

Delphinapterus leucas. By Barbara E. Stewart and Robert E. A. Stewart

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Delphinapterus Lacépède, 1804

- Delphinapterus* Lacépède, 1804:xli, 243. Type species *Delphinapterus beluga* Lacépède.
Beluga Rafinesque, 1815:60, renaming of *Delphinapterus* Lacépède.
Delphinaptera Bowdich, 1821:86, emendation of *Delphinapterus* Lacépède.
Delphinaster Gray, 1821:310, misprint for *Delphinapterus* Lacépède.
Delphinopterius Cuvier, 1829:517, misprint for *Delphinapterus* Lacépède.
Delphis Wagler, 1830:34. Type species *Delphinus leucas* Pallas, 1776, by monotypy.
Argocetus Gloger, 1842:xxxiv, 169. Type species the "beluge" by monotypy.

CONTEXT AND CONTENT. Order Cetacea, Suborder Odontoceti, Family Monodontidae. *Delphinapterus* and *Monodon* are the only genera; each is monotypic and generally no subspecies are recognized.

Delphinapterus leucas (Pallas, 1776)

Beluga

- Delphinus leucas* Pallas, 1776:85, footnote. Type locality mouth of Ob River, northeastern Siberia, U.S.S.R.
B[alaena] albicans Müller, 1776:7. Type locality not available to authors.
D[elphinus] phocaena albus Kerr, 1792:363. Type locality St. Lawrence River.
Delphinapterus beluga Lacépède, 1804:xli, 243. Type locality Arctic seas and the North Atlantic Ocean, particularly Davis Strait.
Delphinus albians Nilsson, 1820:403. A misprint for *albicans*.
Delphinus leucaster Gray, 1821:310. A misprint for *D. leucas* Pallas.
Delphinus canadensis Desmarest, 1822:516. Type locality seas of Canada.
Delphinus (Delphinapterus?) kingii Gray, 1827:375. Type locality uncertain; the holotype, a skull, agrees with those of Alaskan beluga.
Catodon candicans Lesson, 1828:192, footnote. A lapsus for *albicans*.
Beluga borealis Lesson, 1828:440, 192. New name for *Delphinus leucas* Pallas.
Beluga glacialis Lesson, 1828:194, pl. 3, fig. 2 (animal with name in caption). Type locality Firth of Forth, Scotland.
C[atodon] sibbaldi Fleming, 1828:29. Type locality Kairston, Orkney Island, Great Britain.
Beluga catodon Gray, 1846:29. Type locality Greenland.
Beluga rhinodon Cope, 1865:274. Type locality Upernavik, Greenland.
Beluga declivis Cope, 1865:274. Type locality probably Greenland.
Beluga concreta Cope, 1865:278. Type locality probably Greenland.
Beluga angustata Cope, 1866:293. Type locality Upernavik, Greenland.
Delphinapterus freimani Klumov, 1935:26-28, fig. 2. Type locality White or Barents Sea.
Delphinapterus dorofeevi Klumov and Barabash, 1935:24. Type locality Okhotsk Sea.

DIAGNOSIS. Adult beluga are easily distinguished from the narwhal, *Monodon monoceros*, by skin color and dentition (Pippard, 1985), but neonates may be confused. Newborn beluga are dark brown, grey-brown, or blue-grey; narwhal are slate grey (Kleinenberg

et al., 1969; Reeves and Tracey, 1980). Juveniles are more readily distinguished: beluga are various shades of gray; narwhal have patches of white about the anus and genital slit. Adults have distinct coloration: beluga are white; narwhal are almost white ventrally, black dorsally, and have a mottled skin pattern on the sides of the body and upper fluke surfaces (Kleinenberg et al., 1969; Reeves and Tracey, 1980).

Beluga have a maximum of 40 homodont teeth, all of which are erupted and typically worn at the tip in mature animals. Narwhal have no buccal teeth, although adult males and rarely females, have tusk-like teeth derived from anterior-maxillary papillae.

GENERAL CHARACTERS. Adult body size varies geographically, smaller beluga occurring in sub-Arctic estuaries, mid-sized beluga in partially oceanic influenced Arctic waters, and larger beluga in southern sub-Arctic areas under direct oceanic influence (Sergeant and Brodie, 1969). Adults weigh up to 1,500 kg and range in length from 2.6 to 6.7 m (Kleinenberg et al., 1969; Sergeant and Brodie, 1969). Males are larger than females.

