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17

Dall's Porpoise *Phocoenoides dalli* (True, 1885)

Warren J. Houck and Thomas A. Jefferson

Genus and Species

Taxonomy

Dall's porpoise was originally described as *Phocoena dalli* by F. W. True (1885) based on a specimen collected in August 1873 by W. H. Dall west of Adak Island in the Aleutian Islands, Alaska. In 1911, R. C. Andrews described a new species of porpoise, *Phocoenoides truei*, proposed the new genus *Phocoenoides*, and placed the previously described species *Phocoena dalli* in this genus. The validity of the new genus is well established; however, the relationship between the two named forms in the genus, i.e. Dall's porpoise, *P. dalli*, and True's porpoise, *P. truei*, has remained controversial. They have been called species (Andrews, 1911), subspecies (Kuroda, 1954), and colour morphs of the same species, *P. dalli* (Houck, 1976). This problem has been discussed by Houck (1976), Kasuya (1978, 1982), Jefferson (1988), and others. Investigators since Andrews generally have agreed that the differences are below the species level, and most recent work supports the idea of colour morphs. In the remainder of this chapter, these named forms will be referred to as *dalli*-type and *truei*-type.

Barnes (1985) considered *Phocoenoides* to be more closely related to *Australophocaena* than to the other two genera in this family (*Phocoena* and

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Neophocaena). He proposed the new subfamily Phocoenoidinae to include these two extant genera, plus fossil forms. Recent molecular genetic evidence, however, does not support this affinity (Rosel *et al*., 1995).

Common names

Following the nomenclature of Hershkovitz (1966), other common names include Dall porpoise, white-flank porpoise, spray porpoise, ishi-iruka (Japanese), rikuzen-iruka (Japanese), and belokrylaya morskaya svinya (Russian).

Distribution

Range

The distribution of Dall's porpoise, as shown in Fig. 1, is confined to the North Pacific Ocean and adjacent seas. In the eastern North Pacific, a beach-cast specimen (California Academy of Sciences #16237) is known from as far south as Scammon's Lagoon (approximately 28°N). Morejohn (1979) reported an additional specimen from the same locality. However, Dall's porpoises are seldom seen south of 32°N in the summer (Ridgway, 1966; Morejohn, 1979). The distribution extends northwards along the continental shelf and slope, through the

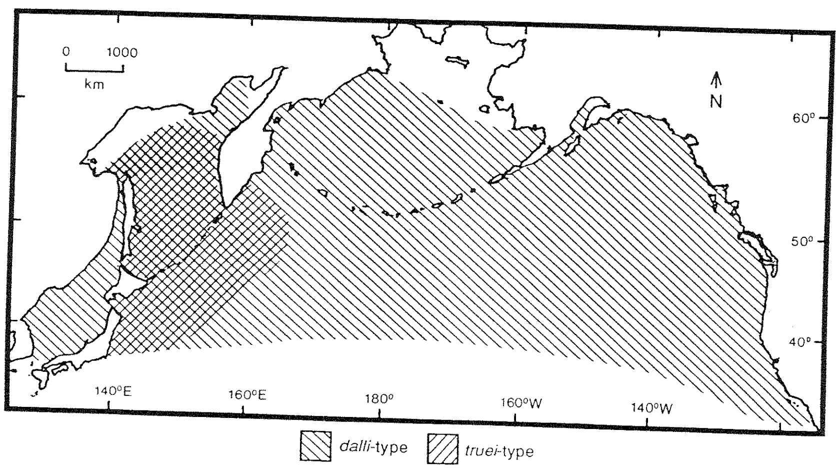


FIG. 1 Geographical distribution of *Phocoenoides*. This genus is confined to the colder waters of the North Pacific Ocean and adjacent seas.

Gulf of Alaska, throughout the Bering Sea (except for the shallow eastern flats) and, according to Sleptsov (1961), penetrates the Bering Strait into the Chukchi Sea on occasion. In the western Pacific, Kasuya (1978) reported the range to extend as far south as 35°N (central Honshu, Japan) in the winter. *Phocoenoides* also occurs in the Okhotsk Sea and Sea of Japan. In the central North Pacific, the *dalli*-type (Fig. 2) is known at least as far south as 39°N and over 1100 km from the nearest land (Jones *et al*., 1987).

The distribution of the *truei*-type (Fig. 2) is much more restricted. It is generally found in the western Pacific, along the east coast of Japan and the Kurile Islands, from about 35°N in the south to 54°N in the north (Kasuya, 1978), and it is sympatric with the *dalli*-type in this area and in the Okhotsk Sea (Miyashita, 1991). *Truei*-types have been captured as far east as the western Aleutians (ca. 180°), and recently a single neonate having the *truei*-type pattern has been reported from the central California coast (Szczepaniak *et al*., 1992). This record should not be taken to imply that the eastern Pacific is a normal part of the range of the *truei*-type. *Truei*-types are not known from the Sea of Japan, where the *dalli*-type is common. Within the area of overlap, both mixed

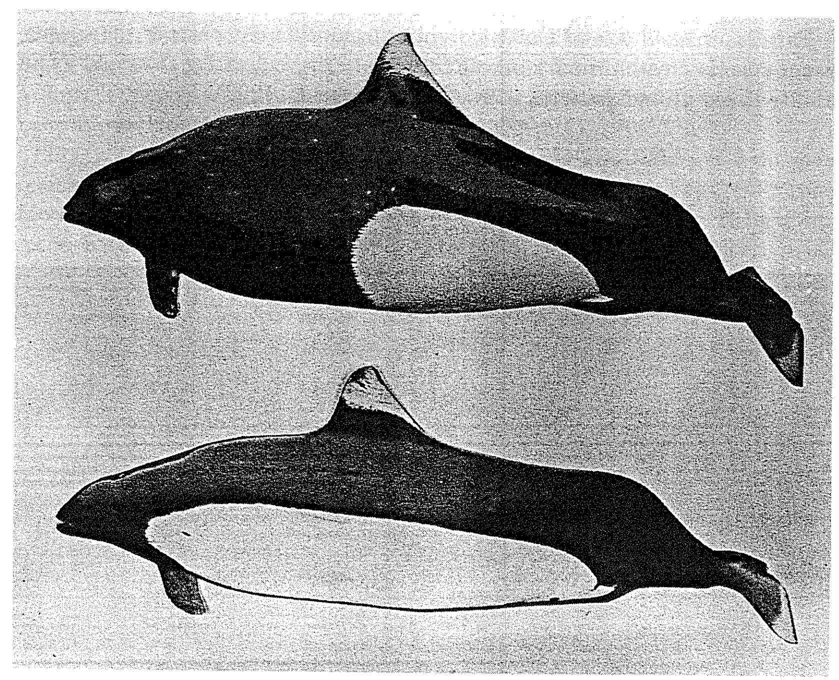


FIG. 2 Large adult male Dall's porpoises, showing the species' body shape, coloration, and two major colour types: *dalli*-type (top) and *truei*-type (bottom).

and unmixed schools are found. Miyazaki *et al.* (1984) reported on mixed schooling behaviour and the possibility of interbreeding between these types off Japan.

