Stenella longirostris (Gray, 1828)

Spiner Dolphin


CONTEXT AND CONTENT. Order Cetacea, Suborder Odontoceti, Family Delphinidae, Subfamily Delphininae (Fraser and Purves, 1960). Genus Stenella contains five species (Mead and Brownell, 1993). Three subspecies are recognized (Perrin, 1990):

S. l. longirostris (Gray, 1828:1). Type locality unknown. Deep pelagic waters of the tropical Atlantic Ocean; Indian Ocean; and western, southern and central Pacific Ocean.

S. l. orientalis (Perrin, 1990:457). Type locality “ca. 120 km off the coast of Guatemala in the eastern tropical Pacific.” Offshore eastern Pacific Ocean.

S. l. centroamericanus (Perrin, 1990:461). Type locality “9°47’ N, 85°42’ W (Gulf of Nicoya, Pacific coast of Costa Rica).” Coastal eastern Pacific Ocean from Gulf of Tehuantepec in southern Mexico to Gulf of Panama.

DIAGNOSIS. The skull can be confused with those of two other species in the genus (S. coeruleoalba and S. cymene) and Delphis; all have a relatively long and narrow, dorsoventrally flattened rostrum, a large number of small slender teeth (about 40–60 in each row), medially convergent premaxillae, and sigmoid ramus (Heyning and Perrin, 1994; Perrin et al., 1981). It differs from Delphis in lacking strongly defined palatal grooves. The rostrum is narrower at the base (57–84 mm—Perrin and Gilpatrick, 1994) than in S. coeruleoalba (93–120 mm—Perrin et al., 1994a). Tooth counts and all skull measurements marginally overlap those of S. cymene (Perrin and Mead, 1994), but the skull of S. longirostris is proportionately longer and narrower (Perrin et al., 1981).

Externally (Fig. 1), the rostrum is relatively long and narrow and with a distinct demarcation from the melon, as in the four other Stenella species, Delphinus, and Tursiops. It lacks the distinctive cross-cross lateral color pattern diagnostic of Delphinus (Heyning and Perrin, 1994). It differs from sympatric Tursiops, S. attenuata, T. frontalis, and S. coeruleoalba in having a triangular or subtriangular (vs. strongly falcate) dorsal fin. It also differs from Tursiops in having a longer, more slender rostrum, from adults of S. attenuata and T. frontalis in lacking dorsal spots (although some specimens of T. frontalis from the offshore North Atlantic may also lack spots—Perrin et al., 1987; Perrin et al., 1994b), from S. attenuata in lacking a stripe from flipper to gape, and from S. attenuata in lacking the complex system of lateral eye-to-anus stripe with subtending stripe diagnostic of that species. The shoulder blaze typical of Tursiops and S. coeruleoalba is usually absent. The tripartite color pattern in S. l. longirostris is very similar to that of S. cymene, but it lacks a “moustache” mark on the rostrum and the margins of the flipper stripe are parallel rather than anteriorly convergent. It is also proportionately more slender and has a proportionately longer rostrum than S. cymene (Perrin et al., 1981).

GENERAL CHARACTERS. The spinner is a small and slender dolphin, length of 1.824 sexually mature adults ranged from 129 to 235 cm (Perrin and Gilpatrick, 1994), and weight in 33 adults ranged from 23 to 78 kg (Perrin et al., 1989). Ranges of other external measurements follow (in cm, with sample sizes in parentheses; does not include dwarf form from Southeast Asia described below): tip of upper jaw to apex of melon 11–20 (132), tip of upper jaw to end of gape 23–33 (136), tip of upper jaw to umbilical scar 75–101 (121), tip of upper jaw to tip of dorsal fin 83–117 (95), girth at axilla 67–98 (122), anterior length of flipper 25–30 (35), width of flipper 8–11 (35), span of flukes 30–53 (125), height of dorsal fin 15–25 (33—Perrin and Gilpatrick, 1994).

