely high concentrations of persistent organic pollutant residues have been found in the tissues of *Tursiops* in many parts of the world, with males accumulating higher concentrations than females with age (Kucklick et al., 2011; Jepson et al., 2016). Cockcroft et al. (1989b) suggested that first-born calves of South African bottlenose dolphins received 80% of their mother's body burden of contaminant residues (polychlorinated biphenyls and dieldrin), perhaps leading to increased neonatal mortality but also reducing levels of contaminants in the mothers. Studies along the west coast of Florida monitoring contaminant concentrations in identifiable resident dolphins supported these findings, with high concentrations in first-born calves and nulliparous females and lowered levels in females while lactating (Wells et al., 2005; Yordy et al., 2010). Accumulation of contaminants in tissues of males have reached levels that theoretically could impair testosterone production and thus reduce reproductive ability. Preliminary findings suggest that even relatively low levels of PCBs and DDT metabolites can result in a decline in bottlenose dolphin immune system function, health, and reproductive success (Lahvis et al., 1995; Schwacke et al., 2002). Other anthropogenic chemical contaminants, such as perfluoroalkyl compounds, are of emerging concern.

Research following the catastrophic 2010 *Deepwater Horizon* oil spill found significant impacts of the spill on bottlenose dolphin health, survival, and reproduction. In comparison to reference populations, dolphins in heavily oiled Barataria Bay, Louisiana exhibited

Copyright © 2017. Elsevier Science & Technology. All rights reserved.

a high prevalence of moderate-to-severe lung disease, consistent with studies of humans and other animals exposed to petroleum-associated chemicals, along with serum biochemical abnormalities and low measures of adrenal hormones (both cortisol and aldosterone) indicative of hypoadrenocorticism (Schwacke et al., 2014). Significantly lower reproductive success and interannual survival were also found (Lane et al., 2015).

Direct human interactions with wild dolphins through provisioning, dolphin watching, and swimming have created increasing concern (Samuels and Bejder, 2004; Powell and Wells, 2011). Inappropriate and risky foraging behaviors, involving approaching anglers or provisioners, are passed maternally from one generation to the next through social learning. Bottlenose dolphins suffer mortality and serious injury from collisions with boats (Wells et al., 2008), relative abundance may decline with increased dolphin-watching tours (Bedjer et al., 2006), and dive patterns, heading, synchronicity, time spent feeding and resting, aerial behaviors, and communications may change in the presence of vessels (Nowacek et al., 2001; Hastie et al., 2003; Guerra et al., 2014).

Although there are many threats operating on local populations and areas where populations are in decline, for example, in the Mediterranean Sea (Bearzi et al., 2008), *T. truncatus* is widespread and abundant, and as a species it does not appear to merit concern for major global population decline. Therefore, *T. truncatus* has been classified by the IUCN as "Least Concern." However, climate change has the potential for yet-to-be-determined large-scale impacts on bottlenose dolphins (Wells 2010).

See Also the Following Articles

Bottlenose Dolphin: *Tursiops aduncus*, Indo-Pacific Bottlenose Dolphin ■ Delphinids, Overview

References

Au, W.L. (1993). *Sonar of Dolphins.* Springer Verlag, New York.

Baird, R.W., Gorgone, A.M., McSweeney, D.J., Ligon, A.D., Deakos, M.H., Webster, D.L., Schorr, G.S., Martien, K.M., Salden, D.R., and Mahaffy, S.D. (2009). Population structure of island-associated dolphins: Evidence from photo-identification of common bottlenose dolphins (*Tursiops truncatus*) in the main Hawaiian Islands. *Mar. Mamm. Sci.* **25**(2), 251–274.

Barnes, L.G. (1990). The fossil record and evolutionary relationships of the genus *Tursiops*. In "The Bottlenose Dolphin", (S. Leatherwood, and R.R. Reeves, Eds), pp. 3–26. Academic Press, San Diego, CA.

Barros, N.B., and Odell, D.K. (1990). Food habits of bottlenose dolphins in the southeastern United States. In "The Bottlenose Dolphin", (S. Leatherwood, and R.R. Reeves, Eds), pp. 309–328. Academic Press, San Diego, CA.

Bearzi, G., Fortuna, C.M., and Reeves, R.R. (2008). Ecology and conservation of common bottlenose dolphins *Tursiops truncatus* in the Mediterranean Sea. *Mammal. Rev.* **39**(2), 92–123.

Bedjer, L., et al. (10 authors) (2006). Decline in relative abundance of bottlenose dolphins exposed to long-term disturbance. *Conserv. Biol.* **20**, 1791–1798.

Berens McCabe, E., Gannon, D.P., Barros, N.B., and Wells, R.S. (2010). Prey selection in a resident common bottlenose dolphin (*Tursiops truncatus*) community in Sarasota Bay, Florida. *Mar. Biol.* **157**(5), 931–942.

Bruck, J.N. (2013). Decades-long social memory in bottlenose dolphins. *Proc. R. Soc. B* **280**, 20131726.

Buckstaff, K.C., Wells, R.S., Gannon, J.G., and Nowacek, D.P. (2013). Responses of bottlenose dolphins (*Tursiops truncatus*) to construction and demolition of coastal marine structures. *Aquat. Mamm.* **39**, 174–186.

Caldwell, D.K. (1955). Evidence of home range in the bottlenosed dolphin. *J. Mamm.* **36**, 304–305.

Caldwell, D.K., and Caldwell, M.C. (1972). *The World of the Bottlenosed Dolphin.* J. B. Lippincott Co, Philadelphia, PA.

Caldwell, M.C., Caldwell, D.K., and Tyack, P.L. (1990). Review of the signature-whistle hypothesis for the Atlantic bottlenose dolphin. In "The Bottlenose Dolphin" (S. Leatherwood, and R.R. Reeves, Eds), pp. 199–234. Academic Press, San Diego, CA.

Castilho, C.S., Pedone-Valdez, F., Bertuol, F., Fruet, P., Genoves, R.C., Di Tullio, J.C., Caon, G., Hoffmann, L.S., and Freitas, T.R.O. (2015). Insights about the genetic diversity and population structure of an offshore group of common bottlenose dolphins (*Tursiops truncatus*) in the Mid-Atlantic. *Genet. Mol. Res.* **14**(2), 3387–3399.

Cockcroft, V.G., Cliff, G., and Ross, G.J.B. (1989a). Shark predation on Indian Ocean bottlenose dolphins *Tursiops truncatus* off Natal, South Africa. *South Afr. J. Zool.* **24**, 305–309.

Cockcroft, V.G., De Kock, A.C., Lord, D.A., and Ross, G.J.B. (1989b). Organochlorines in bottlenose dolphins *Tursiops truncatus* from the east coast of South Africa. *South Afr. J. Mar. Sci.* **8**, 207–217.

Cotter, M.P., Maldini, D., and Jefferson, T.A. (2012). "Porpicide" in California: Killing of harbor porpoises (*Phocoena phocoena*) by coastal bottlenose dolphins (*Tursiops truncatus*). *Mar. Mamm. Sci.* **28**(1), E1–E15.

Daura-Jorge, F.G., Cantor, M., Ingram, S.N., Lusseau, D., and Simões-Lopes, P.C. (2012). The structure of a bottlenose dolphin society is coupled to a unique foraging cooperation with artisanal fishermen. *Biol. Lett.* **8**, 702–705.

DeMaster, D.P., and Drevenak, J.K. (1988). Survivorship patterns in three species of captive cetaceans. *Mar. Mamm. Sci.* **4**, 297–311.

Duffield, D.A., and Wells, R.S. (2002). The molecular profile of a resident community of bottlenose dolphins, *Tursiops truncatus*. In "Molecular and Cell Biology of Marine Mammals", (C.J. Pfeiffer, Ed.), pp. 3–11. Krieger Publishing Company, Melbourne.

Elliser, C.R., and Herzing, D.L. (2011). Replacement dolphins? Social restructuring of a resident pod of Atlantic bottlenose dolphins, *Tursiops truncatus*, after two major hurricanes. *Mar. Mamm. Sci.* **27**(1), 39–59.

Elliser, C.R., and Herzing, D.L. (2016). Long-term interspecies association patterns of Atlantic bottlenose dolphins, *Tursiops truncatus*, and Atlantic spotted dolphins, *Stenella frontalis*, in the Bahamas. *Mar. Mamm. Sci.* **32**(1), 38–56.

Guerra, M., Dawson, S.M., Brough, T.E., and Rayment, W.J. (2014). Effects of boats on the surface and acoustic behaviour of an endangered population of bottlenose dolphins. *Endangered Species Res.* **24**, 221–236.

Hastie, G.D., Wilson, B., Tufft, L.H., and Thompson, P.M. (2003). Bottlenose dolphins increase breathing synchrony in response to boat traffic. *Mar. Mamm. Sci.* **19**, 74–84.

Hershkovitz, P. (1966). Catalog of Living Whales. *US Natl. Mus. Bull.* 246. Smithsonian Institution, Washington, DC.

Herzing, D.L., Moewe, K., and Brunnick, B.J. (2003). Interspecies interactions between Atlantic spotted dolphins, *Stenella frontalis*, and bottlenose dolphins, *Tursiops truncatus*, on Great Bahama Bank, Bahamas. *Aquat. Mamm.* **29**, 335–341.

Irvine, B., Wells, R.S., and Gilbert, P.W. (1973). Conditioning an Atlantic bottle-nosed dolphin, *Tursiops truncatus*, to repel various species of sharks. *J. Mamm.* **54**, 503–505.

Janik, V.M., and Sayigh, L.S. (2013). Communication in bottlenose dolphins: 50 years of signature whistle research. *J. Comp. Physiol. A* **199**, 479–489.

Jensen, F.H., Beedholm, K., Wahlburg, M., Bejder, L., and Madsen, P.T. (2012). Estimated communication range and energetic cost of bottlenose dolphin whistles in a tropical habitat. *J. Acoust. Soc. Am.* **131**(1), 582–592.

Jepson, P.D., Deaville, R., Barber, J.L., Aguilar, A., Borrell, A., Murphy, S., Barry, J., Brownlow, A., Barnett, J., Berrow, S., Cunningham, A.A., Davison, N.J., ten Doeschate, M., Esteban, R., Ferreira, M., Foote, A.D., Genov, T., Giménex, J., Loveridge, J., Llavona, A., Martin, V., Maxwell, D.L., Papachlimitzou, A., Penrose, R., Perkins, M.W.,

Copyright © 2017. Elsevier Science & Technology. All rights reserved.

Smith, B., de Stephanis, R., Tregenza, N., Verborgh, P., Fernandez, A., and Law, R.J. (2016). PCB pollution continues to impact populations of orcas and other dolphins in European waters. *Nat. Sci. Rep.* **6**, 18573.

King, S.L., and Janik, V.M. (2013). Bottlenose dolphins can use learned vocal labels to address each other. *Proc. Natl. Acad. Sci. USA* **110**(32), 13216–13221.

King, S.L., and Janik, V.M. (2015). Come dine with me: food-associated social signalling in wild bottlenose dolphins (*Tursiops truncatus*). *Anim. Cogn.* **18**, 969–974.

Kucklick, J., Schwacke, L., Wells, R., Hohn, A., Guichard, A., Yordy, J., Hansen, L., Zolman, E., Wilson, R., Litz, J., Nowacek, D., Rowles, T., Pugh, R., Balmer, B., Sinclair, C., and Rosel, P. (2011). Bottlenose dolphins as indicators of persistent organic pollutants in waters along the US East and Gulf of Mexico coasts. *Environ. Sci. Technol.* **45**, 4270–4277.

Lahvis, G.P., Wells, R.S., Kuehl, D.W., Stewart, J.L., Rhinehart, H.L., and Via, C.S. (1995). Decreased lymphocyte responses in free-ranging bottlenose dolphins (*Tursiops truncatus*) are associated with increased concentrations of PCBs and DDT in peripheral blood. *Environ. Health Perspect.* **103**, 67–72.

Lane, S.M., Smith, C.R., Balmer, B.C., Barry, K.P., McDonald, T., Mitchell, J., Mori, C.S., Rosel, P.E., Rowles, T.K., Speakman, T.R., Townsend, F.I., Tumlin, M.C., Wells, R.S., Zolman, E.S., and Schwacke, L.H. (2015). Survival and reproductive outcome of bottlenose dolphins sampled in Barataria Bay, Louisiana, USA following the *Deepwater Horizon* oil spill. *Proc. R. Soc. B* **282**, 20151944.

Leatherwood, S., and Reeves, R.R. (1982). Bottlenose dolphin (*Tursiops truncatus*) and other toothed cetaceans. In "Wild Mammals of North America: Biology, Management, Economics", (J.A. Chapman, and G.A. Feldhamer, Eds), pp. 369–414. Johns Hopkins University Press, Baltimore, MD.

Leatherwood, S., and Reeves, R.R. (1990). *The Bottlenose Dolphin*. Academic Press, San Diego, CA.

LeDuc, R.G., Perrin, W.F., and Dizon, A.E. (1999). Phylogenetic relationships among the delphinid cetaceans based on full cytochrome *b* sequences. *Mar. Mamm. Sci.* **15**, 619–648.

Martien, K.K., Baird, R.W., Hedrick, N.M., Gorgone, A.M., Thieleking, J.L., McSweeney, D.J., Robertson, K.M., and Webster, D.L. (2012). Population structure of island-associated dolphins: Evidence from mitochondrial and microsatellite markers for common bottlenose dolphins (*Tursiops truncatus*) around the main Hawaiian Islands. *Mar. Mamm. Sci.* **28**(3), E208–E232.

McBride, A.F., and Hebb, D.O. (1948). Behavior of the captive bottle-nose dolphin, *Tursiops truncatus. J. Comp. Physiol. Psychol.* **41**, 111–123.

Mead, J.G., and Potter, C.W. (1990). Natural history of bottlenose dolphins along the central Atlantic coast of the United States. In "The Bottlenose Dolphin", (S. Leatherwood, and R.R. Reeves, Eds), pp. 165–195. Academic Press, San Diego, CA.

Mead, J.G., and Potter, C.W. (1995). Recognizing two populations of the bottlenose dolphin (*Tursiops truncatus*) off the Atlantic coast of North America: Morphological and ecological considerations. *Int. Biol. Res. Inst. Rep.* **5**, 31–43.

Nowacek, D.P. (2005). Acoustic ecology of foraging bottlenose dolphins (*Tursiops truncatus*), habitat-specific sound use of three sound types. *Mar. Mamm. Sci.* **21**, 587–602.

Nowacek, S.M., Wells, R.S., and Solow, A.R. (2001). Short-term effects of boat traffic on bottlenose dolphins, *Tursiops truncatus*, in Sarasota Bay, Florida. *Mar. Mamm. Sci.* **17**, 673–688.

O'Brien, J.K., and Robeck, T.R. (2012). The relationship of maternal characteristics and circulating progesterone concentrations with reproductive outcome in the bottlenose dolphin (*Tursiops truncatus*) after artificial insemination, with and without ovulation induction, and natural breeding. *Theriogenology* **78**(3), 469–482.

Owen, E.C.G., Hofmann, S., and Wells, R.S. (2002). Ranging and social association patterns of paired and unpaired adult male bottlenose dolphins, *Tursiops truncatus*, in Sarasota, Florida, provide no evidence for alternative male strategies. *Can. J. Zool.* **80**, 2072–2089.

Perrtree, R.M., Sayigh, L.S., Williford, A., Bocconcelli, A., Curran, M.C., and Cox, T.M. (2016). First observed wild birth and acoustic record of a possible infanticide attempt on a common bottlenose dolphin (*Tursiops truncatus*). *Mar. Mamm. Sci.* **32**(1), 376–385.

Parsons, K.M., Durban, J.W., and Claridge, D.E. (2003). Male–male aggression renders bottlenose dolphin (*Tursiops truncatus*) unconscious. *Aquat. Mamm.* **29**, 360–362.

Parsons, K.M., Durban, J.W., Claridge, D.E., Herzing, D.L., Balcomb, K.C., and Noble, L.R. (2006). Population genetic structure of coastal bottlenose dolphins (*Tursiops truncatus*) in the northern Bahamas. *Mar. Mamm. Sci.* **22**, 276–298.

Powell, J.R., and Wells, R.S. (2011). Recreational fishing depredation and associated behaviors involving common bottlenose dolphins (*Tursiops truncatus*) in Sarasota Bay, Florida. *Mar. Mamm. Sci.* **27**, 111–129.

Quérouil, S., Silva, M.A., Freitas, L., Prieto, R., Magalhães, S., Dinas, A., Alves, F., Matos, J.A., Mendonça, D., Hammond, P.S., and Santos, R.S. (2007). High gene flow in oceanic bottlenose dolphins (*Tursiops truncatus*) of the North Atlantic. *Conserv. Genet.* **8**, 1405–1419.

Quick, N.J., and Janik, V.M. (2012). Bottlenose dolphins exchange signature whistles when meeting at sea. *Proc. R. Soc. B* **279**, 2539–2545.

Quintana-Rizzo, E., Mann, D.A., and Wells, R.S. (2006). Estimated communication range of social sounds used by bottlenose dolphins (*Tursiops truncatus*). *J. Acoust. Soc. Am.* **120**, 1671–1683.

Reynolds III, J.E., Wells, R.S., and Eide, S.D. (2000). *Biology and Conservation of the Bottlenose Dolphin*. University of Florida Press, Gainesville, FL.

Rice, D.W. (1998). Marine Mammals of the World: Systematics and Distribution *Special Publication No. 4, Society for Marine Mammalogy*. Allen Press, Lawrence.

Robinson, K.P., O'Brien, J.M., Berrow, S.D., Cheney, B., Costa, M., Eisfeld, S.M., Haberlin, D., Mandleberg, L., O'Donovan, M., Oudejans, M.G., Ryan, C., Stevick, P.T., Thompson, P.M., and Whooley, P. (2012). Discrete or not so discrete: Long distance movements by coastal bottlenose dolphins in the UK and Ireland. *J. Cetacean Res. Manage.* **12**, 365–372.

Rogers, C.A., Brunnick, B.J., Herzing, D.L., and Baldwin, J.D. (2004). The social structure of bottlenose dolphins, *Tursiops truncatus*, in the Bahamas. *Mar. Mamm. Sci.* **20**, 688–708.

Rossman, S., Stolen, M., Barrros, N.B., Gandhi, H., Ostrom, P.H., Stricker, C.A., and Wells, R.S. (2015). Individual specialization in the foraging habits of female bottlenose dolphins living in a tropically diverse and habitat rich estuary. *Oecologia*. doi:10.1007/s00442-015-3241-6.

Rowles, T.K., Schwacke, L.H., Wells, R.S., Saliki, J.T., Hansen, L., Hohn, A., Townsend, F., Sayre, R.A., and Hall, A.J. (2011). Evidence of susceptibility to morbillivirus infection in cetaceans from the United States. *Mar. Mamm. Sci.* **27**, 1–19.

Samuels, A., and Bejder, L. (2004). Chronic interaction between humans and free-ranging bottlenose dolphins near Panama City Beach, Florida, USA. *J. Cetacean Res. Manage.* **6**, 69–77.

Schwacke, L.H., Voit, E.O., Hansen, L.J., Wells, R.S., Mitchum, G.B., Hohn, A.A., and Fair, P.A. (2002). Probabilistic risk assessment of reproductive effects of polychlorinated biphenyls on bottlenose dolphins (*Tursiops truncatus*) from the southeast United States coast. *Environ. Toxicol. Chem.* **21**, 2752–2764.

Schwacke, L.H., Smith, C.R., Townsend, F.I., Wells, R.S., Hart, L.B., Balmer, B.C., Collier, T.K., De Guise, S., Fry, M.M., Guillette Jr., L.J., Lamb, S.V., Lane, S.M., McFee, W.E., Place, N.J., Tumlin, M.C., Ylitalo, G.M., Zolman, E.S., and Rowles, T.K. (2014). Health of common bottlenose dolphins (*Tursiops truncatus*) in the Gulf of Mexico following the *Deepwater Horizon* Oil Spill. *Environ. Sci. Technol.* **48**, 93–103.

Scott, M.D., and Chivers, S.J. (1990). Distribution and herd structure of bottlenose dolphins in the eastern tropical Pacific Ocean. In "The

Copyright © 2017. Elsevier Science & Technology. All rights reserved.

Bottlenose Dolphin", (S. Leatherwood, and R.R. Reeves, Eds), pp. 387–402. Academic Press, San Diego, CA.

Scott, M.D., Wells, R.S., and Irvine, A.B. (1990). A long-term study of bottlenose dolphins on the west coast of Florida. In "The Bottlenose Dolphin" (S. Leatherwood, and R.R. Reeves, Eds), pp. 235–244. Academic Press, San Diego, CA.

Sellas, A.B., Wells, R.S., and Rosel, P.E. (2005). Mitochondrial and nuclear DNA analyses reveal fine scale geographic structure in bottlenose dolphins (*Tursiops truncatus*) in the Gulf of Mexico. *Conserv. Genet.* **6**, 715–728.

Shane, S.H., Wells, R.S., and Würsig, B. (1986). Ecology, behavior and social organization of the bottlenose dolphin: A review. *Mar. Mamm. Sci.* **2**, 34–63.

Simard, P., Lace, N., Gowans, S., Quintana-Rizzo, E., Kuczaj II, S., Wells, R.S., and Mann, D.A. (2011). Low frequency narrow-band calls in bottlenose dolphins (*Tursiops truncatus*): signal properties, function and conservation implications. *J. Acoust. Soc. Am.* **130**, 3068–3076.

Tobeña, M., Escánez, A., Rodríguez, Y., López, C., Ritter, F., and Aguilar, N. (2014). Inter-island movements of common bottlenose dolphins *Tursiops truncatus* among the Canary Islands: online catalogues and implications for conservation and management. *Afr. J. Mar. Sci.* **36**, 137–141.

Torres, L.G., and Read, A.J. (2009). Where to catch a fish? The influence of foraging tactics on the ecology of bottlenose dolphins (*Tursiops truncatus*) in Florida Bay, Florida. *Mar. Mamm. Sci.* **25**, 797–815.

Toth, J.L., Hohn, A.A., Able, K.W., and Gorgone, A.M. (2011). Patterns of seasonal occurrence, distribution, and site fidelity of coastal bottlenose dolphins (*Tursiops truncatus*) in southern New Jersey, U.S.A. *Mar. Mamm. Sci.* **27**, 94–110.

Twiner, M.J., Flewelling, L.J., Fire, S.E., Bowen-Stevens, S.R., Gaydos, J.K., Johnson, C.K., Landsberg, J.H., Leighfield, T.A., Mase-Guthrie, B., Schwacke, L., Van Dolah, F.M., Wang, Z., and Rowles, T.K. (2012). Comparative analysis of three brevetoxin-associated bottlenose dolphin (*Tursiops truncatus*) mortality events in the Florida Panhandle region (USA). *PLoS One* **7**, e42974.