Habitat

Phocoenoides inhabits both the neritic and oceanic zones, although the major populations are oceanic. Porpoises of this genus rarely come close to shore, except in areas of relatively deep water. Sightings are common along the central and northern California coastlines (Sullivan and Houck, 1979; Jefferson, 1991), and they are common in the deep inshore waters of Washington, British Columbia, and Alaska (Leatherwood *et al.*, 1982). Dohl *et al.* (1983) reported only 28% of their sightings in water less than 180 m deep, and Pike and MacAskie (1969) had frequent sightings as far as 2400 km off the coast of British Columbia.

Dall's porpoise is a cold water species that inhabits water with temperatures of 3–24 °C (Kasuya, 1978; Miyashita and Kasuya, 1988), but generally avoids water warmer than about 17–18 °C (Norris and Prescott, 1961; Kasuya and Jones, 1984; Jones *et al.*, 1987). According to Leatherwood *et al.* (1982) and Ohsumi (1975), it is not found in the southern extremes of its range during the summer or warm water months.

Patterns in skull size of Dall's porpoises from different parts of the species' range correlate with primary productivity patterns, indicating that food availability affects growth patterns (Amano and Miyazaki, 1992).

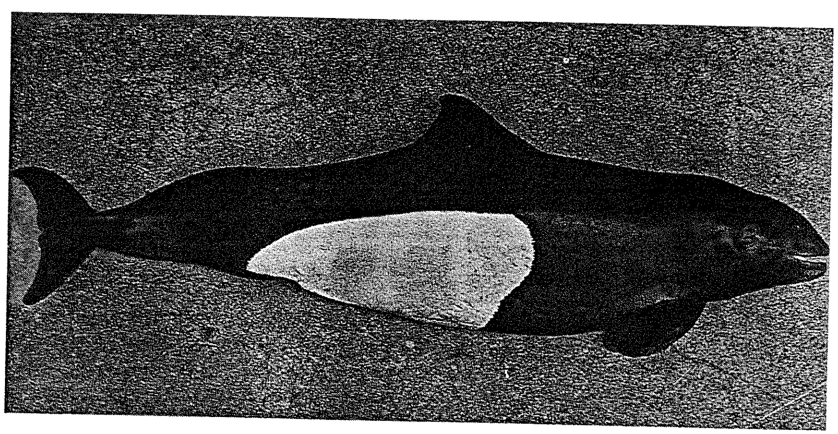


FIG. 3 A newborn Dall's porpoise of the *dalli*-type (total length 101 cm). The absence of white "trim" or "frosting" on the dorsal fin and flukes is an age characteristic.

External Characteristics

Colour pattern

The colour pattern of adults is highly contrasting black and white (Fig. 2). The primary body colour is black; there is a large white patch on each flank, extending ventrally across the abdomen onto the other flank. In adults, the trailing edge of the flukes and the upper two-thirds or so of the dorsal fin are usually light grey to white (this is termed "trim" or "frosting"), and the extent of this lightening is highly variable. The lateroventral part of the tail stock often has a white or light grey pattern on it. The remainder of the head and body is black.

There are two major colour patterns, with many minor variations (Figs 2 and 3). The primary difference is in the extent of the lateral white blaze. In the *dalli*-type the blaze extends anteriorly at least to the level of the dorsal fin, but does not reach to the flippers. In the *truei*-type the lateral blaze extends to or beyond the flippers. In addition to these two commonly occurring types, completely black (Nishiwaki, 1966), white (Joyce *et al.*, 1982), and grey (Morejohn *et al.*, 1973; Hall, 1979) types have been reported. Also, some porpoises with brown rather than black backgrounds and some with the lateral blaze marked with black speckling are known. Kasuya (1978) listed 14 different minor pattern groups. Types apparently intermediate between *dalli*- and *truei*-types also have been found (Houck, 1976).

The colour pattern changes with age. Newborns are dark and light grey instead of black and white, with no trim (Fig. 3). As the animals age, coloration intensifies to black and white, and the trim develops and lightens (Morejohn, 1979; Kasuya, 1982; Jefferson, 1990). Morejohn *et al.* (1973) described sexual dimorphism in the colour patterns of the urogenital area; however, there is great individual variation that was not accounted for by these researchers (see Jefferson, 1990).

Size and shape

Dall's porpoises are born at a length of about 100 cm (Fig. 3), and the growth rate for both sexes is similar during the first two years, after which males grow somewhat faster (Kasuya, 1978; Newby, 1982). For most populations, the maximum size is about 210 cm for females and 220 cm for males, but males from the southern Okhotsk Sea grow to as large as 239 cm (R. L. Brownell Jr, personal communication). Mizue *et al.* (1966) gave a maximum weight of approximately 170 kg, but some Dall's may reach nearly 200 kg.

The body shape of Dall's porpoise is relatively stocky (Fig. 2). The head has no prominent beak, but is typically porpoise-like in that it forms a rapidly tapering cone. In adults, the body and caudal peduncle are deeper than in most other small cetaceans. The flippers are terminally rounded, and small in adults. The dorsal fin is triangular to slightly falcate and wide-based, often with a recurved tip. Previously unpublished external measurements for several individuals are presented in Table 1.

The head and flippers of newborn calves are relatively larger than in adults (Amano and Miyazaki, 1993; see Fig. 3). Sexual dimorphism in this species is moderate. Males grow longer and heavier than females (Kasuya, 1978; Newby, 1982). As is true for cetaceans in general, the distance between the anal and genital openings is much greater in males than in females. In adult males, the caudal peduncle is deeper than in females, and discernible sexual differences in dorsal fin shape, fluke shape, and post-anal hump depth also have been reported (Jefferson, 1990; Amano and Miyazaki, 1993).

Internal Anatomy

Skull

The skull of *Phocoenoides* (Fig. 4) is distinctive in several ways. It is large, relative to that of other phocoenids; an adult male may have a condylobasal length of 34 cm. The cranium may be as much as 1.7 times wider than its length. The rostrum is broad and short; its length usually is less than 1.5 times its basal breadth and only slightly more than 0.4 times the condylobasal length (Table 2). In profile, the skull of this species differs from those of both *Neophocaena* (finless porpoise) and *Phocoena* (harbour and Burmeister's porpoises) in that the posterior part of the maxillary bends dorsally abruptly to form the anterior face of the cranium. These "maxillary shields" make an angle of approximately 130° with the axis of the rostrum. In *Neophocaena* and *Phocoena* this angle is much flatter. In dorsal view the anterior surface of the cranium is greatly flattened. The suture between the nasal bones is only slightly more anterior than the lateral margins of the "maxillary shields". In older animals, the transverse ridge formed by the top of the frontals may slightly overhang the posterior edge of the maxillaries. In *Neophocaena* and *Phocoena* the anterior surface of the cranium is rounded.