The most common color pattern (as in S. l. longirostris) is tripartite, consisting of a dark gray dorsal field or cape, lighter lateral field, and white or very light-gray ventral field (Fig. 1; Perrin, 1972; Perrin and Gilpatrick, 1994). The ventral margin of the cape dips over the eye, is lowest below the dorsal fin, passes dorsally about halfway between the dorsal fin and the flukes, and is parallel to the ventral margin of the lateral field on the anterior half of the animal. A medium-gray flipper stripe extends anteriorly to the eye and is usually set off ventrally by a narrow light line. A dark eye stripe of variable width passes forward from the dark eye spot to or near the apex of the melon. In some individuals it may meander onto the top of the rostrum (Perrin, 1997). The blowhole stripe is relatively indistinct and is bordered by narrow light lines. A mesial dark stripe on the rostrum broadens anteriorly to yield a black-tipped beak. A dark lip mark borders the gape. The white ventral field may be flecked with gray.

The tripartite nature of the color pattern may be obscured by a dark dorsal overlay in S. l. orientalis and S. l. centroamericanus in the far-eastern Pacific (Perrin, 1972, 1990), and the dorsal fin in large adult males of these subspecies may be relatively large and erect or distantly canted forward (Perrin, 1990; Perrin and Gilpatrick, 1994). The forward cast of the dorsal fin is correlated with development of a large ventral protuberance just behind the anal region. More offshore spinners from further to the west are intermediate in coloration between the orientalis/centroamericanus pattern and that typical of S. l. longirostris (Perrin et al., 1991). The dorsal overlay is less dense and less extensive, yielding a faint cape and a more extensive ventral field. The margin of the ventral field may be speckled. These highly variable animals, called “white-belly spinner dolphins”, may represent hybridization between the distinctive spinner dolphins to the east and those in the central

FIG. 1. Gray’s spinner dolphin (Stenella longirostris longirostris) from the Caribbean. Photograph courtesy of H. E. Winn.
Pacific; this is supported inter alia by greater variability in length (larger SD) as well as coloration than in waters to the east and west (Perrin et al., 1991).

The spinner dolphin varies geographically in size as well as coloration (Dizon et al., 1994; Perrin and Gilpatrick, 1994; Perrin et al., 1985). In the eastern Pacific, average lengths of adult females of S. l. orientalis and S. l. centroamericanus were 171 cm (n = 687, range 152–193, SD 6.0) and 199 cm (n = 12, range 193–211), respectively. Seventeen adult females of S. l. longirostris from the Gulf of Mexico averaged 189 cm (177–204) and 17 males averaged 193 cm (173–208). Recent aerial photogrammetry of spinner dolphins around the Ilo Maristas Island in Mexican waters suggest that the “eastern” spinners there may differ in size from those farther to the south and offshore (Perryman and Westlake, 1998). A dwarf form that occurs in the Gulf of Thailand and elsewhere in inner Southeast Asia (Perrin and Dolar, 1996; Perrin et al., 1989; Perrin, in litt.) may reach sexual and cranial maturity at 130 cm or less. The few external data available for this undescribed subspecies suggest that the appendages (dorsal fin, flippers, and flukes) are proportionately larger than for other spinner dolphins.

The skull (Fig. 2) typically has a relatively small braincase, long rostrum, very shallow palatal grooves, small temporal fossa, sigmoid ramus, and about 50 small teeth in each row. Ranges of tooth counts and selected measurements follow for specimens from around the world (in mm, with sample size in parentheses—Perrin and Gilpatrick, 1994): upper teeth, 44–64 per row (128); lower teeth, 42–62 per row (150); condylodial length, 335–464 (112); length of rostrum, 213–304 (112); length of rostrum at base, 57–84 (119); width of rostrum at ¾ length, 24–39 (106); preorbital width, 111–137 (118); zygomatic width, 121–171 (116); parietal width, 103–140 (117); length of temporal fossa, 41–61 (119); height of temporal fossa, 29–50 (118); length of ramus, 257–399 (116); tooth diameter, 2.1–3.0 (32). Sexual dimorphism is slight, e.g., less than in S. attenuata (Douglas et al., 1986).

