disturbed, a mother vocalizes to her pup and the pup responds with a bawl sound and moves close to the mother. An observation of a newborn pup reported it swimming in icy water from one floe to another. Pups wean after about 1 month of nursing.

Subadult seals are rarely seen as they are presumably in open water north of the pack ice. Longevity is unknown, but is at least 21 years. The exact age of sexual maturity is uncertain, but based on analysis of reproductive tracts is estimated at 3–4 years of age in females and 2–7 years in males. At birth, pups are 105–120 cm in length and weigh 17–27 kg.

VI. Interactions with Humans

Ross seals have little fear of humans because there are no natural land predators in Antarctica (unlike pinnipeds in the Arctic who adapt to polar bear predators). There is no record of extensive harvest of this species, except for scientific collection. A variety of Antarctic investigators from Britain, France, America, Soviet Union, Australia, and New Zealand reported sightings of Ross seals from ships. However, there have been no ice-camp or land-based studies of this species.

Although no major threats to Ross seal populations have been identified, changes in pack ice due to climate change may influence their pack-ice habitat and prey distribution. The Ross seal is totally protected under the Antarctic Treaty and the Convention for the Conservation of Antarctic Seals. In January 1998, the Environmental Protection Protocol to the Antarctic Treaty was ratified, implementing environmental measures such as the banning of mining and oil drilling in Antarctica for at least 50 years, along with the banning of refuse disposal and the use of pesticides in the region. Because the species inhabits dense pack ice, it is doubtful that ecotourism has an impact on it.

See Also the Following Articles

Antarctic Marine Mammals ■ Earless Seals

References

Barrett-Hamilton, G. E. H. (1901). Zoologie: Seals. Result. *In* "Voyage *S. Y. Belgica* 1897–1899. Exped. Antarctica Belge." pp. 1–20.

Erickson, A. W., Gilbert, J. R., and Ortis, J. (1971). Distributional ecology of Antarctic seals. *In* "Proceedings of the Symposium on Antarctic Ice and Water Masses" (G. Deacon, ed.), pp. 55–75. SCAR, Cambridge.

Gray, J. E. (1844). Mammalia. 1. The seals of the Southern Hemisphere. *In* "The Zoology of the Voyage of the *HMS Erebus and Terror*, 1839–1843," p. 1. E.W. Jansen, London.

Hofman, R. J., Erickson, A., and Siniff, D. B. (1973). The Ross seal (*Ommatophoca rossi*). *Publ. New Ser.*, Suppl. Paper.

King, J. E. (1969). Some aspects of the anatomy of the Ross seal (*Ommatophoca rossi*). *Brit. Ant. Surv. Sci. Rep.* **63**, 1–54.

Nowak, R. M. (1999). "Walker's Mammals of the World, Vol. II," 6th Ed. The Johns Hopkins University Press, Baltimore.

Øristland, T. (1970). Sealing and seal research in the Southwest Atlantic pack ice, September–October 1964. *In* "Antarctic Ecology" (M. W. Holdgate, ed.), Vol. 1, pp. 367–3765. Academic Press, London.

Rogers, T. L. (2003). Factors influencing the acoustic behaviour of male phocid seals. *Aquat. Mamm.* **29**, 247–260.

Reeves, R. R., Stewart, B. S., and Leatherwood, S. (1992). "The Sierra Club Handbook of Seals and Sirenians." Sierra Club Books, San Francisco.

Scheffer, V. (1958). "Seals, Sea Lions and Walruses: A Review of the Pinnipedia." Stanford University Press, Stanford, CA.

Scheffer, V. (1976). Standard measurements of seals. *J. Mammal.* **48**, 459–462.

Solyanick, G. A. (1964). Experiment in marking seals from small ships. *Sov. Ant. Exped. Bull.* **5**, 212.

Stacey, R. A. (2006). Vocalizations of Antarctic Ross seals (*Ommatophoca rossii*). Masters Thesis, Western Illinois University, Moline, IL.

Stirling, I. (1966). A technique for handling live seals. *J. Mammal.* **47**, 543–544.

Thomas, J. A., DeMaster, D. P., Stone, S., and Andriashek, D. (1980). Observations of a newborn Ross seal pup (*Ommatophoca rossi*). *Can. J. Zool.* **58**, 2156–2158.

Tikhimirov, E. A. (1975). Biology of the ice forms of seals in the Pacific section of the Antarctic. *Rapp. P. V. Reun. Cons. Int. Explor. Mer.* **169**, 409–412.