The teeth of Dall's porpoises are smaller than those of *Phocoena* (some are only about 1 mm in diameter), and are not as clearly spatulate (although some of the teeth have crowns broader than the roots). There is a slight constriction between the crown and the root. These small teeth erupt only a short distance through the gums, which are rough and may help the teeth in grasping such slippery prey as squid (Morejohn, 1979). Miller (1929) described the gums of this species in detail. The tooth counts are highly variable, although most individuals have 21–28 teeth per tooth row (Table 2). In most cases, a greater number of teeth is found in the lower jaw. The teeth in the premaxillary region are rudimentary, and thus quite variable in number. Probably this variation is also partially a

TABLE 1 Unpublished external measurements from Dall's porpoises taken in Japanese waters.[a] All measurements are in cm. The numbers in parentheses are percentages of the total body length

	HSU #2694 ♂, *dalli*-type		HSU #2695 ♂, *truei*-type		HSU #2696 ♀, *dalli*-type		HSU #2697 ♀, *truei*-type		HSU #2698 ♂, *dalli*-type		HSU #2699 ♀, *truei*-type	
Total length (straight line)	185	(100)	178	(100)	187	(100)	173	(100)	180	(100)	187	(100)
Tip of upper jaw to centre of eye	18	(10)	18.5	(10)	19	(10)	18	(10)	19	(11)	18.5	(10)
Length of gape	9	(05)	9	(05)	9.5	(05)	9.5	(05)	10	(06)	10	(05)
Tip of upper jaw to anterior insertion of flipper	28	(15)	28.5	(16)	28.5	(15)	27.5	(16)	28	(16)	27	(14)
Tip of upper jaw to tip of dorsal fin	86	(46)	81	(46)	87	(47)	78	(45)	83	(46)	82	(44)
Flipper length (anterior insertion to tip)	21.5	(12)	21	(12)	22	(12)	19.5	(11)	22	(12)	23	(12)
Height of dorsal fin	15	(08)	18.5	(10)	16	(09)	13.5	(08)	15.5	(09)	18	(10)
Width of flukes	45.5	(25)	51	(29)	46	(25)	41	(24)	46	(26)	54	(29)

[a] HSU indicates the collection of Humboldt State University.

TABLE 2 Unpublished skull measurements from Dall's porpoises taken in Japanese waters.[a] All measurements are in cm. The numbers in parentheses are percentages of the total skull length

	HSU #2694 ♂, *dalli*-type		HSU #2695 ♂, *truei*-type		HSU #2696 ♀, *dalli*-type		HSU #2697 ♀, *truei*-type		HSU #2698 ♂, *dalli*-type		HSU #2699 ♀, *truei*-type	
Total length (condylobasal)	32.9	(100)	32.6	(100)	31.3	(100)	33.1	(100)	34.2	(100)	32.0	(100)
Length of rostrum	13.2	(40)	12.8	(39)	12.4	(40)	14.6	(44)	14.0	(41)	13.1	(41)
Tip of rostrum to anterior nares	16.7	(51)	17.0	(52)	16.1	(51)	18.3	(55)	18.9	(55)	17.0	(53)
Width of rostrum at base	9.6	(29)	9.5	(29)	9.2	(29)	9.2	(28)	10.4	(30)	9.6	(30)
Width of rostrum at midpoint	5.6	(17)	5.1	(16)	6.0	(19)	5.3	(16)	6.4	(19)	5.8	(18)
Max. width of cranium (parietals)	17.3	(53)	18.8	(58)	16.2	(52)	17.0	(51)	17.5	(51)	17.5	(55)
Total length of mandible right side	25.1	(76)	25.0	(77)	24.1	(77)	25.8	(78)	26.8	(78)	25.3	(79)
Length of mandibular symphysis	4.2	(13)	3.9	(12)	3.4	(11)	4.2	(13)	3.6	(11)	3.6	(11)
Number of teeth right side:												
upper	31		26		22		24		24		24	
lower	32		24		25		25		31		26	

[a] HSU indicates the collection of Humboldt State University.

reflection of the fact that the premaxillary teeth are tiny and may be lost easily during skeletal preparation.

P. dioptrica (spectacled porpoise) has a higher braincase, a shorter and wider rostrum, and lower tooth counts (Hamilton, 1941; Brownell 1975; Barnes, 1985). It also has a shorter skull, with a maximum condylobasal length of 31.5 cm (Brownell, 1975).

Postcranial skeleton

Dall's porpoises have greatly elongated and slender dorsal and lateral processes on their vertebrae, and compressed centra (Miller, 1930). The total number of vertebrae in this genus is variable, ranging from 86 to 98, with a mean of 91.8–93.7 for different populations, and a mode of 96 (Walker and Sinclair, 1990; W. J. Houck, unpublished data). Although much of this variability is real, it must be noted that some low counts can be attributed to losses in skeletal preparation. The vertebral formula is C_7, $T_{15–18}$, $L_{24–27}$, $Ca_{44–49}$ = 92–98 (Tomilin, 1957; Nishiwaki, 1963, 1972). The cervical vertebrae are fused into a unit; the sutures between the first six centra usually are indistinct; the separation between the centra of C6 and C7 is clear. The neural spine of C1, the atlas, is bifurcate. *Australophocaena* has fewer vertebrae (66–70) and shorter vertebral processes (Brownell, 1975; Barnes, 1985).

The usual number of ribs is 18 pairs, but 17 is not unusual. The ribs are also long and slender, compared with other species (Miller, 1930). The first 12 pairs are two-headed, while the remaining five or six pairs have single heads. The last rib is a "floating rib" and can be easily missed in preparation of the skeleton. A pair of cervical ribs, or a single small one (approximately 2 cm long) is not uncommon.

Organs, tissues and physiology

Relative to other small cetaceans, Dall's porpoise has a large skeletal muscle mass, relatively small brain, thick tracheal cartilage rings, large deeply folded vestibular sacs, and large adrenals and thyroid (Ridgway, 1966; Ridgway *et al.*, 1966; Pilleri and Gihr, 1970; Mead, 1975; Morejohn, 1979; Curry, 1992). Fatty pads lining the lungs are unique to this species and serve no known function (Ridgway, 1966).

Very little has been published on organ weights of *Phocoenoides*, although Miyazaki *et al.* (1986) presented a complete set of organ and body part weights for a stranded animal from Japan. The most significant studies have been the heart weight research of Ridgway and Johnston (1966). They found a mean heart weight of 1.31% of body weight in *Phocoenoides*, 0.85% in *Lagenorhynchus obliquidens* (Pacific white-sided dolphin), and 0.54% in *Tursiops truncatus* (bottlenose dolphin). This sequence reflects the postulated relative metabolic rates and activity levels of these three species, and more recent work supports this as well

(Ridgway and Kohin, 1995). McCormick (1969) never observed captive Dall's porpoises to engage in any activity resembling sleep, and although oxygen consumption rates have not been studied, they probably have one of the highest metabolic rates of all small cetaceans (see Ridgway, 1966; Ridgway and Johnston, 1966). Of these three species, *P. dalli* was found to have also the highest mean blood volume and packed-cell volume (haematocrit) (Ridgway and Johnston, 1966). For blood oxygen content, which is probably a better indicator of physiological capabilities, these same investigators found that *P. dalli* has a value nearly three times that of *Tursiops*.