Geographic variation in the skull is pronounced (Douglas et al., 1986, 1992; Perrin, 1975, 1990; Perrin et al., 1989), primarily in overall skull size and proportional length of the rostrum. Skulls of animals from the pelagic eastern Pacific tend to be smaller and have shorter rostra than those of specimens from the coast of Central America and from the Central and South Pacific to the west. Similar variation may occur in other oceans, but the large samples necessary for its detection are not yet available. The smallest adult skulls known (also with the lowest tooth counts) are from the Gulf of Thailand (Perrin et al., 1989). Averages (±SD for samples ≥30) of tooth counts and selected skull measurements for the two eastern Pacific subspecies and the dwarf form from Thailand follow (in mm, with sample size and range in parentheses): S. l. orientalis, upper teeth per row, 52.6 ± 3.16 (32, 46–61); lower teeth per row, 38.5 ± 2.39 (37, 35–46); condylodial length, 386.5 (26, 331–407); length of rostrum, 245.5 (26, 218–262); width of rostrum at base, 72.1 (26, 66–77); width of rostrum at ¾ length, 30.5 (26, 26–36); preorbital width, 132.3 (29, 127–138); zygomatic width, 146.4 (29, 139–153); parietal width, 125.9 (29, 119–132); length of temporal fossa, 48.5 (29, 41–57); height of temporal fossa, 30.6 (29, 22–37); length of ramus, 329.1 (27, 301–348); S. l. centroamericanus, (n = 5) for all counts and measurements) upper teeth per row, 55.3 (53–57); lower teeth per row, 50.3 (51–59); condylodial length, 428.6 (416–439); length of rostrum, 279.0 (266–288); width of rostrum at ¾ length, 29.8 (26–32); preorbital width, 134.2 (131–138); zygomatic width, 150.4 (149–152); parietal width, 128.8 (127–130); length of temporal fossa, 49.6 (46–57); height of temporal fossa, 36.4 (34–42); length of ramus, 369.6 (358–379); dwarf form, lower teeth per row, 45.4 (40, 43–46); condylodial length, 342.5 (n = 4 for all measurements, 335–352); length of rostrum, 219.8 (215–224); width of rostrum at base, 61.0 (57–66); width of rostrum at ¾ length, 25.0 (24–27); preorbital width, 115.5 (111–120); zygomatic width, 125.8 (121–130); parietal width, 104.8 (103–108); length of temporal fossa, 45.8 (42–49); height of temporal fossa, 38.0 (36–40); length of ramus, 293.3 (287–303, Perrin, 1990; Perrin and Dolar, 1996; Perrin et al., 1989).

The number of vertebrae ranges from 69 to 77 (n = 90); the typical formula is 7C, 15T, 18L, 22CA, total 73. The number of vertebrae may vary geographically; seven spinners from the Gulf of Thailand had 69–71 (average 69.7), 38 from the Philippines had 70–73 (average 71.6), and 50 from the eastern Pacific had 70–77 (average 73.9, Perrin and Dolar, 1996; Perrin and Gilpatrick, 1994).

DISTRIBUTION. *Stenella longirostris* is pantropical, inhabiting tropical, subtropical, and some warm-temperate waters of the world (Fig. 3; after Jefferson et al., 1993 and taking into account data in Balanche et al., 1996; Chou, 1994; Corbett, 1994; Dolar and Perrin, 1996; Eyre, 1995; Leatherwood et al., 1982; Miyashita et al., 1996; Perrin and Gilpatrick, 1994; Reiner et al., 1996; Secchi and Siciliano, 1995; Shimada and Pastene, 1995; Smith et al., 1995; Wang, 1996; Zhou et al., 1995). For some areas, e.g., the eastern tropical Pacific, the distribution is known in some detail. For other regions within the overall likely range, very little is known, e.g., the central Indian Ocean and the Southeast Atlantic (Perrin and Gilpatrick, 1994). It is, however, primarily a tropical species and does not occur in subantarctic waters of South America as indicated by Marucci and Pilleri (1971). An extralimital record from New Zealand (Perrin and Gilpatrick, 1994) is still well north of subantarctic waters. To date, this species has not appeared in the fossil record.