The forehead is rounded and prominent (Fig. 1). A nuchal constriction is apparent and the head is flexible laterally. Beluga lack a dorsal fin, but have a prominent dorsal ridge. The flippers are short and wide and in adult males the distal edge curls upward. The degree of curl increases with age (Sergeant, 1962; Vladyskov, 1943).

Skin color changes with age as noted above. The transition to the white adult color generally is completed by 9 years for males and by 11 years for females (Sergeant, 1973).

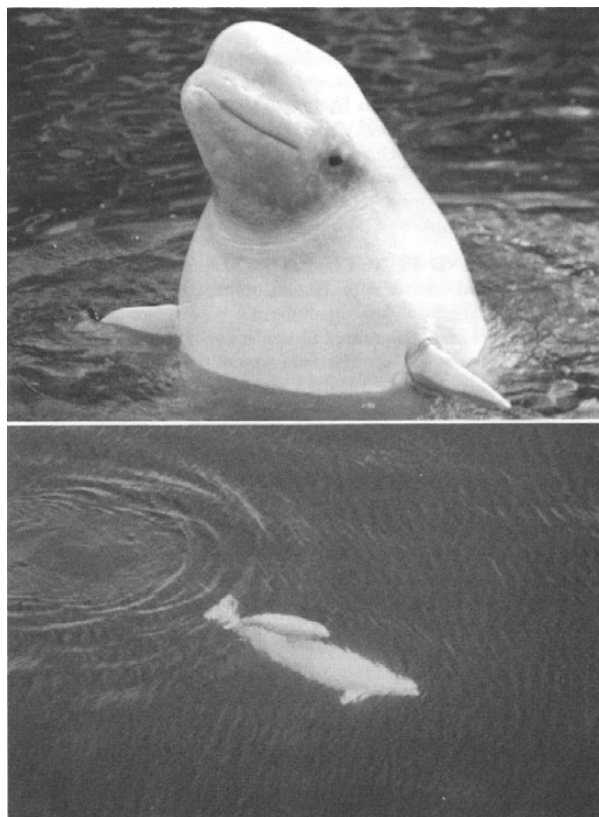


FIG. 1. Adult female *Delphinapterus leucas* (above) in the Vancouver Aquarium and female with calf (below) in the Churchill River, Manitoba, Canada. Photos by R. Stewart.



FIG. 2. Distribution of *Delphinapterus leucas*.

DISTRIBUTION. Beluga occur in Arctic and sub-Arctic waters of North America and Eurasia. The northernmost area of the range is off Ellesmere Island, West Greenland, and Spitsbergen, about 82°N. The southernmost belugas occupy areas in the St. Lawrence River estuary (47 to 49°N), White Sea, Okhotsk Sea, Gulf of Alaska, and James Bay (Ivashin and Mineev, 1981; Sergeant, 1962; Smith and Hammill, 1986; Fig. 2). Southern extralimital records are: 47°N, Loire River, France; 39°N, New Jersey, U.S.A.; 47°N, Puget Sound, U.S.A.; 46°N, Sea of Japan (Gurevich, 1980; Reeves and Katona, 1980; Sergeant et al., 1970; Vladikov, 1944).

The isolated resident population in the Gulf of St. Lawrence is a relict of a larger post-glacial group that penetrated the then Champlain Sea further west to Ottawa, Canada (Sergeant, 1962, 1986). The modern distribution in the Gulf of St. Lawrence has been further reduced by hydroelectric development (Sergeant and Brodie, 1975). A population decline is attributed to a loss of suitable habitat, to pollution, and to historic over-exploitation (Reeves and Mitchell, 1984; Sergeant, 1986).

FOSSIL RECORD. Late Miocene fossils from western North America indicate monodontids were extant at least 5 mya (Gaskin, 1982). *Delphinapterus* was likely trapped in the Arctic basin sometime during a Tertiary cold period (Gaskin, 1982).

Seventeen fossil beluga have been located in Pleistocene clay and sand deposits in eastern Ontario, Quebec, and Vermont. The fossils indicate an extensive beluga distribution in the Champlain Sea approximately 11,000 years ago (Harington, 1977, 1981).

FORM AND FUNCTION. The skin lacks sweat and other glands. The epidermis is 5 to 12 mm thick and has a spiny and a horny layer. The well-developed dermis consists of reticular and papillary layers and is separated from the hypodermis (fat or blubber layer) by a boundary layer. The thickness of the blubber layer varies with age, sex, reproductive status, seasonality, and location on the body. Within an individual, blubber varies from 4 to 27 cm; it is thickest above the upper jaw on the forehead, and is thinnest around the peduncle (Kleinenberg et al., 1969). Blubber and flippers represent approximately 43% of total body mass (Sergeant and Brodie, 1969).

