

D

Dall's Porpoise

Phocoenoides dalli

THOMAS A. JEFFERSON

I. Characteristics and Taxonomy

Typical of the porpoise family, Dall's porpoise has a stocky body, and it has a short, wide-based, triangular dorsal fin (Fig. 1). The dorsal fin is slightly falcate at the tip, but the entire fin may be canted forward in adult males (Jefferson, 1990). The tail stock is deepened, especially in adult males, and males also have a prominent post-anal hump of connective tissue. There is an extremely short, poorly defined beak. The flippers and flukes are small, and the fluke blades may also be canted forward in older individuals.

The color pattern is diagnostic. "Dall's" are largely dark gray to black with a large, ventrally continuous white patch that extends up about halfway on each flank. In addition, there is light gray to white frosting, or trim, on the upper part of the dorsal fin and on the trailing edges of the flukes. Some other light patches may exist, particularly around the base of the tail stock. Newborn animals are muted in color and do not have the fluke and dorsal fin frosting, which develops with age in older animals.

There are two major color morphs, one with a flank patch that extends forward to about the level of the dorsal fin (*dalli* type) and the other with a flank patch extending to about the level of the flippers (*truei* type). These forms were variously considered as separate species and subspecies in the past, but most recent work suggests that they are in fact color variants, with few or no other phenotypic



Figure 1 Dall's porpoise mother and calf killed in a Japanese salmon driftnet south of the Aleutian Islands in the mid-1980s. Such large-scale kills have now been much reduced, due to a United Nations ban on oceanic driftnet fishing.

differences. However, genetic analyses have confirmed that they do form separate populations (Escorza Trevino *et al.*, 2004), and Rice (1998) still considered them as separate subspecies. Other color types (all-black, all-white, and forms intermediate between *dalli* and *truei* types) have also been observed.

Dall's porpoises reach maximum known lengths and weights of about 239 cm and 200 kg. Males grow longer and heavier than females, and adult males have secondary sexual characteristics (as discussed earlier). There is a great deal of geographical variation; size, shape, and coloration differences have been documented among different areas of the species' range (Amano and Miyazaki, 1992).

The SKULL of Dall's porpoise is larger than that of most other phocoenids and may reach 340 mm in length. The rostrum is wide at the base and relatively short. There are prominent "maxillary shields" that make an angle of about 130° with the rostrum axis (Houck and Jefferson, 1999). Tooth counts are highly variable, but generally number 21–28 per tooth row. The TEETH are shaped like grains of rice (not strongly spatulate, as in *Phocoena*) and are extremely small, the smallest of any species of cetacean. They often do not rise above the level of the gums and are considered by many to be rudimentary. Dall's porpoises have an unusual skeleton, with extremely long, slender dorsal, and lateral processes on the vertebrae. Total vertebral counts generally number 92–98.

Recent studies of mtDNA and morphology suggest that the previous classification of Dall's porpoise and the spectacled porpoise (*Phocoena dioptrica*) in the same subfamily was erroneous (Rosel *et al.*, 1995; Fajardo-Mellor *et al.*, 2006). These two species do not appear to be closely related, and their similarities may be the result of CONVERGENT EVOLUTION.

Intergeneric hybrids between Dall's porpoises and harbor porpoises (*Phocoena phocoena*) have been examined and described (Baird *et al.*, 1998; Willis *et al.*, 2004). Free-ranging hybrids are regularly observed around Vancouver Island, British Columbia, suggesting that such hybridization events may not be all that rare and supporting the hypothesis of a close relationship between these two species.

The species was named after William H. Dall, who collected the type specimen in Alaska in 1873. Other English common names include True's porpoise, white-flank porpoise, and spray porpoise.

II. Distribution and Abundance

Dall's porpoise is found only in the North Pacific Ocean and adjacent seas (Bering Sea, Okhotsk Sea, and Sea of Japan), from about 32–35°N (southern California and southern Japan) in the south to about 63°N (central Bering Sea) in the north. When water temperatures are unseasonably cold, they may extend down to around Scammon's Lagoon, Baja California, Mexico (Morejohn, 1979). On rare occasions, they may also go through the Bering Strait into the Chukchi Sea. Up to 10 different stocks are recognized, based on studies of morphology, genetics, and ecological parameters (see review in Houck and Jefferson, 1999). Sex-biased dispersal and migration patterns have been elucidated from molecular genetic analyses (Escorza Trevino *et al.*, 2004).