Rough-Toothed Dolphin
Steno bredanensis

Thomas A. Jefferson

I. Characteristics and Taxonomy

Rough-toothed dolphins are named for the vertical ridges, or wrinkles, on their teeth, which give them a roughened appearance. Other English common names include black porpoise, steno, and slopehead.

The rough-toothed dolphin is very distinctive when seen at close quarters. It is the only long-beaked dolphin with a smoothly sloping melon that does not contain any hint of a crease as it blends into the upper beak (Fig. 1). These dolphins are not particularly slender, and the anterior part of the body may be stocky. The large flippers are set farther back on the body than in most other small cetaceans. They are equal to about 17–19% of the body length. The dorsal fin is tall and generally only slightly falcate. Some large males have a hump of connective tissue posterior to the anus, which gives the appearance of a pronounced keel. Weight is up to 155 kg. Males grow to larger sizes than females (known maximums of 265 and 255 cm, respectively); some evidence suggests they may occasionally reach 280 cm. Females may have proportionately longer beaks (Miyazaki, 1980; Miyazaki and Perrin, 1994).

The color pattern is moderately complex but consists generally of shades of black, white, and gray (Fig. 1). The body is countershaded, with a white belly and black to dark gray back. The sides are a medium shade of gray and are separated from the darker back by the margins of a dorsal cape that is narrow between the blowhole and the dorsal fin and wider behind the fin. The lower sides and mouth area are often dotted with white patches, splotches, and spots. In warm tropical waters, the belly and the lower jaw may be tinged with pink. Some of the white spots are thought to be scars from bites inflicted by cookie-cutter sharks and perhaps squid. Young animals (Fig. 2) have a muted color pattern and generally lack the white spots (Miyazaki and Perrin, 1994).

The skull (adult CBL ~472–555 mm) can be distinguished from those of all other dolphins (except humpback dolphins, *Sousa* spp.) by their size and combination of long beak, concave rostral and maxillary margins, long mandibular symphysis, and large temporal fossae. Tooth counts can be used to distinguish them from humpback dolphins: rough-toothed dolphins have 19–26 teeth in each upper tooth row and 19–28 teeth in each lower row, and humpback dolphins usually have greater than 30. The teeth are ridged. Other differences from the skull of the humpback dolphin are the relatively large orbits

and the prominent and long cylindrical ridge on the ventral part of the frontal bones in rough-toothed dolphins (Van Waerebeek *et al*., 1999). The postcranial skeleton is heavily built, and total vertebral counts generally range from 65 to 67.

Traditionally, morphological characters have been used to infer a close relationship between the rough-toothed dolphin and two other genera of dolphins (*Sotalia* spp., the tucuxi and costero; and *Sousa* spp., the humpback dolphins). Recent genetic analyses (LeDuc *et al*., 1999) have supported the relationship with *Sotalia* (in the subfamily Stenoninae), but not with *Sousa*, which groups phylogenetically with the Delphininae. In captivity, hybrids between *Steno* and *Tursiops truncatus* (common bottlenose dolphin) have been born (Dohl *et al*., 1974).

II. Distribution and Abundance

The rough-toothed dolphin is a tropical to warm temperate species and is found in oceanic waters worldwide (Miyazaki and Perrin, 1994). For instance, it prefers waters greater than 1500-m deep off Hawaii (Baird *et al*., 2008). However, it can also be found over the continental shelf in some shallow, coastal waters (e.g., Brazil–Flores and Ximinez, 1997). Records from the Atlantic Ocean are mostly from between the southeastern United States and southern Brazil across to the Iberian Peninsula and tropical West Africa, with some (probably extralimital) records from the English Channel and the North Sea. The normal range includes the Gulf of Mexico, Caribbean Sea, and Mediterranean Sea. In the Pacific, it occurs from central Japan and northern Australia across to southern Baja California, Mexico, and southern Peru. In the eastern tropical Pacific, it is generally associated with warm tropical waters lacking major upwelling. The range includes the southern Gulf of California and the South China Sea. Records from the west coast of the continental United States and New Zealand are considered extralimital. In the poorly studied Indian Ocean, there are only a few scattered records, but the species probably has an extensive distribution there north of about 20°S.

There are no estimates of global abundance, and surveys to estimate abundance have not been conducted in most parts of the species' range. However, about 985 occur in the northern Gulf of Mexico (Mullin and Fulling, 2004) and about 146,000 are found in the eastern tropical Pacific (Wade and Gerrodette, 1993). Almost nothing is known about population or stock structure in this species.