Beluga have two mammae, one on each side of the ventral genital slit (Sergeant, 1962). Beluga milk contains 27% fat, 59% water, 11% protein, and 1% lactose, as is consistent with aquatic mammals (Lauer and Baker, 1969). The caloric density of beluga milk varies with lactational state and ranges from 5,400 to 8,400 calories/g dry weight.

The skull is asymmetric and elongate due to an extended rostrum (Fig. 3). There are 49 to 54 vertebrae: 7 unfused C, 11 to 12 T, 6 to 12 L, and 21 to 26 Ca. The typical mammalian forelimb is modified into a flipper. The pelvic girdle is absent and there are no hind limbs. Small pelvic bones (10 to 15 cm in adult males, shorter in females) are not attached to the vertebral column and serve only as sites of attachment for muscles of the urogenital system (Kleinenberg et al., 1969).

Tooth eruption starts at 2 years and is only partially complete by 3 years (Brodie, 1971). The upper teeth appear first and usually



FIG. 3. Dorsal, ventral, and lateral views of the skull and lateral view of the mandible of *Delphinapterus leucas* from western Hudson Bay (3.55 m subadult male, no. 14306). Greatest length of cranium is 53.8 cm. Photos courtesy of Manitoba Museum of Man and Nature, Winnipeg, Manitoba.

are more numerous until eruption is complete. The full set of 40 conical teeth rarely is attained and the number of teeth in each jaw may vary (Doan and Douglas, 1953; Kleinenberg et al., 1969). The teeth of juveniles are tritubercular, bearing small auxiliary cusps on each side of the anterior and posterior faces of the tooth (Douglas, 1951; Kleinenberg et al., 1969), however these cusps are quickly worn off. Enamel is present in unerupted teeth but is quickly eroded in erupted teeth (Ishiyama, 1987). The thin (7–10 μ m) enamel is prismless, made of fine crystal groups perpendicular to the surface and has incremental lines roughly parallel to the surface (Ishiyama, 1987). Teeth in old beluga are worn at the crown due to abrasion of teeth with those from the opposing jaw (Doan and Douglas, 1953; Sergeant, 1973). The teeth of females do not erupt as far and wear less at the tip (Sergeant, 1973) than those of males, which are longer (maximum 8 cm) and have thicker cementum (International Whaling Commission, 1980a; Sergeant, 1973). Growth-layer groups deposited in both dentine and cementum may be counted in longitudinal thin sections for age estimates (Brodie, 1969a, 1971; Goren et al., 1987; Sergeant, 1973, 1981).

The 13 dorsal muscles connecting the skull to the body are

paired and well developed, and, with the neck muscles, allow mobility of the head. All muscles of the vertebral column end at the tail in tendons attached to the caudal vertebrae. This allows for vertical movements of the tail. Contraction of special muscles is responsible for lateral tail movements. As in other cetaceans, the cerebellum is well developed as is the cortex of the prosencephalon hemispheres. Hearing appears to be the most developed of the senses and there are no olfactory structures. Beluga have well-developed trigeminal and facial nerves (Kleinenberg et al., 1969).

Acoustically, beluga have exceptional abilities to discriminate size, shape, and textures, and have directional capabilities (Brodie, 1969b; Fish and Mowbray, 1962). Such echolocatory sounds are generated either by passage of air through the nasal diverticula surrounding the blowhole (Gaskin, 1982; Harrison and King, 1965) or in the larynx with subsequent serial transmission through the palato-pharyngeal muscle, bones of the skull, and the rostrum or connective tissue of the melon (Harrison and King, 1965; Pilleri, 1980, 1982). Captive beluga which discriminated complex planar targets had peak emission energies of 40, 80, and 120 kHz (Gurevich and Evans, 1976). At peak energies (100 kHz), a male beluga demonstrated three click-interval patterns in detecting a target at 80 m (Au et al., 1987). The main beam was angled up about 5° from the plane defined by the beluga's teeth (Au et al., 1987). This angle is similar to that (7°) used by a beluga using a surface-reflected path to increase detection performance in a noisy environment (Penner et al., 1986). Returning sound waves probably impinge on both the external auditory meatus and the intramandibular fat body for subsequent internal transmission (Gaskin, 1982; Harrison and King, 1965).