FORM AND FUNCTION. Anatomical and physiological descriptions include those of the esophagus and stomach (Harrison et al., 1970), small intestine (Harrison et al., 1977), gonads (Harrison et al., 1972), gross cephalic anatomy ( Cranford et al., 1996), cranial nucleus ellipticus (Nieto and Nieto, 1984), islets of Calleja (Nieto and Nieto, 1986), countercurrent heat exchange vascular system (Savol et al., 1992), cutaneous vascular structure (Zukoski, 1974), kidney (Cave and Aunonier, 1966), cornea (Dral and Dudok van Heel, 1974), hemoglobin (Baluda et al., 1972; De Monte and Pilleri, 1979; Sharp, 1975), enzymes (Malvin and Vander, 1967), and
Fig. 3. Geographic distribution of the spinner dolphin. Modified from Jefferson et al. (1993). A = range of *S. l. longirostris*, B = *S. l. orientalis*, C = *S. l. centroamericanus* (coastal), D = known range of dwarf form (Gulf of Thailand).

ONTOGONY AND REPRODUCTION. The system of stripes on the head (the “bridle”) develops from a single anlage consisting of a band across the back of the head in fetuses of roughly 100 mm (Perrin, 1997). Postnatal development of the skull and postcranial skeleton was described by Perrin (1975) and embryology of the terminal airway system by Drabek and Koopman (1963).

Growth and reproduction are summarized in Perrin and Gilpatrick (1994). Gestation is ca. 10 months. Average length at birth in *S. l. orientalis* is 77 cm, and average length at one year is 133 cm; for the hybrid whitebelly form, average length at birth is 76 cm and at one year, 137 cm (Perrin and Henderson, 1984; Perrin and Reilly, 1984; Perrin et al., 1977). Length of nursing is 1–2 years. Calves are born at ca. 3-year intervals. Both males and females undergo a growth spurt at about the onset of puberty. Females on average attain sexual maturity at about 165–180 cm and 4–7 years, depending on the population and the hypothesis of tooth-layer deposition rate. Males undergo a sharp increase in testis weight at body length of 160–180 cm and age 7–10 years, however, some large and externally mature animals have immature testes or ovaries; social factors may influence sexual maturation. Ovulation may be spontaneous (Renshawe et al., 1980). Ovulation rate is variable with age and population but is about once per year in mature animals. Breeding is seasonal, more sharply so in some regions than in others (Barlow, 1984). Seasonal hormonal cycles have been demonstrated for both males and females in *S. l. longirostris*, with correlated changes in some behaviors involving genital contact (Wells, 1984; Wells and Norris, 1994). The most likely breeding system is polygyny (Wells and Norris, 1994). Males of the highly dimorphic eastern spinner attain greater testis size than males of the hybrid whitebelly form (Perrin et al., 1977); this may indicate some difference in breeding systems in the two populations, because, as pointed out by Kemagy and Trombiak (1986), pronounced sexual dimorphism is generally inversely correlated with sperm competition (trend to polyandry).

Approximately 1% of adult females are postreproductive, as evidenced by shrunk, non-active ovaries containing scars of previous ovulatory function. The reason for this is unknown but may be related to some non-reproductive social function of elderly females that contributes to inclusive fitness.

Almost nothing is known of the biology of the dwarf form of the spinner dolphin in Southeast Asia, but four specimens, probably sexually mature, from the Gulf of Thailand ranged from 129 to 137 cm (range for thousands of specimens from other parts of the world was 152–235 cm—Perrin et al., 1989).

ECOLOGY. Spinner dolphins are usually associated with inshore waters, islands, or banks, but in the eastern tropical Pacific they occur in large schools hundreds of miles from the nearest land in waters typified by unusual conditions of shallow mixed layer, shoal and sharp thermocline, and relatively low annual variation in surface temperature (Au and Perryman, 1985). They are usually seen together with pantropical spotted dolphins (*S. attenuata*), yellowfin tuna (*Thunnus albacares*), and birds of several species (Norrish, 1994; Perrin, 1968, 1969). Reilly (1990) and Fiedler and Reilly (1994) found seasonal shifts of the preferred habitat of spinner dolphins, as well as year-to-year variation in habitat distribution, and differences in the habitats of the eastern and western bellies populations (the former preferring regions of relatively more shoal thermocline). The dwarf spinner of Southeast Asia apparently inhabits shallow coral reef areas.

