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Right Whale Dolphins *Lissodelphis borealis* (Peale, 1848) and *Lissodelphis peronii* (Lacépède, 1804)

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Genus and Species

Taxonomy

The genus *Lissodelphis* (Gloger, 1841) consists of two species of finless dolphins in the family Delphinidae. There is some question as to their validity (Honacki *et al.*, 1982), but at present most researchers regard them as separate species. The right whale dolphins are sometimes classified in a separate subfamily, Lissodelphinae (Fraser and Purves, 1960), but this subfamily designation has not been widely accepted.

The genus *Lissodelphis* has a relatively complicated taxonomic history, reviewed by Hershkovitz (1966) and Jefferson and Newcomer (1993).

Common names

The northern right whale dolphin, *Lissodelphis borealis*, is also referred to as the Pacific right whale porpoise, delfín liso del norte (Spanish), kita semi-iruka (Japanese), severnyi kitovidnyi delfin (Russian), besperyi delfin (Russian), and rett-delphin (Norwegian). The southern right whale dolphin, *Lissodelphis peronii*, is also called the southern right whale porpoise, mealy-mouthed porpoise, tunina (= tonina) sin aleta (Spanish), delfín liso austral (Spanish), minami semi-iruka (Japanese), dauphin de Péron (French), and yuzhnyi kitovidnyi delfin (Russian).

Distribution

Range

The northern right whale dolphin is a North Pacific endemic (Fig. 1) that is normally distributed from 30° to 50°N in the eastern Pacific (Leatherwood and Walker, 1979) and 35° to 51°N in the western Pacific (Sleptsov, 1961; Nishiwaki, 1967). Movements beyond this range occur occasionally, as evidenced by sightings as far south as 29°N off Baja California, Mexico (Leatherwood and Walker, 1979), and as far north as 59°N in the Gulf of Alaska and just south of the Aleutian Islands in the central Pacific (Kajimura and Loughlin, 1988). The northernmost sightings are generally from summer months and the southernmost from winter months.

Scammon (1874) reported sightings as far north as the Bering Sea, but there are no other records from north of the Aleutian Islands. Okada and Hanaoka's (1940) report of this species in the "northern sea of Japan" apparently refers to the seas of Japan, in this case the Pacific coast, and not to the Sea of Japan proper.

Movements south and inshore for winter months and north and offshore for summer months have been reported for both sides of the Pacific (Kasuya, 1971; Leatherwood and Walker, 1979). Peak periods of abundance off southern California coincide with peak occurrence there of market squid (*Loligo opalescens*) (Leatherwood and Walker, 1979).

The southern right whale dolphin has a circumpolar distribution, generally between the Subtropical and Antarctic Convergences, in the Southern Hemisphere (Gaskin, 1968a; Fig. 1). Northernmost records are from near Pucusana, Peru (12°30'S) off western South America (Van Waerebeek *et al.* 1991) and from about 23°S off western South Africa (Brown, 1982). The northward-flowing Humboldt (Peru Coastal) and Benguela current systems may allow this cold-water species to extend its range northward in these areas (Brown, 1973, 1982). The southern limit of this species' distribution extends south of the Antarctic Convergence to about 58–61°S in some years (Cruickshank and

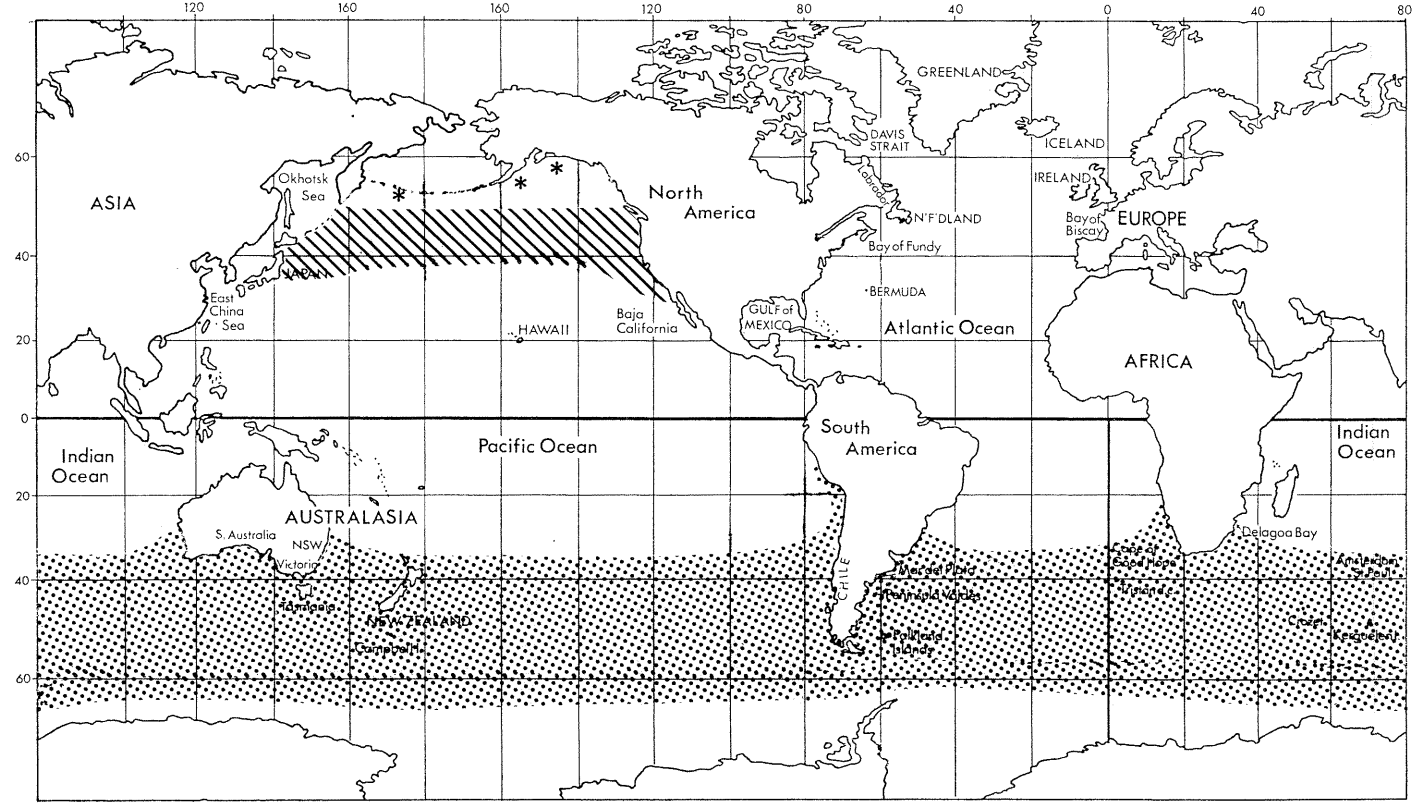


FIG. 1 Approximate ranges of *Lissodelphis borealis* (hatched) and *L. peronii* (stippled). Asterisks (*) indicate extralimital northern right whale dolphin sightings in Kajimura and Loughlin (1988).