Dall's porpoise is a cold water species, the Pacific white-sided dolphin is a more temperate species, and the bottlenose dolphin is a warm water species. While one would expect the thickness of the blubber layer to be greatest in the colder water species, Ridgway and Johnston (1966) found just the opposite, with mean blubber thicknesses of 1, 2, and 3 cm for these three species, respectively. This paradox seems best explained by the suggestion that Dall's porpoise has a higher metabolic rate, by which body temperature is maintained. The food consumption rates of captive animals of these three species support a higher metabolic rate for Dall's porpoise.

Recent studies have shown that the retina of the Dall's porpoise is similar to that in other species of cetaceans (Murayama *et al.*, 1995). Calculi have been found in the nasal diverticula of Dall's porpoises (Curry *et al.*, 1994).

Life History and Population Dynamics

Growth and reproduction

Almost all age data have been obtained by sectioning teeth longitudinally, then staining and counting the cementum layers (Kasuya, 1978; Perrin and Myrick, 1980). These cementum layers become difficult to interpret with increasing age, causing problems in aging older animals. Age data may be obtained also from length data for smaller individuals (Kasuya, 1978).

Reproductive parameters for various Dall's porpoise populations are summarized in Table 3. *Truei*-types attain sexual maturity at body lengths 12–17 cm greater than *dalli*-types of most populations (Kasuya and Shiraga, 1985), although *dalli*-types in the Sea of Japan/Okhotsk Sea reach maturity at lengths similar to those of the *truei*-type population (Amano and Kuramochi, 1992). Everywhere that this species has been studied, there appears to be a calving peak in the summer months (Okada and Hayashi, 1951; Kasuya, 1978; Newby, 1982; Jones *et al.*, 1987; Jefferson, 1989). A single neonate from northern California of 100.7 cm in length (Fig. 3) was found on 7 August with its teeth unerupted but with the umbilicus healed (W. J. Houck, unpublished data).

TABLE 3 Reproductive parameters estimated for various Dall's porpoise populations

Parameter	Population: Pacific coast of Japan (*truei*)[a]	Sea of Japan/ Okhotsk Sea[b]	NW North Pacific[c]	Bering Sea[c]
Length at birth (cm)	—	~ 100	97	—
Length at sexual maturity (cm)				
Male	195.7	192	175–180	180–185
Female	186.5	187	174–177	182
Age at sexual maturity (yrs)				
Male	7.9	—	3.6–4.0	4.0–5.0
Female	6.8	—	4.5	4.4
Calving season	Aug.–Sept.	May–June	mid June–late July	mid July–?
Length of gestation (months)	11.4	7–9	10.7	—
Length of lactation (yrs)	2	—	—	—
Calving interval (yrs)	3	—	1	—

[a] Data from Kasuya (1978).
[b] Data from Okada and Hayashi (1951) and Amano and Kuramochi (1992).
[c] Data from Jones *et al.* (1985, 1987, 1988).

The length of the lactation period is very difficult to estimate accurately. It is thought generally that lactation is much shorter than the 2 years estimated by Kasuya (1978), and probably less than 4 months (Loeb, 1972; Newby, 1982).

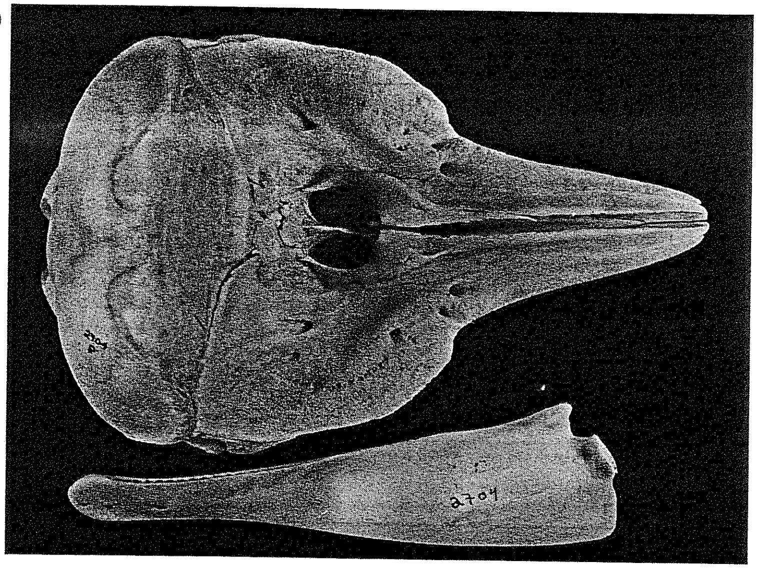
Mortality

The only known predator other than humans, is the killer whale (*Orcinus orca*). Killer whales have been observed preying on Dall's porpoises, and have been found with Dall's porpoise remains in their stomachs (Rice, 1968; Pike and MacAskie, 1969; Barr and Barr, 1972; Morejohn, 1979). Several authors have also suggested sharks as possible predators, and Newby (1982) illustrated a possible shark attack wound; however, because of the great speeds achieved by Dall's porpoises, sharks seem unlikely to be major predators (Morejohn, 1979).

Abundance

Several stocks have been recognized, based largely on geographic variation in morphology and colour patterns, parasite loads, and densities of mother/calf pairs (see Kasuya and Ogi, 1987; Walker, 1990; Walker and Sinclair, 1990;

(A)



(B)

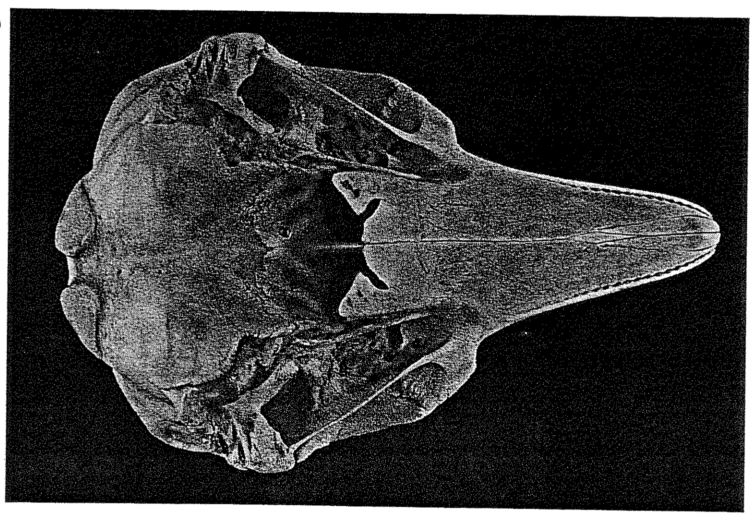


FIG. 4 Skull of *Phocoenoides dalli* (Humboldt State University #2704, female, condylobasal length 28.7 cm): (A) dorsal view of cranium and lateral view of mandible and (B) ventral view of cranium.