The heart of the beluga is broad and flat and the rounded apex is formed by both ventricles. The morphology is partially related to diving performance and is consistent with marine mammals that may dive deeply for protracted periods (Bisaillon et al., 1987). Two trained beluga dove comfortably for up to 15 min and to a depth of 400 m. A maximum dive of 647 m was attained (Ridgway et al., 1984). Approximate blood measures are: hematocrit, 52%; hemoglobin, 20.0 g/100 ml; blood volume, 127 ml/kg (Ridgway et al., 1984). Blood-oxygen capacity ranges from 25 to 28 volume % (Dhindsa et al., 1974; Ridgway et al., 1984).

Beluga have one respiratory opening, a crescent-shaped blow hole on the top of the head. The larynx serves only as a further passage for air to the trachea; no vocal cords are present. The larynx lies rostral to the level of the atlas and extends to the presphenoid synchondrosis (Kleinenberg et al., 1969). This laryngeal position may allow a beluga to simultaneously swallow and echolocate (Reidenberg and Laitman, 1987). The cartilaginous tracheal rings are closed and form a non-collapsible tube. The lungs are elongate and single-lobed (Kleinenberg et al., 1969).

Prey is held by the beluga's hard lips and teeth, while the mobile tongue aids in orientation and swallowing (Kleinenberg et al., 1969). No mastication occurs. The stomach is three-chambered, providing a large surface area for rapid digestion (Gaskin, 1982; Treacy and Crawford, 1981). The cecum is absent. The oblong, oval kidney may contain up to 400 lobes and the ureters empty into a small pyriform bladder. The urethra is short; 10 to 16 cm in adult males and 20 to 25 cm in adult females. The small, lobular prostate is scattered about the colliculus seminalis, the distal portion of the vas deferens, and the beginning of the urogenital canal. The adrenals are flat and lie anterior to the kidney, adjacent to the diaphragm (Kleinenberg et al., 1969).

Two functional ovaries are present and the uterus is bicornuate (Brodie, 1971; Doan and Douglas, 1953; Harrison and King, 1965; Sergeant, 1962). The vaginal and urethral openings, clitoris, mammae, and anus lie in the same fold on the ventral surface near the tail. This fold is further anterior in males than it is in females (Kleinenberg et al., 1969). The testes are abdominal (Harrison and King, 1965).

ONTOGENY AND REPRODUCTION. Mating occurs in the spring and the timing varies geographically (Brodie, 1971), although in most areas conceptions peak in May (Brodie, 1971; Doan and Douglas, 1953; Kleinenberg et al., 1969). Alaskan beluga mate from late February to June with a presumed peak in March and a few beluga in Hudson Bay may mate in June to September (Doan and Douglas, 1953).

Implantation of the one fetus (rarely two) occurs 80% of the time in the left uterine horn (Brodie, 1971; Doan and Douglas,

1953; Sergeant, 1962). Placentation is diffuse, epitheliochorial (Harrison and King, 1965), and the estimated gestation period is 14 to 15 months (Brodie, 1971; Sergeant, 1962, 1973).

Peak calving time varies geographically: late March in west Greenland (Sergeant, 1962); end of June in western Hudson Bay and Bering Sea (Sergeant, 1986); July in the Chukchi Sea, Mackenzie River, and St. Lawrence River (Sergeant, 1986; Sergeant and Hoek, 1974); late July to early August in Cumberland Sound (Brodie, 1971). Neonate length varies geographically and ranges from 120 to 183 cm, the average is 150 cm (Kleinenberg et al., 1969; Ognetev, 1981; Sergeant, 1973). Newborn beluga mass is 35 to 85 kg (Gurevich, 1980; R. E. A. Stewart, original data).

Lactation extends for approximately 20 to 24 months (Brodie, 1969b, 1971; International Whaling Commission, 1980b; Sergeant, 1973), although solid food supplements the diet of milk after the first year (Brodie, 1971; Sergeant, 1973). Because a calf stays with the mother through a successive breeding period, most full reproductive cycles encompass 36 months (Brodie, 1971; International Whaling Commission, 1980b; Sergeant, 1973; Seaman and Burns, 1981), although a smaller proportion of beluga may have biennial breeding cycles (Mitchell, 1975).