Brown, 1981; Goodall and Galeazzi, 1985; Kasamatsu *et al.* 1988), with the southernmost records from about 64°S (Brownell, 1974; Kasamatsu *et al.* 1989). However, the limit of the Antarctic Convergence is highly variable from year to year, and the southern right whale dolphin's distribution likely reflects this.

Melliss' (1885) report of the southern right whale dolphin as far north as St Helena (16°00′S, 5°45′W) is considered erroneous (Perrin, 1985), and reports of this species in the North Pacific off Japan actually refer to anomalously coloured northern right whale dolphins (Ogawa, 1937; Tobayama *et al.* 1969).

There is some suggestion of inshore and northward summer movements by southern right whale dolphins from sighting records off South Africa (Cruickshank and Brown, 1981); however, Rose and Payne (1991) suggested that southern right whale dolphins may be year-round residents off Namibia, southern Africa. Although the sample size is still small, north of 25°S off western South America more fresh specimens and sighting records have been registered in July–September than in all other months combined, suggesting a northern migration in the austral winter and spring (Van Waerebeek *et al.* 1991).

Habitat

Right whale dolphins are observed most often in cool, deep, offshore waters with temperatures of 8–19°C (*L. borealis*, Leatherwood and Walker, 1979) and 1–20°C (*L. peronii*, Cruickshank and Brown, 1981; Kasamatsu *et al.*, 1988). They are sometimes seen nearshore, especially where deep water approaches the coast, and the northern species apparently prefers "coastal-type" waters in the California Current system (Smith *et al.*, 1986).

External Characteristics

Colour pattern

The major difference between the species is the colour pattern (Fig. 2). The northern species is mostly black, with a white ventral band running from the fluke notch to the gular region; this band widens slightly in the genital area (more so in females than in males: Leatherwood and Walker, 1979) and widens again to cover the entire ventrum between the flippers. There is also a white patch just behind the tip of the lower jaw (Fig. 3), and crescent-shaped patches on the flukes are brushed light grey dorsally and white ventrally (Fig. 4). An uncommonly occurring colour variant, termed "swirled", with more extensive white areas has been reported from both sides of the Pacific (Ogawa, 1937; Tobayama *et al.* 1969; Leatherwood and Walker, 1979; Black and Jefferson, 1992).

Southern right whale dolphins are mostly black dorsally and white ventrally. The sharp border between black and white is high on the posterior flank, dips

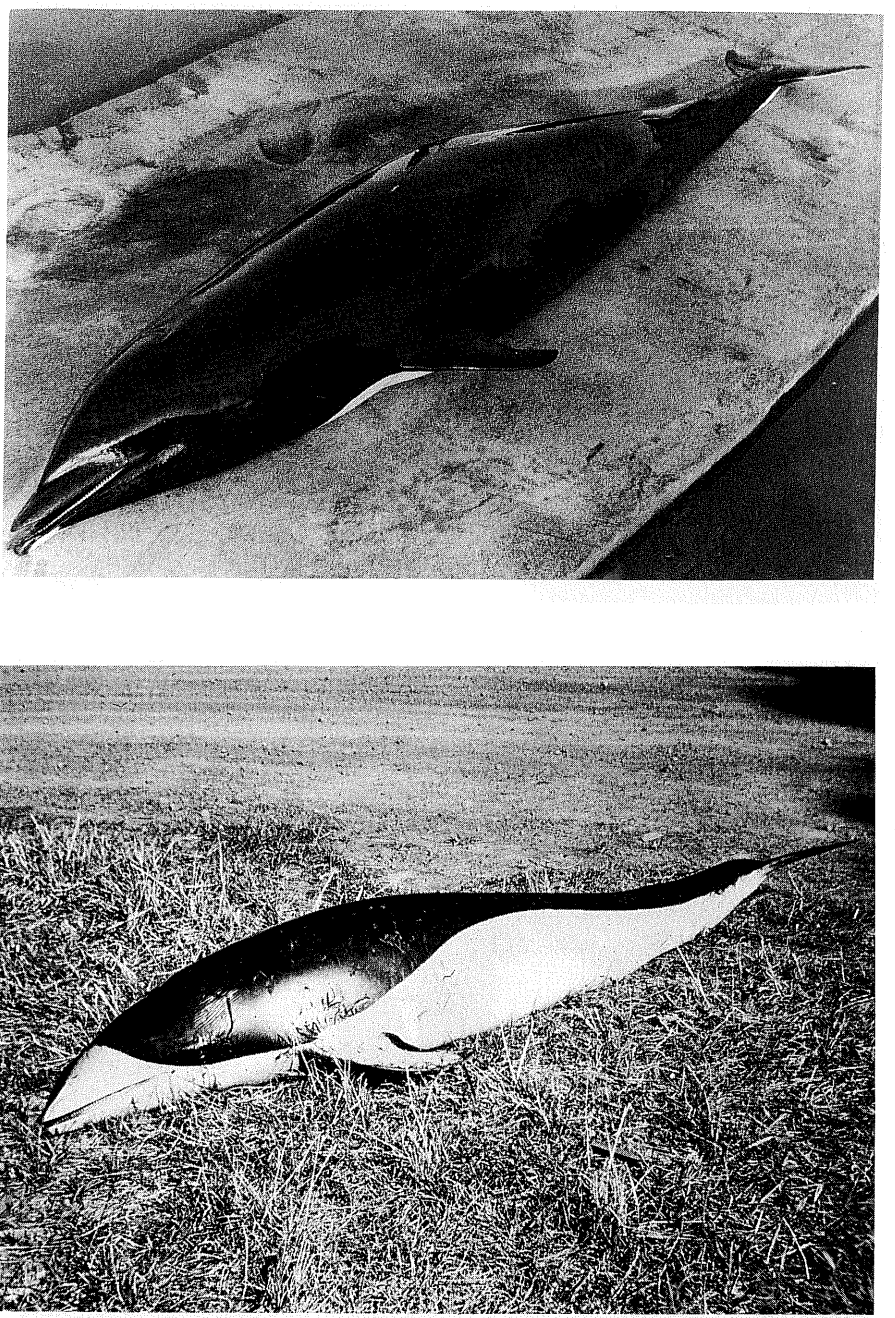


FIG. 2 Lateral views of northern (top) and southern (bottom) right whale dolphins. Photos by F. G. Wood (top) and R. Abel (bottom).