Predators include sharks and probably killer whales (*Orcinus Orca*), as well as possibly false killer whales (*Pseudorca crassidens*), pygmy killer whales (*Feresa attenuata*), and short-finned pilot whales (*Globicephala macrocephalus*—Norrish, 1994; Perrin and Gilpatrick, 1994). Parasites may cause direct or indirect mortality (Perrin and Powers, 1980). External commensals include the remora *Remieia australis* and the stalked barnacle *Conchoderma aurita*. Internal parasites include the nematodes *Anisakis simplex*, *Halocercus delphini*, and *Mastigonomia stellata*; the trematodes *Zoalophotrema pacificum*, *Campula rochebruni*, and *Naistrema*; the cestodes *Tetraphyllus forsteri*, *Stroblocephalus triangularis*, *Phyllobothrium delphini*, and *Monorygma grimaldi*; and the acanthocephalans *Bulusoma vasculosum* and *B. balanae* (Perrin and Gilpatrick, 1994). Natural diseases and pathology recorded in wild spinner dolphins include irregular thickening of walls of small arteries and arterioles, degeneration and scarring of the myocardium, focal myocarditis, basophilic degeneration, lung lesions caused by *Halocercus delphini*, myxoid neurofibromas, neoplasm of islet cell origin in the pancreas, focal interstitial inflam-
mation of the kidney, infected rickets, glomeruloclesclerosis, arte-
riosclerosis, neoplasm of tubular epithelial origin, and splenic changes indicative of reaction to an infectious agent (Perrin and Gilpatrick, 1994).

The diet includes primarily small (<20cm) mesopelagic fishes, squid, and sergestid shrimps obtained in dives to depths of at least 200–300 m (Perrin and Gilpatrick, 1994). Prey items identified from stomach contents in the eastern tropical Pacific and Hawaii include fishes of the families Mętynophiδe, Pliothetidię, Breg-
macerotidae, Meleagriphii, Bathyagridae, Scolepidiidae, Stre-
mateidae, Paralipidae, Aponidae, Carapidae, Holocentridae, and Bythitidae; cephalopods of the families Ocytocheițae, Ome-
matiidae, Sphincteridae, Chirolophiiidae and Lagenidię; and small crustaceans of the families Gammaridae, Enypniatidae, Sergestidae, Pasiphaeidae, and Ophiolepidae (Perrin and Gilpat-
rick, 1994; Würsig et al., 1994a). The dwarf spinner dolphin in Southeast Asia may feed primarily on reef and shallow-water benthi-
crustaceans (Perrin et al., 1989).

Spinner dolphins are killed incidentally in large numbers in fish-
ing nets around the world, most notably in tuna purse seines in the
eastern tropical Pacific (Barlow et al., 1995; Bjarne et al., 1994; 
Blaylock et al., 1995; Palacios and Gernrodde, 1996; Perrin and Dolar, 1996; Perrin et al., 1994c, 1996; Wade, 1993), where mor-
tality ranged into the tens of thousands annually during the 1980s after even larger kills in the 1960s and 1970s. The population of S. l. orientalis has been estimated to have been reduced by at least two-thirds from its original size in 1960 (Wade, 1993, 1994). Trends in some life-history parameters consistent with positive reproductive
response to population decline have been detected, but sur-
nvivance rate has apparently declined, the reverse of what would be expected (Chivers and Demaster, 1994).

Contaminants assessed in spinner dolphins include persistent organochlorine residues (India—Tanabe et al., 1990; BTCs (In-
dia—Swata et al., 1990); Hg, DDT, dieldrin, and PCBs (Gaskin et al., 1974); Hg, Cd, Cr, Cu, Mn, Ni, Se, Zn, SDDT, and PCBs (east-
ern tropical Pacific—André, 1988), and radioactive isotopes of Pb, Cs, and K (Calmet et al., 1992). Tanabe et al. (1988) described capacity and mode of PCB metabolism.

BEHAVIOR. The behavior of the spinner dolphin has been intensively studied in Hawaiian waters by Norris et al. (1994c), and the following is briefly abstracted from their reports.