Dall's porpoise is a cold-water species, avoiding tropical/subtropical waters. This is an oceanic species that is found in deep offshore waters, but also in deeper nearshore and inshore waters along the west coast of North America. There are seasonal inshore–offshore and north–south movements in both the eastern and western North Pacific (Forney and Barlow, 1998; Houck and Jefferson, 1999), but in most areas these are poorly defined.

Current global abundance is not well established (due to lack of survey data for some areas and probable biases in available estimates),

but it was thought to number over 1.2 million individuals in the 1980s (Buckland *et al.*, 1993). There are thought to be around 104,000 along the Pacific coast of Japan, 554,000 in the Okhotsk Sea, 83,000 in Alaska, and 100,000 along the US west coast.

III. Ecology

Prey of Dall's porpoise include a wide variety of small fishes and cephalopods (several dozen species have been identified—see Houck and Jefferson, 1999). The most common prey items include schooling fishes (such as herrings, anchovies, mackerels, and sauries), mesopelagic fishes (such as myctophids and deep-sea smelts), and squids. KRILL, decapods, and shrimps have been found in some stomachs, but these are not considered to be common prey items. Amano and Miyazaki (1992) found that the skulls of Dall's porpoises grew to larger sizes in areas with higher productivity, suggesting that food availability may affect growth. Dall's porpoises in some areas appear to feed preferentially at night on vertically migrating fish and squid associated with the deep scattering layer (DSL).

Dall's are thought to be deep divers and capable of feeding at great depths; however, very few dives have been measured directly. The first dive depth data were obtained from a single individual in the transboundary area between British Columbia and Washington State. Seventeen dives were recorded, the deepest to 94 m (Hanson and Baird, 1998). However, Dall's porpoises are probably capable of much deeper dives.

Several internal parasites have been identified from various areas of the body of this species, and these parasites can cause disease and pathology which can even lead to death (see review in Houck and Jefferson, 1999). The trematode fluke, *Nasitrema*, appears to be particularly serious and has been implicated in the stranding and subsequent deaths of several specimens. Whale lice have also been found on the external surface of the body.

Large sharks, and especially killer whales, are predators. Several attacks by killer whales on Dall's porpoises have been observed in recent years, and it appears that killer whales may be major predators on this species, at least in Alaskan waters.

IV. Behavior and Physiology

Small groups are most common, although large aggregations of several hundred to about one thousand have been reported on occasion (Houck and Jefferson, 1999). Groups of over 20–30 are rather uncommon. Very little is known of the group structure of this species, except that group composition appears to be quite fluid. Recently, evidence of mate guarding behavior, whereby a male maintains longer associations with females (presumably to exclude other males from mating with them) has been documented (Willis and Dill, 2007). This is probably related to a polygynous mating system.

Dall's porpoises are very fast swimming and active animals. They are often seen moving very quickly, slicing along the surface, creating a sloppy, V-shaped splash. These are called rooster tail splashes (Fig. 2). However, aerial behavior, such as breaching and leaping out of the water, is virtually nonexistent. Dall's porpoises are willing and capable bow riders and will converge on the bow of a fast-moving boat from all around. They have even been seen to “snout ride” on bow waves pushed forward by the heads of large whales (like blue and humpback whales). When moving more slowly, they roll at the surface in a subdued behavior more typical of other species of porpoises (Fig. 3).

The physiology of this species has not been extensively studied, but some work mostly related to diving physiology has been done.



Figure 2 Most often when Dall's porpoises are seen at sea, they are swimming very fast and “roostertailing,” as this porpoise is doing while riding the bow wave of a research vessel in Southeast Alaska.