Vollmer, N.L., and Rosel, P.E. (2013). A review of common bottlenose dolphins (*Tursiops truncatus truncatus*) in the northern Gulf of Mexico: Population biology, potential threats, and management. *Southeastern Nat.* **13**, 1–43.

Wells, R.S. (2003). Dolphin social complexity: Lessons from long-term study and life history. In "Animal Social Complexity: Intelligence, Culture, and Individualized Societies", (F.B.M. de Waal, and P.L. Tyack, Eds), pp. 32–56. Harvard University Press, Cambridge.

Wells, R.S. (2010). Feeling the heat – potential climate change impacts on bottlenose dolphins. *Whalewatcher J. Am. Cetacean Soc.* **39**(2), 12–17.

Wells, R.S. (2014). Social structure and life history of common bottlenose dolphins near Sarasota Bay, Florida: Insights from four decades and five generations. In "Primates and Cetaceans: Field Research and Conservation of Complex Mammalian Societies", (J. Yamagiwa, and L. Karczmarski, Eds), pp. 149–172. Primatology Monographs, Springer, Tokyo, Japan.

Wells, R.S., and Scott, M.D. (1990). Estimating bottlenose dolphin population parameters from individual identification and capture–release techniques. In "Individual Recognition of Cetaceans: Use of Photo-identification and Other Techniques to Estimate Population Parameters" (P.S. Hammond, S.A. Mizroch, and G.P. Donovan, Eds), pp. 407–415. *Rep. Int. Whal. Comm.* Spec. Iss. No. 12.

Wells, R.S., and Scott, M.D. (1999). Bottlenose dolphin *Tursiops truncatus* (Montagu, 1821). In "Handbook of Marine Mammals", (S.H. Ridgway, and R. Harrison, Eds), **6**the Second Book of Dolphins and Porpoises, pp. 137–182. Academic Press, San Diego, CA.

Wells, R.S., Scott, M.D., and Irvine, A.B. (1987). The social structure of free-ranging bottlenose dolphins. In "Current Mammalogy", (H.H. Genoways, Ed.), Vol. 1, pp. 247–305. Plenum Press, New York.

Wells, R.S., Hansen, L.J., Baldridge, A., Dohl, T.P., Kelly, D.L., and Defran, R.H. (1990). Northward extension of the range of bottlenose dolphins along the California coast. In "The Bottlenose Dolphin" (S. Leatherwood, and R.R. Reeves, Eds), pp. 421–431. Academic Press, San Diego, CA.

Wells, R.S., Tornero, V., Borrell, A., Aguilar, A., Rowles, T.K., Rhinehart, H.L., Hofmann, S., Jarman, W.M., Hohn, A.A., and Sweeney, J.C. (2005). Integrating life history and reproductive success data to examine potential relationships with organochlorine compounds for bottlenose dolphins (*Tursiops truncatus*) in Sarasota Bay, Florida. *Sci. Total Environ.* **349**, 106–119.

Wells, R.S., Allen, J.B., Hofmann, S., Bassos-Hull, K., Fauquier, D.A., Barros, N.B., DeLynn, R.E., Sutton, G., Socha, V., and Scott, M.D. (2008). Consequences of injuries on survival and reproduction of common bottlenose dolphins (*Tursiops truncatus*) along the west coast of Florida. *Mar. Mamm. Sci.* **24**, 774–794.

Wells, R.S., McHugh, K.A., Douglas, D.C., Shippee, S., Berens McCabe, E.J., Barros, N.B., and Phillips, G.T. (2013). Evaluation of potential protective factors against metabolic syndrome in bottlenose dolphins: Feeding and activity patterns of dolphins in Sarasota Bay, Florida. *Front. Endocrinol.* **4**, 139.

Wood, F.G., Caldwell, D.K., and Caldwell, M.C. (1970). Behavioral interactions between porpoises and sharks. *Invest. Cetacea* **2**, 264–277.

Würsig, B., and Würsig, M. (1979). Behavior and ecology of the bottlenose dolphin, *Tursiops truncatus*, in the South Atlantic. *Fish. Bul.* **77**, 399–412.

Yordy, J., Wells, R.S., Balmer, B.C., Schwacke, L., Rowles, T., and Kucklick, J.R. (2010). Life history as a source of variation for persistent organic pollutant (POP) patterns in a community of common bottlenose dolphins (*Tursiops truncatus*) resident to Sarasota Bay, FL. *Sci. Total Environ.* **408**, 2163–2172.

Zaechsmar, J.R., Dwyer, S.L., and Stockin, K.A. (2013). Rare observations of false killer whales (*Pseudorca crassidens*) cooperatively feeding with common bottlenose dolphins (*Tursiops truncatus*) in the Hauraki Gulf, New Zealand. *Mar. Mamm. Sci.* **29**(3), 555–562.

BOTTLENOSE DOLPHIN, *TURSIOPS ADUNCUS*, INDO-PACIFIC BOTTLENOSE DOLPHIN

John Y. Wang

This species was initially named *Delphinus aduncus*. *Tursiops* is the combination of the Greek words *Tursio* for dolphin and *ops* for appearance; *aduncus* is Latin meaning hooked (possibly referring to the lower jaw being slightly upturned distally). Another common name is Indian Ocean bottlenose dolphin.

I. Characteristics and Taxonomy

Species status of *T. aduncus* gained wide acceptance after studies demonstrated two morphotypes of *Tursiops* were reproductively isolated in sympatry (Wang et al., 1999, 2000a,b). However, there is still taxonomic uncertainty within *T. aduncus*. For example, the Shark Bay (Western Australia) bottlenose dolphins are very well studied yet their species identity remains uncertain (in this review, they are treated as *T. aduncus*). Polyphyly of *T. aduncus* was also suggested and there are notable differences in the mtDNA between dolphins from the eastern and western extremes of the species' distribution (Perrin et al., 2007). However, only one single species (with no subspecies) is currently recognized. Although population

Copyright © 2017. Elsevier Science & Technology. All rights reserved.

structure studies are relatively few, analyses of differences in cranial, pigmentation, acoustic and molecular characters across several locations support the species comprising many relatively small, resident and isolated populations (e.g., Hawkins, 2010; Oremus et al., 2015).

Controversy also exists over the sister taxa of *T. aduncus*. Early analysis of mtDNA and later molecular studies suggested that *T. truncatus* was not the closest relative of *T. aduncus*. However, this view was inconsistent with osteological characters, which showed *T. aduncus* to be very similar to *T. truncatus*, to the point that distinguishing between the two species is difficult. More recent studies combining many independent molecular characters and better sampling of species have swayed support back to monophyly for *Tursiops* (e.g., McGowen, 2011; Amaral et al., 2012).

This species is smaller than *T. truncatus*, reaching a maximum length of about 2.7 m and weighing about 200 kg but dolphins in some regions are noticeably smaller, growing not much longer than about 2.3 m. Males may be slightly larger but sexual dimorphism is not obvious. The dorsal fin, flippers and flukes of *T. aduncus* are larger and broader (relative to body size) than those on *T. truncatus*, but overall the body appears more slender: the snout is longer and thinner, the melon is less bulbous, and the head has a more pointed profile (Fig. 1). The relative length of the rostrum, as a proportion of the total body length or the distance from the tip of the rostrum to the middle of the eye, is greater than for *T. truncatus*. In Chinese waters, the rostrum length (excluding young calves) is also longer than in *T. truncatus* regardless of body length. Overall, dolphins of the waters of the northern Philippines, Solomon Islands, China, Taiwan, South Korea, and Japan appear to be longer, more massive, and possess longer beaks than those from Indonesia, Western Australia, and South Africa, which have a "stubbier" appearance.

Pigmentation of *T. aduncus* is fairly simple with a dark to medium gray dorsal surface (often appearing as a cape) progressing to light gray on the flanks and a light spinal blaze may be present. The belly is whitish, often with a pinkish hue and in most regions, there is dark spotting. The intensity and specific body locations of the ventral spotting appear to vary regionally and individually, but in general development of spotting is similar (Fig. 2). Spotting on the venter begins around the onset of sexual maturity and becomes more intense and darkens with age. The mouth line and tip of the beak also become whiter with age. Calves are generally lighter in overall color and are unspotted. Spotting patterns may be cues for individual recognition, indicating maturity stage or group membership. Spotting on dolphins in some populations can begin at body lengths of 1.6 m and can become intense at less than 2.2 m, whereas in other populations, spotting may not start to develop until at least 2.2 m long. In a few regions, dolphins may remain more or less unspotted throughout their lives.

There are only a few, subtle distinguishing features between the skulls of *T. aduncus* and *T. truncatus*, some of which may not hold everywhere. The skull of *T. aduncus* is relatively smaller and possesses a narrower rostrum with a prominent premaxillary convexity or "pinch" that is situated at about one-third of the rostral length anterior of the base of the rostrum. The position of the premaxillary convexity is also reflected externally by a longer beak compared with that of *T. truncatus*. The width of the external nares (relative to the parietal width) is also greater in *T. aduncus*. Teeth of *T. aduncus* are generally smaller in diameter and more numerous than in *T. truncatus* (in Chinese and South African waters, *T. aduncus* has 23–29 teeth in each row, whereas *T. truncatus* possesses 19–27 teeth per row).

T. aduncus has fewer vertebrae than *T. truncatus* (total vertebral count for *T. aduncus* is 59–62, whereas it is 64–67 for *T. truncatus*). Although these distributions do not overlap, a slight overlap in vertebral formulae was found in southern Australia. There may also be slight differences in the morphology of the cervical vertebrae between the two species.

The presence of *T. aduncus* from various regions has been supported by analyses of mtDNA sequences. MtDNA control regions of *T. aduncus* and *T. truncatus* differ by several fixed nucleotide bases and are highly divergent (at least 4.4%) from each other (e.g., Wang

Figure 2 *Indo-Pacific bottlenose dolphins in the Red Sea (Photo by Beno Steinacher).*

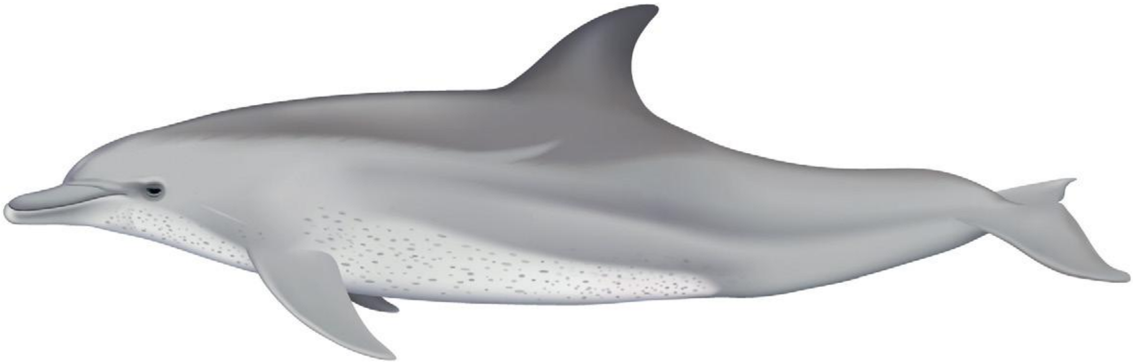

Figure 1 *Indo-Pacific bottlenose dolphin,* Tursiops aduncus *(Illustration by Uko Gorter).*

Copyright © 2017. Elsevier Science & Technology. All rights reserved.

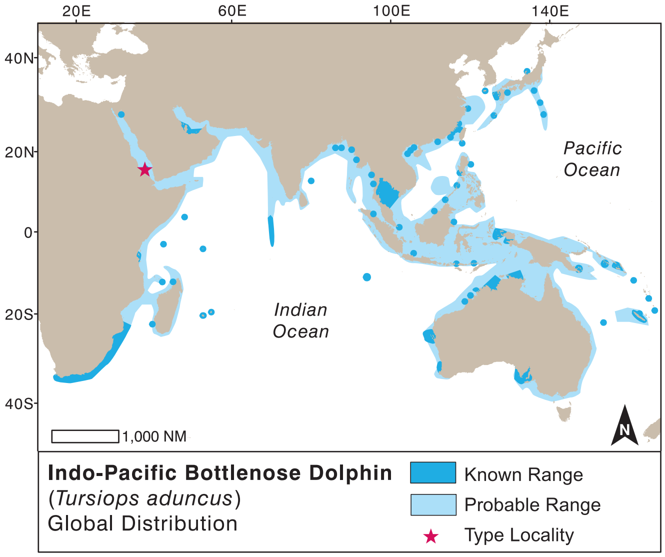

Figure 3 *Indo-Pacific bottlenose dolphin distribution. Adapted by Nina Lisowski from Jefferson, T.A., Webber, M.A., and Pitman, R.L. (2015). "Marine Mammals of the World: A Comprehensive Guide to Their Identification," 2nd ed. Elsevier, San Diego, CA.*

et al., 1999). Notable differences in mtDNA sequences within this species have been reported but it is unclear what they represent taxonomically.

II. Distribution and Abundance

Due to the fairly recent recognition of *T. aduncus* as a distinct species, distribution information is patchy. The species is widespread throughout coastal waters of the Indian and western Pacific oceans extending from Melanesia in the east, across the northern rim of the Indian Ocean (including the Red Sea), to the southern tip of South Africa (including the islands of Madagascar, Réunion, Mauritius, the Seychelles, and Mayotte of the Comoros Archipelago) in the west and from the northern coastal waters of central Honshu (Japan) through Southeast Asia to southern Australia (Fig. 3). However, there is clear discontinuity in this expansive distribution with several small isolated or semi-isolated, resident or seasonal populations around many islands and various study sites. With thousands of islands in the Indo-Pacific region, more such populations are certain.

There is no global abundance estimate for the species and local abundance estimates are still relatively few. Abundance estimates exist for various sites in Japan, Solomon Islands, Australia, and South Africa and for the waters of Jeju Island (South Korea), Swatch-of-No-Ground (Bangladesh), Zanzibar, and Mayotte (e.g., Smith et al., 2013; Pusineri et al., 2014). Local abundance appears relatively low (a few tens to several hundred being most common) but it can be the most frequently observed cetacean in some areas. In the Swatch-of-No-Ground, large annual abundance estimates of roughly 2000–2500 individuals were reported but these are diminutive compared to the enormous (>28,000) estimate obtained by a study on dolphins of Algoa Bay, South Africa (Reisinger and Karczmarski, 2010). Such exceptionally large estimates in these regions deserve further attention. Because population structure and boundaries are poorly understood, local estimates must be interpreted cautiously as they may not represent biological entities but rather the number of individuals found in study areas.

Even though information is limited, there are concerns that this species has experienced declines in some regions (e.g., the Arabian Gulf, Vietnamese waters, Chinese waters, waters of the Solomon Islands) due to intentional captures and fisheries bycatch. Even in Shark Bay, which is still relatively pristine, a decline in dolphin numbers has been observed and the activities of tour operators targeting the dolphins have been suggested as the cause of the decline; this further emphasizes the particular vulnerability of this nearshore species to human activities, even those that are usually considered to be fairly benign.

III. Ecology

Continental shelf waters with rocky and coral reefs, sandy bottom, or sea grass beds seem to be the preferred habitat of this species. It is most commonly found in water less than 100 m deep. In some areas, dolphins may concentrate in and around estuaries but they do not seem to frequent low salinity, turbid, muddy waters. Around oceanic islands, inshore and lagoon waters are the main habitat. Although generally considered a resident species, occasional long-distance (hundreds of kilometers) movement across deep oceanic waters can occur. Its main distribution is in tropical to warm temperate waters of the Indian and western Pacific oceans, where sea surface temperature varies between 20 and 30°C. However, it can also be found in cooler (the lowest temperature recorded was 8°C) waters off Jeju Island, northern coast of central Honshu, northern China, southern Australia, and South Africa.

Tursiops aduncus has overlapping distributions with many species but mainly *T. truncatus*, *Sousa* spp., *Neophocaena phocaenoides*, *Stenella longirostris*, *S. attenuata*, and *Orcaella* spp. Whenever both species of *Tursiops* spp. are sympatric (e.g., waters of central and southern China, western and southern Taiwan, the southern half of Japan, Philippines, Australia, South Africa, Réunion Island, Mayotte, Solomon Islands, New Caledonia), *T. aduncus* occupies more inshore coastal areas but where *T. aduncus* is sympatric with *Sousa chinensis*, the distribution of the former species tends to be in slightly deeper waters. Mixed species schools with *T. truncatus*, *Pseudorca crassidens*, *Delphinus*, *Sousa* spp., and *Stenella longirostris* have been documented but interspecific associations differ regionally (e.g., *S. chinensis* has not been observed with *T. aduncus* in Taiwanese waters where both species exist).

A great variety of fish and cephalopod species are known prey of this species but great geographical variability in diet exists (e.g., Kiszka et al., 2014). The primary prey species are benthic and reef-dwelling fish and cephalopods that are found over continental shelf waters but epipelagic and mesopelagic species can also be consumed in considerable numbers in some areas. The most common prey species are less than 300 mm long and belong to the families Apogonidae, Belonidae, Carangidae, Clupeidae, Congridae, Mugilidae, Sciaenidae, Engraulidae, Sepioteuthidae, Sepiidae, Sepiolidae, Loliginidae, and Octopodidae. Infrequently, small benthic sharks may also be eaten. Prey choice and size may be related to habitat types, age, sex, or reproductive status of individuals and there appears to be little overlap with the prey species of *T. truncatus*. The daily food requirement of captive adult dolphins is about 4%–5% of their body mass but can increase with lower water temperatures.

Many foraging tactics are employed to capture various prey species in differing habitats and locations. Some techniques are unique, involve tool use, and culturally transmitted vertically through learning (e.g.,

Copyright © 2017. Elsevier Science & Technology. All rights reserved.

Krützen et al., 2014). Foraging methods used by dolphins of the Shark Bay population include: sticking the rostrum into sea grass beds or the seafloor to search for fish ('bottom grubbing"), using tail slaps to flush out prey ("kerplunking"), chasing prey onto beaches where dolphins follow to catch them ("beach hunting"), carrying marine sponges to protect the tip of the beak from abrasion on the ocean floor ("sponging"), and the lifting of large gastropod shells above the water to dislodge fish hidden inside ("conching" or "shelling").

Little is known about the predators of *T. aduncus* in most regions. Sharks are a main cause of mortality for some populations, with the main predators being tiger shark (*Galeocerdo cuvieri*), white shark (*Carcharodon carcharias*), bull shark (*Carcharhinus leucus*), and dusky shark (*C. obscurus*). For some populations, shark-bite frequency is very high (e.g., >74% of the noncalf dolphins in Shark Bay bear scars from shark attacks). Shark-bite scars are much less frequent in Moreton Bay (eastern Australia) and South African waters, at about 37% and 10%–20%, respectively (however, it is uncertain if these data include both *T. aduncus* and *T. truncatus*). There are also some indications that small sharks may behave as micropredators by taking small bites out of dolphins living around oceanic islands (e.g., Mikura Island), where some dolphins possess scars that have been attributed to "cookie-cutter" sharks. There is no record of predation by killer whales. However, the stomach contents of a young killer whale (stranded in southern Australia) contained parts of at least three *T. aduncus* (along with at least two other delphinid species) but due to suspicious human interference, this should not be considered a reliable record of killer whale predation. In addition to predation, dolphins have died as a result of accidental injuries caused by needlefish, spines of a sting ray, and airway obstruction by carpet shark, porcupine fish, and extensive papillomatosis within the blowhole (e.g., Byard et al., 2010).

There are few studies on parasites and pathogens. Ectoparasites reported include the cirripede *Xenobalanus globicipitis* and cyamids. Endoparasites include nematodes in the pterygoid sinuses (possibly *Crassicauda* sp.) and in the lungs and respiratory tract (*Halocercus lagenorhynchi*, *Stenurus ovatus*) and cestodes of the genus *Phyllobothrium* in the blubber (mainly around the urogenital region) and possibly *Monorygma* internally. Fecal (and vomit) sampling of Red Sea dolphins revealed a plethora of parasites (some potentially zoonotic) of the gastrointestinal tract. At least 21 species of protozoans (including *Cryptosporidium* spp., *Giardia* spp., and *Sarcocystis* spp., Ciliata sp., Holotrichia sp., and Dinoflagellata sp.), seven trematodes (*Nasitrema* spp., *Zalophotrema* spp., *Pholeter gastrophilus*), two nematodes (*Anisakis typica*, *Capillaria* sp.), and one cestode (*Diphyllobothrium* sp.) were recorded (see Kleinertz et al., 2014). Exposure to *Toxoplasma* was also detected for dolphins from Western Australia and the Solomon Islands. *Brucella* and viral (morbillivirus and poxviruses) infections have also been detected (e.g., van Bressem et al., 2009; Stephens et al., 2014). Lobomycosis-like disease was reported from Japan, Mayotte, and South Africa and a high prevalence of a nodular skin disease (also suspected to be fungal) was found on dolphins in Japan (van Bressem et al., 2013).

IV. Behavior and Physiology

Group size is small being most commonly between 20 and 50 individuals with the larger groups tending to contain calves. In Japanese waters, groups of >100 individuals are quite common. In Taiwan, no group greater than about 35 individuals has been recorded in recent times even though past drive-hunting in the Penghu Islands may have caught hundreds in single drives (the last drive in 1993 captured only about 20 individuals, which may be indicative of local depletion after decades of unregulated hunting). In South African waters, larger groups up to 2000 individuals, comprising many smaller units, have been reported. Different communities have been found in various locations but these can change naturally or due to human activities.

Social organization is best described as fission–fusion but individual associations can vary greatly across regions (see Connor and Krützen, 2016; Tsai and Mann, 2013). Males can have complex alliance strategies to improve access to reproductive females while females can associate with each other to reduce shark predation, help rear calves, and thwart male coercion. In some regions, associations appear to have correlations with kinship. Mother–offspring bonds are very strong. Neonates have an intense following response and mothers are very possessive of their offpring (they have even been observed to stay with and protect deceased offspring for extended periods).

In general, the species appears to exhibit year-round residency within limited coastal waters and there is some evidence of seasonal movement. However, migration, in the strict sense, does not occur. Both sexes appear to exhibit strong philopatry but whether males are more dispersive is debatable. Long distant (hundreds of kilometers) movements of individuals have been recorded and in at least one case, the movement was believed to be permanent (Shirakihara et al., 2012). Based on limited studies, individual home ranges appear to be small being in the tens to low hundreds of km^2 (with males having larger ranges than females) (e.g., Sprogis et al., 2016a). There appears to be spatial and social sexual segregation in some areas but not in others (e.g., Fury et al., 2013). Swimming speed is usually between 1.5 and 4 km/hr, but high-speed bursts can reach at least 16–19 km/hr. Submergence time is typically short (<5–10 min) and maximum dive depth is likely shallower than 200 m.