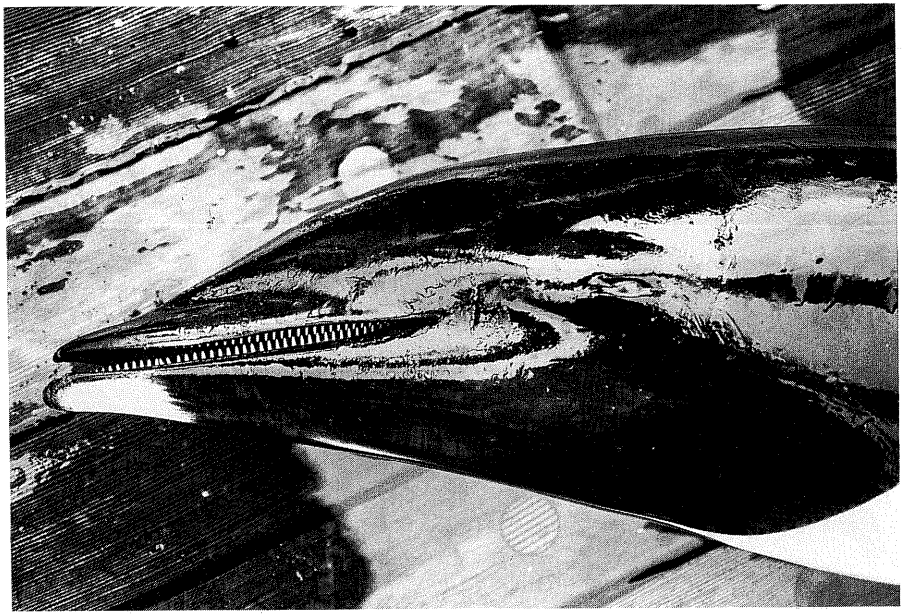


FIG. 3 Close-up of the head of a northern right whale dolphin, showing the short beak, and fine, sharply pointed teeth that are characteristic of the genus. (Photo by M. W. Newcomer.)

FIG. 4 Ventral view of the flukes of a northern right whale dolphin. (Photo by M. W. Newcomer.)

lower to the flipper insertion, then sweeps upward and across the melon in front of the blowhole. The beak, anterior melon, and flippers (except for a thin black band on the trailing edges) are white. The dorsal surface of the flukes tends to be dark grey instead of black. Several different types of colour variants have been reported in this species, including those with white spots on the head, those with variations in the extent of black and white on the body and appendages, an animal with a "grey dappled back", an entirely black animal, and a possibly all-white individual (Brown, 1973; Baker, 1981; Cruickshank and Brown, 1981; J. S. Grove, *in litt.* 12 June 1990; Rose and Payne, 1991).

TABLE 1 External measurements of a northern right whale dolphin neonate (IS 56, California Academy of Sciences Acc. No. 3813), provided by I. Szczepaniak (numbers in parentheses correspond to standard measurements in Norris, 1961)

Measurement	mm
Total length (1)	970
Snout to anterior insertion of flipper (10)	285
Snout to axillary insertion of flipper	355
Snout to external ear (5)	195
Snout to blowhole (9)	145
Snout to eye (2)	170
Length of gape (4)	115
Snout to base of beak (3)	20
Fluke notch to centre of anus	255
Fluke notch to centre of umbilicus	400
Fluke notch to centre of genital opening	325
Fluke span (34)	145
Fluke depth	70
Anterior length of flipper (29)	190
Axillary length of flipper (30)	130
Maximum width of flipper (31)	55
Girth, head	410
Girth, anterior to flipper	410
Girth, posterior to flipper (21)	420
Maximum girth, 435 mm from tip of snout (22)	435
Girth at penis	280
Anal slit length (26)	5
Genital slit length (26)	55
Umbilical slit length	30
Penis length	100
Blowhole length (27)	5
Blowhole width (27)	20
Eye length (24)	16
Ear length (28)	0.5

As in many small cetaceans, calves of both species have been reported to have a muted colour pattern, with brown or grey areas instead of black and white. They attain adult coloration some time in their first year. A 97-cm northern right whale dolphin calf appeared to possess adult coloration (I. Sczcepaniak, personal communication), however this may have been an artefact of *post-mortem* darkening (W. A. Walker, *in litt.* 20 May 1990).

Size and shape

Both species of *Lissodelphis* are characterized by the complete absence of a dorsal fin or dorsal ridge, a slender, dorso-ventrally compressed body, a straight mouthline, a moderately well-defined, but short beak, small recurved flippers with pointed tips, located about one-quarter of the way back from the snout tip, and small slightly concave flukes with a deep median notch (Figs 2–4).

Both species apparently reach lengths of about 3 m; the largest measured specimens were 3.1 m (*L. borealis*, Leatherwood and Walker, 1979) and 2.97 m (*L. peronii*, Van Waerebeek *et al.*, 1991). Males apparently grow larger than females.

Previously unpublished external measurements of a 97-cm northern right whale dolphin neonate (IS 56) are presented in Table 1.

Weight

Maximum recorded weight is 113 kg for a 282-cm northern right whale dolphin (Leatherwood and Walker, 1979) and 116 kg for a 251-cm southern right whale dolphin (Van Waerebeek and Oporto, 1990).

Internal Anatomy

The following discussion is based on knowledge gained from very few specimens, especially in the case of the southern right whale dolphin.

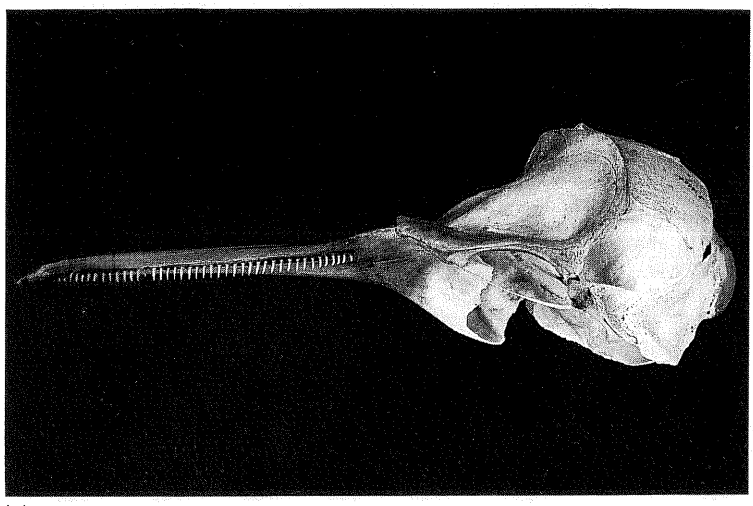
Skull

The skull of both species of *Lissodelphis* is slender and the bones are light (True, 1889; Okada and Hanaoka, 1940; Fig. 5). Skull measurements, previously unpublished, of seven northern right whale dolphins are presented in Table 2. True (1889) could find little to differentiate the crania of these two species. The condylobasal length of the northern species ranges up to at least 474 mm (Table 2), and represents about 2.17 times the width of the skull (Nishiwaki, 1972). Maximum recorded condylobasal length is 441 mm for the southern species (K. Van Waerebeek, unpublished). Baker (1981) considered the skull of the southern right whale dolphin to closely resemble that of the striped dolphin