The age at first pregnancy ranges from 4 to 7 years, with a mean of 5 years (Brodie, 1971; Mitchell, 1975; Ognetev, 1981; Seaman and Burns, 1981; Sergeant, 1973). Sperm production can occur in testes >200 g (Sergeant, 1973) and the testes mass increases from 50 to 300 g at body lengths between 290 and 330 cm (Finley et al., 1982; Sergeant, 1973). This sexual maturation in males occurs between 7 and 9 years of age and generally coincides with the development of white skin color (Brodie, 1971; International Whaling Commission, 1980b; Seaman and Burns, 1981; Sergeant, 1973). Males may not attain social maturity concomitantly with sexual maturity; the breeding system is likely polygynous (Fraker, 1980; Sergeant, 1962). The variation seen in blubber thickness of females is associated with gestation and lactation, and is not apparent in males (Sergeant and Brodie, 1969).

Corpora albicantia are apparent in mature ovaries, but accessory corpora lutea and luteinized follicles may obscure the reproductive history of a female based on corpora albicantia (Brodie, 1971, 1972; Kleinenberg et al., 1969; Sergeant, 1973). A typical female may have a maximum of 10 pregnancies in a full reproductive lifetime (Sergeant, 1973).

Longevity estimates range from 20 to 30+ years (Brodie, 1971; International Whaling Commission, 1980b; Mitchell, 1975; Sergeant and Brodie, 1975). However, these estimates are vulnerable to errors caused by tooth wear.

ECOLOGY. Polar bears (*Ursus maritimus*), killer whales (*Orcinus orca*), humans (*Homo sapiens*), and to a limited extent, walrus (*Odobenus rosmarus*) prey upon beluga (Freeman, 1973; Kleinenberg et al., 1969; Lowry et al., 1987; Mitchell and Reeves, 1981; Sergeant and Brodie, 1969; Smith, 1985; Smith and Taylor, 1977). Beluga in savvats or ice entrapments are particularly vulnerable and may starve, suffocate, or be intensively hunted (Freeman, 1968; Ivashin and Shevlyagin, 1987; Kapel, 1977; Kemper, 1980; Mitchell and Reeves, 1981). The white shark (*Carcharodon carcharias*) is a potential predator in the Gulf of St. Lawrence (Pippard, 1985).

Beluga harbor three trematodes (*Odhneriella seymouri*, *Leucasiella arctica*, and *L. mironovi*), one cestode (*Diphyllbothrium lanceolatum*), eight species of nematode (*Anisakis kuikenthali*, *A. simplex*, *Terrenova decipiens*, *Stenurus arctomarinus*, *S. minor*, *S. pallasii* (= *Pharurus pallasii*, Kenyon and Kenyon, 1977), *Otopocaeurus oserskoi*, *Crassicauda giliakiana*) and one acanthocephalan (*Corynosoma strumosum*) (Kleinenberg et al., 1969). *L. arctica*, *A. simplex*, *S. arctomarinus*, *S. pallasii* (= *Pharurus pallasii*), *O. oserskoi* (= *P. pallasii*), *Crassicauda* sp. and *C. strumosum* have also been reported in beluga (Brodie, 1971; Doan and Douglas, 1953; Kenyon and Kenyon, 1977; Wazura et al., 1986) as have *Hadwenius seymouri*, *Trichenella* sp., and *Contra-caecum* sp. (Arvy, 1979; Wazura et al., 1986).

A rare aneurysm occurred in the pulmonary trunk of a male beluga found dead in the St. Lawrence River. The beluga was infected with *Pharurus pallasii* and had high levels of polychlorinated biphenyls in its tissues, but the cause of the aneurysm could not be determined (Martineau et al., 1986). Another male beluga from the same area had a transitional cell carcinoma of the urinary bladder (Martineau et al., 1985). Although urinary bladder cancer in humans

in this region had been linked to polycyclic aromatic hydrocarbons, the cause of this tumour could not be identified.

Polychlorinated biphenyls recorded in stranded beluga from the St. Lawrence River ranged from 5.7 to 576.0 $\mu\text{g/g}$ in blubber, 0.227 to 71.58 $\mu\text{g/g}$ in liver, and 0.399 to 31.65 $\mu\text{g/g}$ wet weight in kidney. Total DDT ranged from 0.233 to 53.8 $\mu\text{g/g}$ in blubber, 0.03 to 7.985 $\mu\text{g/g}$ in liver, and 0.177 to 3.461 $\mu\text{g/g}$ wet weight in kidney (Martineau et al., 1987). Concentrations of 1.72 $\mu\text{g/g}$ of polychlorinated biphenyls and 2.04 $\mu\text{g/g}$ of total DDT were found in milk of stranded beluga from the same area (Massé et al., 1986). Addison and Brodie (1973) reported DDT levels in blubber, liver, and muscle of beluga from the Mackenzie Delta as 2 to 4 ppm, 0.02 ppm, and 0.01 ppm wet weight, respectively.