V. Life History

Demographic information is limited and mostly from studies on the dolphins of the waters of Shark Bay, Mikura Island, and southern Australia (e.g., Steiner and Bossley, 2008; Kemper et al., 2014). Mean annual birth rate varies from 0.064 to 0.071, mean fecundity rate is 0.239, and mean recruitment rate is 0.068. The sex ratio at birth is about equal, but there are more males at subadulthood and more females at adulthood suggesting that females may have higher survivorship to adulthood, but it was uncertain why the sex ratio would be skewed toward males prior to adulthood. Mortality of first-year calves varies between 0.13 and 0.30 (being especially high for those of primiparous females) and calf mortality was about 0.40–0.46. Typically, age of sexual maturity for both sexes is about 10–15 years (with males being slightly earlier) and there is great geographic variation in length at sexual maturation. In Shark Bay, dolphins can reach sexual maturity between <1.9 and 2.1 m long, whereas South African dolphins are slightly larger (2.1–2.4 m long). Larger minimum size at sexual maturation is likely to be found in colder waters. Studies have shown that each dental growth layer group (GLG) is consistent with a year but old dolphins can be difficult to age because the pulp cavities of teeth become occluded (usually coinciding with physical maturity) so maximum age is unknown but estimated at >40 years for males and >50 years for females. Estimates of apparent survivorship vary between 0.94 and 0.99 (e.g., Sprogis et al., 2016b).

Ovulation is spontaneous and sporadic. The left ovary is larger (with more corpora) than the right and appears to begin activity earlier. Males have relatively small mature testes compared with other delphinids, but are still large (combined testes mass ~2 kg) relative to other mammals. Calving seasons are broad with most births occurring in the months with highest water temperatures. Gestation lasts about 12 months and interbirth interval is usually

Copyright © 2017. Elsevier Science & Technology. All rights reserved.

between 3 and 6 years but can be as low as 2–3 years; females that lose calves early can become pregnant soon afterward and give birth the following year. Females can be simultaneously pregnant and lactating with nursing usually lasting 3–5 years but can be as short as 18–20 months. Size at birth is about 1 m long and about 9–15 kg in mass.

There is little information on growth but given large regional differences in body size, growth curves are sure to vary. Like most marine mammals, growth is rapid in the earliest years of life. For South African animals (Ross, 1984), the length-to-mass function is $M = 8.0 \times 10^{29} X^{3.057}$ (where M = mass in kilograms and X = length in millimeters).

VI. Interactions With Humans

Direct and incidental catches and habitat degradation are the most concerning threats to this species. In many regions, it has been killed (usually by some form of spear) for human consumption and bait for shark or crustacean fisheries (e.g., Philippines, Taiwan, east Africa, Australia) as well as out of malice. It is also a preferred species for captive display throughout Asia. The infamous drive hunt of the Penghu Islands (which ceased in the early 1990s) and more recent captures from the waters of Indonesia and the Solomon Islands supplied dolphins for several aquariums and tourist resorts including in Taiwan, Hong Kong, Europe, Mexico, and Dubai. With the recent interest and rapid expansion of dolphinarium numbers in China, more pressure will likely be put on this vulnerable species.

Incidental net entanglement is likely the greatest concern; see Shirakihara and Shirakihara (2012). In the 1980s, up to 2000 dolphins per year were caught in northern Australian waters by a Taiwanese shark driftnet fishery. After strict Australian regulations, the fishery moved into neighboring Indonesian waters and continued largely unmonitored. Bycatch levels in Chinese waters are poorly known but with >3.5 million gillnets being used in coastal waters (not including those of Taiwan), there is great concern. The species is also known to feed behind bottom trawl nets. This behavior increases the risk of incidental capture and rate of shark attacks (as the dolphins are focused on the trawls, which also attract sharks) and can alter the social organization of dolphins. Even hand-line fisheries (in areas without gillnets) have been shown to injure and kill dolphins. In South African and Australian waters, concerning numbers of dolphins have been killed by entanglement in protective nets used to protect bathers from sharks and tuna (in aquaculture cages) from predators.

Habitat destruction and displacement by heavy industrialization, coastal development, expansion of industrial aquaculture and mariculture operations in many parts of the distribution of *T. aduncus* continues at a rapid pace. Moreover, the pollution that accompanies such activities further contributes to the degradation of water quality. Because the species tends to be in small, localized groups and in inshore waters, coastal degradation can have devastating impacts on these groups.

Even activities that are usually considered relatively benign toward cetaceans can also affect this vulnerable species. Dolphin-watch boats (even at low levels) have affected the behavior of dolphins and appear to have caused a decline in dolphin abundance in Shark Bay (Bejder et al., 2006). Dolphin-swim tours have altered natural dolphin behavior and dolphin-feeding tours have increased calf mortality and decreased reproductive success of the provisioned females. Increased boating traffic can alter the swimming and acoustic behavior of some dolphins and sometimes result in collisions that are fatal to dolphins.

Tursiops aduncus is classified by the IUCN Red List of Threatened Species as "Data Deficient." However, there are serious concerns about the depletion of some populations that have yet to be assessed. The species is well protected by national laws throughout most of its distribution but adequate enforcement is lacking almost everywhere. A few marine protected areas have been established but their effectiveness remains to be determined.

Copyright © 2017. Elsevier Science & Technology. All rights reserved.

References

Amaral, A.R., Jackson, J.A., Möller, L.M., and Beheregaray, L.B. (2012). Species tree of a recent radiation: the subfamily Delphininae (Cetacea, Mammalia). *Mol. Phylo. Evol.* **64**, 243–253.

Byard, R.W., Tomo, I., Kemper, C.M., Gibbs, S.E., Bossley, M., Machado, A., and Hill, M. (2010). Unusual causes of fatal upper aerodigestive tract obstruction in wild bottlenose dolphins (*Tursiops aduncus*). *Forensic Sci. Med. Pathol.* **6**, 207–210.

Bejder, L., et al. (2006). Decline in relative abundance of bottlenose dolphins exposed to long-term disturbance. *Cons. Biol.* **20**, 1791–1798.

Connor, R.C., and Krützen, M. (2015). Male dolphin alliances in Shark Bay: changing perspectives in a 30-year study. *Anim. Behav.* **103**, 223–235.

Fury, C.A., Ruckstuhl, K.E., and Harrison, P.L. (2013). Spatial and social sexual segregation patterns in Indo-Pacific bottlenose dolphins (*Tursiops aduncus*). *PloS One* **8**(1), e52987.

Hawkins, E.R. (2010). Geographic variations in the whistles of bottlenose dolphins (*Tursiops aduncus*) along the east and west coasts of Australia. *J. Acoust. Soc. Am.* **128**, 924–935.

Kemper, C.M., Trentin, E., and Tomo, I. (2014). Sexual maturity in male Indo-Pacific bottlenose dolphins (*Tursiops aduncus*): evidence for regressed/pathological adults. *J. Mammal.* **95**, 357–368.

Kiszka, J.J., Méndez-Fernandez, P., Heithaus, M.R., and Ridoux, V. (2014). The foraging ecology of coastal bottlenose dolphins based on stable isotope mixing models and behavioural sampling. *Mar. Biol.* **161**, 953–961.

Kleinertz, S., Hermosilla, C., Ziltener, A., Kreicker, S., Hirzmann, J., Abdel-Ghaffar, E., and Taibert, A. (2014). Gastrointestinal parasites of free-living Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) in the Northern Red Sea, Egypt. *Parasitol. Res.* **113**, 1405–1415.

Krützen, M., Kreicker, S., MacLeod, C.D., Learmouth, J., Kopps, A.M., Walsham, P., and Allen, S.J. (2014). Cultural transmission of tool use by Indo- Pacific bottlenose dolphins (*Tursiops* sp.) provides access to a novel foraging niche. *Proc. R. Soc. B* **281**, 20140374.

McGowen, M.R. (2011). Toward the resolution of an explosive radiation—a mulitlocus phylogeny of oceanic dolphins (Delphinidae). *Mol. Phylo. Evol* **60**, 345–357.

Oremus, M., Garrigue, C., Tezanos-Pinto, G., and Baker, C.S. (2015). Phylogenetic identification and population differentiation of bottlenose dolphins (*Tursiops* spp.) in Melanesia, as revealed by mitochondrial DNA. *Mar. Mamm. Sci.* **31**, 1035–1056.

Perrin, W.F., Robertson, K.M., van Bree, P.J.H., and Mead, J.G. (2007). Cranial description and genetic identity of the holotype specimen of *Tursiops aduncus* (Ehrenberg, 1832). *Mar. Mamm. Sci.* **23**, 343–357.

Pusineri, C., Barbraud, C., Kiszka, J., Caceres, S., Mougnot, J., Daudin, G., and Ridoux, V. (2014). Capture-mark-recapture modelling suggests an endangered status for the Mayotte Island (eastern Africa) population of Indo-Pacific bottlenose dolphins. *Endangered Species Res.* **23**, 23–33.

Reisinger, R.R., and Karczmarski, L. (2010). Population size estimate of Indo-Pacific bottlenose dolphins in the Algoa Bay region, South Africa. *Mar. Mamm. Sci* **26**, 86–97.

Shirakihara, M., and Shirakihara, K. (2012). Bycatch of the Indo-Pacific bottlenose dolphin (*Tursiops aduncus*) in gillnet fisheries off Amakusa-Shimoshima Island, Japan. *J. Cetacean Res. Manage.* **12**, 345–351.

Shirakihara, M., Shirakihara, K., Nishiyama, M., Iida, T., and Amano, M. (2012). Long-distance movements of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) and habitat preference of two species of bottlenose dolphins in eastern Kyushu, Japan. *Aquat. Mamm* **38**, 145–152.

Smith, H.C., Pollock, K., Waples, K., Bradley, S., and Bejder, L. (2013). Use of the robust design to estimate seasonal abundance and demographic parameters of a coastal bottlenose dolphin (*Tursiops aduncus*) population. *PloS One* **8**(10), e76574.

Sprogis, K.R., Raudino, H.C., Rankin, R., MacLeod, C.D., and Bejder, L. (2016a). Home range size of adult Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) in a coastal and estuarine system is habitat and sex-specific. *Mar. Mamm. Sci* **32**, 287–308.

Sprogis, K.R., Pollock, K.H., Raudino, H.C., Allen, S.J., Kopps, A.M., Manlik, O., Tyne, J.A., and Bejder, L. (2016b). Sex-specific patterns in abundance, temporary emigration and survival of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) in coastal and estuarine waters. *Front. Mar. Sci* **3**, 12.

Steiner, A., and Bossley, M. (2008). Some reproductive parameters of an estuarine population of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*). *Aquat. Mamm* **34**, 84–92.

Stephens, N., Duignan, P.J., Wang, J., Bingham, J., Finn, H., Bejder, L., Patterson, I.A.P., and Holyoake, C. (2014). Cetacean morbillivirus in coastal Indo-Pacific bottlenose dolphins, Western Australia. *Emerg. Infect. Dis.* **20**, 666–670.

Tsai, Y.-J.J., and Mann, J. (2013). Dispersal, philopatry, and the role of fission-fusion dynamics in bottlenose dolphins. *Mar. Mamm. Sci.* **29**, 261–279.

Van Bressem, M.-F., Shirakihara, M., and Amano, M. (2013). Cutaneous nodular disease in a small population of Indo-Pacific bottlenose dolphins, *Tursiops aduncus*, from Japan. *Mar. Mamm. Sci.* **29**, 525–532.

Van Bressem, M.-F., Raga, J.A., Di Guardo, G., Jepson, P.D., Duignan, P.J., Siebert, U., Barrett, T., de Oliveira Santos, M.C., Moreno, I.B., Siciliano, S., Aguilar, A., and Van Waerebeek, K. (2009). Emerging infectious diseases in cetaceans worldwide and the possible role of environmental stressors. *Dis. Aquat. Org.* **86**, 143–157.

Wang, J.Y., Chou, L.-S., and White, B.N. (1999). Mitochondrial DNA analysis of sympatric morphotypes of bottlenose dolphins (genus *Tursiops*) in Chinese waters. *Mol. Ecol.* **8**, 1603–1612.

Wang, J.Y., Chou, L.-S., and White, B.N. (2000a). Differences in the external morphology of two sympatric species of bottlenose dolphins (genus *Tursiops*) in the waters of China. *J. Mamm.* **81**, 1157–1165.

Wang, J.Y., Chou, L.-S., and White, B.N. (2000b). Osteological differences between two sympatric forms of bottlenose dolphins (genus *Tursiops*) in Chinese waters. *J. Zool. (London)* **252**, 147–162.

BOTTLENOSE WHALES

Hyperoodon ampullatus and H. planifrons

HILARY B. MOORS-MURPHY

Bottlenose whales (bottle-nosed whales) are toothed whales (order: Cetacea, suborder: Odonticeti) of the family Ziphiidae: the beaked whales.

I. Characteristics and Taxonomy

Bottlenose whales are medium-sized whales 6–10m in length (Mead, 1989). They have a large bulbous melon (forehead) and pronounced beak (Figs 1 and 2). Like other beaked whales, they have a falcate dorsal fin two-thirds down their back, small flippers, two ventral throat grooves, and no median notch in their tail flukes. Their color varies between chocolate brown to gray to yellow, with lighter flanks and belly. Coloration and head shape are indicative of sex and age (Fig. 2; Gowans et al., 2000). Calves are gray with dark eye patches; adult females and immature males have a smooth rounded forehead. Mature males develop a flat, squared-off forehead that gets whiter with age due to their maxillary crests becoming larger and heavier (Mead, 1989). The dense forehead of males may be used for male–male competition; head-butting has been observed (Gowans and Rendell, 1999). Females and immatures have no erupted teeth, while adult males have two erupted teeth at the tip of the lower jaw (Mead, 1989) that are rarely visible in live animals.

Two species are currently recognized under the genus *Hyperoodon*—the northern bottlenose whale (*H. ampullatus*) and the southern bottlenose whale (*H. planifrons*).

II. Distribution and Abundance

Northern bottlenose whales are found only in the North Atlantic Ocean in cold temperate, subarctic, and Arctic waters (Fig. 3). They tend to occur in waters >500m, with a preference for deep continental slope waters of 800–1800m. They are generally not found in partially enclosed areas such as the Gulf of St Lawrence, Hudson Bay, or Mediterranean Sea. Whaling data indicate six areas of concentration: the Scotian Shelf and off Labrador/southern Baffin Bay in the western Atlantic, and off east Greenland/Iceland/Jan Mayan/Faroe Islands, southwest of Svalbard (Norway), off Andenes (northern Norway), and off Møre (western Norway) in the eastern Atlantic (Whitehead and Hooker, 2012). The western Atlantic concentrations are managed as separate populations in Canada (COSEWIC, 2011; DFO, 2016). The "Scotian Shelf population" is listed as *endangered* under the Canadian Species at Risk Act (SARA). It consists of ~140 individuals and has been stable since the 1980s when photographic identification studies began (Fig. 4; O'Brien and Whitehead, 2013). These whales occur mainly in three submarine canyons of the Scotian Shelf that are designated as critical habitat of the population: the Gully, Shortland, and Haldimand canyons. The "Baffin Bay-Davis Strait-Labrador Sea population" was assessed as *special concern*, and is not currently listed under the SARA. Little is known about this population, but ecological and genetic evidence supports the separation of these two western Atlantic populations. There are some genetic linkages between the Baffin Bay-Davis Strait-Labrador Sea population and individuals sampled off Iceland (Dalebout et al., 2006), but stock structure in the eastern Atlantic remains unclear. Abundance estimates off Iceland and the Faeroe Islands range from 5000 to 28000 animals; there are no abundance estimates for Norway (Whitehead and Hooker, 2012).

Southern bottlenose whales occur widely throughout the Southern Hemisphere mainly south of 30°S (Fig. 3; Mead 1989). Like their northern congener, they also appear to prefer deep waters (e.g., Sekiguchi et al., 1993). Kasamatsu and Joyce (1995) report that beaked whales are most common between 58 and 62°S particularly in the South Atlantic, and provide a population estimate of about 600,000 beaked whales.

III. Ecology

Like other beaked whales, bottlenose whales regularly dive deeply to forage. Northern bottlenose whales show a high degree of feeding specialization, predominately eating *Gonatus* squid, though fish and invertebrates are occasionally consumed (MacLeod et al., 2003). Time-depth recorders have shown that they dive to depths >800m approximately every 80min (maximum dive >1400m). Most dives go close to the seafloor suggesting benthic or bathypelagic feeding behavior (Hooker and Baird, 1999).

Stomach content analyses of six southern bottlenose whales show that this species feeds primarily on squid (MacLeod et al., 2003).

IV. Behavior and Physiology

Bottlenose whales are typically observed in small groups of up to ten individuals, though groups of up to 20 animals of mixed

Copyright © 2017. Elsevier Science & Technology. All rights reserved.

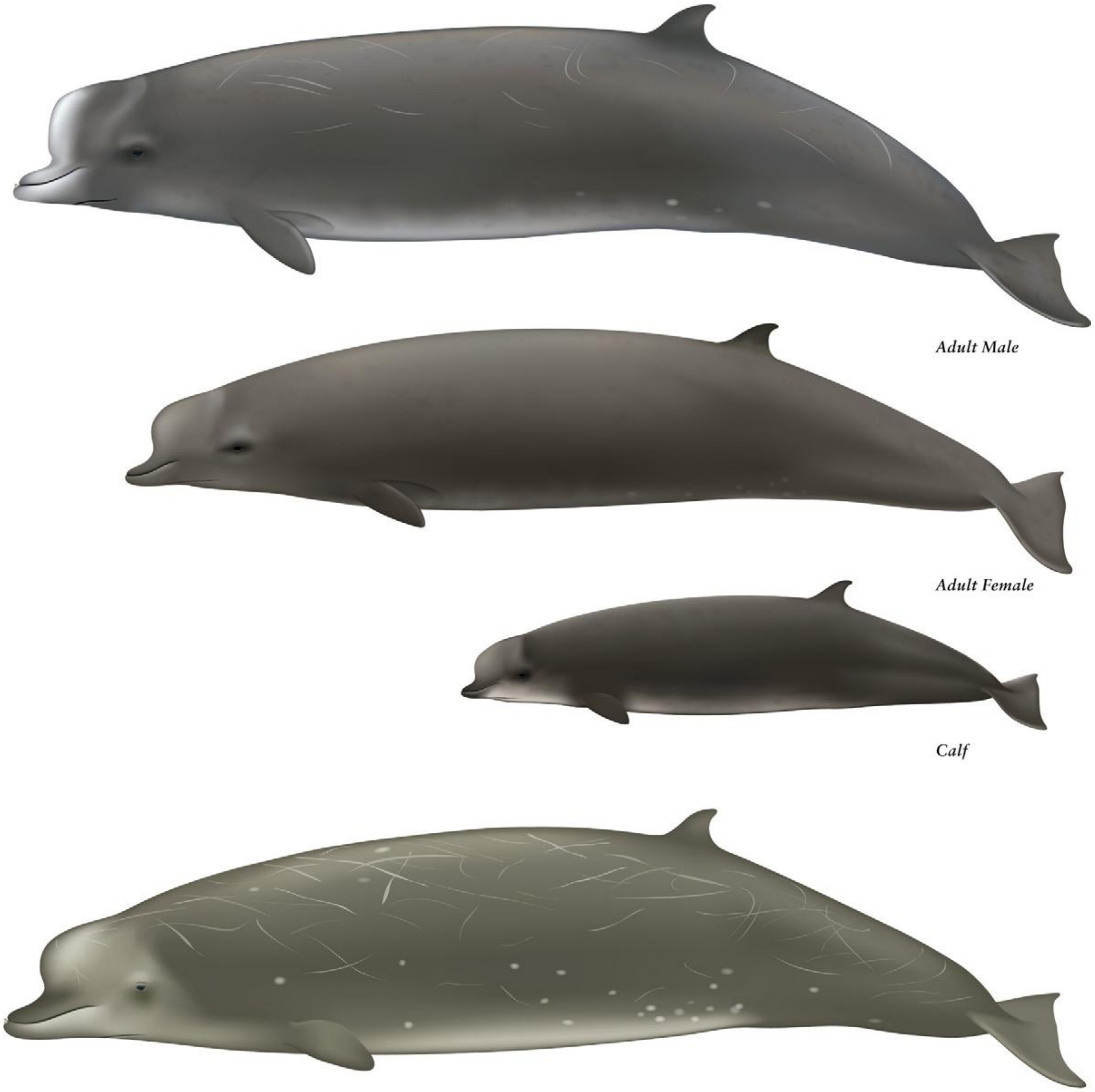

Figure 1 *Northern bottlenose whale,* Hyperoodon ampullatus *and southern bottlenose whale,* H. planifrons. *Adult male (top), adult female (upper middle) and calf (lower middle) northern bottlenose whales. Adult southern bottlenose whale (bottom) (Illustrations by Uko Gorter).*

Figure 2 *Melon (forehead) of a northern bottlenose whale calf (A), female/immature male (B), and (C) a mature male (Photos by (A) Whitehead Lab, Dalhousie University, (B) and (C) H. Moors-Murphy).*

Copyright © 2017. Elsevier Science & Technology. All rights reserved.

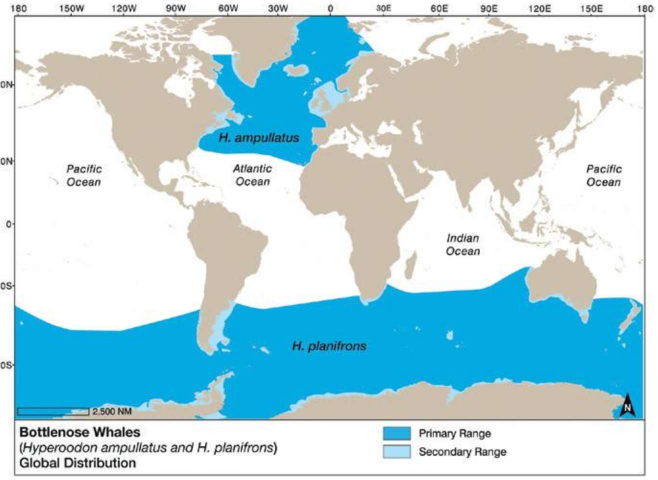

Figure 3 *Northern (H. ampullatus.) and southern (H. planifrons.) bottlenose whale distribution. Adapted by Nina Lisowski from Jefferson, T.A., Webber, M.A., and Pitman, R.L. (2015). "Marine Mammals of the World: A Comprehensive Guide to Their Identification," 2nd ed. Elsevier, San Diego, CA.*

Figure 4 *Individual northern bottlenose whales are identified by unique marks and coloration patterns on their dorsal fins and backs (Photos by Whitehead Lab, Dalhousie University).*

age/sex classes have been reported. Social behavior has only been studied in the Scotian Shelf northern bottlenose whale population. These whales display a fission–fusion society structure where associations among individuals change frequently. Females show no preferential associations while males have more structured relationships, forming associations between individuals that last 1–2 years (Gowans et al., 2001). Northern bottlenose whales often approach and investigate boats. This characteristic was exploited by whalers who also learned that when a northern bottlenose whale was harpooned its companions would not leave it until it was dead, allowing multiple individuals to be taken (Mead, 1989).