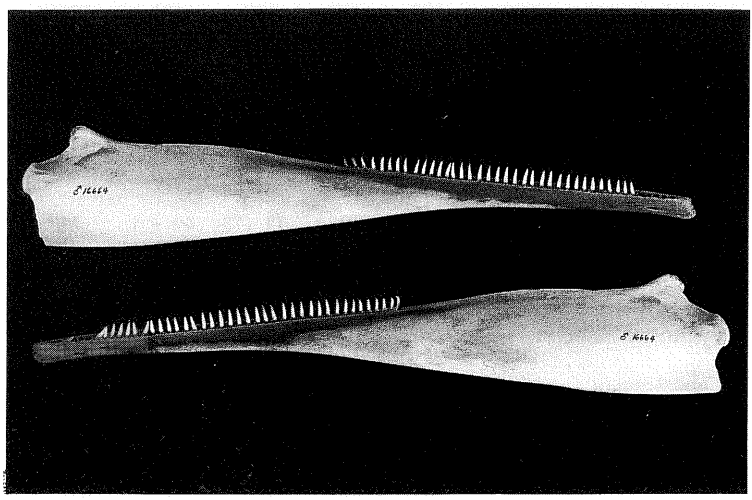
TABLE 2 Skull measurements (in mm) for seven northern right whale dolphin specimens (following Perrin, 1975)

Measurement	US National Museum (USNM) Number						
	290625	290626	8160	286872	270981	286882	286883
Condylobasal length	436	474	440*	427	420	416*	417*
Rostrum length	256	267	193*	242	229	224	224*
Rostrum basal width	107	106	108	115	114	104	107
Rostrum width at 3/4 length	33	40	—	37	42	—	46
Rostrum width at ½ length	50	60	61	54	57	55*	55
Width of premaxillaries at same point	28	32	33	32	33	37*	31
Tip of beak to blowhole	296	317	258*	289	275	257*	276
Tip of beak to pterygoid	309	339	269*	294	295	279*	292*
Preorbital width	163*	174	173	174	175	162	166
Postorbital width	182	188	192	189	187	180	184
Orbital width	166	173	177	172	179	170	172
Nares width	54	54	53	52	52	51	53
Zygomatic width	180	193	192	192	184	184	186
Greatest width of the premaxillaries	75	81	78	75	82	74	79
Width of braincase across parietals	160	165	163	157	159	168	168
Cranial height	146	139	138	136	135	140	135
Cranial length internal	119*	130	129	128	128	130	126
Number of teeth							
UR	48 + 2	50 + 1	33*	42 + 3	42 + 1	46*	44*
UL	48 + 1	50 + 2	38*	42 + 3	43 + 1	47*	50*
LR	54	51	49	46	48	53	50
LL	52	51	48	46	46	51	51
Tooth row length							
UR	208	229	170*	203	187	174	—
UL	206	224	147*	202	182*	169	188
LR	217	224	207	209	197	189	199*
LL	214	223	204	199	195	188	194*
Mandible length							
R	369	400	376	356	366	346	351
L	369	401	376	356	368	346	350
Coronoid length							
R	64	71	69	62	65	66	63
L	62	68	68	64	64	68	60
Symphysis length							
R	45	61	55	61	53	50	50
L	45	60	57	58	51	48	51
Post-temporal length							
R	61	68	69	60	59	65	67
L	58	53	—	—	60	67	65
Post-temporal height							
R	49	70	53	41	49	50	51
L	45	52	54	38	48	47	51

*Damaged (measurement or count not accurate).



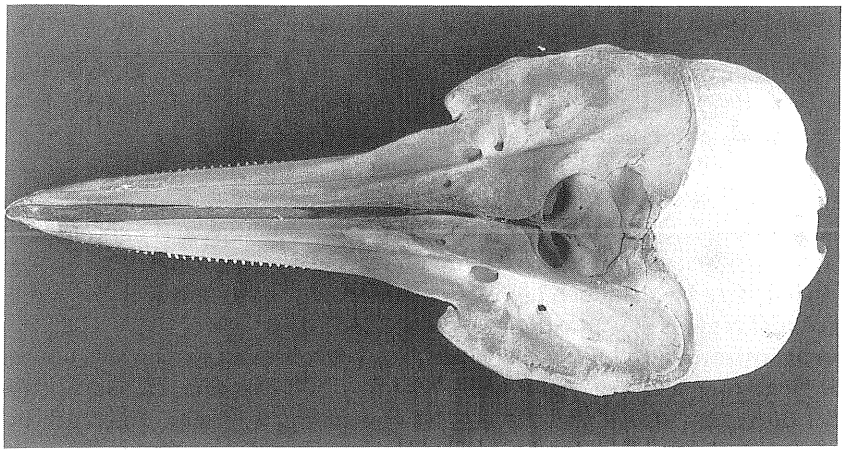
(a)



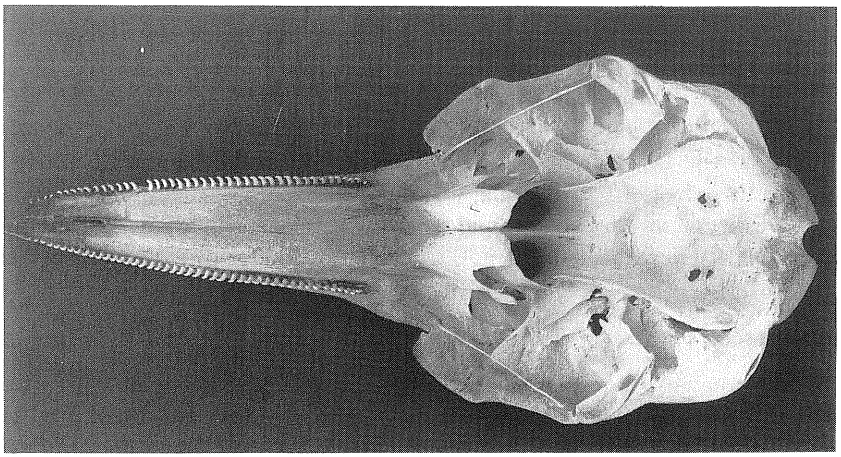
(b)

FIG. 5 Northern right whale dolphin skull: lateral view of cranium (a), lateral view of mandibles (b), dorsal view of cranium (c), and ventral view of cranium (d). (Photos by M. W. Newcomer.)