Figure 1 *A group of rough-toothed dolphins swimming just below the surface in clear waters off Hawaii showing the species' distinctive characteristics. Photo by R. W. Baird.*

III. Ecology

The ecology of the species is quite poorly studied (Miyazaki and Perrin, 1994). There have been only a few reports of feeding habits. In the wild, it feeds on a variety of fish and cephalopod species, some coastal and some oceanic. Some large fish may be taken, as suggested by the robust dentition of the species. Algae have been found in the stomachs of stranded specimens, but they may have been ingested incidentally.

Rough-toothed dolphins frequently associate with other species of cetaceans, especially other delphinids in the eastern tropical Pacific, where they also often associate with flotsam. Lone animals have been seen with short-finned pilot whales (*Globicephala macrorhynchus*) and Fraser's dolphins (*Lagenodelphis hosei*) in the Sulu Sea.

Little is known of diseases and pathology, but Japanese animals have been observed with osteopathological conditions. Only a handful of internal parasites have been recorded, although there are undoubtedly others. Externally, cyamid whale lice have been observed, and the cookie-cutter shark is a partial predator.

IV. Behavior and Physiology

Detailed, long-term behavioral ecology studies on rough-toothed dolphins have only been conducted in the past decade or so, and our

Figure 2 *A rough-toothed dolphin mother and calf surface in Hawaiian waters. The narrow dorsal cape and smoothly sloping forehead show well in this photo. Photo by R. W. Baird.*

knowledge is only beginning to accumulate. There now have been such studies in several areas, including the Canary Islands, Caribbean (Honduras), and Hawaii (Ritter, 2002; Gotz *et al.*, 2006; Kuczaj and Yeater, 2007). They are found in moderate-sized groups, most commonly of 10–20, although larger groups have been seen in some areas—up to 50 in the Canary Islands (Ritter, 2002), over 50 in the eastern tropical Pacific, 300 in Hawaii, and 160 in the Mediterranean. Mass STRANDINGS have been recorded in several areas.

These animals are not generally fast swimmers and they often appear rather sluggish in the wild. They do ride bow waves and are known for their habit of skimming along the surface at moderate speed with a distinctive splash. Synchronous swimming in tight formation is common, and recently it has been suggested to facilitate "eavesdropping" on the echolocation clicks of other individuals (Gotz *et al.*, 2006; Kuczaj and Yeater, 2007). Although not highly acrobatic, various leaps and other aerial behaviors have been seen. Photoidentification of individual dolphins has only recently been conducted, and preliminary results suggest that rough-toothed dolphins may have more stability in their associations than do other species of small delphinids (Kuczaj and Yeater, 2007). Few studies of site fidelity have been conducted, but in the Hawaiian Islands, site fidelity appears to be high and inter-island movements relatively rare (Baird *et al.*, 2008).

Although the maximum recorded dive was only to 70 m, rough-toothed dolphins can probably dive much deeper than this. Behavioral and morphological evidence suggests that they are well adapted for long, deep dives. Submergences of up to 15 min have been recorded. A variety of clicks and whistles have been recorded from these dolphins. Highly directional ECHOLOCATION clicks, with some pulses as high as 200 kHz, are known.

The physiology of the rough-toothed dolphin has not been well studied, and not much is known, other than that they have some anatomical adaptations that tend to be associated with deep-diving.

V. Life History

Detailed studies of life history have only been conducted in Japanese waters. There, males reach sexual maturity at about 14 years and 225 cm, and females at 10 years and 210–220 cm. The maximum age is 32–36 years, although some animals may live significantly longer (Miyazaki, 1980; Miyazaki and Perrin, 1994). Length at birth is thought to be about 1 m.

VI. Interactions with Humans

Rough-toothed dolphins have been held captive in a number of oceanaria, and some success has been encountered in keeping them alive in the captive environment, especially in Hawaii (Dohl *et al.*, 1974). One lived for over 12 years in captivity. They have been found to be bold and inventive, and one "creative porpoise" at Sea Life Park in Hawaii astounded its trainers by grasping the concept of inventing novel behaviors (Pryor *et al.*, 1969). Although they generally do not survive long, several live-stranded animals have also been kept-captive, and some have been released back to sea.

Although not generally the major target, rough-toothed dolphins have been taken in directed dolphin fisheries in Japan, Sri Lanka, Indonesia, the Solomon Islands, Papua New Guinea, St. Vincent, West Africa, and possibly St. Helena in the South Atlantic (Miyazaki and Perrin, 1994). Probably much more significant is the incidental kill of dolphins in fishing nets. Takes in tuna purse-seine nets are known for the eastern tropical Pacific, and gillnet catches have been documented at least in Sri Lanka, Brazil, and the offshore North Pacific. This is one of the main species involved in stealing bait from fishermen's hooks off Hawaii, and sometimes animals get caught on the hooks as well (Nitta and Henderson, 1993). Undocumented catches probably occur in most other areas of the range as well.