V. Life History

Northern bottlenose whales reach sexual maturity at age 8–13 and give birth to a single offspring every 2 years, following a gestation period of 12 months. The lactation period was estimated to last at least 1 year. Males reach sexual maturity around 7–9 years of age. The oldest individual recorded from whaling data was 37 years old (Benjaminsen and Christensen, 1979). Sightings and acoustic data indicate that the Scotian Shelf population is a year-round resident population, while in other areas individuals may migrate seasonally.

Little is known about southern bottlenose whale reproduction. Calving is thought to take place off South Africa in spring and early summer. There is some evidence to suggest a northward migration in winter (Sekiguchi et al., 1993).

VI. Interactions With Humans

Northern bottlenose whales were one of the only beaked whale species targeted by whaling. They were harvested heavily throughout their range from 1880 to 1920 and 1937 to 1973, with more than 60,000 kills reported (though this is likely an underestimate). Whaling resulted in population declines from which some populations are likely still recovering. Currently, the most important threats to northern bottlenose whales include entanglement in fishing gear, anthropogenic noise, and contaminants (DFO, 2016).

See Also the Following Articles

Toothed Whales ■ Diving Physiology ■ Diving Behavior

References

Benjaminsen, T., and Christensen, I. (1979). The natural history of the bottlenose whale, *Hyperoodon ampullatus* (Foster). In "Behavior of Marine Animals", (H.G. Winn, and B.L. Olla, Eds), Vol. 3, pp. 143–164. Plenum Press, New York.

COSEWIC (2011). COSEWIC assessment and status report on the northern bottlenose whale *Hyperoodon ampullatus* in Canada. Committee on the Status of Endangered Wildlife in Canada, Ottawa. xii + 31 pp.

Dalebout, M.L., Ruzzante, D.E., Whitehead, H., and Øien, N.I. (2006). Nuclear and mitochondrial markers reveal distinctiveness of a small population of bottlenose whales (*Hyperrodon ampullatus*) in the Western North Atlantic. *Mol. Ecol.* **15**, 3115–3129.

DFO (2016). Recovery Strategy for the Northern Bottlenose Whale, (*Hyperoodan ampullatus*), Scotian Shelf population, in Atlantic Canadian Waters. *Species at Risk Act Recovery Strategy Series.* Fisheries and Oceans Canada, Ottawa. vii + 70 pp.

Gowans, S., and Rendell, L. (1999). Head-butting in northern bottlenose whales (*Hyperoodon ampullatus*): a possible function for big heads? *Mar. Mamm. Sci.* **15**, 1342–1350.

Gowans, S., Dalebout, M.L., Hooker, S.K., and Whitehead, H. (2000). Reliability of photographic and molecular techniques for sexing northern bottlenose whales (*Hyperoodon ampullatus*). *Can. J. Zool.* **78**, 1224–1229.

Gowans, S., Whitehead, H., and Hooker, S.K. (2001). Social organization in northern bottlenose whales (*Hyperoodon ampullatus*); not driven by deep water foraging. *Anim. Behav.* **62**, 369–377.

Hooker, S.K., and Baird, R.W. (1999). Deep-diving behavior of northern bottlenose whale, *Hyperoodon ampullatus* (Cetacea: Ziphiidae). *Proc. R. Soc. Lond. B* **266**, 671–676.

Kasamatsu, F., and Joyce, G.G. (1995). Current status of odontocetes in the Antarctic. *Antarc. Sci.* **7**, 365–379.

MacLeod, C.D., Santos, M.B., and Pierce, G.J. (2003). Review of the data on diets of beaked whales: evidence of niche separation and geographic segregation. *J. Mar. Biol. Assoc. UK* **83**, 651–665.

Mead, J.D. (1989). Bottlenose whales – *Hyperoodon ampullatus* (Forster, 1770) and *Hyperoodon planifrons* (Flower, 1882). In "Handbook of Marine Mammals, Volume 4: River Dolphins and Larger Toothed Whales", (S.H. Ridgeway, and S.R. Harrison, Eds), pp. 321–348. Academic Press, New York.

O'Brien, K., and Whitehead, H. (2013). Population analysis of Endangered northern bottlenose whales on the Scotian Shelf seven years after the establishment of a Marine Protected Area. *Endang. Species Res.* **21**, 273–284.

Sekiguchi, K., Klagies, N., Findlay, K., and Best, P.B. (1993). Feeding habits and possible movements of southern bottlenose whales (*Hyperoodon planifrons*). *Symp. Polar Biol.* **6**, 84–97.

Whitehead, H., and Hooker, S.K. (2012). Uncertain status of the northern bottlenose whale *Hyperoodon ampullatus*: population fragmentation, legacy of whaling and current threats. *Endang. Species Res.* **19**, 47–61.

Copyright © 2017. Elsevier Science & Technology. All rights reserved.

BOWHEAD WHALE

Balaena mysticetus

J. Craig George, David Rugh and R. Suydam

I. Characteristics and Taxonomy

The bowhead whale (*Balaena mysticetus*), also referred to as the Greenland right whale in the North Atlantic, is a member of the family *Balaenidae* which inhabits the ice-associated regions of the Arctic and subarctic seas (Tomilin, 1957; Moore and Reeves, 1993). Bowheads are characterized by a highly arched rostrum (hence the name "bowhead"), black skin, thick blubber, long baleen, the lack of a dorsal fin, and a rotund profile (Fig. 1). They begin life in freezing sea water in spring often in heavy sea ice. Adults can be 19 m in body length and exceed 80 metric tons in mass; however, some individuals may have exceeded 24 m and 100 metric tons based on observations by Inuit hunters and credible Yankee whaling records. Yankee whalers reported a single animal yielded 375 cast-barrels of oil, suggesting a mass comparable to the largest blue whales.

Bowheads have a white chin patch extending posteriorly that is highly variable in size and shape. The skin around the genital region, peduncle, eye, and flukes gradually becomes whiter with age. The bowhead exhibits a number of superlatives among Cetacea. These include: the thickest blubber, thickest skin, greatest longevity, longest baleen, lowest body core temperatures, and proportionally the largest head of any cetacean (George et al., 1993; Haldiman and Tarpley, 1993). Their baleen rack is extensive with a total of 600–640 plates, the longest of which exceeds 4 m. Head size (skull) increases through life from ~30% to ~35% body length. Fluke width averages 34% of the body length and increases slightly through life.

II. Distribution and Abundance

Bowheads have a circumpolar distribution across the arctic and subarctic seas (Fig. 2). Researchers distinguish four breeding populations defined by geographic regions and genetic independence. The small Okhotsk Sea stock is entirely restricted to the Sea of Okhotsk in eastern Russia and is genetically the most divergent population. The Bering-Chukchi-Beaufort Seas stock (BCB) occupies the waters from the Bering Sea to western Arctic Canada as the name implies, and is genetically distinct (Givens et al., 2010; LeDuc et al., 2009) from both the Okhotsk stock and the Eastern Canadian stock (formerly the Hudson's Bay/Davis Strait stock). Genetic analyses of archeological samples indicate that the fourth stock, the Spitsbergen stock, was genetically isolated only from the Okhotsk stock, while they appear to share recent genetic exchange with the BCB and EC stocks (Alter et al., 2012).

The abundance of the largest and best-studied stock, the BCB stock, was estimated in 2011 at 16,820 whales (95% CI: 15,176–18,643) (Givens et al., 2010) with a 3.7% annual rate of increase. The BCB whales winter in the Bering Sea, (Citta et al., 2012) generally well within the sea ice, and most migrate annually back and forth to the Eastern Beaufort Sea (Fig. 3). Satellite telemetry has shown some excursions into the Canadian Archipelago and into the Northeast Passage along the Chukotka coast.

Recent estimates for the Eastern Canadian stock put it at 6447 (CV 26%) animals (Doniol-Valcroze et al., 2015) and the Okhotsk Stock appears to be about 300 animals (Vladimirov, 1994). Recent surveys suggest the Spitsbergen stock, originally the largest at over 25,000 animals, may now number in the low 100s (Stafford et al., 2012).

III. Ecology

Stomach examinations indicate that bowheads feed primarily on zooplankton, with copepods (~12 species) and euphausiids (2 species), being the dominant prey items. However, several species of fish (e.g., arctic cod and sandlance) and a variety of benthic and epibenthic invertebrate species have been identified as well, in lower abundance. Combined, these total over 100 prey species (Lowry, 1993). Feeding is common in summer and fall with 75% of landed whales having prey remains in their stomachs. Winter feeding in the Bering Sea likely occurs in some years. Limited feeding occurs during spring migrations evidenced by relatively low stomach prey volumes. When animals reach the Eastern Beaufort Sea in May they appear to feed extensively throughout the summer. The ecological significance of bowheads as a high-arctic zooplankton predator is not well understood, but since recovery from near extirpation, their importance in the arctic food web is presumably increasing.

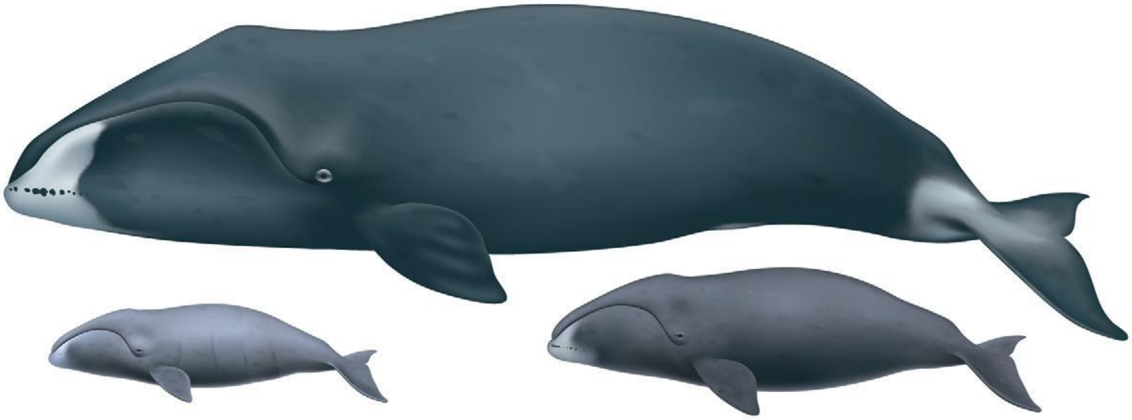

Figure 1 *Bowhead whale,* Balaena mysticetus *Top: Adult, Bottom Left: Neonate, Bottom Right: 6 Month Old Calf (Autumn) (Illustrations by Uko Gorter).*

Copyright © 2017. Elsevier Science & Technology. All rights reserved.

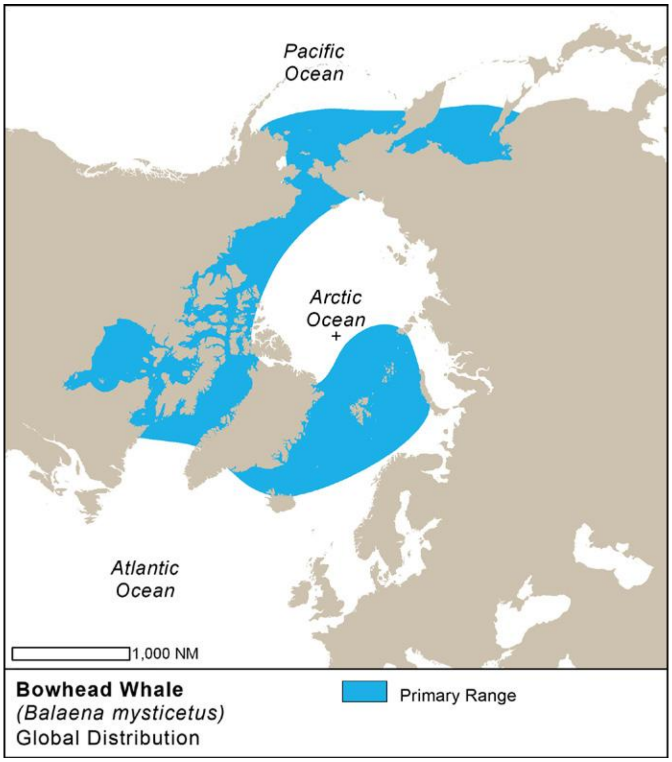

Figure 2 *Bowhead whale distribution. Map produced by Anders Skoglund, Norwegian Polar Institute.*

Figure 3 *A bowhead whale migrating through sea ice. Bowheads are highly adapted to life in sea ice but thrive and feed during ice-free summers (Photograph by Gerrady Zelensky).*

Aside from Eskimo hunters, killer whales (*Orcinus orca*) are the only bowhead predators. Recent studies suggest that the proportion of killer whale attacks has increased. In Alaskan waters approximately 12% of the bowheads show evidence of killer whale attacks but it is higher for EC bowheads (Reinhart et al., 2013; George et al., 2015).

Bowhead whales adeptly navigate sea ice and can break through sea ice in order to breathe. Researchers and native hunters have reported bowheads breaking ice 20–100 cm in thickness (George et al., 1989). The rostrum is strongly arched with the nares at the apex. The "bowed" head is partly an adaptation to breathing through small cracks, breaking ice and accommodating their tremendous baleen racks.

IV. Behavior and Physiology

Bowheads can feed effectively on small, relatively low density prey. The majority of their feeding takes place within the water column but bottom feeding and surface skim feeding are also very common (Würsig et al., 1985). Feeding near the bottom is evidenced by benthic species, occasional small pebbles in the gut, and mud plumes around them as they surface (Mocklin et al., 2012).

During the spring migration, BCB bowheads migrate in loose aggregations or pulses. While some large adults and lone adult females arrive randomly through the spring migration (Rugh et al., 2008), immature animals consistently migrate first, followed by mid-sized age/length animals, and finally the mother and calf pairs with a few large males.

Being a coastal species, bowhead dives tend to be relatively shallow <200 m, but dives to 400 + m are not uncommon (Heide-Jørgensen et al., 2013; Quakenbush et al., 2013) Maximum dive duration has been measured up to 85 min by both whale hunters and researchers. Core body temperatures are the lowest measured for a large cetacean at a mean 33.8°C and they possibly have low metabolic rates (George et al., 2009).

Bowheads have a diverse and complex vocal repertoire that includes simple calls and songs, sung during the winter and early spring. Songs differ from year to year. Songs can be several minutes long, "multivoiced" (can make tones at several frequencies) and span a frequency range from 20 Hz to over 5000 Hz. It is likely that songs play a role in mating behavior (Würsig and Clark, 1993; Stafford et al., 2012).

V. Life History

Bowheads apparently conceive in March and have a 13–14-month gestation period; however, sexual activity has been observed from spring through fall. Calves are born April through June with peak calving in mid-to-late May for BCB whales (George et al., 2004). A neonate weighs ~1000 kg at birth and they grow rapidly to 10–12 metric tons in their first year. Following weaning between 6 and 12 months, growth in body length slows or may cease entirely for about 4 years (George et al., 1999; Lubetkin et al., 2004; Lubetkin, 2008). Post weaning subadults actually lose weight through this period, partly by means of dramatic bone loss where resources are presumably redirected as the large head and extensive baleen rack grows (George et al., 2016).

Sexual maturity is achieved around 13.4 m in females at ~25 years and around 12.5–13 m in males (Rosa et al., 2012; Koski, 1993). Maximum age based on the "eye lens aging" method (aspartic acid racemization) suggests they can exceed 200 years in age. The oldest individuals (> 150 years) have been males; however, some females have been estimated to reach 140 years (George et al., 1999; Rosa et al., 2012; George et al., 2011).

VI. Interactions With Humans

Several indigenous cultures evolved around hunting bowheads and using their products for food, fuel, and building materials. Consequently, the bowhead provides both cultural and nutritional sustenance to many arctic communities. Inuit of North America, eastern Asia, Canada, and Greenland have hunted bowheads for

Copyright © 2017. Elsevier Science & Technology. All rights reserved.

1000–2000 years varying by region. Hunting such enormous animals requires close coordination of a large group of people, sophisticated tools, and complex hunting strategies (Harritt et al., 1995; Stoker and Krupnik, 1993). Sustainable aboriginal hunting from the BCB stock continues under the guidance of the International Whaling Commission with an annual quota of 67 strikes per year in Alaska and Chukotka.

Commercial bowhead whaling started in the North Atlantic in the 1600s by European whalers. The initial interest was oil from blubber. Following the discovery of petroleum, the oil market rapidly dried up, but a market for baleen developed which led to the final phase of bowhead whaling, which had a devastating effect on some stocks. The "crash" in the baleen market around 1910 due to the discovery of baleen substitutes abruptly ended the fishery and may have saved some stocks from extirpation (Bockstoce, 1986).

Interactions between bowheads and commercial fishing operations in the Bering Sea appear to be increasing. In the BCB stock, about 12% of the population exhibit entanglement injuries and several beach cast dead bowheads have been found entangled with commercial crab gear. Several animals have also been photographed during aerial surveys entangled in fishing gear. The annual mortality from entanglement remains unknown but is probably modest considering the current high rate of population increase.

Summer sea ice extent and thickness is diminishing rapidly; however, BCB bowheads currently appear to be responding positively to ice reduction via strong population increase and good body condition (George et al., 2015). Regardless, it is unknown how bowheads will ultimately respond.

References

Alter, E.S., Rosenbaum, H.C., Postma, L.D., Whitridge, P., Gaines, C., Weber, D., Egan, M.G., Lindsay, M., Amato, G., Dueck, L., Brownell, R.L., Heide-Jørgensen, M.-P., Laidre, K.L., Caccone, G., and Hancock, B.L. (2012). Gene flow on ice: the role of sea ice and whaling in shaping Holarctic genetic diversity and population differentiation in bowhead whales (*Balaena mysticetus*). *Ecol. Evol.* **2**(11), 2895–2911.

Citta, J.J., Quakenbush, L.T., George, J.C., Small, R.J., Heide-Jorgensen, M.P., Brower, H., Adams, B., and Brower, L. (2012). Winter movements of bowhead whales (*Balaena mysticetus*) in the Bering Sea. *Arctic* **65**, 1.

Doniol-Valcroze, T., Gosselin, J.-F., Pike, D., Lawson, J., Asselin, N., Hedges, K., and Ferguson, S. (2015). Abundance estimate of the Eastern Canada – West Greenland bowhead whale population based on the 2013 High Arctic Cetacean Survey. *DFO Can. Sci. Advis. Sec. Res. Doc.* **2015/058**, v + 27 p.

George, J.C., Bada, J., Zeh, J., Scott, L., Brown, S.E., O'Hara, T., and Suydam, R. (1999). Age and growth estimates of bowhead whales (*Balaena mysticetus*) via aspartic acid racemization. *Can. J. Zool.* **77**, 571–580.

George, J.C., Druckenmiller, M.L., Lairdre, K.L., Suydam, R., and Person, B. (2015). Bowhead whale body condition and links to summer sea ice and upwelling in the Beaufort Sea. *Prog. Oceanogr.* **136**, 250–262. doi:10.1016/j.pocean.2015.05.001.

George, J.C., Follmann, E., Zeh, J., Sousa, M., Tarpley, R.J., and Suydam, R. (2011). A new way to estimate whale age using ovarian corpora counts. *Can. J. Zool.* **89**, 840–852.

George, J.C., Stimmelmayr, R., Suydam, R., Usip, S., Givens, G., Sformo, T., and Thewissen, J. (2016). Severe bone loss as part of the life history strategy of bowhead whales. *PLoS One* **11**(6), e0156753.

Givens, G.H., Huebinger, R.M., Patton, J.C., Postma, L.D., Lindsay, M., Suydam, R.S., George, J.C., Matson, C.W., and Bickham, J.W. (2010). Population genetics of bowhead whales (*Balaena mysticetus*) in the western Arctic. *Arctic* **63**(1).

Givens, G.H., Edmondson, S.L., George, J.C., Suydam, R., Charif, R.A., Rahaman, A., Hawthorne, D., Tudor, B., DeLong, R.A., and Clark, C.W. (2016). Horvitz-Thompson whale abundance estimation adjusting for uncertain recapture, temporal availability variation and intermittent effort. *Environmetrics* **27**, 134–146.

Haldiman, J.T., and Tarpley, R.T. (1993). Anatomy and physiology. In "The Bowhead Whale", (J.J. Burns, J.J. Montague, and C.J. Cowles, Eds), Special publication No. 2 of the Society of Marine Mammalogy.

Harritt, R.K., Jolles, C.Z., and McCartney, A.P. (1995). Introduction. In "Hunting the Largest Animals. Native Whaling in the Western Arctic and Subarctic. Studies in Whaling No. 3 Occasional Publication No. 36", (A.P. McCartney, Ed.), The Canadian Circumpolar Institute, University of Alberta, Canada.

Heide-Jørgensen, M.P., Laidre, K.L., Nielsen, N., Hansen, R., and Røstad, A. (2013). Winter and spring diving behavior of bowhead whales relative to prey. *Anim. Biotelem.* **1**, 15.

Mocklin, J., Rugh, D., Moore, S., and Angliss, R. (2012). Using aerial photography to investigate evidence of feeding by bowhead whales. *Mar. Mamm. Sci.* **28**(3), 602–619.

Quakenbush, L.T., Small, R.J., Citta, J.J. (2013). Satellite tracking of bowhead whales: movements and analysis from 2006 to 2012. U.S. Dept. of the Interior, Bureau of Ocean Energy Management, Alaska Outer Continental Shelf Region, Anchorage, AK. OCS Study BOEM 2013-01110. 60 pp. + appendices.

Rugh, D.J., Koski, W.R., George, J.C., and Zeh, J.E. (2008). Interyear re-identifications of bowhead whales during their spring migration past Barrow, Alaska, 1984–1994. *J. Cetacean Res. Manage.* **10**(3), 195–200.

Reinhart, N.R., Ferguson, S.H., Koski, W.R., Higdon, J.W., LeBlanc, B., Tervo, O., Jepson, P.D. (2013). Occurrence of killer whale *Orcinus orca* rake marks on Eastern Canada-West Greenland bowhead whales *Balaena mysticetus*. Published online. *Pol. Biol.* doi:10.1007/s00300-013-1335-3.

Würsig, B., and Clark, C.W. (1993). Behavior. In "The Bowhead Whale" (K. Burns, J.J., Montague, and C.J. Cowles, Eds), Spec. Ed. 2. Society for Marine Mammalogy, Allen Press, Lawrence, KS.

Würsig, B., Dorsey, E.M., Fraker, M.A., Payne, R.S., and Richardson, W.J. (1985). Behavior of bowhead whales, *Balaena mysticetus*, summering in the Beaufort Sea: A description. *U.S. Fish. Bull.* **83**, 357–377.