(C)

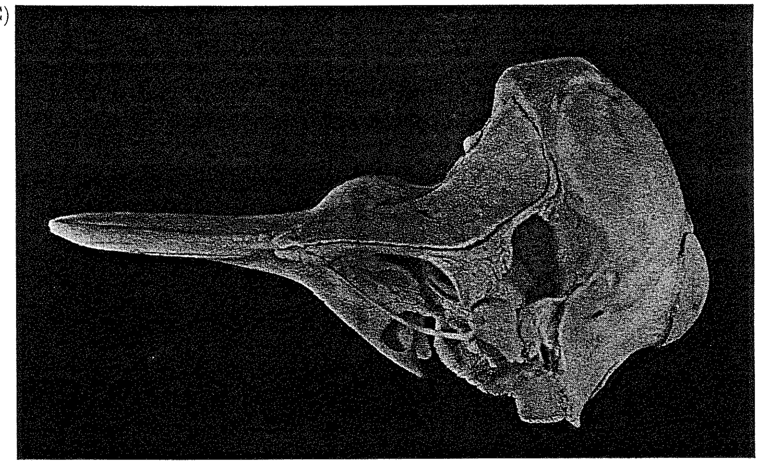


FIG. 4 *Continued* (C) Lateral view of cranium.

International Whaling Commission, 1991; Amano and Miyazaki, 1992). Genetic techniques also have been applied in recent years (Winans and Jones, 1988). Eight stocks (seven *dalli*-type and one *truei*-type) are currently recognized by the International Whaling Commission (1992).

The National Marine Fisheries Service, in cooperation with the government of Japan, has conducted sighting surveys since 1978 for the purpose of estimating the abundance of Dall's porpoise throughout much of its range. Estimates using line and strip transect methods have given a range of 1.4–2.8 million animals in the North Pacific and Bering Sea (Jones *et al.*, 1987). The most recent estimate is 1 186 000 (CV = 0.09) (Buckland *et al.*, 1993). Animal movement and other factors result in violations of some of the assumptions of the analyses, which bias population estimates.

Recently, several estimates for smaller portions of the species' range have been produced. Turnock *et al.* (1995) estimated that there are 141 800 in the western North Pacific. In the waters off the Pacific coast of Japan, Miyashita and Kasuya (1988) have estimated a total of 104 000 Dall's porpoises, more than half of them *truei*-types. Miyashita (1991) estimated the three stocks that inhabit the Sea of Okhotsk to number about 554 000 in total. Along the west coast of the United States there are estimated to be 2150 Dall's porpoises off coastal Washington and Oregon (Green *et al.*, 1992) and 78 400 off California (Barlow, 1995).

Behaviour

Social organization

Dall's porpoises are social animals, but group structure is thought to be fluid as in many other small cetaceans (Miller, 1990). Usually they are seen in groups of 2–12 animals; singles are relatively rare. Larger groups are known as well. They form aggregations of up to 20 or so for feeding and playing in Monterey Bay, California (Jefferson, 1991), and Pike and MacAskie (1969) recorded many large groups of over 30 in inshore waters of British Columbia. Scheffer (1950) reported a group of several thousand in the Gulf of Alaska, and Sullivan and Houck (1979) reported one of approximately 1000 off northern California. A group of about 3000 was seen passing through Stephens Passage, in southeastern Alaska (Jones *et al.*, 1987). Such large groups generally appear to be temporary aggregations of several smaller schools.

Usually Dall's porpoises do not arrange themselves in any discernible order; however, there are notable exceptions. Norris and Prescott (1961) described groups of 20–100 travelling in single file in southern California waters. So far, this behaviour has not been reported elsewhere, nor since, from southern California.

Swimming and diving

Dall's porpoises are extremely fast swimmers and may be the fastest of all the small cetaceans. Speeds as high as 32 km/hr (Ridgway and Johnston, 1966) and 55 km/hr (Leatherwood and Reeves, 1986) have been recorded or estimated, although such high speeds probably can be maintained only for short bursts. Law and Blake (1994) accurately measured maximum speed for wild Dall's porpoises at 22 km/hr.

Respiratory rates of wild individuals are difficult to obtain, except when they are bowriding. Jefferson (1987), while studying wild Dall's porpoises in British Columbia, did not record any dives in excess of 4 min. However, the sample was small and dives of over 5 min probably occur. Individual specimens are difficult to identify and track (see Miller, 1990; Jefferson, 1991). Ridgway (1972) found a mean respiratory rate of 3.2 per min in captivity, which is about the same as that for several other small cetaceans.

Dall's porpoises make a characteristically sloppy splash when surfacing to breathe while travelling quickly. This splashing has come to be known as "roostertailing" (Fig. 5). These distinctive splashes can be seen from long distances at sea and make the presence and identification of the animals known considerably before the porpoises themselves can be seen. When they decrease their speed and roll slowly at the surface, these splashes are not produced, and this type of surfacing is called "slow rolling". Slow rolling Dall's porpoises have been found to travel at about 5 km/hr (Jefferson, 1987). A third type of surfacing, recognized and named "fast surfacing" by Jefferson (1987), involves fast travel below the surface, but without the roostertail splash upon surfacing.

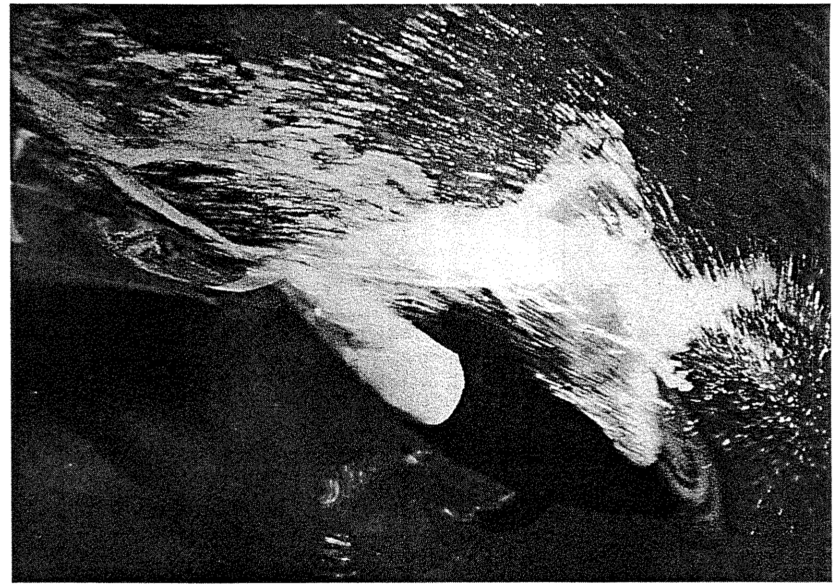


FIG. 5 Dall's porpoise at sea, showing the characteristic "roostertail" splash.