Belugas may minimize mortality by summering in Arctic and sub-Arctic estuaries where potentially competitive species, such as the harbour porpoise (*Phocoena phocoena*), are not thermally adapted to reproduce and by wintering in icebound areas not easily penetrated by killer whales (Sergeant and Brodie, 1969; Smith and Taylor, 1977). Possible cetacean competitors of beluga in the St. Lawrence River estuary are minke (*Balaenoptera acutorostrata*) and fin (*B. physalus*) whales, white-sided dolphin (*Lagenorhynchus acutus*), and harbour porpoise, all of which feed on capelin (*Mallotus villosus*), herring (*Clupea*), and smelt (*Osmerus mordax*; Pippard, 1985).

Mature males tend to herd together, as do females, calves, and immatures. A sex ratio of 1:1 is thought to be realistic (Doan and Douglas, 1953; Finley et al., 1982; Seaman and Burns, 1981; Sergeant, 1973), although commercial catches and subsistence hunter-kills may reflect sampling bias and the spatial separation of the sexes (Fraker, 1980; Richard and Orr, 1986).

Ovulation rate is 0.5 based on the number of ovarian scars corrected for luteinized follicles and second ovulations (Sergeant, 1973). Pregnancy rate, expressed as a proportion of all females, is 0.256 (Sergeant, 1973), as a proportion of mature females is 0.139 (Doan and Douglas, 1953; Douglas, 1951), and as a proportion of total population is 0.143 (Sergeant, 1973). Birth rates based on the numbers of calves counted compared to the total number of beluga seen range from 0.08 to 0.15 (Sergeant, 1962, 1973, 1986). Gross-annual reproduction rates in various estuaries range from 0.056 to 0.121 (Braham, 1984); the International Whaling Commission (1980b) accepted about 0.10. Sergeant (1973) suggested a mortality rate of 0.095 between 2 and 6 months of age. Richard and Orr (1986) critically reviewed previous estimates to calculate net annual reproductive rates and concluded a maximum would be 7.7%.

The discreteness of most populations is not well understood. Some populations, such as that in Cumberland Sound, may not experience any immigration or emigration, while other breeding populations may intersperse in common wintering areas (International Whaling Commission, 1980b).

Current sizes of populations and exploitation rates (annual catch adjusted to include percent loss) are: 5,000+, 3 to 4%, Alaska (International Whaling Commission, 1981); 400 to 600, 22+%, Cumberland Sound (Richard and Orr, 1986); 750 to 2,000, ca. 20%, eastern Hudson Bay (Smith and Hammill, 1986); 12,000 to 14,000, 9 to 10%, western Greenland (International Whaling Commission, 1980b); ca. 500, 0%, St. Lawrence River (Sergeant, 1986).

Beluga are adapted to cold and ice (Gaskin, 1982; Sergeant and Brodie, 1975), but are limited seasonally by heavy pack ice and landfast ice where breathing holes cannot be maintained. Thus, the distribution of most populations changes with the distribution of solid ice and dense pack ice.

In winter, belugas are restricted to polynyas or loose pack ice (Gurevich, 1980; Jonkel, 1969; Stirling and Calvert, 1983; Stirling et al., 1981). Beluga may break open breathing holes in ice up to 20 cm thick (Finley and Renaud, 1980) with their melon (Freeman, 1968; Kleinenberg et al., 1969; Mitchell and Reeves, 1981) or dorsal ridge (Fraker, 1979; Sergeant, 1973; Stirling, 1980). The characteristic breathing holes and body impressions left by beluga resting under thin ice are described as ice cupolas (Finley and Renaud, 1980), conical elevations (Mitchell and Reeves, 1981), and domes (McVay, 1973). In spring and autumn, beluga may be observed following ice edges closely and penetrating areas with ice cracks (Stirling, 1980).

In summer, when coastal areas are largely ice-free, beluga are seen frequently in these shallow waters (Berzin, 1981; Brodie, 1971; Doan and Douglas, 1953; Ivashin and Mineev, 1981; Kapel, 1977; Kapel and Petersen, 1982; Ognetov and Potelov, 1984; Seaman

and Burns, 1981; Sergeant and Hoek, 1974). At this time, beluga of all populations move locally into estuaries of large rivers such as the Churchill, Mackenzie, and Amur. The large summer aggregations are thought to be related primarily to calving and neonate survival, feeding, or molting (Berzin et al., 1986; Finley et al., 1982; Kleinenberg et al., 1969; Mitchell, 1975; Sergeant, 1962, 1973; Stirling et al., 1981).