(*Stenella coeruleoalba*), but to have a shorter, more pointed rostrum. The rostrum of both species of *Lissodelphis* is elongated, and tapers to a sharp point (True, 1889; Okada and Hanaoka, 1940; Baker, 1981). The rostral length is slightly more than twice its width (True, 1889; Nishiwaki, 1963, 1972). The premaxillae are widely and progressively separated through to the rostrum tip, and the pterygoid bones are also separated (True, 1889; Okada and Hanaoka, 1940;



(c)



(d)

FIG. 5 *Continued.*

Baker, 1981). Kasuya (1973) described and illustrated the tympano-periotic complex of the northern right whale dolphin, and noted that its size is most similar to that of *Stenella*. Fraser and Purves (1960) presented a detailed description of the ventral aspect of the skull of this species.

The mandibles of right whale dolphins are long and slender, with a short symphysis (True, 1889; Okada and Hanaoka, 1940; Tomilin, 1957; Baker, 1981). The teeth are small, slender, and sharp, and tooth counts for each jaw are 37–54 (*L. borealis*, Okada and Hanaoka, 1940; Table 2) and 39–50 (*L. peronii*, K. Van Waerebeek, unpublished). Nishiwaki (1972) stated that in general there were slightly more teeth in the lower jaw.

Postcranial skeleton

Like the skull, many elements of the postcranial skeleton of right whale dolphins have been described as light, narrow, or weakly built (Okada and Hanaoka, 1940). Nishiwaki (1963, 1972) reported vertebral counts for the northern species of 88–90, with the following formula: C_7, T_{14-15}, L_{29-30}, and Ca_{37-39}; however, Tobayama *et al.* (1969) gave the formula as C_7, T_{14-17}, L_{29-33}, and $Ca_{35-40} = 88-92$. Characteristic of the delphinids, the atlas and axis are fused. Relative to other species of oceanic dolphins (i.e. *Delphinus* and *Stenella*), right whale dolphins have a much higher vertebral count, particularly in the lumbar and caudal regions (Okada and Hanaoka, 1940).

There are normally 14–17 pairs of vertebral ribs, four to six of which are two-headed in the northern right whale dolphin (Okada and Hanaoka, 1940; Tobayama *et al.*, 1969), and 13 pairs of vertebral ribs, five of which are two-headed and one free-floating in the southern species (Baker, 1981). The northern species has 7–10 pairs of sternal ribs (Okada and Hanaoka, 1940; Tobayama *et al.*, 1969) and the southern species has eight (Baker, 1981). The sternum is "peculiar in shape", with four lobe-like processes (Okada and Hanaoka, 1940).

The phalangeal formula is I_{1-2}, II_{7-8}, III_{5-6}, IV_3, and V_{2-3} (Nishiwaki, 1963; Tobayama *et al.*, 1969), but Nishiwaki (1972) subsequently reported nine phalanges in the third digit, which is likely an error. The scapulae are wide relative to their height (True, 1889; Okada and Hanaoka, 1940).

Other aspects of the postcranial skeleton are described by Okada and Hanaoka (1940) for the northern, and by Baker (1981) for the southern species.

Organs, tissues, and physiology

There has been little work on the soft anatomy and physiology of right whale dolphins. Schenkkan (1973) and Mead (1975) described and illustrated the anatomy of the nasal sac area, and stated that *Lissodelphis* shows no significant difference from the general delphinid plan. Blubber measurements for both species have been reported to be about 1–2 cm (Scheffer and Slipp, 1948; Leatherwood and Walker, 1979; Baker, 1981). Morejohn (1979) reported a northern right whale dolphin specimen with no evidence of external ear openings.

Sharp (1975) studied the electrophoretic and oxygen dissociation properties of 11 northern right whale dolphins, and found that they shared the same haemoglobin form as the Pacific white-sided dolphin (*Lagenorhynchus obliquidens*). The lipid composition of northern right whale dolphin jaw and melon fats was reported by Litchfield *et al.* (1975).

Life History and Population Dynamics

Growth and reproduction

Reproductive data have been published for a total of 11 male and 12 female northern right whale dolphins from the eastern North Pacific (Wick, 1969; Harrison *et al.*, 1972; Walker, 1975; Leatherwood and Walker, 1979; Sullivan and Houck, 1979; Cowan *et al.*, 1986). Collectively, these data suggest that males reach sexual maturity at lengths between 212 and 220 cm, and females at about 200 cm. The 114-cm adult female reported by Sullivan and Houck (1979) is an error. The correct length was 164–165 cm and the specimen was not an adult (W. J. Houck, *in litt.* 7 March 1990).

Miyazaki (1986) summarized data on one 196-cm immature male and 21 females of various lengths from the western Pacific. These data suggest that females reach maturity between 206 and 212 cm.

Neonatal length for northern right whale dolphins is unknown, but small calves seen at sea have been estimated to be 80–100 cm long (Leatherwood *et al.*, 1982), although some very small calves were estimated to be 60–70 cm long (Norris and Prescott, 1961). The calving season is not known, but most sightings of small calves are from winter (Dohl *et al.*, 1983) or early spring (Leatherwood and Walker, 1979; Leatherwood *et al.*, 1982).

As far as we know, the smallest northern right whale dolphin measured was a 97-cm male stranded in central California on 3 February 1986 (IS 56). This animal still had foetal folds and rostral hairs, but the umbilical remnant had probably been removed by gulls (I. Szczepaniak, personal communication).

Almost nothing is known of the reproductive biology of the southern right whale dolphin. Females of 229 cm and 218 cm, and a male of 251 cm were all mature (Baker, 1981; Van Waerebeek and Oporto, 1990). Five pregnant females that stranded in November 1988 had near term foetuses (Cawthorn, 1990), and one stranded in April 1988 had a 102-cm near-term foetus (Van Waerebeek and Oporto, 1990). An intact 86-cm neonate, possibly premature, was recovered from the stomach of a large Patagonian toothfish (*Dissostichus eleginoides*) (Van Waerebeek *et al.*, 1991).

Mortality

Strandings of right whale dolphins are not common (Leatherwood and Walker, 1979; Cruickshank and Brown, 1981), however Woodhouse *et al.* (1985) reported on the unprecedented stranding of 23 individual northern right whale dolphins along southern California beaches in 1981. Increasing numbers of southern right whale dolphins have stranded on beaches of north-central Chile in the last few years, but apparently involve mostly by-caught animals discarded from fishing nets (Van Waerebeek *et al.* 1991).