These porpoises rarely, if ever, leap from the water. Yocom (1946), in his account of Dall's porpoises west of San Francisco, mentioned leaping in several instances. It seems likely that he confused the splashes associated with roostertailing with those caused by leaping animals.

Dall's porpoises frequently will approach vessels at high speed and position themselves in front of and alongside the bow, although often they weave in and out of the bow wave with jerky movements (Fig. 6). Bowriding appears to be a play activity, most commonly undertaken by younger animals (Kasuya and Jones, 1984; Jefferson, 1991). They may swim in the normal position, on their sides as if to look at the observers on the bow, or occasionally upside down. This play may last anywhere from a few minutes to over half an hour. They terminate the "game" by veering off to the side at high speed or simply outracing the vessel. Certain vessels seem to be preferred over others; perhaps a combination of speed and bow configuration of some vessels produces pressure waves more to their liking. It is possible that sound may also be a factor.

Bowriding behaviour may have been learned from their association with larger cetaceans. Morejohn (1979) recorded associations with gray (*Eschrichtius*

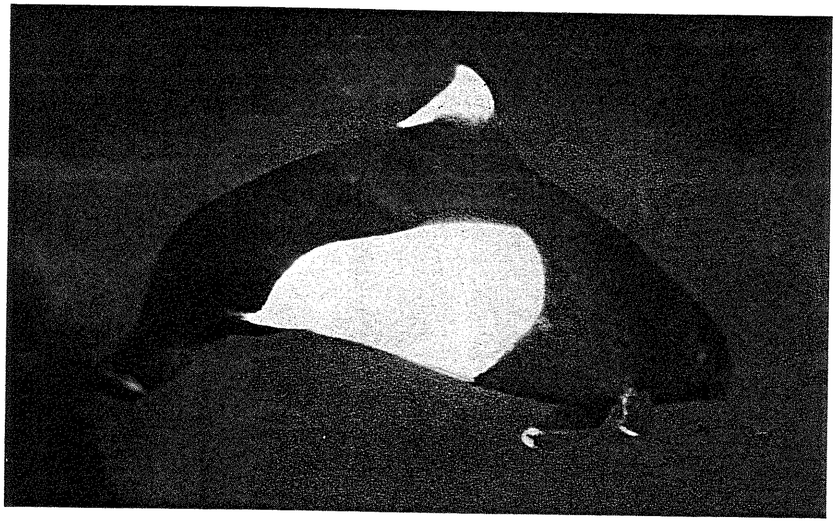


FIG. 6 Bowriding Dall's porpoise on its side just below the surface.

robustus) and fin (*Balaenoptera physalus*) whales, and Dall's porpoises have been observed "bow riding" on the pressure waves produced by the heads of surfacing blue whales (*Balaenoptera musculus*) (Jefferson, 1991) and humpback whales (*Megaptera novaeangliae*) (T. A. Jefferson, unpublished observations). Associations with other smaller marine mammals are relatively uncommon.

Feeding

The diet of Dall's porpoise consists primarily of small fish and squid; size and abundance probably determine the prey (Table 4). Norris and Prescott (1961) found that prey items were all less than 25 cm in length. This is not surprising, as the teeth of this species are slender and incapable of shearing bites from larger prey.

Loeb (1972), in her study of Dall's in Monterey Bay, found that Pacific hake (*Merluccius*), juvenile rockfish (*Sebastes*), and market squid (*Loligo*) made up 85% of the food items over the year. Off Japan, Wilke and Nicholson (1958) found that squid accounted for 11% of the food items; lanternfish were over 70% of the remainder. The most common prey items in the Sea of Okhotsk were the Japanese pilchard (*Sardinops sagax*) and the squid *Berryteuthis magister* (Walker, 1996). Stomachs of Dall's porpoises from the northwestern North Pacific and Bering Sea contained mostly squid (Mizue *et al.*, 1966; Fiscus and Jones, 1990; Kuramochi *et al.*, 1993), but 33 species of epi- and mesopelagic fishes were also found (Crawford, 1981). Of the fish remains, 94% of the individuals

TABLE 4 Prey species recorded from stomach contents of Dall's porpoise

Scientific name	Common name	Source(s)
FISHES		
Merluccius productus	Pacific hake	Scheffer, 1953; Norris and Prescott, 1961; Loeb, 1972; Morejohn, 1979; Stroud *et al.*, 1981
Laemonema spp.	Hakes	Wilke *et al.*, 1953; Wilke and Nicholson, 1958; Jones, 1981
Trachurus symmetricus	Jack mackerel	Scheffer, 1953; Norris and Prescott, 1961
Scomber japonicus	Chub mackerel	Wilke *et al.*, 1953; Wilke and Nicholson, 1958; Kuzin and Belyaev, 1985
Clupea harengus	Pacific herring	Cowan, 1944; Poke and MacAskie, 1969; Loeb, 1972; Morejohn, 1979; Crawford, 1981
Engraulis mordax	Northern anchovy	Loeb, 1972; Morejohn, 1979; Crawford, 1981; Stroud *et al.*, 1981
Engraulis japonica	Anchovy	Wilke *et al.*, 1953
Cololabis saira	Pacific saury	Sleptsov, 1961; Stroud *et al.*, 1981; Kuzin and Belyaev, 1985
Sardinops sagax	Pacific sardine Japanese pilchard	Kuzin and Belyaev, 1986; Walker, 1996
Sebastes spp.	Rockfishes	Loeb, 1972; Morejohn, 1979
Mallotus villosus	Capelin	Scheffer, 1953; Stroud *et al.*, 1981
Thaleichthys pacificus	Eulachon	Stroud *et al.*, 1981
Tarletonbeania crenularis	Blue lanternfish	Loeb, 1972; Crawford, 1981
Protomyctophum thomsoni	Flashlightfish	Crawford, 1981
Myctophidae	Lanternfishes	Wilke *et al.*, 1953; Wilke and Nicholson, 1958; Loeb, 1972; Morejohn, 1979; Crawford, 1981
Citharichthys sordidus	Pacific sandab	Loeb, 1972; Morejohn, 1979
Oncorhynchus spp.[a]	Salmon	Mizue *et al.*, 1966
Spirinchus starski	Nightsmelt	Loeb, 1972; Morejohn, 1979
Bathylagus spp.	Deep sea smelts	Loeb, 1972; Morejohn, 1979; Crawford, 1981
Chilara taylori	Spotted cuskeel	Morejohn, 1979
Deprilus simillimus	Pacific butterfish	Morejohn, 1979
Microgadus proximus	Pacific tomcod	Jones, 1981
Zoarcidae	Eelpouts	Loeb, 1972; Morejohn, 1979
Macrouridae	Rattails	Loeb, 1972; Morejohn, 1979
Ammodytes hexapterus	Pacific sandlance	Crawford, 1981
Cottidae	Sculpins	Crawford, 1981
Scopelosaurus harryi	Paperbone	Crawford, 1981
Moridae	Moras	Crawford, 1981
Nansenia candida	Bluethroat argentine	Crawford, 1981