Habitat degradation impacts and effects of pollutants are probably somewhat less severe for this species than for other, more-coastal small cetaceans. Although little directed work has been done on environmental contaminants, relatively low levels of PCBs and DDTs have been recorded from the few specimens examined so far (O'Shea *et al.*, 1980). However, conservation-oriented studies are almost nonexistent, and therefore the uncertainty that exists about population status for this species should be acknowledged.

See Also the Following Articles

Captivity ■ Delphinids ■ Skull Anatomy ■ Teeth

References

Baird, R. W., Webster, D. L., Mahaffy, S. D., McSweeney, D. J., Schorr, G. D., and Ligon, A. D. (2008). Site fidelity and association patterns in a deep water dolphin: Rough-toothed dolphins (*Steno bredanensis*) in the Hawaiian Archipelago. *Mar. Mamm. Sci.* **24**, 535–553.

Dohl, T. P., Norris, K. S., and Kang, I. (1974). A porpoise hybrid: *Tursiops X Steno*. *J. Mammal.* **55**, 217–221.

Flores, P. A. de C., and Ximinez, A. (1997). Observations on the rough-toothed dolphin *Steno bredanensis* off Santa Catarina Island, southern Brazilian coast. *Biotemas* **10**, 71–79.

Gotz, T., Verfub, U. K., and Schnitzler, H. U. (2006). "Eavesdropping" in wild rough-toothed dolphins (*Steno bredanensis*). *Biol. Lett.* **2**, 5–7.

Kuczaj, S. A., and Yeater, D. B. (2007). Observations of rough-toothed dolphins (*Steno bredanensis*) off the coast of Utila, Honduras. *J. Mar. Biol. Assoc. U.K.* **87**, 141–148.

LeDuc, R. G., Perrin, W. F., and Dizon, A. E. (1999). Phylogenetic relationships among the delphinid cetaceans based on full cytochrome B sequences. *Mar. Mamm. Sci.* **15**, 619–638.

Miyazaki, N. (1980). Preliminary note on age determination and growth of the rough-toothed dolphin *Steno bredanensis*, off the Pacific coast of Japan. *Rep. Int. Whal. Comm. Spec. Issue* **3**, 171–179.

Miyazaki, N., and Perrin, W. F. (1994). Rough-toothed dolphin *Steno bredanensis* (Lesson, 1828). *In* "Handbook of Marine Mammals" (S. H. Ridgway, and R. Harrison, eds), Vol. 5, pp. 1–21. Academic Press, San Diego, California.

Mullin, K. D., and Fulling, G. L. (2004). Abundance of cetaceans in the oceanic northern Gulf of Mexico, 1996–2001. *Mar. Mamm. Sci.* **20**, 787–807.

Nitta, E. T., and Henderson, J. R. (1993). A review of interactions between Hawaii's fisheries and protected species. *Mar. Fish. Rev.* **55**, 83–92.

O'Shea, T. J., Brownell, R. L., Clark, D. R., Walker, W. A., Gay, M. L., and Lamont, T. G. (1980). Organochlorine pollutants in small cetaceans from the Pacific and South Atlantic oceans, November 1968-June 1976. *Pestic. Monit. J.* **14**, 35–46.

Pryor, K. W., Haag, R., and O'Reilly, J. (1969). The creative porpoise: Training for novel behavior. *J. Exp. Anal. Behav.* **12**, 653–661.

Ritter, F. (2002). Behavioural observations of rough-toothed dolphins (*Steno bredanensis*) off La Gomera, Canary Islands (1995–2000), with special reference to their interactions with humans. *Aquat. Mamm.* **28**, 46–59.

Van Waerebeek, K., Gallagher, M., Baldwin, R., Papastavrou, V., and Al-Lawati-Samira, M. (1999). Morphology and distribution of the spinner dolphin, *Stenella longirostris*, rough-toothed dolphin, *Steno bredanensis*, and melon-headed whale, *Peponocephala electra*, from waters off the Sultanate of Oman. *J. Cetacean Res. Manag.* **1**, 167–178.

Wade, P. R., and Gerrodette, T. (1993). Estimates of cetacean abundance and distribution in the eastern tropical Pacific. *Rep. Int. Whal. Commn.* **43**, 477–493.