Mass strandings have not been reported for northern right whale dolphins, but a few have been reported for the southern species, including one that involved 77 animals (Fraser, 1955; Goodall, 1978; Baker, 1981; Cawthorn, 1990). Some live-stranded southern right whale dolphins have been returned to sea alive, but it is unknown if they survived (Baker, 1981).

There are no records of predation for either species, but it is likely that killer whales (*Orcinus orca*), and possibly large sharks, are at least occasional predators. For the southern species, there may also be other predators, as indicated by the discovery of an intact 86-cm dolphin in the stomach of a 170-cm Patagonian toothfish taken off central Chile in 1983 (Van Waerebeek *et al.*, 1991), and another 87-cm foetus, with the mother's surrounding genital region, in a 360-cm sleeping shark (*Somniosus* cf. *pacificus*) from Chile in 1990 (Crovetto *et al.*, 1992).

Abundance

There are no comprehensive population estimates for either species. Peak populations of northern right whale dolphins have been estimated at 17 800 off southern California (Leatherwood and Walker, 1979), and at around 61 500 off central and northern California (Dohl *et al.*, 1983), making them the second or third most abundant cetacean off California, after *Delphinus delphis* and *Lagenorhynchus obliquidens*.

Preliminary boat surveys and the rapid accumulation of stranding and fishery interaction records in northern Chile suggest that the southern right whale dolphin may be one of the most common cetaceans in this region (Van Waerebeek and Guerra, 1987; Van Waerebeek *et al.*, 1991).

Behaviour

Social organization

Right whale dolphins are highly gregarious. Both species are occasionally seen singly, but more often in groups of up to 2000–3000 for the northern species (Leatherwood and Walker, 1979; Leatherwood *et al.*, 1987) and up to over 1000 for the southern species (Gaskin, 1968b; Cruickshank and Brown, 1981). Average herd sizes for the northern right whale dolphin are about 100 in the eastern Pacific (Leatherwood and Walker, 1979) and 200 or more in the western Pacific (Nishiwaki, 1972). Mean herd size is 210 individuals for southern right whale dolphins off Chile (Van Waerebeek *et al.*, 1991).

Herd configurations reported for both species are similar (Cruickshank and Brown, 1981) and have been described in detail for the northern species by Leatherwood and Walker (1979). One of four distinct types is usually observed: (1) tightly packed groups, (2) herds with prominent subgroups, (3) V-formations, or (4) "chorus-lines".

Feeding

Right whale dolphins prey primarily on mesopelagic fishes (especially lanternfish, family Myctophidae) and squid (Table 3). Both species may dive to depths in excess of 200 m in search of food (Fitch and Brownell, 1968; Baker, 1981).

Association with other animals

Right whale dolphins have been reported to occur with many other species of marine mammals (Table 4), but are most often seen in association with dolphins of the genus *Lagenorhynchus*, with which they intermix freely, and with pilot whales (*Globicephala* spp.).

Swimming and diving

Swimming behaviour described for both species is remarkably similar (summaries by Leatherwood and Walker, 1979 for *L. borealis*, and Cruickshank and Brown, 1981 for *L. peronii*). Slow-moving groups are undemonstrative, typically exposing only the head and blowhole to respire. Fast-moving herds may employ one of two strategies: (1) swimming just below the surface, rapidly surfacing to breathe, then resubmerging, or (2) swimming rapidly at the surface, where they manifest characteristic low angle leaps and create a considerable surface disturbance (Fig. 6). The long slender bodies of right whale dolphins may allow them to reduce drag by taking several tail strokes while the bulk of the body is out of the water (Au and Weihs, 1980; Norris and Dohl, 1980).

Right whale dolphins are fast swimmers, but there have been few direct speed measurements at sea. Reported speeds have been as high as 34 km hr^{-1} for northern (Leatherwood and Walker, 1979) and 22 km hr^{-1} for southern (Cruickshank and Brown, 1981) right whale dolphins.

Individuals have been noted to dive for periods of 10–75 sec, but entire herds have dived for up to 6.25 min (*L. borealis*, Leatherwood and Walker, 1979) and 6.5 min (*L. peronii*, Cruickshank and Brown, 1981).

Aerial and other behaviour

While in the fast-swimming mode, both species have also been seen to perform belly-flops, fluke-slaps, and side-slaps (Fig. 7). Rose and Payne (1991) reported

TABLE 3 Stomach contents of right whale dolphins

Prey type	Family	Species	Sources
Lissodelphis borealis			
Squids	Unidentified squid		1, 2, 3
	Gonatidae	Unidentified gonatids	4
		Gonatus sp.	5
	Enoploteuthidae	*Abraliopsis* sp.	5
	Histioteuthidae	*Histioteuthis* sp.	5
	Loliginidae	*Loligo opalescens* (?)	6
	Onychoteuthidae	*Onychoteuthis* sp.	7
Fishes	Bathylagidae	*Leuroglossus stilbius*	1
	Paralepididae	*Lestidium ringens*	1
	Myctophidae	Unidentified myctophids	8
		Symbolophorus californiensis	1
		Diaphus theta	1, 8
		Lampadena urophaos	8
		Lampanyctus cf. *ritteri*	8
		Lampanyctus ritteri	1
		Stenobrachius leucopsarus	1
		Triphoturus mexicanus	1, 8
		Ceratoscopelus townsendi	1
		Tarletonbeania crenularis	1
	Merlucciidae	*Merluccius productus*	2, 8
	Scomberesocidae	*Cololabis saira*	1
	Melamphaidae	*Scopelogadus bispinosus*	8
		Melamphaes lugubris	1
	Centrolophidae	*Icichthys lockingtoni*	8
Lissodelphis peronii			
Squids	Ommastrephidae	*Dosidicus gigas*	9
		Notodarus sloani	10
	Gonatidae	*Gonatus antarcticus*	9
	Mastigoteuthidae	*Mastigoteuthis* sp.	9
	Cranchiidae	Unidentified cranchids	9
Fishes	Bathylagidae	*Bathylagus* sp.	9
	Photichthyidae	*Vinciguerria* sp.	9
	Myctophidae	Unidentified myctophids	9
		Hygophum hanseni	9
		Lampanyctus cf. *intricarius*	9
		Lampanyctus parvicauda	9
	Merlucciidae	*Macruronus novaezelandiae*	10
	Engraulididae	*Engraulis ringens*	11
	Atherinidae	*Odontesthes ragia*	11
	Carangidae	*Trachurus murphyi*	11

[1]Leatherwood and Walker, 1979; [2]Woodhouse *et al.*, 1985; [3]Scheffer and Slipp, 1948; [4]Sullivan and Houck, 1979; [5]Clarke, 1986; [6]Norris and Prescott, 1961; [7]Beach *et al.*, 1985; [8]Fitch and Brownell, 1968; [9]Torres and Aguayo, 1979; [10]Baker, 1981; [11]Van Waerebeek and Oporto, 1990.