BOW-RIDING

Bernd Würsig

One of the most fascinating behaviors of dolphins is when they ride the bow pressure waves of boats. Dolphins probably have been bow-riding since swift vessels plied the seas, propelled by oar, sail, or very recently in the history of seafaring, motor. The Greeks wrote of bow-riding in the eastern Mediterranean and Aegean Seas by what were most likely common bottlenose (*Tursiops truncatus*), short-beaked common (*Delphinus delphis*), and striped dolphins (*Stenella coeruleoalba*).

Bow-riding consists of dolphins, porpoises, and other smaller toothed whales (and occasionally sea lions and fur seals) positioning themselves to be lifted up and pushed forward by the circulating water generated to form a bow pressure wave of an advancing vessel (Lang, 1966; Hertel, 1969). Dolphins are exquisitely good at bow-riding, able to fine-tune their body posture and position with only small movements of flippers, to be propelled along entirely by the pressure wave, often with no tail (or fluke) beats needed.

Copyright © 2017. Elsevier Science & Technology. All rights reserved.

Figure 1 *Common dolphins (*Delphinus delphis*) on the bow of a sailing vessel off Panama (Photo by Bernd Würsig).*

Figure 2 *Two bottlenose dolphins (*Tursiops truncatus*) leap for a breath between rides on the bow of a shrimp vessel near shore in the Gulf of Mexico (Photo by Bernd Würsig).*

Bow-riders at the periphery of the pressure wave do need to beat their flukes, and so do bow-riders of a slowly moving vessel or one with a very sharp cutting instead of pushing bow.

There is often quite a bit of jostling for position at the bow; dominant animals of a group might edge others to less favorable positions, or one animal may simply replace another that is displaced from the bow (Fig. 1). Bow-riding dolphins tend to emit sounds that are normally associated with high levels of social activity (Brownlee and Norris, 1994).

While many species of dolphins, porpoises, and small toothed whales ride bow waves, some do not; and in some species, certain populations do not. Bottlenose dolphins (*Tursiops* spp.) are bow-riders the world over, but even they do not ride in some areas (even where they are not hunted) or on some types of vessels. For example, off the shores of Texas in the Gulf of Mexico, they generally do not approach vessels smaller than 15 m long to bow-ride, apparently finding the smaller bows not worth their while. Instead, they "hitch a ride" on oil tankers and freighters or sometimes they are attracted to larger shrimping vessels en route to and from the shrimping grounds, at times bow-riding for 20 or more kilometers at a stretch. Dolphins ride underwater, and must leave their position to breathe, leaping forward at an angle to the surface before falling back toward the advancing bow in a welter of foam (Fig. 2). Dolphins also ride the stern waves (or wakes) of boats, which present a different hydrodynamic challenge than bow-riding; and in some areas, dolphins that do not approach the bow will nevertheless ride in the influence of a large (or fast small) vessel's wake.

Most oceanic dolphins ride bow waves, with notable exceptions in areas of intensive hunting (by being harpooned or gaffed), or in the case of tuna vessels in the eastern Tropical Pacific, where vessels chase dolphins to net the tuna affiliated with a dolphin school (Perrin, 1968). However, riding the bow is also "mood dependent"; dusky dolphins (*Lagenorhynchus obscurus*), for example, do not approach vessels when they have not fed for two or more days. These same dolphins race toward a boat from several kilometers during and after social/sexual activities that take place immediately after bouts of feeding on schooling anchovy (Würsig and Würsig, 1980).

Why do dolphins bow-ride? It has been proposed that bow-riding is a mechanism to efficiently travel from one place to another (Williams et al., 1992). However, this is unlikely, for one often sees bow-riding dolphins after some time heading back to whence they picked up the vessel. Instead of for locomotion, it is more likely that riding the bow is usually (but perhaps not always) for play. There are not many wild adult mammals that habitually engage in activities just for the fun of them, although the list is growing with detailed observations in nature.

Bow-riding was not "invented" by dolphins as a sport when human-made vessels first came on the scene. Instead, it appears to have been adapted from other wave-riding forms. Dolphins ride on the lee slopes of large oceanic waves and on the curling waves (or surf) that are formed as oceanic waves touch nearshore bottom (these two "rides" are hydrodynamically quite different; Hertel, 1969). Dolphins "body surf" much as do humans, but dolphins are generally much better surfers than humans. Dolphins also ride the bow waves of surging whales such as baleen whales and sperm whales (*Physeter macrocephalus*). Dolphins even "entice" whales to surge ahead by rapidly crossing back and forth in front of a whale's eyes and snout. The whale surges forward in response (and apparent annoyance), often blowing forcefully during the surge. An abrupt bow wave is formed, and the previously heckling dolphins line up in the wave, apparently enjoying its momentary pressure effect. This activity can go on with one whale for 30 min or more, until the whale tires and surges less or not at all.

See Also the Following Articles

Aerial Behavior ■ Group Behavior ■ Playful Behavior

References

Brownlee, S.M., and Norris, K.S. (1994). The acoustic domain. In "The Hawaiian Spinner Dolphin" (K.S. Norris, B. Würsig, R.S. Wells, and M. Würsig, Eds), pp. 161–185. University of California Press, Berkeley, CA.

Hertel, H. (1969). Hydrodynamics of swimming and wave-riding dolphins. In "The Biology of Marine Mammals" (H.T. Anderson, Ed.), pp. 31–63. Academic Press, New York.

Lang, T.G. (1966). Hydrodynamic analysis of cetacean performance. In "Whales, Dolphins, and Porpoises", (K.S. Norris, Ed.), pp. 410–434. University of California Press, Berkeley.

Perrin, W.F. (1968). The porpoise and the tuna. *Sea Front.* **14**, 166–174.

Williams, T.M., Friedl, W.A., Fong, M.L., Yamada, R.M., Sedivy, P., and Haun, J.E. (1992). Travel at low energetic cost by swimming and wave-riding bottlenose dolphins. *Nature* **355**, 821–823.

Copyright © 2017. Elsevier Science & Technology. All rights reserved.

Würsig, B., and Würsig, M. (1980). Behavior and ecology of the dusky dolphin *Lagenorhynchus obscurus*, in the South Atlantic. *Fish. Bull.* **77**, 871–890.

BRAIN

J.G.M. Thewissen

The brains of marine mammals are first and foremost mammal brains, and as such they share the features of all mammal brains. These include being dominated by the large cerebrum and smaller cerebellum that both overhang all the other nervous structures in the cranial cavity. The groups of marine mammals evolved from different terrestrial ancestors, and the differences in the brains of those ancestors can still be seen in the brains of their aquatic descendants, in spite of the aquatic adaptations that their bodies acquired in parallel. As a result, there are few similarities between the brains of the groups of marine mammals beyond those that they have in common with all mammals.

As with all brains, the shape of marine mammal brains is a compromise between specific neural adaptations of the groups in question and constraints from unrelated but nearby parts of the head. An example of such specific neural adaptations is the enlarged hearing areas of the brain of odontocetes. An example of skull shape affecting brain shape is the short and wide shape of cetacean brain with its anterior parts more or less folded underneath. This is related to the posteriorly shifted nostrils (the blowhole), and the telescoping of cetacean skulls.

I. Brain Size

The largest brain on the planet weighs more than 9 kg and belongs to the sperm whale. However, this says little about the intellectual abilities of that species. In general, larger mammals have larger brains (Fig. 1), for the simple reason that each cube of tissue of a mammalian body needs a smaller cube of brain to regulate the functions that are basic to each cell, such as cell metabolism and physiological homeostasis. Some tissues (such as blubber) have fewer of such functions and thus need less brain to regulate them, but overall, the relation holds. Instead, functions such as higher thinking and the analysis of sophisticating sensory information (from echolocation for instance) require great processing power of the brain and that goes beyond what is needed for those basic functions. Hence, brain size is commonly studied using the encephalization quotient (Jerison, 1973): EQ = (brain weight in grams)/0.12 (body weight in grams)$^{0.67}$. At any one body size, a mammal with an average-sized brain has an EQ of 1, whereas a species with a larger than average brain has an EQ higher than that, and a smaller than average brain has an EQ smaller than 1. For instance, cats have an EQ of 1, and among cetaceans, beaked and sperm whales and river dolphins have EQs between 1 and 3, but in delphinids EQ is between 3 and 5 (Marino et al., 2004). Pinniped EQs are between 1 and 2.5 and sirenian EQs are less than 0.6. In general, pinniped brains are similar in size to those of land carnivores of the same body size (Worthy and Hickie, 1986). Humans have the highest EQ on Earth: 7, much higher than their extant sister group, the EQ of chimpanzees is 2.5. The human lineage increased its brain size in the geologically recent past, and only surpassed the EQs of the dolphin around 2 million years ago. For most of Cenozoic history, delphinids were the mammals with the highest EQ.

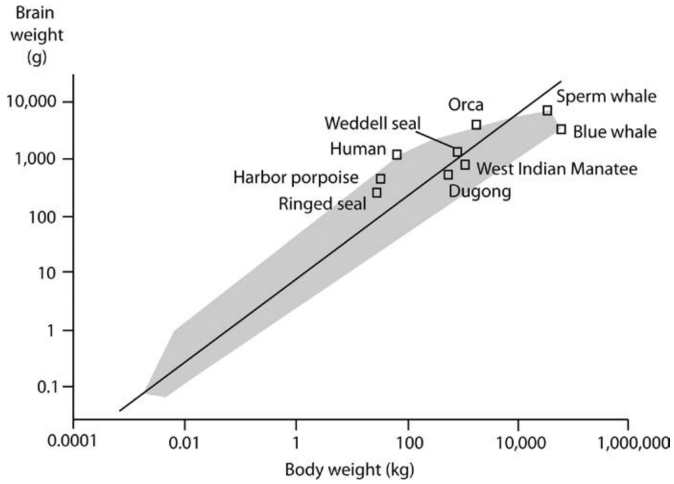

Figure 1 *Body size of mammals plotted against brain weight, both on a logarithmic axis. The gray field includes data on a range of diverse mammals, and some marine mammals and humans are indicated as individual points.*

Thick blubber does confound the importance of EQ. The EQ of the bowhead whale is 0.4, similar to that of a rabbit. Since blubber and other fat make up 40%–50% of the weight of a bowhead whale and since these tissues need less brain tissue to regulate them, a bowhead's EQ should be corrected for that. If we subtract all the fat from the bowhead body weight, the recalculated EQ for a bowhead is 0.6, still low.

One problem is that brain sizes cannot be directly determined for fossil species, since brains do not fossilize. Paleontologists usually measure the volume of the inside of the braincase (the endocast) as an estimate for brain size, but this is problematic in cetaceans, as some of species have large nets of blood vessels (retia mirabilia) around the brain that add to the endocranial volume, but are not part of the brain. In a bowhead whale, the brain only takes up 35%–40% of the endocranial volume. But that percentage varies greatly, in delphinoids, brain volume approximates endocranial volume and those volumes can be used to approximate EQ.

II. Forebrain

The largest part of the forebrain in mammals is the cerebrum, which consists of paired hemispheres. In vertebrate brains, the surface area of the cerebrum constrains, in part, how many neurons can be packed, and is thus related to processing power. In many mammals, the surface area of the cerebrum is enlarged by being folded into ridges (gyrus) and valleys (sulci), a process called gyrification. Greater gyrification suggests greater processing ability, and the smooth-surfaced brains that lack gyrification are described as lissencephalic. The cerebrum of sirenians (Reep et al., 1989; Reep and O'Shea, 1990) is lissencephalic in contrast to that of their modern terrestrial sister group, elephants. It is likely that the lissencephalic shape is primitive for this group, as indicated by impressions of the inside of the cranial cavity (endocasts) of ancient sirenians and their ancestors.

The cerebrum of the earliest cetaceans from the Eocene is also lissencephalic (as far as can be determined from their endocasts), but gyrification occurs in both odontocete and mysticete lineages. Among modern odontocetes (Morgane and Jacobs, 1972),

Copyright © 2017. Elsevier Science & Technology. All rights reserved.

gyrification is distinctly greater in the delphinoids than in other families such as platanistids. This is consistent with the high degree of encephalization in delphinoids.

Significant parts of the odontocete cortex are devoted to visual and auditory fields. In odontocetes, the olfactory parts of the cerebrum are missing, and they are small in mysticetes. In otters, the cortical areas devoted to somatic sensory projections from the forelimb are enlarged compared to other carnivores. Otters have a sophisticated sense of touch in their forefeet, needed when they manipulate food, and this part of the brain is involved with this.

Connections between left and right cerebral hemispheres (anterior commissure and corpus callosum, Tarpley and Ridgway, 1994) of cetaceans and pinnipeds are smaller than those of land mammals. This suggests that the two hemispheres of the cerebrum have greater independence than in other mammals. This is consistent with the ability of cetaceans and pinnipeds to show signs of sleeping with one hemisphere, while the other is awake. In contrast, the corpus callosum of phocids is large.

The pineal gland is a part of the brain that is hidden deep in the furrow between left and right hemispheres of the cerebrum. This structure is absent in postnatal odontocetes (sperm whale, dolphins) as well as sirenians, but present in some or all mysticetes (humpback and fin whale). In contrast, the gland is enormous in phocid seals. This gland produces melatonin, regulates sleep patterns, and is involved with sex hormone production. It is possible that the melatonin in cetaceans is instead produced by the retina.

III. Cerebellum

The cerebellum of mammals is mostly involved with fine motor control. The cerebellum of cetaceans, especially mysticetes, is large, and displays morphologies associated with the modification of the forelimb, the loss of the hind limb, and the development of the fluke (Jansen, 1954). Based on the endocast, the cerebellum of Eocene whales is enormous, and reaches further dorsal than the cerebrum (Fig. 2). The cerebellum of phocids is covered by the greatly enlarged cerebrum, and the cerebellum of sirenians is small.

IV. Cranial Nerves

In all vertebrates, there are 12 pairs of nerves that emerge from the brain and that are related to all functions of the head and many functions in other parts of the body. These are called the cranial nerves and the specific functions of individual cranial nerves are similar across mammals. For instance, the fifth cranial nerve of all mammals carries sensory information from the face to the brain. The size of nuclei of the brain to which the cranial nerves project (are connected), in general, matches the importance of that nerve's functions. The olfactory nerve (cranial nerve I) is absent in investigated odontocetes and olfaction is lacking in them. The nervous structures associated with olfaction (olfactory bulb) are small in mysticetes when compared to most mammals, but relatively large when compared to the same structures in apes and humans. It is likely that mysticetes have a sense of smell that is more acute than that of humans. The first cranial nerve of phocids is smaller than that of their land carnivore ancestors. The optic nerve (cranial nerve II) of odontocete species living in muddy waters, such as the Ganges dolphin (*Platanista gangetica*) is strongly reduced (Purves and Pilleri, 1973), consistent with their near-blind status. In phocid seals, the optic nerve is one of the largest cranial nerves (Wohlert et al., 2016), an indication of how important vision is for seals.

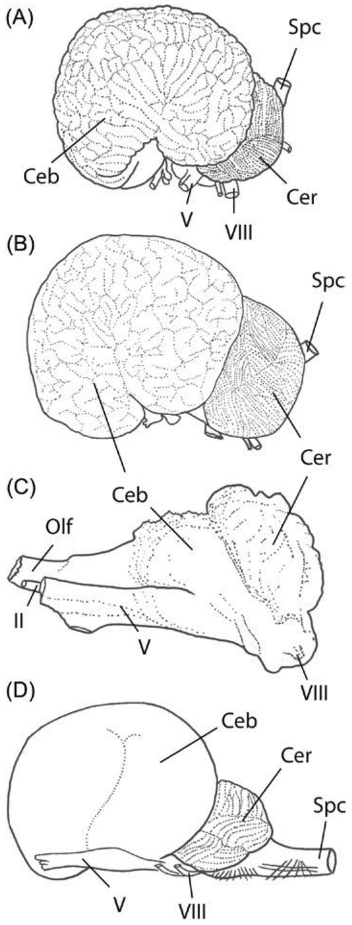

Figure 2 *Marine mammal brains (modern mammals) and endocast (fossil) in left lateral view (not to scale). The endocast is an impression of the inside of the cranial cavity; it shows not only some surface features of the brain, but also those of other anatomical structures. (A) Brain of an odontocete (*Tursiops truncatus, *after Oelschläger and Oelschläger, 2002), (B) a mysticete (*Megaptera novaeangliae *after Breathnach, 1955), (C) an extinct Eocene whale (*Basilosaurus isis, *after Dart, 1923), and (D) a sirenian (*Trichechus, *after Murie, 1885). Ceb, cerebellum; Cer, cerebrum; Olf, olfactory tract; SpC, spinal cord. Cranial nerves indicated by their roman numeral, II, optic nerve; V, trigeminal nerve; VIII, vestibulocochlear nerve.*

The motor and sensory parts of the trigeminal nucleus (cranial nerve V, trigeminal nerve) of mysticetes is the largest of the cranial nerves and is much larger than that of odontocetes. The motor neurons in this nerve control the chewing muscles, whereas the sensory parts receive general sense information from the face, including the vibrissae of some species, and the sensitive lips. Otters have many vibrissae and their trigeminal nerve is large too (Oelschläger and Oelschläger, 2002).

The facial nerve (cranial nerve VII) is large in cetaceans as it controls the muscles near the blow hole which in odontocetes are involved in producing sounds. In sperm whales, this is usually the largest cranial nerve, as it innervates the muscles associated with sound production in the massive rostrum. The facial nerve and nucleus of sirenians is large, as the muscles of the muzzle are innervated by it and are used in grazing. Hearing is of great importance in odontocetes, and the sensory nerve related to it, the vestibulocochlear nerve (cranial nerve VIII), is the largest cranial nerve in delphinoids, and much larger than that of mysticetes.

Copyright © 2017. Elsevier Science & Technology. All rights reserved.

V. Conclusion

The brain receives information from and sends information to all parts of the body. As such, parts of the brain represent all parts of the body, and the relative size, organization, and complexity reflect the importance of those body parts. Therefore, the brain is a dynamic organ evolutionarily, and the comparative study of the size, organization, and complexity of its parts can give clues into the current status of an animal's adaptations. On evolutionary time scales, the brain changes as organs change and great changes in bodies of marine mammals occurred as their land mammal ancestors took to the water. For instance, in the evolution of cetaceans, an early stage of experimentation with the sense organs took place, when these organs had to change to respond to water-borne, instead of air-borne stimuli (Fig. 3). Brain evolution records much of these changes and is a window into the sensory landscape of a marine mammal, the way in which it perceives the world around it.

See Also the Following Articles

Hearing ■ Intelligence ■ Sensory Biology ■ Skull ■ Vision

References

Breathnach, A.S. (1955). The surface features of the brain of the humpback whale (*Megaptera novaeangliae*). *J. Anat.* **89**, 343–354.

Dart, R.A. (1923). The brain of the Zeuglodontidae. *Proc. Zool. Soc. London* **1923**, 615–654.

Jansen, J. (1954). In "Aspects of Cerebellar Anatomy", (J. Jansen, and A. Brodal, Eds), pp. 13–81. J. G. Tanum, Oslo.

Jerison, H.J. (1973). *Evolution of the Brain and Intelligence.* Academic Press, New York. 482 p.

Marino, L., McShea, D.W., and Uhen, M.D. (2004). Origin and evolution of large brains in toothed whales. *Anat. Rec.* **281A**, 1247–1255.

Morgane, P.J., and Jacobs, M.S. (1972). Comparative anatomy of the cetacean nervous system. In "Functional Anatomy of Marine Mammals", (R.J. Harrison, Ed.), pp. 117–244. Academic Press, London.

Murie, J. (1885). Further observations on the manatee. *Trans. Zool. Soc. London* **64**, 19–48.

Oelschläger, H.H.A., and Oelschläger, J.S. (2002). Brain. In "Encyclopedia of Marine Mammals", (W.P. Perrin, B. Würsig, and J.G.M. Thewissen, Eds), 1st ed., pp. 133–158. Academic Press, San Diego, CA.

Purves, P.E., and Pilleri, G. (1973). Observations on the ear, nose, throat, and eye of *Platanista indi. Investig. Cetacea (Berne)* **5**, 13–57.

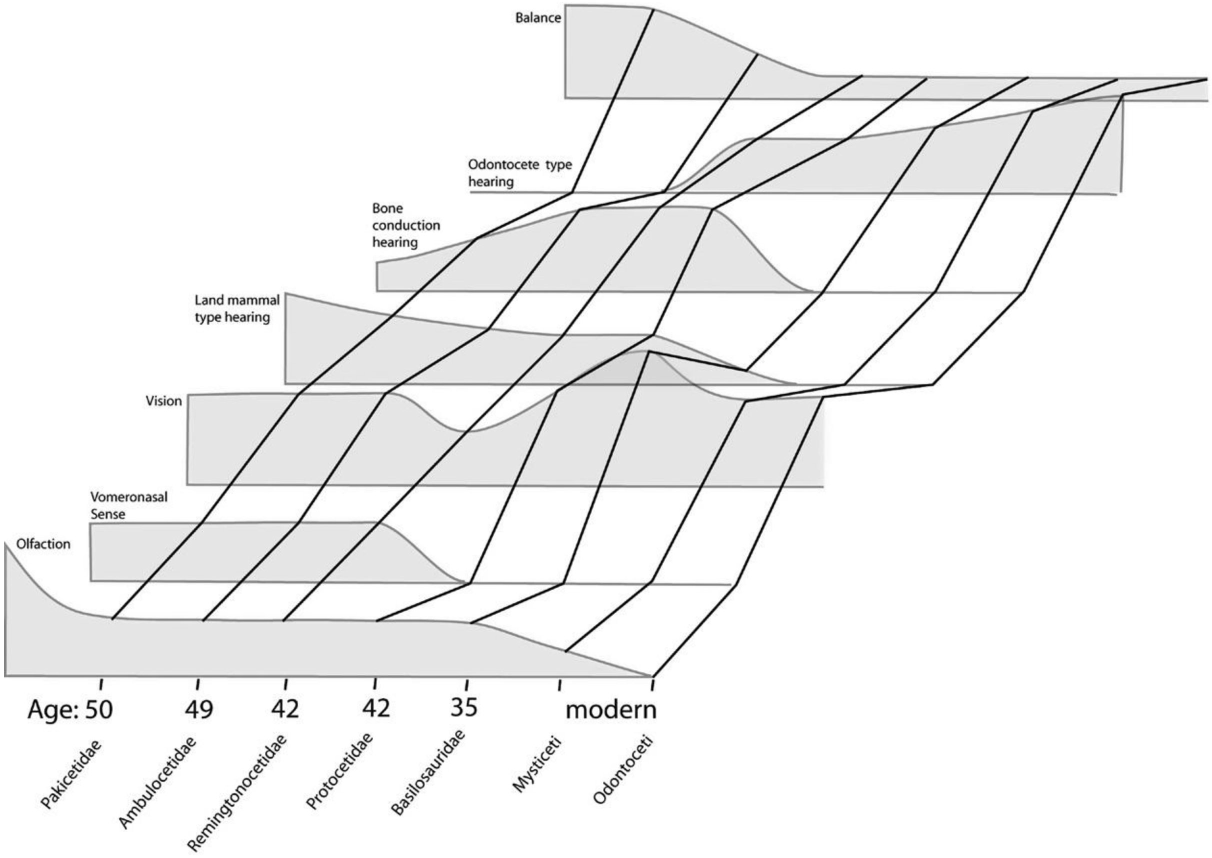

Figure 3 *The importance of different sense organs changed during the evolution of* Eocene cetaceans, *as different sense organs adapted at different times to the watery environment (modified after Thewissen and Nummela, 2007). This process passed through a number of stages of experimentation, from pakicetids (shallow, freshwater waders), to variously adapted, but amphibious cetaceans (ambulocetids, remingtonocetids, and protocetids) and to basilosaurids, mysticetes, and odontocetes (obligate marine swimmers). Families of cetaceans are discussed in chapters Archaeocetes, Archaic, and Basilosaurids and Kekenodontids and hearing mechanisms are discussed in Hearing. Ages are in millions of years ago and are indicative, here given one age for each taxon concerned.*

Copyright © 2017. Elsevier Science & Technology. All rights reserved.