continued

TABLE 4 *Continued*

Scientific name	Common name	Source(s)
Pleurogrammus monopterygius	Atka mackerel	Crawford, 1981
Ichthyococcus sp.	Gonostomatid	Crawford, 1981
Stichaeidae	Pricklebacks	Crawford, 1981
Stomatiatiodae	Stomatiatiods	Crawford, 1981
Otophidium taylori	Cusk eel	Loeb, 1972
Peprilus simillimus	Pompano	Loeb, 1972; Morejohn, 1979
Anoploma fimbria	Sablefish	Loeb, 1972; Morejohn, 1979
Lampanyctus regalis	Pinpoint lampfish	Loeb, 1972; Morejohn, 1979
Liparis sp.	Snailfish	Loeb, 1972; Morejohn, 1979
Melamphaediae	Bigscales	Crawford, 1981
Opistoproctidae	Spookfishes	Crawford, 1981
Paralepididae	Barracudinas	Wilke *et al.*, 1953; Wilke and Nicholson, 1958; Crawford, 1981
Benthabella dentata	Pearleye	Crawford, 1981
Pleuronectidae	Righteye flounders	Stroud *et al.*, 1981
Theragra chalcogramma	Walleye pollock	Crawford, 1981; Walker 1996
Anguilliformes	Eels	Loeb, 1972
CEPHALOPODS		
Loligo opalescens	Market squid	Scheffer, 1953; Norris and Prescott, 1961; Ridgway, 1966; Loeb, 1972; Morejohn, 1979; Stroud *et al.*, 1981
Sepiolidae	Bobtail cuttlefishes	Morejohn, 1979
Ommastrephes sloani	Flying squid	Wilke *et al.*, 1953; Wilke and Nicholson, 1958; Sleptsov, 1961
Ommastrephidae	Flying squids	Morejohn, 1979
Onychoteuthis spp.	Hooked squids	Stroud *et al.*, 1981; Kuzin and Belyaev, 1985; Fiscus and Jones, 1990
Watasenia scintillans	Sparkling enope squid	Wilke *et al.*, 1953; Wilke and Nicholson, 1958
Octopoteuthis sp.	Octopus squid	Stroud *et al.*, 1981
Octopoteuthidae	Octopus squids	Morejohn, 1979
Gonatidae	Gonatid squids	Loeb, 1972; Morejohn, 1979; Stroud *et al.*, 1981; Fiscus and Jones, 1990
Gonatopsis spp.	? squid	Kuramochi *et al.*, 1993
Gonatus onyx	? squid	Kuramochi *et al.*, 1993
Berryteuthis spp.	? squid	Kuramochi *et al.*, 1993; Walker, 1996
Abraliopsis sp.	? squid	Loeb, 1972; Stroud *et al.*, 1981
Enoploteuthidae	Enope squids	Morejohn, 1979; Fiscus and Jones, 1990
Histioteuthis sp.	Jewell squid	Fiscus and Jones, 1990

continued

TABLE 4 *Continued*

Scientific name	Common name	Source(s)
Histioteuthidae	Jewell squids	Morejohn, 1979
Chiroteuthis sp.	? squid	Fiscus and Jones, 1990
Cranchiidae	Cranch squids	Stroud *et al.*, 1981; Fiscus and Jones, 1990
Bolitaenidae	Bolitaenid squids	Fiscus and Jones, 1990
Octopus sp.	Octopus	Loeb, 1972; Morejohn, 1979
OTHER INVERTEBRATES		
Euphausiidae[a]	Krill	Crawford, 1981
Decapoda[a]	Decapods	Wilke *et al.*, 1953; Morejohn, 1979
	Shrimp	Mizue and Yoshida, 1965

[a] Not considered a regular prey item.

were myctophids (lanternfish), with *Protomyctophum* accounting for 78% of all the fishes consumed.

The high percentage of deepwater and vertically migrating fishes in the diet of Dall's porpoises from many areas indicates that the porpoises were either feeding at night or at great depths, most likely both (see Morejohn, 1979; Crawford, 1981; Stroud *et al.*, 1981).

Movements

This species is present throughout much of its range year-round. This is true for at least central California (Morejohn, 1979; Jefferson, 1991), northern California (W. J. Houck, unpublished data), Puget Sound, Washington (Miller, 1990), and British Columbia (Pike and MacAskie, 1969). In these areas, waters remain cool (about 9–15 °C) year-round.

Norris and Prescott (1961) found Dall's porpoises in southern California waters only in the winter, generally when the water temperature was less than 15 °C. Inshore/offshore movements off southern California and British Columbia have been postulated (Brown and Norris, 1956; Pike and MacAskie, 1969). Although movements in the eastern Pacific also have a north/south component (Leatherwood *et al.*, 1982), there appear to be more distinct north/south movements in the western Pacific (Nishiwaki, 1967; Kasuya, 1978; Amano and Kuramochi, 1992).

These movements may be temperature-related or, as Morejohn (1979) postulated, food-dependent. Miyazaki *et al.* (1984) found that *truei*-type porpoises and mixed schools generally were found in warmer waters, while *dalli*-types were found in both warmer and colder waters.

Movement patterns of individual porpoises have not been studied well. Hall (1979) reported evidence of a summer home range in porpoises of this species from Prince William Sound, Alaska, and Miller (1989, 1990) reported resightings over various distances and periods of time of photoidentified Dall's porpoises in Puget Sound. One porpoise tagged in Prince William Sound was resighted 90 days later at a straight line distance of 821 km away (Hall, 1979).

Sound production

Only pulsed sounds, no pure-tone whistles, have been recorded from this species. The clicks produced by Dall's porpoises have been found to be similar to those known from other phocoenids and dolphins of the genus *Cephalorhynchus* (Evans *et al.*, 1988). They consist of high frequency (mostly 120–150 kHz), narrow-band single and double pulses (Awbrey *et al.*, 1979). The pulses are of short duration; single pulses are about 500 μs and double pulses are about 250 μs (Evans *et al.*, 1988). These sounds presumably are used for echolocation.

Parasites and Disease

Dall's porpoises suffer from a variety of parasitic infestations (Table 5). There has been some limited work on the diseases and pathology of this species (Ridgway, 1966; Dailey and Walker, 1978; Conlogue *et al.*, 1985; Cowan *et al.*, 1986). The trematode fluke *Nasitrema*, which infests and produces lesions in the respiratory system and brain, has been implicated as a possible causal factor in single strandings of Dall's porpoises in southern California (Dailey and Walker, 1978). Walker (1990) found certain parasites useful as stock indicators.