Figure 3 A Dall's porpoise slow rolls in Monterey Bay, California. This is an adult male, based on the forward-canted dorsal fin (the animal is moving left to right).

Dall's have a thin blubber layer, large skeletal muscle mass, thick tracheal cartilage rings, deeply folded vestibular sacs, fatty pads lining the lungs, relatively small brain, and large adrenal and thyroid glands. They also have relatively high blood oxygen content. In addition, they appear to have a relatively high metabolic rate and interestingly, captive animals were never seen to sleep (see review in Houck and Jefferson, 1999).

V. Life History

Growth and reproductive parameters have been estimated for several populations in the central and western North Pacific, based on large samples of specimens killed in various fisheries. Length at birth is about 100 cm. Estimates of length and age at sexual maturity range from about 172 to 187 cm and 4–7 years for females, and from 175 to 196 cm and 3.5–8 years for males (Ferrero and Walker, 1999; see Houck and Jefferson, 1999 for a review). Gestation lasts about 10–12 months. The length of lactation is not well known (but is most likely <1 year). The calving season is in the summer for all populations that have been studied to date, although sometimes calves may be born outside of the main calving season (Jefferson, 1989). There appears to be significant geographic variation in growth and life history parameters.

VI. Interactions with Humans

Small numbers of Dall's porpoises have been kept in captivity in oceanaria and research institutes in the United States and Japan, but most individuals have not survived very long. Due to their poor record of survival in captivity and their apparent intractability, they are not currently a species that is sought after for captive display.

A number of human-caused threats to Dall's porpoise populations have been identified, including environmental POLLUTION and habitat alteration. However, the most serious threats are clearly the various fishery kills of this species (review in Houck and Jefferson, 1999). These include directed kills in Japanese waters and INCIDENTAL CATCHES in various fisheries (most prominently several drift gillnet fisheries) throughout the range. The most heavily impacted populations were those in the central and western North Pacific. Between 1981 and 1990, over 45,000 Dall's porpoises were killed in Japanese driftnet fisheries, and between 1981 and 1994, more than 247,000 were directly taken in a Japanese harpoon fishery (Houck and Jefferson, 1999). Fortunately, these kills have been greatly reduced in recent years.

See Also the Following Articles

Bow-Riding ■ Geographic Variation ■ North Pacific Marine Mammals ■ Porpoises ■ Overview