Daily movements in the open-water season are influenced by tides in some locations: beluga ascend rivers or estuaries on flood tides and descend on ebb tides (Pippard, 1985). Beluga in the Mackenzie estuary do not show such movements. Beluga may make long-range movements up various river systems such as the Amur and Rhine (Kleinenberg et al., 1969).

Beluga eat a wide variety of benthic and pelagic prey in shallow and coastal waters although diets vary with season, location, age, and body size (Freeman, 1968; Gaskin, 1982; Kleinenberg et al., 1969; Seaman et al., 1982; Sergeant, 1962). Important prey species include capelin, Arctic cod (*Boreogadus saida*), sand lance (*Ammodytes*), char (*Salvelinus*), herring, cisco and whitefish (*Coregonus*), smelt, saffron cod (*Eleginus navaga*), Greenland cod (*Gadus ogac*), burbot (*Lota lota*), salmon (*Onchorhynchus*), sculpins (*Myoxocephalus*), decapod crustaceans, including spider crab (*Hyas arctatus*), and many shrimp species, squid, and octopus (Bradstreet, 1982; Doan and Douglas, 1953; Douglas, 1951; Pippard, 1985; Seaman et al., 1982; Sergeant, 1962, 1973; Sergeant and Hoek, 1974; Vladikov, 1944; Watts and Draper, 1986). Small stones, sand, and mud may be ingested during benthic foraging.

In 1979, there were 19 beluga in captivity in North America, with an average captive longevity of 3.8 years (range, 1 to 17; Cornell et al., 1982). At that time three beluga had been born in captivity (captive and wild breedings not distinguished) and none was alive (Cornell et al., 1982). Since 1979, permits have been granted for the removal of an additional 24 beluga from Canadian waters for North American aquaria (R. Moshenko, in litt.). In 1982, at least three beluga were captive in Europe (Pilleri, 1982).

Plasma levels of alanine aminotransferase and creatine kinase are diagnostic for liver and muscle damage respectively, caused by parasites, disease, or trauma (Geraci and St. Aubin, 1979). In captivity, beluga may be carriers of human-associated yeasts that are potential opportunistic pathogens, including *Candida albicans* (Buck, 1980; Dunn et al., 1982). This infection can be treated with ketoconazole and levamisole hydrochloride (Dunn et al., 1982). Vibrios are apparently uncommon in wild beluga, but may infect beluga in captivity (Buck and Spotte, 1986).

Aboriginal hunting techniques have changed with the introduction of modern technology and with alteration of native lifestyles. The traditional kayak, harpoon, and float methods are still in limited use in the Thule district and in West Greenland (International Whaling Commission, 1980b; Kapel, 1977), but other subsistence hunters now use high-powered rifles, motorboats, and snowmobiles to pursue beluga (Hunt, 1979; Kemper, 1980). Driving, herding, and netting in shallow nearshore waters are common capture techniques in the summer (Hunt, 1979; Kemper, 1980; Seaman and Burns, 1981). The rifle-first method of shooting beluga before securing it with a float or drogue, now associated with most native hunts has led to a substantial increase in the wounded-but-lost and killed-but-lost rates (Finley et al., 1982; International Whaling Commission, 1980b; Kemper, 1980). Muktuk (the Vitamin C-rich skin plus a small amount of attached blubber) and meat are the principal items taken. Previously, commercial fisheries such as those operating in Cumberland Sound, Northwest Territories, and Churchill, Manitoba, during the early to mid-1900s, rendered the oil for industrial and edible products, salted the hides for export, and processed the meat for human consumption and for use on mink (*Mustela vison*) farms (Doan and Douglas, 1953; Kemper, 1980; Mitchell and Reeves, 1981). Traditional applications also included the use of beluga leather for dog harnesses, blubber for cooking and lamp (kudlik) oils, and stomachs for berry and meat containers (Doan and Douglas, 1953; Sergeant, 1962).

A brief sport-fishery existed in the early 1970s in Churchill, Manitoba, but was closed for economic and humane reasons. Mercury concentrations 5 ppm (wet weight) in beluga caused the closure of a net fishery at Whale Cove, Northwest Territories, between 1961 and 1970 (Sergeant, 1981).