TABLE 4 Associations of right whale dolphins with other species of marine mammals

Order, Family	Species	Sources
Lissodelphis borealis		
Cetacea, Delphinidae	*Lagenorhynchus obliquidens*	1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11
	Delphinus delphis	4, 12
	Tursiops truncatus	6
	Grampus griseus	3, 5, 6, 7, 8, 11
	Globicephala sp.	2, 3, 6, 8, 10
Cetacea, Phocoenidae	*Phocoenoides dalli*	2, 4, 7, 8
Cetacea, Ziphiidae	*Berardius bairdii*	6
	Mesoplodon sp.	8
Cetacea, Physeteridae	*Physeter macrocephalus*	8
Cetacea, Balaenopteridae	*Megaptera novaeangliae*	6, 8, 13
	Balaenoptera borealis	6, 13
	Balaenoptera physalus	6
Cetacea, Eschrichtiidae	*Eschrichtius robustus*	4
Pinnipedia, Otariidae	*Zalophus californianus*	4
Lissodelphis peronii		
Cetacea, Delphinidae	*Globicephala* sp.	14, 15, 16, 17, 18, 19, 20, 21
	Lagenorhynchus cruciger	18, 19, 20
	Lagenorhynchus obscurus	14, 21, 22
	Delphinus delphis	23, 24
	Tursiops truncatus	21
Cetacea, Balaenopteridae	*Balaenoptera physalus*	18

[1]Klumov, 1959; [2]Norris and Prescott, 1961; [3]Fiscus and Niggol, 1965; [4]Leatherwood, 1974; [5]Wahl, 1977; [6]Leatherwood and Walker, 1979; [7]Braham, 1983; [8]Dohl *et al.*, 1983; [9]Kasuya and Jones, 1984; [10]Baird and Stacey, 1991; [11]Black and Jefferson, 1992; [12]Smith *et al.*, 1986; [13]Brownell, 1964; [14]Cruickshank and Brown, 1981; [15]Laws and Nieuwenhujis, 1981; [16]Bastida and Bastida, 1984; [17]Enticott, 1986; [18]Miyazaki and Kato, 1988; [19]Kasamatsu *et al.*, 1988; [20]Kasamatsu *et al.*, 1989; [21]Rose and Payne, 1991; [22]Fraser, 1955; [23]J. S. Grove, *in litt.* 12 June 1990; [24]Van Waerebeek and Guerra, 1987.

an interesting behaviour pattern in southern right whale dolphins off southern Africa. In a loose herd, one animal began leaping out of the water, circling the entire school. Then the entire school exploded outwards, with animals swimming directly away from the centre in all directions. This was observed on two consecutive days, but has not been reported elsewhere.

The behaviour of right whale dolphins relative to ships is highly variable; they may approach them and ride the bow wave or may actively avoid them (Leatherwood and Walker, 1979; Cruickshank and Brown, 1981; Rose and Payne, 1991). Apparently, at least for the northern species, bow-riding occurs more often in the company of other species (Leatherwood *et al.*, 1987).

Northern right whale dolphins have reportedly been observed "standing by" injured school mates (Cassin, 1858), but Caldwell and Caldwell (1966) considered the identification of species here questionable. Little else is known of their social behaviour.

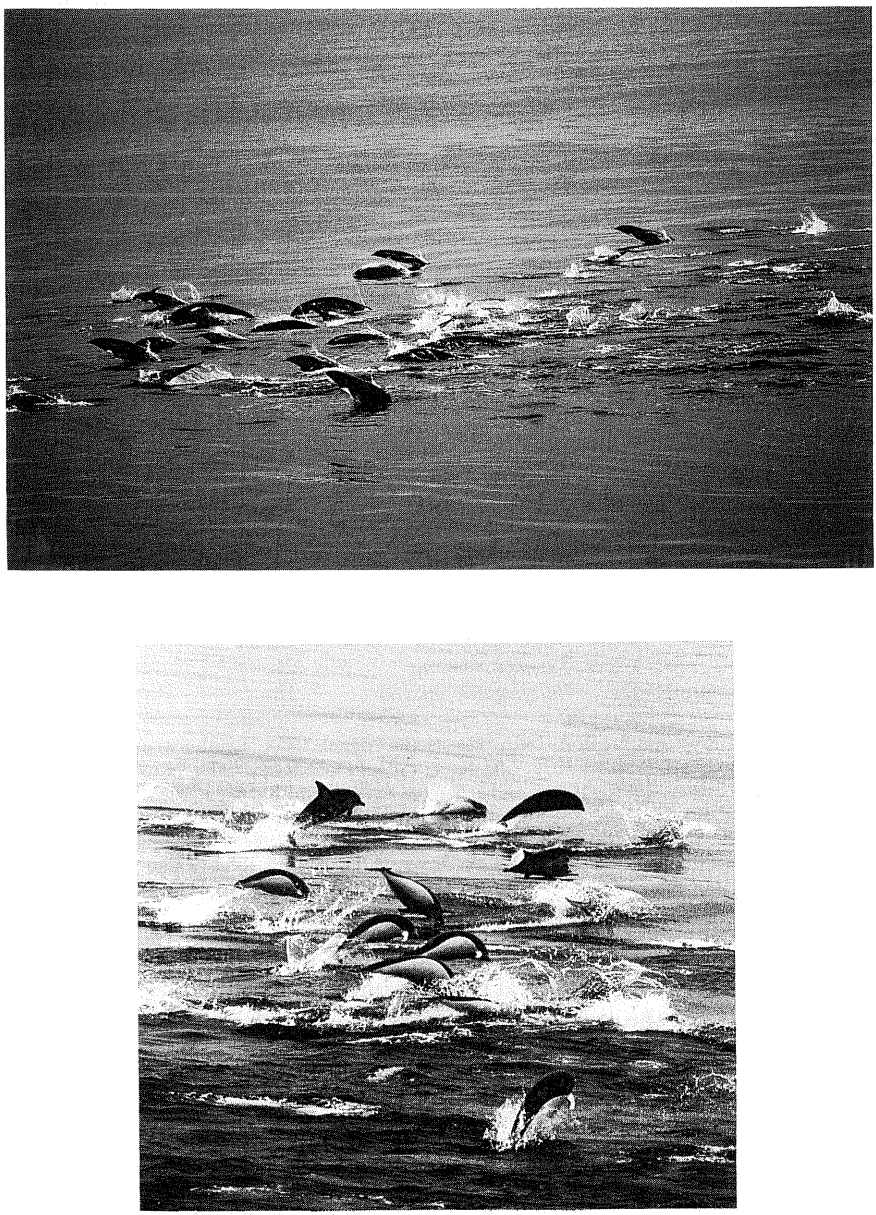


FIG. 6 Low angle leaps of northern (top) and southern (bottom) right whale dolphins. The bottom photo also shows an entirely black southern right whale dolphin and an association with the common dolphin (*Delphinus delphis*). (Photos by M. W. Newcomer (top) and J. S. Grove/Eye on the World Photography (bottom).)