Reep, R.L., and O'Shea, T.J. (1990). Regional brain morphometry and lissencephaly in the Sirenia. *Brain, Behav. Evol.* **35**, 185–194.

Reep, R.L., Johnson, J.I., Switzer, R.C., and Welker, W.I. (1989). Manatee cerebral cortex: cytoarchitecture of the frontal region in *Trichechus manatus latirostris*. *Brain, Behav. Evol.* **34**, 365–386.

Tarpley, R.J., and Ridgway, S.H. (1994). Corpus callosum size in delphinid cetaceans. *Brain, Behav. Evol.* **44**, 156–165.

Thewissen, J.G.M., and Nummela, S. (2007). Toward an integrative approach. In "Sensory Evolution on the Threshold, Adaptations in Secondarily Aquatic Vertebrates", (J.G.M. Thewissen, and S. Nummela, Eds), pp. 333–340. University of California Press, Berkeley, CA.

Wohlert, D., Kröger, J., Will, M., Schmitt, O., Wree, A., Czech-Damal, N., Siebert, U., Folkow, L., and Hanke, F.D. (2016). A comparative morphometric analysis of three cranial nerves in two phocids: the hooded seal (*Cystophora cristata*) and the harbor seal (*Phoca vitulina*). *Anat. Rec.* **299**, 370–378.

Worthy, A.J., and Hickie, J.P. (1986). Relative brain size in marine mammals. *Am. Nat.* **128**, 445–459.

BREATHING

Patrick J.O. Miller and Marjoleine M.H. Roos

I. Introduction

Breathing, technically termed *respiration*, is of fundamental importance to the energetics of all animals. Breathing enables uptake of oxygen that is the final electron receptor in aerobic metabolism, and the offload of carbon dioxide that forms as a byproduct of aerobic metabolism. Unlike mammals on land that live within an air medium and are always able to breathe, marine mammals at sea need to physically position themselves by coming to the sea surface to respire, and undergo apnea (breath-holding) when underwater.

Perhaps driven by the risk inherent in attempting to breathe while submerged, marine mammals are generally considered to have adapted to be conscious breathers, with the role of behavioral control of breathing long recognized (Craig and Påsche, 1980). Marine mammals can behaviorally control both the timing of breaths and the amount of gas exchanged. The active opening of the blowholes (cetaceans) or nostrils (pinnipeds, sirenians, and marine carnivores) is an energy-saving adaptation to their aquatic life, avoiding the requisite for constant muscle contraction to prevent water entering the respiratory tract while submerged. Cetaceans stop breathing when they lose consciousness under many anesthesia procedures, requiring careful mechanical breathing assistance. Inconsistent results from experiments with altered gas mixtures (Butler, 1982) make it difficult to conclude whether oxygen deficit or carbon dioxide accumulations are the specific cue to trigger breathing in marine mammals, but such a trigger to breathe would need to be suppressed until the animal is at the sea surface and able to safely breathe.

All marine mammals are expected to benefit from greater capacity to remain submerged for long periods of time, to maximize the time spent foraging and conducting other important activities at depth. It is anticipated that a diver in general would not fully deplete its oxygen stores; vital organs such as the brain and central nervous system require oxygen to function, although anaerobic metabolism is well documented for other body tissues. A diver is expected to have some reserve capacity to accommodate any unforeseen apnea elongation in case dive times (and associated apnea) need to be extended to find breathing holes or avoid predators, without it being fatal. Accordingly, marine mammals have greater oxygen stores than terrestrial mammals. However, different selective pressures among marine mammals for accessing prey at greater depth, and associated dive durations, have led to large differences in the total body oxygen stores and their distribution across the lungs, blood, and muscle (Ponganis, 2011). Relatively small oxygen stores (21 mL/kg) have been measured for shallow diving manatees, and intermediate oxygen-store values (36–57 mL/kg) for most cetaceans and pinnipeds. Deep-diving specialists among pinnipeds and cetaceans have notably greater oxygen stores (69–97 mL/kg), though to date it has not been possible to measure the total oxygen stores of deep-diving beaked whales. There is a clear inverse trend between total-body oxygen stores and the proportion of the store carried in the lungs during dives, with larger oxygen stores occurring primarily within highly adapted blood and muscle compartments (Ponganis, 2011). Phocid seals generally dive upon exhalation, behaviorally reducing their lung oxygen store during dives (Kooyman and Sinnett, 1982). Cetacean diving specialists such as sperm and beaked whales have rather small lungs and gas oxygen stores during dives despite diving with full lungs (Miller et al., 2016). Otariid seals, manatees, and other cetaceans are believed to dive upon inspiration with larger gas volumes and oxygen stores in their lungs. Hyperventilation in pinnipeds and large tidal volumes in cetaceans are adaptations that enable rapid gaseous exchange of oxygen and carbon dioxide with blood hemoglobin stores during breathing intervals. Increased heart rates (tachycardia) at the surface lead to rapid restoration of oxygen stores as hemoglobin stores, replenished at the lungs, are transported to replenish myoglobin stores in muscle.

Marine mammals breathe at a much slower rate overall than terrestrial mammals of similar size (Mortola and Limoges, 2006), with breathing occurring during surface intervals. Breathing behavior is determined by each individual, influenced not only by physiological but also biological, behavioral, social, and ecological factors. For efficient foraging, it is expected that marine mammals optimize oxygen use and simultaneously optimize the way they replenish oxygen stores (timing and rate of breathing) to maximize the time spent actively foraging at depth. It is therefore expected that divers use oxygen balance strategies, depleting their oxygen stores vastly, to maximize oxygen uptake during breathing. Kramer (1988) applied the "marginal value theorem" (Charnov, 1976) to aquatic air breathers to determine the optimal time allocation during a dive cycle, including surface time related to oxygen replenishment and dive time related to energy uptake. This ground-laying approach for a "theory of optimal breathing" has been applied in studies on many diverse divers ranging from birds to pinnipeds to large whales.

II. Breathing and Breathing Patterns

Among cetaceans, mysticetes, the baleen whales, have two blowholes whereas odontocetes, the toothed whales, have one. The blowhole leads to the trachea, which is disconnected from the esophagus and ends in the lungs. The blowhole is normally closed when the controlling muscles are relaxed. Muscles must contract to open the blowhole and move the nasal plug so that it no longer blocks the airway. A cetacean's blowhole is centered dorsally, high at the top of the head. As the exception, the sperm whale's (*Physeter macrocephalus*) blowhole is located on the anterior top end of the head, highly skewed to the left. The dorsal position of their blowhole makes it relatively effortless for cetaceans to take in air while at the

Copyright © 2017. Elsevier Science & Technology. All rights reserved.

sea surface, as they can breathe without having to lift their head out of the water. Whereas adult cetaceans break the surface rather gracefully and smoothly with most of their body remaining submerged, neonates often break the surface showing their entire head plus a large part of their body when coming up for air. Cetaceans usually initiate expiration prior to the blowhole breaking the surface. The explosive nature of the expiration, the "blow," creates the small droplets that make the respiration visible. In the past, people believed that this spray represented water that the whale had swallowed, but later this theory was deemed impossible given their anatomy. The strong expiration simply clears the upper respiratory passages and the area around the blowholes of any residual water, and the blow expirate also contains mucus from airways and lungs. Because the blowholes of a baleen whale lie in rather deep folds, their blow could contain a larger amount of water (Fig. 1). The blow is one of the most apparent whale behaviors that humans can observe at the surface, and the shape of the blow can help in the identification of the whale species from a distance.

Porpoises, delphinids, and other small toothed whale species respire in less than 1 s. The bottlenose dolphin (*Tursiops truncatus*) completes an exhalation and inhalation cycle in approximately one-third of a second. With a tidal volume of 10 L, flow rates through the air passages can be as high as 162 L/s. In gray whale (*Eschrichtius robustus*) calves, the duration of expiration and inhalation is closer to 1.5 s, but the tidal volume can be as great as 62 L, and the maximum flow rate as great as 202 L/s. However, on average it takes adults from larger whale species approximately 2 s to perform a single respiration cycle. In strong contrast to humans and other terrestrial mammals, the short powerful blow in cetaceans is accomplished by steady high flow rates throughout almost the complete expiration. Gas flows through the external nares at speeds up to 200 m/s during expiration and 44 m/s during the immediately following inspiration.

Vast differences in breathing behavior and patterns exist both across and within cetacean species. Most cetaceans take only one breath per surfacing, but usually take a sequence of breaths between dives. Breathing patterns of cetaceans vary depending on their behavior and activity level. Shallow diving odontocetes, including dolphins and porpoises, take breaths with relatively steady intervals of 1–2 min. Prolonged dives of the moderate sized killer whales (*Orcinus orca*) are in general under 8 min, with on average 40 s breath intervals during breathing bouts of approximately five breaths. Baleen whales, including the large blue whales (*Balaenoptera musculus*), typically dive for 4 min on average, followed by a breathing bout of about 3–5 breaths. The deep-diving beaked whales replenish their oxygen deficit after long dives during recovery periods by taking a series of breaths, each in a subsequent surfacing event, before diving to depth again. While most species of cetaceans only occasionally "log" or drift at the sea surface while breathing, such logging behavior is the primary posture for breathing in sperm whales. Sperm whales generally dive for 30–50 min, after which they remain at the surface for about 9 min. The somewhat longer interdive breath intervals of beaked whales often last 45–70 min. It is hypothesized that the final breaths in breathing sequences are performed to offload carbon dioxide, accumulated during breath-hold, rather than uploading oxygen (Boutilier et al., 2001).

The breaths of sirenians and marine carnivores are not generally as conspicuous as those of cetaceans. Manatees (*Trichechus manatus*) and dugongs (*Dugong dugon*) breathe through their nostrils located dorsally near the front of their head (Fig. 2), which are opened and closed with precise timing in relation to breathing. Low metabolic rates combined with large tidal volumes enable sirenians to maintain aerobic metabolism taking single breaths between dives of varying depth and duration (Reynolds, 1981).

Pinniped breathing using more anterior-oriented nostrils (Fig. 3) is inconspicuous, but can be recorded when they are on land or in captivity using video and acoustic methods, or using heart-rate patterns as an indirect measure. Breathing at sea can also be observed using sound-recording loggers attached to the animals. Interestingly, pinnipeds appear to have similar breathing patterns on land as they do at sea, with short breathing periods separating longer-duration periods of apnea, though some individual animals have lower resting breathing rates in water than on land (Mortola and Limoges, 2006). A hyperventilation pattern of breathing during surfacing periods between dives at sea has been well-documented for phocid seals, with northern (*Mirounga angustirostris*) and southern elephant seals (*M. leonina*) shown to typically breathe at a rate of ~15 breaths/min during 2–3 min duration surfacing periods (Le Boeuf et al., 2000). The detailed breathing patterns of otariids and walrus (*Odobenus rosmarus*) are less-well described than those of phocid seals, which could provide a fruitful topic of future research.

Figure 1 *Breathing behavior of fin whale (Photo by Erminia Ricci).*

Figure 2 *A West Indian manatee breathing (Photo by Katsufumi Sato).*

Copyright © 2017. Elsevier Science & Technology. All rights reserved.

Figure 3 *A Weddell seal breathing within an ice hole near McMurdo U.S. Antarctic Station, with an Antarctic tooth fish (Dissostichus mawsoni) it brought up with it (Photo by Katsufumi Sato).*

III. Behavioral State

Marine mammal breathing patterns and intervals also depend on their behavioral state. Different behaviors have different functions (e.g., foraging, traveling, resting, socializing, fleeing) and influence swimming modes, and therefore timing of breaths. Within behavior classes it is expected that animals will use consistent breathing patterns, depending upon the level of activity. In general, breath intervals during feeding and resting are longer than the median breath-hold, whereas intervals tend to shorten during exercise. Longer breathing intervals are required to accomplish deeper (hence longer duration) dives during foraging. Foraging or hunting strategies shape oxygen usage and breath timing, and it has been proposed that marine mammals, as other divers, should prepare for such dives by taking up additional oxygen during the preceding breathing bout (Kramer, 1988).

Most marine mammals breathe during either a continuous period resting at the surface (pinnipeds, sperm whales) or by taking single breaths (other cetaceans) during short and low-energy surfacing events. Small-to-moderate sized cetaceans and otariids at times leap completely out of the water at high speeds, so-called porpoising. During this high activity level they are forced to stay close to the surface in order to resurface to breathe and replenish their depleted oxygen stores at regular intervals. This efficient way of respiring allows the animal to spend most of its travel time below the surface or in the air where drag, and thus locomotion cost, is reduced (Williams, 2001). Compared to intervals during normal breathing bouts, breathing events during porpoising are relatively equally distributed in time with longer breath intervals that likely increase oxygen uptake per breath (Roos et al., 2016).

In general, breath intervals of marine mammals appear to increase during rest. Sleep apnea on land is well documented for diverse pinnipeds, though most research has focused on phocid seals (Deacon and Arnould, 2009). Respiration rates during breathing periods associated with sleep apnea of phocid seals on land are substantially lower than during surfacings of presumably awake animals at sea. The longest duration dives of West Indian manatees (*T. manatus*) occur during underwater rest, though longer periods resting at the surface have been reported for dugongs. Breath-hold of resting humpback whales (*Megaptera novaeangliae*) logging at the surface is longer than their average breath-hold. Resting bowhead whales (*Balaena mysticetus*) float up and down without forward movement, either breathing at constant intervals or staying at the surface while breathing several times before submerging again.

Figure 4 *A group of killer whales surfacing to breathe (Photo by Olga Filatova).*

The need to breathe consciously raises the question of how marine mammals control breathing during sleep when active control of breathing is reduced. There are two primary breathing patterns during sleep across marine mammals that seem to be shaped by taxon-specific mechanisms and behavioral patterns during sleep. Some marine mammals produce unihemispheric brain waves associated with sleep, which indicates that there is one cerebral hemisphere that is always awake to control surfacing and breathing (Lyamin et al., 2008). It has been proposed that breathing during such periods while resting at the surface may be partly automatic (McCormick, 1969). A number of marine mammals have been recorded to drift motionless underwater, which is thought to be more compatible with bi-hemispheric sleep. In this case, it is thought that sleep must be interrupted to enable voluntary control of breathing after return to the sea surface.

IV. Social Aspects of Breathing

Species that are social and behave in groups, such as most of the family Delphinidae, are expected to be partly constrained by conspecifics' decision-making and physiological abilities that vary with age and body size. Killer whale breathing events within matrilines (Fig. 4) show greater synchronicity compared to those with other subgroups in a pod (Ray et al., 1986). Similar overall breathing rates across different body sized killer whales indicate a strategy of physiological compromise is followed, whereby large males underutilize their capacity to accommodate the lesser capacity of smaller group members (Miller et al., 2010).

Though the exact function driving diverse patterns of breathing synchrony in cetaceans remains undetermined, it has been shown to reflect more complex social or stressful situations and can be performed by groups, same sex pairs of the same age class, as well as mother–calf and escort–calf pairs (Sakai et al., 2010). For instance, breathing synchrony in bottlenose dolphin pods is positively correlated with boat presence. Breathing synchrony among members of bottlenose dolphin male alliances is more common in more highly social situations. Spinner dolphins (*Stenella longirostris*) have been observed

Copyright © 2017. Elsevier Science & Technology. All rights reserved.

breathing synchronously even when diving 50m or more apart, possibly hunting together at depth. Killer whales often synchronize breathing patterns, for instance, while chasing gray whales, as they coordinate harassment of the intended prey. It is hypothesized that synchronous swimming and breathing in mother–calf pairs is due to the calf swimming in the echelon position near the belly of mother, so that it can save locomotion costs without falling behind. In contrast, asynchronous surfacing times of sperm whales enable alloparental care to small group members, so that some noncalves are in foraging dives while others are available to take care of calves at the surface.

See Also the Following Articles

Brain ■ Circulatory System ■ Diving Physiology ■ Diving Behavior ■ Feeding Strategies and Tactics ■ Swimming

References

Boutilier, R.G., Reed, J.Z., and Fedak, M.A. (2001). Unsteady-state gas exchange and storage in diving marine mammals: The harbor porpoise and gray seal. *Am. J. Physiol. Regul. Integr. Comp. Physiol.* **281**, R490–R494.

Butler, P.J. (1982). Respiratory and cardiovascular control during diving in birds and mammals. *J. Exp. Biol.* **100**, 195–221.

Charnov, E.L. (1976). Optimal foraging, the marginal value theorem. *Theor. Popul. Biol.* **9**(2), 129–136.

Craig Jr., A.B., and Påsche, A. (1980). Respiratory physiology of freely-diving harbor seals (*Phoca vitulina*). *Physiol. Zool.* **53**, 419–432.

Deacon, N.L., and Arnould, J.P.Y. (2009). Terrestrial apnoeas and the development of cardiac control in Australian fur seal (*Arctocephalus pusillus doriferus*) pups. *J. Comp. Phyiol. B* **179**, 287–295.

Kooyman, G.L., and Sinnett, E.E. (1982). Pulmonary shunts in harbor seals and sea lions during simulated dives to depth. *Physiol. Zool.* **55**, 105–111.

Kramer, D.L. (1988). The behavioral ecology of air breathing by aquatic animals. *Can. J. Zool.* **66**, 89–94.

Le Boeuf, B.J., Crocker, D.E., Grayson, J., Gedamke, J., Webb, P.M., Blackwell, S.B., and Costa, D.P. (2000). Respiration and heart rate at the surface between dives in northern elephant seals. *J. Exp. Biol.* **203**, 3265–3274.

Lyamin, O.I., Manger, P.R., Ridgway, S.H., Mukhametov, L.M., and Siegel, J.M. (2008). Cetacean sleep: An unusual form of mammalian sleep. *Neurosci. Biobehav. Rev.* **32**, 1451–1484.

McCormick, J.G. (1969). Relationship of sleep, respiration, and anesthesia in the porpoise: a preliminary report. *Proc. Natl. Acad. Sci. U. S. A.* **62**, 697–703.

Miller, P.J.O., Shapiro, A.D., and Deecke, V.B. (2010). The diving behaviour of mammal-eating killer whales (*Orcinus orca*): variations with ecological not physiological factors. *Can. J. Zool.* **88**, 1103–1112.

Miller, P., Narazaki, T., Isojunno, S., Aoki, K., Smout, S., and Sato, K. (2016). Body density and diving gas volume of the northern bottlenose whale (*Hyperoodon ampullatus*). *J. Exp. Biol.* **219**, 2458–2468.

Mortola, J., and Limoges, M.J. (2006). Resting breathing frequency in aquatic mammals: a comparative analysis with terrestrial species. *Respir. Physiol. Neurobiol.* **154**, 500–514.

Ponganis, P.J. (2011). Diving mammals. *Comp. Physiol.* **1**, 447–465.

Ray, R.D., Carlson, M.L., Carlson, M.A., Carlson, T., and Upson, J.D. (1986). Behavioral and respiratory synchronization quantified in a pair of captive killer whales. In "Behavioral Biology of Killer Whales", (B. Kirkevold, and J. Lockhard, Eds), pp. 187–209. A.R. Liss Publishing Corporation, New York.

Reynolds III, J.E. (1981). Behaviour patterns in the West Indian manatee, with emphasis on feeding and diving (*Trichechus manatus*, Florida). *Florida Sci.* **44**, 232–242.

Roos, M.M.H., Wu, G.-M., and Miller, P.J.O. (2016). The significance of respiration timing in the energetics estimates of free-ranging killer whales (*Orcinus orca*). *J. Exp. Biol.* **219**, 2066–2077.

Sakai, M., Morisaka, T., Kogi, K., Hishii, T., and Kohshima, S. (2010). Fine-scale analysis of synchronous breathing in wild indo-pacific bottlenose dolphins (*Tursiops aduncus*). *Behav. Process.* **83**, 48–53.

Williams, T.M. (2001). Intermittent swimming by mammals: a strategy for increasing energetic efficiency during diving. *Am. Zool.* **41**, 166–176.

BRYDE'S WHALE

Balaenoptera edeni

Hidehiro Kato and William F. Perrin

Bryde's whales (Fig. 1) are the least known of the large baleen whales. They were long confused with sei whales (*Balaenoptera borealis*), and are similar to Omura's whales.

I. Characteristics and Taxonomy

Bryde's whales were first described by Anderson (1878) based on examination of a stranded whale in Burma. He gave it the scientific name *Balaenoptera edeni*. Olsen (1913) found an unrecognized species among "sei whales" caught in Durban, South Africa, and gave it the scientific name *B. brydei*. Junge (1950) concluded that the two names were synonymous based on examination of a skeleton collected in Singapore. Further studies by Omura (1959) and Best (1960) supported Junge's view, and their conclusion had been generally accepted until recently, with *B. edeni* having priority as the scientific name. Wada and Numachi (1991) found that a small form occurring off the Solomon Islands and Java differed from other Bryde's whales in allozymes. These results suggesting the existence of at least two species were supported by mtDNA analyses reported by Yoshida and Kato (1999); the Solomon Islands and Java whales were more closely related genetically to sei whales than to "ordinary" Bryde's whales. The naming conventions at that point became some permutation of the names *B. brydei*, *B. edeni*, and a third name might be needed. Subsequently, a specimen of the same apparently undescribed species reported by Wada and Numachi (1991) washed ashore in southern Japan, and Wada et al. (2003) described the new species *B. omurai* (see chapter on Omura's Whale). They further suggested that large and small forms of the "ordinary" Bryde's whale should be considered full species, *B. brydei* and *B. edeni*, respectively. However, the degree of differentiation between the two forms could be considered subspecific.

A recent genetic study (Kershaw et al., 2013) using samples/data that covered various localities in the Indian and Pacific regions clearly identified two forms and identified them as *B. edeni brydei* and *B. edeni edeni* for the large and small forms, respectively. Additional analyses by Luksenburg et al. (2015) incorporating both genetic and osteological analyses and a review by Thomas et al. (2016) supported this conclusion.