The beluga is listed on Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora which allows regulated trade under permit. In Canada, beluga are

managed under the Fisheries Act of Canada and are taken solely by Inuit subsistence hunters. An annual quota of 40 beluga was imposed for the Cumberland Sound population in 1979. The St. Lawrence River population is the only North American population that is legally protected from all forms of direct exploitation (Reeves and Mitchell, 1984). In the United States, beluga fall under the Marine Mammal Protection Act of 1972 that prohibits hunting except for a subsistence hunt by Alaskan natives. This act also provides for permitting scientific research on beluga, captures for public display, and importation of beluga.

Some individual beluga may be identified on the basis of persistent natural markings or scars (Gaskin, 1982; Finley et al., 1982; Freeman, 1968; Sergeant, 1986). No permanent or long-term tagging or marking techniques have been successfully developed.

BEHAVIOR. Beluga have a large vocal repertoire and produce echolocatory and auditory scanning sounds almost constantly (Fish and Mowbray, 1962; Morgan, 1979). The two main sounds formed are pulsed click series associated with echolocation and pure tone and modulated whistles (Au et al., 1985; Fish and Mowbray, 1962; Gurevich and Evans, 1976; Sjare and Smith, 1986a, 1986b). The number of whistles emitted by beluga resting, swimming in a directive manner, interacting socially or indicating alarm did not vary. However there were fewer pulsed tones emitted by alarmed whales than by beluga in the other three behavioral groups. Clicks were most common during alarm as well but were also high during direct swimming (Sjare and Smith, 1986b).

Beluga respond to playback of conspecific vocalizations by changing their rate of vocalization, orientation, activity, or dive times (Morgan, 1970, 1979). Transmission of high-frequency vocalizations of killer whale have repelled free-ranging beluga travelling up the Kvichak River, Alaska, to feed on salmon smolt (Fish and Vania, 1971).

When travelling without ice cover, beluga surface in a smooth roll to respire, although neonates may lift the head clear of the water with a jump (Sergeant, 1986). Beluga following ice edges closely may immediately penetrate newly formed cracks and leads (Stirling, 1980). They dive deeply at ice edges and travel under the ice, surfacing at the next available lead (Fraker, 1979, 1980). Beluga may remain submerged for 15 to 20 minutes and may travel up to 2 to 3 km on one dive (Kleinenberg et al., 1969; Ridgway et al., 1984; Seaman and Burns, 1981). Maximum swimming speeds are 16 to 22 km/h (Kleinenberg et al., 1969; Vladykov, 1944).

Size of beluga pods is variable and ranges from small groups of 2 to 10 whales to aggregates of several hundred. Estimates of abundance are confounded by such factors as submerged whales, masking of dark colored neonates and juveniles in turbid waters, height of the survey flight, type of aircraft, and weather such as wind disturbance and sun glare (Brodie, 1971; Doan and Douglas, 1953; Douglas, 1951; Finley et al., 1982; Fraker, 1980; Ognetov and Potelov, 1982; Richard and Orr, 1986).

The maternal-neonate bond is strong; calves stay close to the mother (Fig. 1) and reportedly may ride the mother's back (Sergeant and Brodie, 1975). Females with calves swim slowly in non-erratic courses when hunted, possibly trying to prevent separation from their young (Douglas, 1951).

GENETICS. The diploid number of chromosomes of *Delphinapterus leucas* is 44, the same as other cetaceans. There are four pairs of telocentric chromosomes, the large chromosomes are submetacentric or subtelocentric, and metacentric chromosomes are small (Jarrell and Arnason, 1981).

REMARKS. Historically the beluga was known as the white porpoise, white-squidhound, and, due to its highly vocal nature, the sea canary (Fish and Mowbray, 1962; Sergeant and Fisher, 1957). Beluga are also referred to commonly as belukha or white whale.

There has been a longstanding practice of harvesting beluga. Archaeological evidence indicates beluga whaling occurred in the Mackenzie River estuary at least 500 years ago (McChee, 1974). Thule Eskimos in the eastern Arctic also hunted beluga; their settlements were first established in Cumberland Sound between 1370 and 1650 A.D. (Mitchell and Reeves, 1981). Historical records indicate there were dietary restrictions imposed on consumption of the "hiviting" (beluga) by the mid-thirteenth century for Greenlandic, Icelandic, and Norwegian peoples, likely to prevent sickness associated with trichinosis contamination of the meat (Arvy, 1979).

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