Live Maintenance

Dall's porpoises have been extremely difficult to maintain in captivity. Most attempts have ended with the premature death of the animal. Walker (1975) claimed this to be the most difficult to maintain of all the southern California cetaceans. Of eight porpoises live-captured, half died during capture or transport, two died within 60 days, one lived three months, and the remaining one survived slightly over 15 months. Walker (1975) reported that, although they had a high food intake, they never regained their original capture weight. The last specimen, and another reported by Ridgway (1966), are the only ones known to have survived longer than one year in captivity. Small numbers have also been live-captured in Japan for public display (Kasuya *et al.*, 1984).

TABLE 5 Parasites recorded from Dall's porpoise

Location	Species	Source(s)
Lungs	*Halocercus dalli*	Benson and Groody, 1942; Machida, 1974; Conlogue *et al.*, 1985
	Stenurus minor	Johnston and Ridgway, 1969
	Stenurus sp.	Walker, 1975
Nasal passages/ air sacs	*Nasitrema dalli*	Yamaguti, 1951; Dailey, 1971; Dailey and Walker, 1978; Cowan *et al.*, 1986
	Torynurus dalli	Dailey and Walker, 1978; Cowan *et al.*, 1986
	Pharurus dalli	Dailey, 1971; Kuramochi *et al.*, 1990
	Pharurus sp.	Walker, 1975
	Stenurus minor	Johnston and Ridgway, 1969; Dailey and Walker, 1978; Cowan *et al.*, 1986
	Stenurus truei	Kuramochi *et al.*, 1990
	Stenurus yamagutii	Kuramochi *et al.*, 1990
	Crassicauda sp.	Dailey and Walker, 1978; Cowan *et al.*, 1986
Inner ear	*Pharurus dalli*	Machida, 1974
	Pharurus sp.	Walker, 1975
	Stenurus truei	Machida, 1974
Brain	*Nasitrema* sp.	Cowan *et al.*, 1986
Liver/pancreas/ ducts	*Campula oblonga*	Yamaguti, 1951; Machida, 1974; Walker, 1975; Dailey and Walker, 1978; Conlogue *et al.*, 1985; Cowan *et al.*, 1986
Stomach	*Anisakis simplex*	Dailey, 1971
	Anisakis sp.	Machida, 1974
Urogenital blubber	*Crassicauda* sp.	Walker, 1975, 1990; Dailey and Walker, 1978; Conlogue *et al.*, 1985; Araki *et al.*, 1994
	Placentonema sp.	Ridgway, 1966
Mammaries	*Phyllobothrium* sp.	Dailey and Brownell, 1972; Walker, 1990
	Placentonema sp.	Ridgway, 1966
	Crassicauda sp.	Dailey and Walker, 1978
Intestines	*Bolbosoma* sp.	Machida, 1974
	Corynosoma sp.	Machida, 1974
External	*Neocyamus physeteris*	Leung, 1967

Human Effects

Directed fisheries

Along the coast of northern Japan, Dall's porpoises are taken for human consumption (Table 6). This fishery, in recent years, has been primarily a harpoon fishery, as shooting has been banned (see description of the fishery in Ohsumi, 1972; Miyazaki, 1983). Annual kills in the past were in the thousands, but in the late 1980s they increased to the tens of thousands. The 1988 catch of over 40 000

Dall's porpoises in this fishery (Kasuya, 1992) represented over one-third of the population known to migrate through the fishing area (Miyashita and Kasuya, 1988) and clearly was not sustainable. In recent years, the catch has been reduced somewhat, but still remains high (Table 6).

By-catches

Large numbers of Dall's porpoises are taken also in various gill net fisheries throughout much of their range, especially in the western Pacific and Bering Sea. The largest kills have been in the Japanese mothership and land-based salmon drift net fisheries (Table 6). Catches in the 1960s probably numbered between 10 000 and 20 000 animals per year (Mizue and Yoshida, 1965), but have declined in recent years, concomitant with reduced fishing effort. Since 1978, Japanese, Taiwanese, and Korean drift net fisheries for squid have developed in the area south of the mothership area. Although other species of small cetaceans are caught more frequently, a significant catch of Dall's porpoise is also known. Monitoring beginning in 1989 suggested that as many as 6000 Dall's porpoises may have been taken per year in the squid fisheries (International Whaling Commission, 1992). Although the effect of these takes on Dall's porpoise numbers is uncertain (Hobbs and Jones, 1993), there is evidence for a decline in abundance in the western North Pacific between 1984 and 1986 (Turnock and Buckland, 1995). A global moratorium on pelagic drift net fishing went into effect at the end of 1992, and should reduce or eliminate these kills. Extensive research in take reduction methods in the 1980s was largely ineffective (Hatakeyama *et al.*, 1994).

TABLE 6 Estimated incidental kill of Dall's porpoise in Japanese salmon drift net fisheries and reported direct kill in Japanese harpoon fishery

	Drift net fisheries		
Year	Mothership[a]	Land-based[a]	Harpoon fishery[b]
1981	2862	2936	9 767
1982	5903	6010	12 833
1983	4280	4429	12 776
1984	3355	3356	9 764
1985	3239	2979	10 378
1986	1719	1392	15 457
1987	1011	1229	25 871
1988	222	319	40 853
1989	36	282	29 048
1990	54	134	21 802
1991	—	—	17 634
1992	—	—	11 403
1993	—	—	14 318
1994	—	—	15 947

[a] Data from Jones (1990), Jones *et al.* (1987), and Anonymous (1991).
[b] Data from International Whaling Commission (1992, 1995, 1996), and Kasuya (1992).

Relatively small numbers of Dall's porpoises are known to be taken also in gill net fisheries along the west coast of North America (Lennert *et al.*, 1994) and in drift nets for tuna and billfish in the central Pacific (Jones *et al.*, 1992). Dall's porpoises are taken occasionally in other types of fishing gear as well, such as in trawl nets along the west coast of the United States (see Perez and Loughlin, 1991).

Pollution

In recent years, some work has been done on the levels of pollutants in Dall's porpoise tissues (O'Shea *et al.*, 1980; Tanabe *et al.*, 1983; Subramanian *et al.*, 1986, 1987a). High levels of organochlorines have been found, but the effects of these substances remain largely unknown (Tanabe *et al.*, 1994, 1996; Jarman *et al.*, 1996). It has been discovered that females may transfer organochlorines to their offspring during gestation and especially through lactation (Subramanian *et al.*, 1988), and that testosterone levels in males may be reduced by high levels of PCBs and DDE (Subramanian *et al.*, 1987b). These findings suggest that current levels of contaminants in Dall's porpoise tissues may have detrimental effects on production and calf survival.

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