References

- Amano, M., and Miyazaki, N. (1992). Geographic variation and sexual dimorphism in the skull of Dall's porpoise, *Phocoenoides dalli*. *Mar. Mamm. Sci.* **8**, 240–261.
- Baird, R. W., Willis, P. M., Guenther, T. J., Wilson, P. J., and White, B. N. (1998). An intergeneric hybrid in the family Phocoenidae. *Can. J. Zool.* **76**, 198–204.
- Buckland, S. T., Cattanach, K. L., and Hobbs, R. C. (1993). Abundance estimates of Pacific white-sided dolphin, northern right whale dolphin, Dall's porpoise and northern fur seal in the North Pacific, 1987–1990. *Int. N. Pac. Fish. Comm. Bull.* **53**, 387–407.
- Escorza Trevino, S., Pastene, L. A., and Dizon, A. E. (2004). Molecular analyses of the *truei* and *dalli* morphotypes of Dall's porpoise (*Phocoenoides dalli*). *J. Mammal.* **85**, 347–355.
- Fajardo-Mellor, L., Berta, A., Brownell, R. L., Jr., Boy, C. C., and Goodall, R. N. P. (2006). The phylogenetic relationships and biogeography of true porpoises (Mammalia: Phocoenidae) based on morphological data. *Mar. Mamm. Sci.* **22**, 910–932.
- Ferrero, R. C., and Walker, W. A. (1999). Age, growth, and reproductive patterns of Dall's porpoise (*Phocoenoides dalli*) in the central North Pacific Ocean. *Mar. Mamm. Sci.* **15**, 273–313.
- Forney, K. A., and Barlow, J. (1998). Seasonal patterns in the abundance and distribution of California cetaceans, 1991–1992. *Mar. Mamm. Sci.* **14**, 460–489.
- Hanson, M. B., and Baird, R. W. (1998). Dall's porpoise reactions to tagging attempts using a remotely-deployed suction-cup tag. *MTS J.* **32**, 18–23.
- Houck, W. J., and Jefferson, T. A. (1999). Dall's porpoise *Phocoenoides dalli* (True, 1885). In "Handbook of Marine Mammals" (S. H. Ridgway, and R. Harrison, eds), Vol. 6, pp. 443–472. Academic Press, San Diego.
- Jefferson, T. A. (1988). *Phocoenoides dalli*. *Mamm. Spec.* **319**, 7 pp.
- Jefferson, T. A. (1989). Calving seasonality of Dall's porpoise in the eastern North Pacific. *Mar. Mamm. Sci.* **5**, 196–200.
- Jefferson, T. A. (1990). Sexual dimorphism and development of external features in Dall's porpoise *Phocoenoides dalli*. *Fish. Bull.* **88**, 119–132.
- Morejohn, G. V. (1979). The natural history of Dall's porpoise in the North Pacific Ocean. In "Behavior of Marine Animals, Volume 3: Cetaceans" (H. E. Wimm, and B. L. Olla, eds), pp. 45–83. Plenum Press, New York.
- Rice, D. W. (1998). Marine mammals of the world: Systematics and distribution. *Soc. Mar. Mamm. Spec. Pub.* **4**, 231 pp.
- Rosel, P. E., Haygood, M. G., and Perrin, W. F. (1995). Phylogenetic relationships among the true porpoises (Cetacea: Phocoenidae). *Mol. Phy. Evol.* **4**, 463–474.
- Willis, P. M., and Dill, L. M. (2007). Mate guarding in male Dall's porpoises (*Phocoenoides dalli*). *Ethology* **113**, 587–597.
- Willis, P. M., Crespi, B. J., Dill, L. M., Baird, R. W., and Hanson, M. B. (2004). Natural hybridization between Dall's porpoises (*Phocoenoides dalli*) and harbour porpoises (*Phocoena phocoena*). *Can. J. Zool.* **82**, 828–834.

Delphinids, Overview

RICK LEDUC

I. Introduction

For most species of delphinids, basic aspects of their evolution, physiology, ecology, behavior, and population structure are virtually unknown. Even abundance estimates for many species are very imprecise. For the biologist, dolphin research presents challenges and opportunities in trying to understand individual species and how they fit into marine ecosystems.

II. Taxonomic Overview

The family Delphinidae is one of three extant families (with Phocoenidae and Monodontidae) in the cetacean superfamily Delphinoidea (which also includes two extinct families, Kentriodontidae and Albireonidae). Delphinids likely arose in the mid- to late Miocene (11–12 mya) from kentriodontid-like ancestors and quickly radiated into many different morphological and ecological types. This early radiation produced precursors of many modern forms; many of the early delphinid fossils can be assigned to extant genera, particularly *Tursiops*. Today the Delphinidae is the most speciose family of marine mammals, with 33–35 recognized extant species arranged into 17–19 genera. At present, there is much uncertainty about the evolutionary relationships among the species of delphinids. Of the many recent classifications that have been proposed, two are depicted here. One represents a more traditional view of dolphin taxonomy (Table Ia), and the other is a revised classification based on various recent molecular and morphological phylogenetic analyses (Table Ib). Some of these analyses have led to changes in the number of species in certain genera (*Orcaella* and *Sotalia*) (Beasley *et al.*, 2005; Caballero *et al.*, 2007). In fact, some of the best known genera, such as *Orcinus*, may undergo revision in the number of recognized species (Pitman and Ensor, 2003). There is still uncertainty surrounding the deeper relationships, such as those among the different subfamilies. Also, there will no doubt be additional revisions proposed in the future at the genus level, especially involving the apparently paraphyletic genera *Stenella* and *Tursiops*. In part, this changing nature of delphinid taxonomy is due to the new molecular and analytical tools available to researchers, but it also reflects the uncertainties about evolutionary relationships that have long been recognized by morphological systematists but have yet to be addressed.