FIG. 7 Northern right whale dolphin performing side slaps. (Photo by T. A. Jefferson.)

Sound production

Sounds of northern right whale dolphins have been reported by Fish and Turl (1976) and Leatherwood and Walker (1979). Most commonly heard were clicks with high repetition rates. There were few whistles, especially compared with other oceanic dolphins. The sounds of southern right whale dolphins have not been described.

Parasites and Disease

Woodhouse *et al.* (1985) and Cowan *et al.* (1986) provided the only detailed information on pathology of northern right whale dolphins, based on eight and six stranded specimens, respectively. They reported heart scars, lung abcesses and inflammation, pulmonary oedema, ulceration, and brain lesions in some specimens.

Published parasite records for both species are reviewed in Table 5. Effects of most parasites are largely unknown, but the trematode fluke *Nasitrema* sp. can cause major damage to the air sinuses, inner ears, and brain, and has been

TABLE 5 Parasites of right whale dolphins

Location	Species	Sources
Lissodelphis borealis		
Brain	*Nasitrema* sp.	1, 2, 3
Air sinus/ears	*Crassicauda* sp.	1, 3
	Nasitrema sp.	1, 3, 4
	Nasitrema globicephalae	1, 5
Stomach	*Anisakis* cf. *simplex*	1, 3
Blubber	*Phyllobothrium* sp.	1, 6, 7
	Phyllobothrium delphini	8
Muscle	*Sarcosporidia* sp.	3
Peritoneum	*Monorygma grimaldii*	1
External	*Xenobalanus* sp.	1
	Penella sp.	1, 9
Lissodelphis peronii		
Air sinuses	*Nasitrema* sp.	10, 11
Lungs	*Stenurus* sp.	10
Stomach	*Anisakis simplex*	10, 12, 13
	Unidentified trematode	10
Colon	*Strobilocephalus triangularis*	13
Intestine	*Tetrabothrium forsteri*	13
Liver	*Orthosplanchus antarcticus*	12
	Delphinicola tenuis	13
Blubber	*Phyllobothrium* sp.	12
	Phyllobothrium delphini	10

[1]Dailey and Walker, 1978; [2]Dailey, 1985; [3]Cowan *et al.*, 1986; [4]Walker, 1975; [5]Neiland *et al.*, 1970; [6]Dailey and Brownell, 1972; [7]Woodhouse *et al.*, 1985; [8]Testa and Dailey, 1977; [9]Leatherwood and Walker, 1979; [10]Van Waerebeek and Oporto, 1990; [11]Reyes and Brito, 1990; [12]Baker, 1981; [13]Fernandez, 1987.

implicated as a factor in the stranding and death of some animals (Ridgway and Dailey, 1972; Walker, 1975).

Live Maintenance

Due to the difficulty of capturing and maintaining these open-ocean species, there have been few attempts to live capture right whale dolphins (Mitchell, 1975). One northern right whale dolphin survived in captivity for 15 months (Walker, 1975), but all other captives lived less than 3 weeks (Wood, 1973; Walker, 1975; Reeves and Leatherwood, 1984). There have been no reported attempts to live capture southern right whale dolphins (International Whaling Commission, 1984).

Human Effects

Directed fisheries

Northern right whale dolphins were occasionally taken by nineteenth century whalers (Mitchell, 1975). In the western Pacific, coastal fisheries off Japan have taken them for many years, with 465 reported killed in the harpoon fishery in 1949 (Wilke *et al.*, 1953). Although this fishery mainly targets other small cetaceans, northern right whale dolphins continue to be taken (Miyazaki, 1983).

Southern right whale dolphins were also taken occasionally by whalers in the last century, primarily for their meat (Mitchell, 1975; Cruickshank and Brown, 1981; Goodall and Galeazzi, 1985). They are reportedly infrequently caught off the coasts of Peru and Chile, where they are used as food or crab bait (Aguayo, 1975; Torres and Aguayo, 1979; Goodall and Cameron, 1980; Van Waerebeek and Reyes, 1990).

By-catches

A few incidental catches of northern right whale dolphins occur in purse-seine operations in Japan and the Soviet Union (Klumov, 1959; Ohsumi, 1972), and small numbers have been killed in commercial and experimental salmon drift-net operations in the western and central Pacific (International North Pacific Fisheries Commission, 1981, 1982; International Whaling Commission, 1989). The North Pacific squid driftnet fleets of Japan, Taiwan, and South Korea are known to take northern right whale dolphins (International North Pacific Fisheries Commission, 1990). Total numbers killed in the late 1980s were estimated at about 15 000–24 000 per year, and this mortality is considered to have depleted the population to 24–73% of its pre-exploitation size (Mangel, 1993). Northern right whale dolphins have also been observed entangled in net debris in the western Pacific (Gooder, 1989). The total reported take of northern right whale dolphins by Japan in 1987 was 261 individuals, but this is likely an underestimate of the true numbers taken (International Whaling Commission, 1989).

Although there have been no directed fisheries for northern right whale dolphins in the eastern Pacific, they have been killed incidentally in other activities. Norris and Prescott (1961) and Beach *et al.* (1985) reported beach-stranded specimens that had been shot. Small numbers have been reported taken in American drift nets set for sharks and swordfish off southern California (Diamond *et al.*, 1987), and Oregon and Washington (Stick and Hreha, 1989). A short-lived Canadian experimental driftnet fishery for flying squid killed a total of 13 in 1986 and 1987 (Baird and Stacey, 1991).

Since 1989, there has been evidence of a significant incidental catch of southern right whale dolphins in the rapidly developing swordfish gillnet fishery off northern Chile (see Van Waerebeek *et al.*, 1991).

Pollution

The effects of habitat degradation and pollution on right whale dolphins are unknown, but as Baird and Stacey (1991) pointed out for the northern species, their pelagic habitat is probably safer from human effects than coastal areas are. We know of no published accounts of pollutant levels in right whale dolphins; however, high concentrations of environmental contaminants have been found in other pelagic small cetaceans (O'Shea *et al.*, 1980). The seasonal shoreward movements of right whale dolphins may put them at increased risk during certain times of the year.

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