Bryde's whales are medium-sized balaenopterids. Females are larger than males throughout life, by about 2ft (0.5–0.6m) at full maturity. It is believed they reach 15.5m, but most are much smaller. Animals from coastal stocks are generally smaller than those from migratory pelagic stocks. Southern Hemisphere animals are also larger than Northern Hemisphere animals.

Bryde's whales closely resemble sei whales but have a number of distinctive characteristics. Body color is principally dark smoky gray above and white below, but the dark area extends down to include the throat grooves and the flippers. The boundary between

Copyright © 2017. Elsevier Science & Technology. All rights reserved.

Figure 1 *Bryde's whale,* Balaenoptera brydei *(Illustration by Uki Gorter).*

dark and light areas is diffuse. The rostrum is V shaped as in other balaenopterids. The dorsal fin is extremely falcate with a tapering tip. The flukes are broad with rather straight posterior margins.

Pelagic Bryde's whales bear large numbers of oval pit-like scars from bites by the tropical cookie cutter shark (*Isistius* sp.), which serve as evidence of migration to tropical waters. Such scarring is rare on animals of the coastal form off South Africa; this may also be true for coastal animals in neritic waters off Kochi, southwestern Japan, indicating that those whales do not migrate to tropical waters.

The throat grooves extend to or beyond the navel, whereas those of the sei whale do not reach the navel. The most distinctive external character allowing the discrimination of Bryde's whales from other baleen whales is the presence of three prominent ridges on the rostrum, one in the midline and a paired set parallel to that (Fig. 2). Bryde's whales have 285–350 dark slate-gray baleen plates on each side of the mouth. They are much broader and have coarser bristles than those of sei whales. The longest plate may reach 40 cm in length above the gum. There is a clear difference in the proportion of length to breadth of the plates in South Africa, with those of the inshore form being slenderer than those of the offshore form. Animals in the South Pacific tend to have finer bristles than those in the western North Pacific stock, probably reflecting a difference in their feeding habits.

The skull is relatively broad, short, and flat for a balaenopterid skull. The rostrum is also relatively short and pointed. Its sides are nearly parallel posteriorly but slightly convexly curved anteriorly. The curved and robust mandible is also conspicuous among balaenopterids.

II. Distribution and Abundance

Although there is a general pattern of migration toward the equator in winter and to higher latitudes in summer, Bryde's whales are seen throughout tropical and warm temperate waters of 16.3°C or warmer year round. Their occurrence has been reported from all tropical and temperate waters in the North and South Pacific, Indian Ocean, and South and North Atlantic between 40°N and 40°S (Fig. 3).

Two allopatric forms of Bryde's whale known as the inshore and offshore forms are found off the west coast of South Africa (Best, 1977). The inshore form is restricted to within 20 miles from the coast and is seen there throughout the year. The offshore form occurs in waters over 50 miles from the coast and migrates north to the equator in winter.

III. Ecology

Bryde's whales feed mainly on pelagic schooling fishes such as pilchard, anchovy, sardine, mackerel, herring, and others but also on crustaceans. They are considered opportunistic feeders, unlike sei whales, which feed mainly on copepods. Off South Africa, Bryde whales tend to be dependent on euphausiids in pelagic waters and feed on schooling fishes in coastal waters; thus, feeding habits may be characteristic of stocks (Best, 1977). In the pelagic North Pacific, these whales fed on Japanese anchovy in 1 year and krill in the next (Murase et al., 2007). Bryde's whales are sometimes seen within high-density patches of bonito (*Sarda*) in pelagic waters in

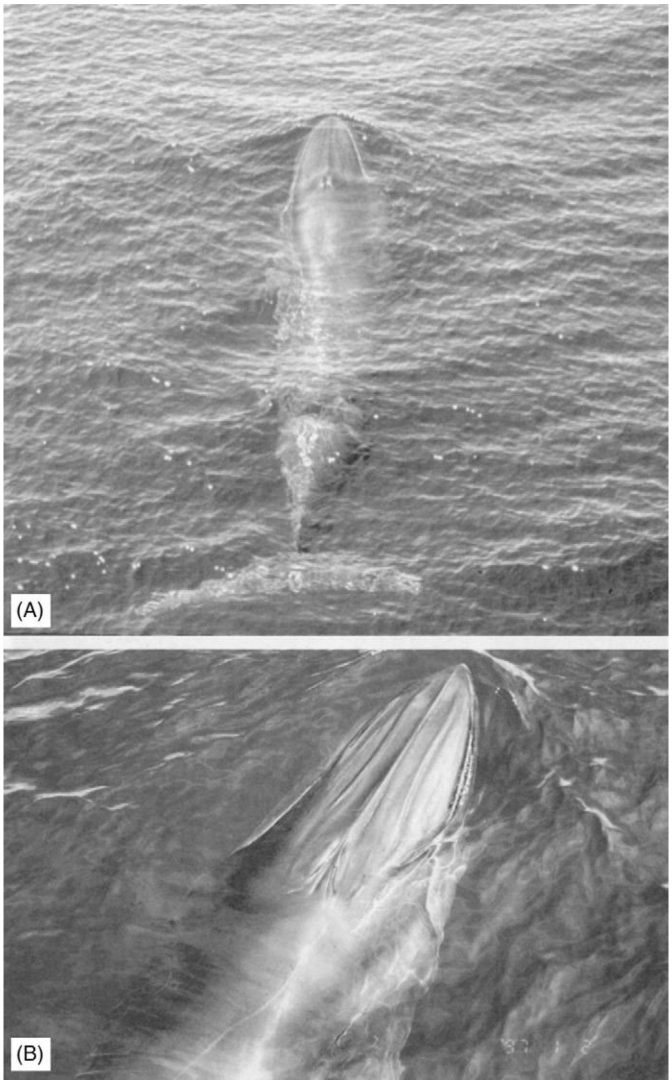

Figure 2 *Dorsal view of the head of* B. brydei, *showing the three longitudinal ridges that are characteristic of the species (Photo by Keiko Sekiguchi).*

Copyright © 2017. Elsevier Science & Technology. All rights reserved.

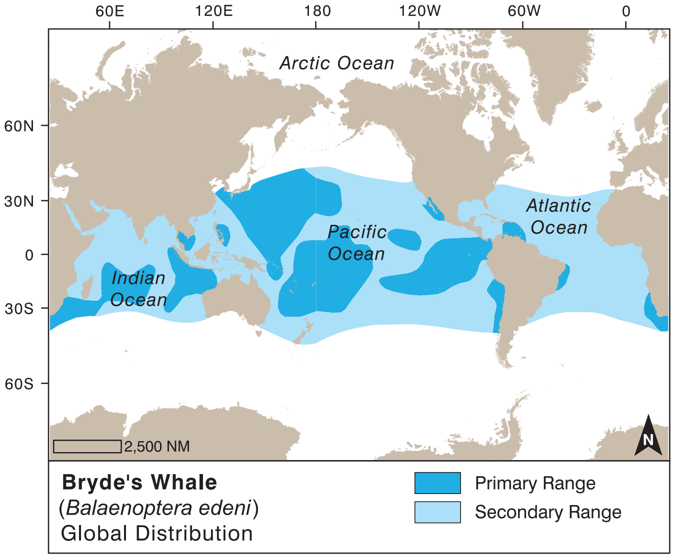

Figure 3 *Bryde's whale distribution. From Jefferson, T.A., Webber, M.A., and Pitman, R.L. (2015). "Marine Mammals of the World: A Comprehensive Guide to Their Identification," 2nd ed. Elsevier, San Diego, CA.*

the North Pacific. This may be a result of two predators chasing the same prey. Similarly, off the coasts of Kochi and Kasasa, southwestern Japan, it is very common to see Bryde's whales feeding in patches of sardines or juvenile tuna, especially in summer. They have also been observed to utilize bubble net foraging with slow circle swimming below the surface.

IV. Behavior and Physiology

Bryde's whales do not gather into large groups. They are usually seen singly or in groups of 2–3 in the North Pacific, with a maximum group size of 12. The blow is 3–4 m high. The dorsal fin is seen after the blow and then sometimes the dorsal keel is seen. They seldom lift their flukes out of the water before diving. It is generally believed that they usually move at 2–7 km/hr but can swim as fast as 20–25 km/hr and dive up to 300 m. Bryde's whales breach more often than other balaenopterids. They produce powerful low-frequency tonal and swept calls similar to the calls of other balaenopterid whales.

V. Life History

Although Bryde's whales have a life history similar to that of other balaenopterids, there are species-specific aspects due to the fact that they remain in tropical and temperate waters throughout the year. As for many other migratory large cetaceans, little is known about the breeding grounds, even for inshore or coastal stocks, although it is generally believed that they must be somewhere in lower latitudes for the migratory stocks. In waters off the inshore waters of the Pacific coast of Japan and the East China Sea, females accompanied by small calves sometimes appear in early spring, but there is no direct evidence that they give birth there. In pelagic stocks, peaks of both mating and calving are in winter; although these are much more diffuse than in other migratory balaenopterids. Gestation lasts for about 11 months. Length at birth is about 4 m. The sex ratio at birth is around 1 (Best, 1977). Lactation lasts about 6 months and calves are weaned at about 7 m in body length. Males attain sexual maturity at 11–11.4 m and females at 11.6–11.8 m in the western North Pacific stock. Best (1977) found length at sexual maturity for the inshore form to be less than for the offshore form off South Africa, by 1 ft in females and 3 ft in males. The mean age at sexual maturity is slightly less than 7 years. Based on the annual ovulation rate (0.42–0.46) for pelagic Bryde's whale stocks, the calving interval is about 2 years. In summary, Bryde's whales have a 2-year reproductive cycle composed of 11–12 months' gestation, 6 months of lactation, and 6 months resting.

VI. Human Interactions

Bryde's whales were not harvested commercially or substantially until recent times; their value became relatively important in the late 1970s with the shift of whaling to the smaller species. However, commercial harvest of this species was prohibited by a moratorium imposed by the International Whaling Commission (IWC) in 1987.

Because Bryde's whales had been mainly exploited after substantial improvement of IWC stock management procedures adopted in 1975 (the New Management Procedure or NMP), stocks have been kept relatively stable.

See Also the Following Articles

Baleen Whales (Mysticeti) ■ Omura's Whale ■ Sei Whale

References

Anderson, J. (1878). *Anatomical and Zoological Researchers: Comprising an Account of the Zoological Results of the Two Expeditions to Western Yunnan in 1868 and 1875.* B. Quaritch, London.

Best, P.B. (1960). Further information on Bryde's whale (*Balaenoptera edeni* Anderson) from Saldanha Bay, South Africa. *Hvalfangst-Tidende* **49**, 201–215.

Best, P.B. (1977). Two allopatric forms of Bryde's whale off South Africa. *Rep. Int. Whaling Comm.* (Special Issue 1), 10–38.

Junge, G.C.A. (1950). On a specimen of the rare fin whale, *Balaenoptera edeni* Anderson, stranded on Pulu Sugi near Singapore. *Zool. Verh.* **9**, 1–26.

Kershaw, F., Leslie, M.S., Collins, T., et al. (2013). Population differentiation of 2 forms of Bryde's whales in the Indian and Pacific Oceans. *J. Hered.* **104**, 755–764.

Luksenburg, J.A., Henriquez, A., and Sangster, G. (2015). Molecular and morphological evidence for the subspecific identity of Bryde's whales in the southern Caribbean. *Mar. Mamm. Sci.* **31**, 1568–1579.

Murase, H., Tamura, T., Kiwada, H., Fujise, Y., Watanabe, H., Ohizumi, H., Yonezaki, S., Okamura, H., and Kawahara, S. (2007). Prey selection of common minke (*Balaenoptera acutorostrata*) and Bryde's whales (*Balaenoptera edeni*) whales in the western North Pacific in 2000 and 2001. *Fish. Oceanogr.* **16**, 186–201.

Olsen, O. (1913). On the external characteristics and biology of Bryde's whale (*Balaenoptera brydei*) a new rorqual from the coast of South Africa. *Proc. Zool. Soc. London* **1913**, 1073–1090.

Omura, H. (1959). Bryde's whale from the coast of Japan. *Sci. Rep. Whales Res. Inst., Tokyo* **14**, 1–33.

Thomas, P.O., Reeves, R.R., and Brownell Jr., R.L. (2016). Status of the world's baleen whales. *Mar. Mamm. Sci.* **32**, 682–734.

Wada, S., and Numachi, K. (1991). Allozyme analyses of genetic differentiation among the populations and species of the *Balaenoptera*. *Rep. Int. Whaling Comm.* (Special Issue 13), 125–154.

Wada, S., Oishi, M., and Yamada, T.K. (2003). A newly discovered species of living baleen whale. *Nature* **426**, 278–281.

Yoshida, H., and Kato, H. (1999). Phylogenetic relationships of Bryde's whales in the western North Pacific and adjacent waters inferred from mitochondrial DNA sequences. *Mar. Mamm. Sci.* **15**, 1269–1286.

Copyright © 2017. Elsevier Science & Technology. All rights reserved.

BURMEISTER'S PORPOISE

Phocoena spinipinnis Burmeister, 1865

JULIO C. REYES

Phocoena spinipinnis was described based on a specimen captured by fishermen at the mouth of La Plata River, Argentina (Brownell and Praderi, 1984; Brownell and Clapham, 1999). It belongs to the family Phocoenidae, whose members share the presence of premaxillary eminences in the skull, a reduced posterior extension of the premaxillae not reaching the nasal and, at least in the living species, small spatulated teeth. The Spanish name for this porpoise is "marsopa espinosa" (spiny porpoise) which refers to the series of dermal tubercles present in the dorsal fin. Some vernacular names include "chancho marino," "tonino" (Peru), and "antonino" (southern Chile). A drawing of the species is in Fig. 1. It occurs in both the South Atlantic and South Pacific Oceans, never far from shore (Fig. 2).

I. Characteristics and Taxonomy

The body of this porpoise is stocky with a small, blunt head lacking a beak and proportionally large flippers (Goodall et al., 1995a; Figs 3 and 4). The dorsal fin is diagnostic: it is placed in the posterior third of the body, triangular in shape, and canted backward; its leading edge bears a series of 2–4 rows of dermal tubercles ending near the tip of the fin (Fig. 5). The tubercles become larger and sharper in older animals. The flukes are medium sized, with rounded tips and an almost straight trailing edge.

Maximum length reported is 200 cm for specimens from Uruguay. On the Pacific coast of South America, the largest male and female reached 182 and 183 cm long, respectively. Maximum known body mass for specimens from the Pacific is 72 kg for a male of 170 cm long ($n = 70$) and 79 kg for a female of 173 cm long ($n = 60$). In the Atlantic, a 191-cm female weighted 105 kg, whereas male of 178 cm length weighed 78 kg.

The coloration of Burmeister's porpoise observed in fresh carcasses and live animals is dark gray, sometimes lead gray, on the back and sides, with a light gray to white area around the abdominal field. There is a well-defined eye patch surrounded by a light gray to white halo. An anterior extension of this eye patch may

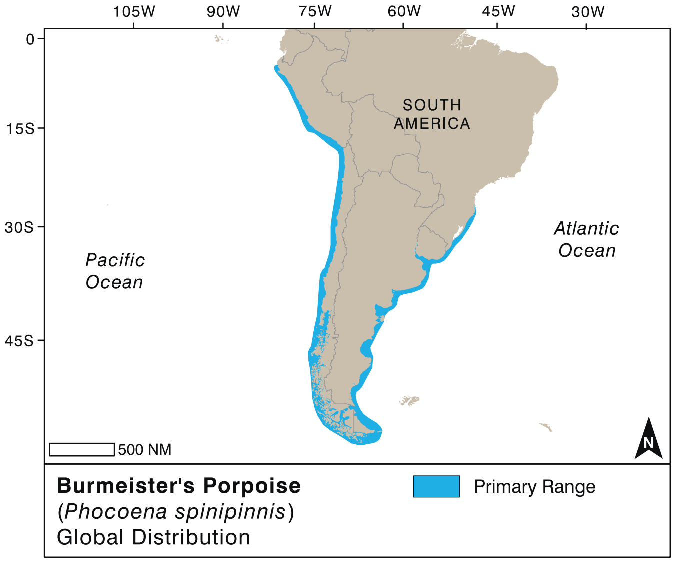

Figure 2 *Burmeister's porpoise distribution. Adapted by Nina Lisowski from Jefferson, T.A., Webber, M.A. and Pitman, R.L. (2015). "Marine Mammals of the World: A Comprehensive Guide to Their Identification," 2nd ed. Elsevier, San Diego, CA.*

Figure 3 *Lateral (top) and ventral (bottom) views of a female* Burmeister's porpoise *from Peru.*

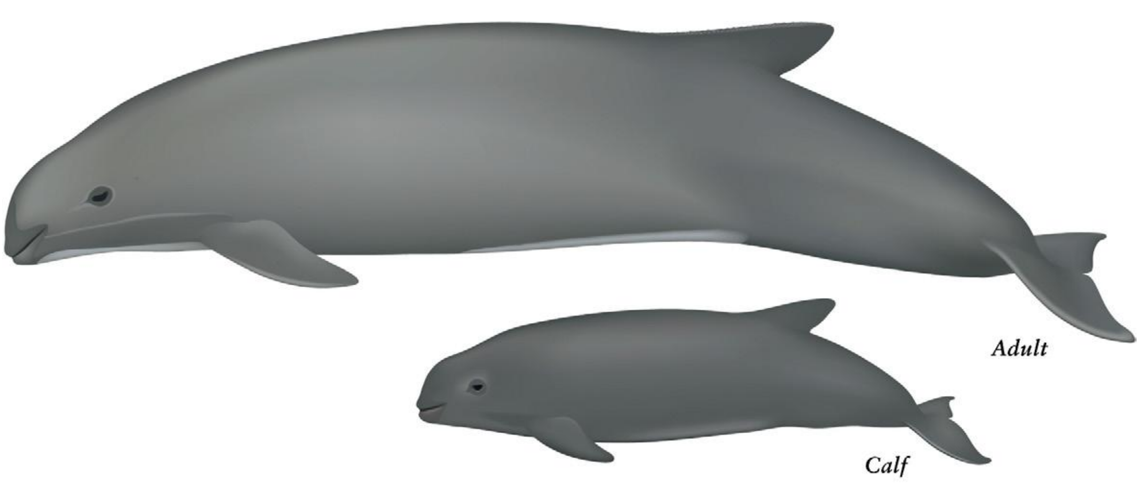

Figure 1 *Burmeister's porpoise,* Phocoena spinipinnis *(Illustrations by Uko Gorter).*

Copyright © 2017. Elsevier Science & Technology. All rights reserved.

Figure 4 *Detail of the head of a* Burmeister's porpoise.

Figure 5 *Dorsal fin of a* Burmeister's porpoise, *showing the dermal tubercles characteristic of the species.*

reach the dark gray lip patch. A wide, dark gray blowhole-to-apex stripe joins the lip patch. The flipper stripe is dark gray, being wide and reaching the lip patch on the right side, and thinner and joining the chin patch on the left side of the head; the flipper stripe may be flanked by thin, light gray stripes. In the abdominal field, coloration of the genital area is sexually dimorphic (Reyes and Van Waerebeek, 1995).

The skull of *Phocoena spinipinnis* resembles those of the harbor porpoise, *P. phocoena*, and the vaquita, *Phocoena sinus*, although it has a less antero-posterior compression of the braincase and the dorsal aspect of the supraoccipital is in line with the plane of the rostrum, whereas in *P. sinus* and *P. phocoena*, this portion of the supraoccipital forms an angle with the long axis of the rostrum. Further characteristics differentiating *P. spinipinnis* from *P. sinus* include a longer rostrum, a larger vertex, fewer alveolar teeth, and hamular processes of pterygoids longer than wide and with mesial borders widely separated. Little information is available on the axial skeleton. Vertebral count is C7, D14, L15, Ca31–35 = 67–71. The first three cervical vertebrae are fused. The first eight pairs of ribs have both capitular and tubercular articulation to the vertebrae. The phalangeal formula is I2, II8, III7, IV4, and V2. Fossil record is limited. A single incomplete fossil calvarium of *P. spinipinnis* is known from Chile, although locality and date are not known for the specimen. Analysis of the mitochondrial DNA control region and cytochrome *b* gene indicates that *P. spinipinnis* is closely related to *P. sinus* and both are related to the spectacled porpoise (*P. dioptrica*) (Rosel et al., 1995).

II. Distribution and Abundance

On the west coast of South America, the northernmost record of Burmeister's porpoise is from Paita, northern Peru (5°01′S), at the latitude where the Humboldt Current veers to the west as it is integrated into the South Equatorial Current (Fig. 2). The distribution extends south along the Peruvian and Chilean coasts to Valdivia, Chile (39°50′S). There are records from the Magellan Strait, the Beagle Channel, and near Cape Horn. On the east side of the continent, this porpoise is reported from Argentina, Uruguay, and up to Santa Catarina State in Brazil (28°48′S) (Brownell and Clapham, 1999; Goodall et al., 1995a) (Fig. 2). Based on specimen records and analysis of oceanographic variables, it has been proposed that the range of this species is continuous from Paita, Peru, to the La Plata River Basin, Argentina. The relatively few records in Uruguay and Brazil are linked to the intrusion of cold waters associated with the Subtropical Convergence (Molina-Schiller et al., 2005). Differences in body size between Pacific and Atlantic Burmeister's porpoises led to the proposal of two different stocks of the species. Analysis of both mitochondrial and nuclear DNA reinforces the existence of a "Peruvian stock" and a "Chilean-Argentinean stock." Further research is needed based on both morphological and molecular analysis for a better determination of the geographic boundaries of these stocks (Corcuera et al., 1995; Rosa et al., 2005). There are no abundance estimates for this species.

III. Ecology

Throughout its range, Burmeister's porpoise is found mainly in coastal waters, over the continental shelf, and up to 50 km from shore, in waters 5–130 m deep and temperatures ranging from 3 to 19.5°C. Sightings and captures are reported in all seasons, although in some areas there seem to be seasonal movements following prey. Seasonal occurrence has also been reported in San Jose Gulf in Argentina.

Burmeister's porpoise feeds mainly on fishes, the species varying with region. In both Peru and Chile, Peruvian anchovy (*Engraulis ringens*), silverside (*Odontesthes regia*), and hake (*Merluccius gayi*) are by far the main preys consumed, together with other small fish and squids. Off Argentina, sardines, tailed hake, shrimps, and squids are preferred. A few specimens examined in Uruguay and Brazil had mostly fish and squids. There is no information on foraging strategies. Parasites commonly found in this porpoise include the nematode *Stenurus australis and S. minor from* the cranial sinuses and the inner ear; the campulid trematode *Nasitrema globicephalae* has also been found in the same location. The lungs may be infected with the nematodes *Halocercus* sp. and *Pseudalius inflexus*. Gastrointestinal parasites include the trematodes *Synthesium tursionis*, *Pholeter gastrophylus*, and *Braunina cordiformis*, and the nematodes *Anisakis typica*, *An. simplex*, *Pseudoterranova* sp. and the acantocephalan *Corynosoma cetaceum* (Corcuera et al., 1995, Reyes and Van Waerebeek, 1995). Parasitic crustaceans of the genus *Isocyamus* have been reported in porpoises from Peru, although prevalence is low. These whale lices are located in fresh wounds, the angle of the mouth, the genital slit, the axillae, and the angle at the base of the dorsal fin. The ectocomensal barnacle *Xenobalanus globicipitis* is found on the tips of flippers, the dorsal fin, and on the flukes of Burmeister's porpoises in Peru, with a maximum of 40 barnacles reported for a single animal. Among viral infections reported in Burmeister's porpoise are at least two papilloma viruses causing genital warts and a poxvirus isolated from tattoo lesions on the skin (Van Bressem et al., 2007).