Spinner dolphins leap high out of the water and rotate as many as 14 times longitudinally (Hester et al., 1963). The function of this spinning behavior is not known, but it may relate to commu-
nication (Norris et al., 1994b). A number of other aerial behaviors were described by Norris et al. (1994d), including nose-outs, tail slaps, flips, head slaps, “salmon leaps,” and side and back slaps.

Spinner dolphins in Hawaii usually return from offshore noctur-
mal feeding grounds to shallow bays where they spend the day in a reduced state of activity (Würsig et al., 1994b). During feeding, they may move some distance along the shore, so the same animals may not be present in the same bay on two successive days. Not all animals go into rest coves every day; some move slowly along the shore between successive nights. Maximum net movement ob-
served in Hawaiian waters was 113 km over 2220 days. In the eastern Pacific, seven tagged spinner dolphins moved minimum distances ranging from 12 nautical miles to 16 to 275 nautical miles over 395 h (Perrin and Gilpatrick, 1994).

Social organization is relatively fluid (Norris and Johnson, 1994). In the ca. 1,000 spinner dolphins off the Island of Hawaii (Ostman, 1994), spinner dolphin society is composed partly of familial units and more broadly of learned associations beyond the family group. Mother-calf bonds are persistent. Mating appears to be promiscu-
ous. Individuals move freely among several sets of companions over periods of minutes, hours, days or weeks. Adult males form coalitions of from a few to about a dozen individuals; these are of
unknown function (Johnson and Norris, 1994), although they may form the several associated core groups that make up a school (Ostman, 1994). Aquatic emissions include wailing calls, which may function in basic organizational and structural signals to regulate school or-
ganization and function; burst-pulse signals, thought to be evocative and vocative in nature; and echolocation click trains (Brownlee and Norris, 1994).

GENETICS. G-band karyotypes are identical to those of S. frontalis and S. attenuata, except for minor band differences ow-

ing to heterochromatin variation (Stock, 1981). However, the C-
band karyotype is sharply different from those of both species, which closely resembled each other. RFPL haplotypes of a portion of the control region of mtDNA were not found to correlate with morphotypic geographic differences in the eastern Pacific, but all were different from haplotypes from northern Australia (Dixon et al., 1991). Analysis of sequences for the same mtDNA region yield-
ed similar results (Garcia-Rodriguez, 1995). The northern Australia sample had low diversity of sequence divergence and low levels of haplotype diversity. The eastern Pacific sample had high levels of haplotype diversity and haplotype sharing between schools, with no concordance with geographical morphotype.

Based on phylogenetic analysis of the entire cytochrome B gene (mtDNA) for all the dolphin species in the genus Stenella, the species in the genus Stenella do not comprise a monophyletic group (LeDuc, 1997) and thus are an artificial taxon. In the paraphyletic array, both S. longirostris and S. attenuata are separated from S. clymene, S. frontalis, and S. coeruleoalba, which are more closely allied with Delphinus and Tursiops. Several polytomies in the best consensus tree resulting from this phylogenetic analysis have yet to be resolved.

REMARKS. Hershkovitz (1966) placed Steno consimilis Malm, 1871 in the synonymy of the spinner dolphin. However, the holotype skull as illustrated by Malm is that of a typical pantropical spotted dolphin, S. attenuata (Perrin et al., 1987).

Other common names are (English) long-snouted dolphin, long-
snouted spinner dolphin, long-beaked dolphin, small-headed dol-
phin, Java Sea dolphin or Ceylon dolphin, Benga-
110
l Indian dolphin, spinner porpoise, spinning porpoise, spinning dol-
phin, spinner, whitebelly spinner porpoise, and whitebelly spinner dolphin; (German) langschwanz Delphin, ostpazifischer Delphin; (French) dauphin à ventre rose; (Spanish) delfín torallón, delfín charumbelo, delfín giradór, delfín de hocico largo, and falsol del-
fín; (Portuguese) golfinho rotador; (Japanese) hoshinaga iruka; (Russian) dlinnososty delphin and vertyashchisyya delfin; (Afri-
kaans) Toldolfijn; (Bahasa Indonesia) temu kira; (in Philippines and Indonesia) lumba-lumba; and (Singhalese) malla.

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MAMMALIAN SPECIES 599


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