Copyright © 2017. Elsevier Science & Technology. All rights reserved.

IV. Behavior and Physiology

Swimming behavior is described as unobtrusive, with little of the body exposed on the surface and gentle rolls when diving, which combined with the low dorsal fin makes difficult spotting this species at sea. On occasions it can swim very fast when approached by a boat. There are no reports of "porpoising" or bowriding, although a few animals have been observed riding waves and leaping out of the water. Underwater speed is estimated at 4 km/hr, while time under the water surface ranges from 1 to 3 min (Goodall et al., 1995b; Brownell and Clapham, 1999). Group size has been usually reported comprising 2–8 individuals. From 27 confirmed sightings, mean group size has been estimated at 7.38, with 78% of the sighted groups containing 1–4 animals. Large aggregations of 50–70 animals are sometimes encountered. A sighting of nearly 150 porpoises was reported off north-central Peru in waters 27–31 m deep. The animals were scattered over a large area in small groups of 1–5 individuals (including several mother–calf pairs) forming a loose association (Van Waerebeek et al., 2002). The cause and frequency of these events are unknown.

V. Life History

In Peru, average length at sexual maturity in females is around 154.8 cm (Goodall et al., 1995a,b; Reyes and Van Waerebeek, 1995). Pregnancy rate has been estimated at 60%, although considering that some fetuses are too small to be noted, this is thought to be an underestimate. Records of pregnant females simultaneously lactating suggest that annual reproduction may take place. Average length at sexual maturity in males has been estimated as 159.9 cm. There is no evidence of seasonality in the male reproductive cycle. The size at birth is around 86 cm. Mating may take place during the austral summer (December through March), with some successful mating occurring outside this season. Gestation may last 11–12 months (Reyes and Van Waerebeek, 1995). Age data are scarce for this species. Maximum estimated age is more than or equal to 12 growth layer groups (GLGs) for a 196-cm female and more than or equal to 5 GLGs for a 179-cm male. Animals from Argentina may reach physical maturity at a length of 200 cm (Corcuera et al., 1995).

VI. Interactions With Humans

The largest capture of Burmeister's porpoise occurs off Peru. Around 200 to more than 400 porpoises are taken annually in Peruvian gillnet fisheries for demersal fishes, including sharks and rays, and used for human consumption (Read et al., 1988; International Whaling Commission, 1994). Although most takes of this species in Peru are incidental, evidence of direct gillnetting on large porpoise aggregations is documented. Small numbers of porpoises are incidentally captured in fisheries off northern Chile; a gillnet fishery for rat fish and sciaenids operating in southern Chile takes a few hundred animals each year, which are used as bait in other fisheries (Lescrauwaet and Gibbons, 1994; Reyes and Oporto, 1994). The number of small cetaceans including Burmeister's porpoises reportedly taken directly for crab bait in southern Chile declined since 1990, due to several factors modifying the fishery's operations. A few animals may be taken in gillnets in Tierra del Fuego, Argentina; evidence of the use of porpoises as human food in the Beagle Channel area dates back some 6500 years (Goodall et al., 1995a). Off the northern coast of Argentina, an estimated 21–25 Burmeister's porpoises are captured every year in gillnet fisheries, while a few are taken in fisheries off Uruguay (Corcuera et al., 1994; Brownell and Clapham, 1999). Organochlorine compounds have been studied in Burmeister's porpoises from northern Argentina. The levels of pollutants (including DDT metabolites and PCBs) in the blubber are considered very low compared with other marine mammals (Corcuera et al., 1995).

References

Brownell Jr., R.L., and Clapham, P.J. (1999). Burmeister's porpoise *Phocoena spinipinnis* Burmeister, 1865. In "Handbook of Marine Mammals", (S. Ridgway, and R. Harrison, Eds), Vol. VI, pp. 393–410. Academic Press, San Diego, CA.

Brownell, R.L., and Praderi, R. (1984). Phocoena spinipinnis. *Mamm. Species* **217**, 1–4.

Corcuera, J., Monzón, F., Crespo, E.A., Aguilar, A., and Raga, J.A. (1994). Interactions between marine mammals and coastal fisheries of Necochea and Claromeco (Buenos Aires province, Argentina). *Rep. Int. Whaling Comm.* (Special Issue 15), 283–290.

Corcuera, J., Monzón, F., Aguilar, A., Borrel, A., and Raga, A. (1995). Life history data, organochlorine pollutants and parasites from eight Burmeister's porpoises, *Phocoena spinipinnis*, caught in northern Argentine waters. *Rep. Int. Whaling Comm.* (Special Issue 16), 365–372.

Goodall, R.N.P., Norris, K.S., Harris, G., Oporto, J.A., and Castello, H.P. (1995a). Notes on the biology of Burmeister's porpoise, *Phocoena spinipinnis*, off southern South America. *Rep. Int. Whaling Comm.* (Special Issue 16), 318–347.

Goodall, R.N.P., Würsig, B., Würsig, M., Harris, G., and Norris, K.S. (1995b). Sightings of Burmeister's porpoise, *Phocoena spinipinnis*, off southern South America. *Rep. Int. Whaling Comm.* (Special Issue 16), 297–316.

International Whaling Commission, 1994. Report of the workshop on mortality of cetaceans in passive fishing nets and traps. *Rep. Int. Whaling Comm.* (Special Issue 15), 1–71.

Lescrauwaet, A.-C., and Gibbons, J. (1994). Mortality of small cetaceans and the crab bait fishery in the Magallanes area of Chile since 1980. *Rep. Int. Whaling Comm.* (Special Issue 15), 485–494.

Molina-Schiller, D.M., Rosales, S.A., and De Freitas, T.R.O. (2005). Oceanographic conditions off coastal South America in relation to the distribution of Burmeister's porpoise, *Phocoena spinipinnis*. *Latin Am. J. Aquat. Mamm.* **4**, 141–156.

Read, A.J., Van Waerebeek, K., Reyes, J.C., McKinnon, J.S., and Lehman, L.C. (1988). The exploitation of small cetaceans in coastal Peru. *Biol. Conserv.* **46**, 53–70.

Reyes, J.C., and Oporto, J.A. (1994). Gillnet fisheries and cetaceans in the southeast Pacific. *Rep. Int. Whaling Comm.* (Special Issue 15), 467–474.

Reyes, J.C., and Van Waerebeek, K. (1995). Aspects of the biology of Burmeister's porpoise from Peru. *Rep. Int. Whaling Comm.* (Special Issue 16), 349–364.

Rosa, S., Milinkovitch, M., Van Waerebeek, K., Berck, J., Oporto, J., Alfaro-Sigueto, J., Van Bressem, M.F., Goodall, N., and Cassens, I. (2005). Population structure of nuclear and mitochondrial DNA variation among South American Burmeister's porpoises (*Phocoena spinipinnis*). *Conserv. Genet.* **6**, 431–443.

Rosel, P.E., Haygood, M.G., and Perrin, W.F. (1995). Phylogenetic relationships among the true porpoises (Cetacea: Phocoenidae). *Mol. Phylogenet. Evol.* **4**, 463–474.

Van Bressem, M.F., Cassonnet, P., Rector, A., Desaintes, C., Van Waerebeek, K., Alfaro-Shigueto, J., Van Ranst, M., and Orth, G. (2007). Genital warts in Burmeister's porpoises: characterization of *Phocoena spinipinnis* papillomavirus type 1 (PsPV-1) and evidence for a second, distantly related PsPV. *J. Gen. Virol.* **88**, 1928–1933.

Van Waerebeek, K., Santillán, L., and Reyes, J.C. (2002). An unusually large aggregation of Burmeister's porpoise *Phocoena spinipinnis* off Peru, with a review of sightings from the eastern South Pacific. *Not. Men. Mus. Nac. Hist. Nat., Chile* **350**, 12–17.

Copyright © 2017. Elsevier Science & Technology. All rights reserved.

BYCATCH

Simon Northridge

Marine mammals sometimes get caught and killed in fishing operations. In many cases, these deaths are entirely unintended by the fishermen and are incidental to the main fishing operation. They are therefore often referred to as incidental catches. More often they are referred to as "bycatches," although this term is also used to describe the capture of some species that, while not the main target of a fishery, still have some value and may therefore be sold. Incidental catches are generally unwanted and discarded. The term *bycatch* is now commonly used to describe any sort of unintended capture of marine life.

Most species of marine mammal that occur in places that are heavily fished have been caught in at least one type of fishing gear, and most types of fishing gear have been reported to ensnare marine mammals. Some captures seem to defy reason. Large whales, for example, may become caught in a single lobster pot line, and porpoises can get caught in simple fish traps that they are able to find their way into, but not out of. One estimate of global bycatch levels suggests that over 300,000 marine mammals per year are killed in fishing operations globally (Read et al., 2006).

In the past, and indeed in some parts of the world today, bycatch of marine mammals might be treated as a useful bonus, and landed for consumption. Since the 1950s, however, fishing technology has changed faster and more completely than ever before, which has led to a reappraisal of the issues surrounding bycatch. Nets have become larger and stronger, new fishing techniques have been devised and fishing intensity throughout the world has increased dramatically, with marine capture fisheries increasing by a factor of four since 1950. Such developments have had unintended negative impacts on nontarget species, including marine mammals, so that bycatches have now become a critical issue for some marine mammal populations. Marine mammals generally reproduce slowly, and their populations are not able to withstand much additional non-natural mortality. The removal of a very small proportion of the population per year may be enough to erode the population. Bycatch is recognized as one of the most important sources of anthropogenic mortality among many species of marine mammals (Reeves et al., 2003; Kovacs et al., 2012). For this reason, many nations now legislate to protect marine mammal populations from deliberate or accidental exploitation, and there are several international agreements with the same aim.

Legislation to protect marine mammals from excessive mortality has resulted from a variety of case studies that have uncovered unsustainable levels of bycatch. Several of these cases have become widely publicized and have generated considerable public attention and debate.

I. Examples

A. Eastern Tropical Pacific Tuna Purse Seine Fishery

The first interaction to be recognized as a serious concern for the conservation of marine mammals was the large-scale capture of pelagic delphinids, mainly *Stenella* and *Delphinus* species in the U.S. tuna purse seine fishery of the eastern tropical Pacific Ocean (ETP). This fishery, which began in the 1950s, involves setting nets around dolphin schools, below which large tuna are known to aggregate. Nets are hauled to catch the fish, but dolphins would often get caught in the process (see Tuna Dolphin).

During much of the 1960s and up to 1972, annual mortalities ranged between 200,000 and 500,000. Thereafter, efforts were made to reduce the kill, but tens of thousands of dolphins were still being killed annually throughout most of the 1980s. Pantropical spotted dolphins (*S. attenuata*) were the most frequently killed species, and numbers of this species in the ETP were more than halved over the 1960s and 1970s. Populations of other species were also severely impacted.

Largely as a result of public pressure, and the introduction of "dolphin safe" tuna retailing, this practice has now been greatly reduced. New techniques have been devised by the skippers to ensure that a very high proportion of the dolphins used in this way to catch tuna are encouraged to escape from the nets before the fish are removed. Under a training and monitoring scheme run by the Inter-American Tropical Tuna Commission, annual dolphin mortality had been reduced to less than 800 animals by 2015. Efforts continue to reduce these figures further still. However, despite the great reduction in the kills, the populations have not shown strong signs of recovery, which may be attributable to continued large-scale chase and capture. (Gerrodette and Forcada, 2005; Wade et al., 2007).

Throughout the world, since the discovery of the effect of the ETP tuna fishery on dolphin populations, it has become clear that there are numerous other fisheries in which marine mammals are being killed in large numbers. In some cases, populations or species have been threatened with extinction. Two of the most severe cases are those concerning the baiji (*Lipotes vexillifer*), which is in fact now thought to be extinct, and the vaquita (*Phocoena sinus*), whose population is at a critically low level. Some pinniped populations have also been severely affected.

B. The Baiji

The baiji, otherwise known as the Chinese river dolphin, inhabited the middle and lower parts of the Yangtze River system in China (see chapter on Baiji). The total population size was thought to have numbered a few hundred in the 1980s, and numerous publications warned of its imminent demise throughout the 1990s and into the present millennium. The major source of mortality for this species was snagging in "rolling hook" fishing lines. These are lines equipped with many closely set, sharp, unbaited hooks designed to snag fish foraging on the river bed in the same areas as the baiji. In one study, 45% of all known baiji deaths were attributed to snagging in rolling hooks. The most recent survey found no remaining baiji and concluded that the species was extinct, probably due to unsustainable bycatch in local fisheries and habitat deterioration (Turvey et al., 2007).

C. The Vaquita

The vaquita is a species of porpoise restricted to the upper part of the Gulf of California in Mexico. Abundance estimates have shown a rapid decline from 567 individuals in 1997, to 245 in 2008, and just 59 individuals in 2015 (CIRVA, 2016). Again, the major source of mortality is incidental catches in fishing operations, in this case gill nets for fish and shrimps. Gill nets are simple long panels of netting that are set to stand in the water with floats along their top and a weighted rope on their bottom edge. Depending on the amount of weight added, they either sit on the seabed floating upward or they float at the surface hanging down. They are not only left to ensnare fish that happen to swim into them, but also catch marine mammals by entangling them. Annual vaquita mortality in gill net fisheries was estimated at around 40–80 per year in the 1990s, which was clearly an unsustainable level of mortality

Copyright © 2017. Elsevier Science & Technology. All rights reserved.

given the size of the population. Despite a comprehensive but temporary ban on all gillnetting in the Upper Gulf of California in 2015, illegal gillnet fishing for totoaba (*Totoaba macdonaldi*, a drum or sciaenid fish) continued to kill vaquitas in 2016. Extinction now appears imminent (CIRVA, 2016), though efforts are being made to develop alternative fishing methods and to combat illegal fishing.

D. Pinnipeds

Much of the research and monitoring of marine mammal bycatch has been focused on small cetaceans, while monitoring, assessment, and mitigation of bycatch in pinnipeds and sirenians is much more restricted. Bycatch is nevertheless one of the main contributing factors to the decline of several species or subspecies of pinniped (Kovacs et al., 2012). The two extant species of monk sea (*Neomonachus schauinslandi and Monachus monachus*) (see Monk seals) are both endangered and in both cases bycatch or entanglement in (discarded) fishing gear has been a contributing factor in their decline (Henderson, 2001; Karamanlidis et al., 2008). The Saimaa seal (*Pusa hispida saimensis*) has also been severely impacted through bycatch in gillnets and other fishing gears in Lake Saimaa, and was listed as critically endangered until very recently. Conservation measures include restrictions on the use of certain types of fishing gear year-round in the main habitat of the Saimaa seal, while other gear types including some gillnets are restricted seasonally in about 60% of the lake to minimize the risk of killing juvenile seals. Alternative fishing gears are also being developed to minimize the risk of bycatch. These measures seem to be working, with a current population estimate of 360 up from less than 200 in the early 1980s.

II. Causes for Concern

There are numerous examples around the world where significant numbers of marine mammals are killed incidentally in fishing operations and where populations may be threatened. It is usually the smaller species and those that occur in continental shelf waters where most fishing is concentrated that are impacted most heavily, and especially those where species' range is limited. Nevertheless, among widely distributed species, local populations can be eliminated or reduced to very low levels through bycatch, though it is often difficult to be absolutely sure of the cause of an observed decline. Examples where bycatch is widely accepted as having substantially affected local populations include those of harbor porpoises (*Phocoena phocoena;* Fig. 1), notably in the Baltic Sea and around the Iberian Peninsula; or Irrawaddy dolphins (*Orcaella brevirostris*) in Malampaya Sound in the Philippines.

Figure 1 *A harbor porpoise entangled in a cod gillnet in the North Sea, one of many hundreds dying this way every year in* European gillnet *fisheries (Photo by Nigel Godden/Sea Mammal Research Unit).*

Throughout the world, other small coastally distributed marine mammal species are victims of bycatch in fishing operations, but the level of such bycatches and the likely impacts remain poorly known in most places. Monitoring bycatch rates and estimating population sizes are expensive, and bycatch events are generally rare and poorly documented, especially when the animal concerned is also rare.

Although most attention worldwide has focused on the potential conservation issues raised by the bycatch of marine mammals, animal welfare considerations are also a serious concern. Whereas some bycatch of marine mammals in fishing operations is an inevitable consequence of fishing, in some nations any large-scale fatalities of marine mammals are publicly unacceptable regardless of whether they are sustainable at a population level.

III. Attempts to Resolve the Problem

Most of the numerically significant bycatches of marine mammals tend to be in static fishing gear, mainly gill nets. Despite the attention focused on this subject in recent years, it is still not known how or why marine mammals become caught in such nets. It is not known, for example, whether mammals are attracted to nets by their curiosity or by the presence of trapped fish, whether they do not notice the netting, or whether they simply do not understand the potential consequence of swimming into it. Despite our ignorance, some progress has been made toward resolving the problem.

The development of pingers, or acoustic beacons, is one effective means of reducing the bycatch of some species. These devices exploit the sensitive hearing of marine mammals by emitting intermittent, short, high-pitched noises that most fish cannot hear but that appear to repel or warn off at least some species of marine mammals. Attached at regular intervals along the length of a gill net, these pocket-sized devices have been shown to reduce the numbers of bycaught marine mammals, mainly harbor porpoises, but also dolphins and sea lions, by up to 90% (Dawson et al., 2012). Pinger use is now mandatory in several fisheries in the United States, EU, and other parts of the world. Pingers certainly appear to be useful, but there are still some concerns about them. If used intensively, there are fears that marine mammals may become excluded from significant parts of their foraging habitats. Pingers need to have their batteries replaced or recharged, and therefore rely on people maintaining them to ensure that they continue to work. This can be an expensive and time-consuming operation that may eventually get overlooked. Finally, pingers themselves are expensive, so that the cost of equipping a net with pingers may exceed the cost of the net. In many less-developed countries, it is unlikely that they will ever become widely used for this reason alone.

Issues with mobile fishing gear are somewhat different. There are or have been several initiatives worldwide that aim to keep marine mammals out of towed or mobile fishing gear. In the ETP tuna fishery referred to earlier, special techniques and net modifications have been developed to help dolphins to escape from the purse seine net once the net has fully encircled the school of tuna. During the "backdown procedure" the skipper manipulates the vessel and net to sink a part of the net float line under the water, enabling the dolphins to escape. This part of the net is also made up with a smaller meshed panel, the Medina panel, reducing the chances of dolphins becoming entangled as they escape. Similarly,

Copyright © 2017. Elsevier Science & Technology. All rights reserved.

in New Zealand, special sea lion escape devices have been designed and used in squid trawls. A large grid is placed near the rear of the net, set at an angle to the vertical plane. Fish can pass through the grid, but larger animals such as sea lions are forced upward and out the net through an escape hatch. Similar devices have been designed and tested to help dolphins escape trawls in the United Kingdom, France, and Australia.

In general, the bycatch of marine mammals is caused by a combination of fishing techniques or gear design and the behavior of the marine mammal. Resolving problematic interactions therefore involves some combination of change to fishing gear use or design and/or the manipulation of marine mammal behavior. Very little is known about the behavior of marine mammals in relation to fishing gear, especially in the context of bycatch. In part this is because of the difficulties of studying marine mammals underwater and the rarity of such events in most cases, which makes observing their occurrence very difficult. Finding solutions to the problem is therefore a slow and arduous process and will normally involve working closely with the fishing industry to find ways of modifying existing gear, or finding alternative fishing methods.

See Also the Following Articles

Baiji ■ Entanglement of Whales in Fishing Gear ■ Fisheries Interactions ■ Monk Seals ■ Ringed Seal ■ Tuna–Dolphin Issue ■ Vaquita

References

CIRVA (2016). Seventh Meeting of the Comité Internacional para la Recuperación de la Vaquita. Ensenada, BC, Mexico.

Dawson, S.M., Northridge, S., Waples, D., and Read, A.J. (2012). To ping or not to ping; the use of active acoustic devices in mitigating interactions between small cetaceans and gillnet fisheries. *Endanger. Spec. Res.* **19**, 201–221.

Gerrodette, T., and Forcada, J. (2005). Non-recovery of two spotted and spinner dolphin populations in the eastern tropical Pacific Ocean. *Mar. Ecol. Prog. Ser.* **291**, 1–21.

Henderson, J.R. (2001). A pre- and post-MARPOL Annex V—Summary of Hawaiian monk seal entanglements and marine debris accumulation in the Northwestern Hawaiian Islands, 1982–1998. *Mar. Pollut. Bull.* **42**, 584–589.

Karamanlidis, A.A., Androukaki, E., Adamantopoulou, S., Chatzispyrou, A., Johnson, W.M., Kotomatas, S., et al. (2008). Assessing accidental entanglement as a threat to the Mediterranean monk seal *Monachus monachus*. *Endanger. Spec. Res.* **5**, 205–213.

Kovacs, K.M., Aguilar, A., Aurioles, D., Burkanov, V., Campagna, C., Gales, N., et al. (2012). Global threats to pinnipeds. *Mar. Mamm. Sci.* **28**, 414–436.

Read, A.J., Drinker, P., and Northridge, S. (2006). Bycatch of marine mammals in U.S. and global fisheries. *Conserv. Biol.* **20**, 163–169.

Reeves, R.R., Smith, B.D., Crespo, E.A., and Sciara, G. N. di (2003). *Dolphins, whales, and porpoises: 2003–2010 conservation action plan for the world's cetaceans.* IUCN Species Survival Commission. IUCN/SSC Cetacean Specialist Group, IUCN, Gland, Switzerland and Cambridge, UK.

Turvey, S.T., Pitman, R.L., Taylor, B.L., Barlow, J., Akamatsu, T., Barrett, L.A., et al. (2007). First human-caused extinction of a cetacean species? *Biol. Lett.* **3**, 537–540.

Wade, P.R., Watters, G.M., Gerrodette, T., and Reilly, S.B. (2007). Depletion of spotted and spinner dolphins in the eastern tropical Pacific: Modeling hypotheses for their lack of recovery. *Mar. Ecol. Prog. Ser.* **343**, 1–14.

Copyright © 2017. Elsevier Science & Technology. All rights reserved.

This page intentionally left blank

Copyright © 2017. Elsevier Science & Technology. All rights reserved.