



Steno bredanensis (Cetacea: Delphinidae)

Authors: West, Kristi L, Mead, James G, and White, Whitney

Source: Mammalian Species, 43(1) : 177-189

Published By: American Society of Mammalogists

URL: <https://doi.org/10.1644/886.1>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Steno bredanensis (Cetacea: Delphinidae)

KRISTI L. WEST, JAMES G. MEAD, AND WHITNEY WHITE

College of Natural and Computational Sciences, Hawaii Pacific University, Kaneohe, HI 96744, USA; kwest@hpu.edu (KLW); volcomcurly@hotmail.com (WW)

Division of Mammals, Smithsonian Institution, Washington, DC 20013-7012, USA; meadj@si.edu (JGM)

Abstract: *Steno bredanensis* (Cuvier in Lesson, 1828) is a small odontocete commonly called the rough-toothed dolphin. A slender, gray dolphin with a slightly darker cape, this species is most easily distinguished from other small delphinids by a gradually sloping forehead and a long rostrum. It is the only species in the genus *Steno*. Despite reports of sightings or stranded specimens from all tropical and subtropical oceans, the species is thought to typically occur in low abundance. The conservation status of *S. bredanensis* is poorly known.

Key words: cetacean, dolphin, marine mammal, odontocete, rough-toothed dolphin

© 26 September 2011 American Society of Mammalogists

Synonymy completed 1 June 2011

DOI: 10.1644/886.1

www.mammalogy.org



Steno Gray, 1846

Steno Gray, 1846:43. Type species *Delphinus rostratus* Cuvier, 1833 (= *Delphinus bredanensis* Cuvier in Lesson, 1828), by monotypy.

Glyphidelphis Gervais, 1859:301. Type species *Delphinus rostratus* Cuvier, 1833 by monotypy.

CONTEXT AND CONTENT. Order Cetacea, suborder Odontoceti, family Delphinidae, subfamily Steninae. The genus *Steno* is monotypic.

Steno bredanensis (Cuvier in Lesson, 1828) Rough-toothed Dolphin

Delphinus rostratus (Desmarest, 1817:160). Type locality “Paimpol, Brittany, France.” Preoccupied by *Delphinus rostratus* Shaw, 1801.

Delphinus frontatus (Cuvier, 1823:278). Type locality unknown.

Delphinus bredanensis Lesson, 1828:206. Replacement name for *Delphinus rostratus* Desmarest, 1817; preoccupied by *Delphinus rostratus* Shaw, 1801.

Delphinus planiceps Schlegel, 1841:27, tab IV. A replacement name for *Delphinus bredanensis* van Breda, 1829.

Delphinorhynchus santonicus Lesson, 1836:330. Type locality “Ile d’Aix, mouth of the Charente River.” Type based on a stranded individual that was not preserved.

Delphinus compressus (Gray, 1843:105). Nomen nudum.

Steno rostratus Gray, 1846:30, 46. Renaming of *Delphinus rostratus* Desmarest, 1817.

Steno compressus Gray, 1846:43, pl. 27. Type locality unknown.

Delphinus (Steno) perspicillatus Peters, 1877:360, Taf. 3.

Type locality “im atlantischen Ocean, in 32° 29’ 7 S. B. und 2° 1’ W. L. Gr. harpunirt wurde.”

Steno bredanensis: Miller and Kellogg, 1955:657–658. First use of current name combination.

Delphinus chamissonis: Herskovitz, 1966:17. Not *Delphinus chamissonis* Wagner, 1846.

CONTEXT AND CONTENT. Context as for genus. Species is monotypic.



Fig. 1.—Pubertal male *Steno bredanensis* from Dolphin Quest French Polynesia, photographed in 2000. Dolphin Quest French Polynesia (The Moorea Dolphin Center) is a captive-care facility that houses dolphins in French Polynesia, located in the South Pacific. Used with permission of the photographer Cecile Gaspar.



Fig. 2.—Dorsal, ventral, and lateral views of the skull and lateral view of mandible of an adult female *Steno bredanensis* (National Museum of Natural History 572792). Note that view of the right mandible has been reversed to align it with the cranium. Specimen is from Wreck Island, Virginia. Condylbasal length of skull is 503 mm. Used with permission of the photographer Michael Potter.

NOMENCLATURE NOTES. The historical nomenclature of *S. bredanensis* is particularly confusing. Schevill (1987) and Flower (1884) have both provided accounts of this history. The fate of the type specimen is unclear and it may have been lost. The relationship between *S. perspicillatus* and *S. bredanensis* is addressed by Fraser (1966).

A series of illustrations of the external appearance and skull of the specimen of *Delphinus bredanensis* from Brest that Lesson (1828:figure 1) described and an account of Cuvier's role in the historical nomenclature of *S. bredanensis* is provided by van Breda (1829:235, 236, 238, plate I—figures 1–6, plate II—figures 1 and 2). This is the paper that is miscited by Hershkovitz (1966:16), following Flower (1884:484) as the authority for *D. planiceps* van Breda. The trivial name *planiceps* does not occur in van Breda (1829).

Hershkovitz (1966:17) follows Wagner's (1846) attribution to "Wiegmann, 1841 (or earlier)" based on Wagner's labeling of his plate CCCLIX (359) as "Delphinus Chamissonis Wiegmann." We surmise that Wagner had seen a manuscript by Wiegmann because we were not able to locate the record in the published literature.

DIAGNOSIS

In the wild, *Steno bredanensis* can most easily be distinguished from other small delphinids by a forehead that gradually slopes into a long and slender rostrum, lacking the demarcation that separates the melon and beak (Fig. 1). Although *Stenella* and the Indo-Pacific bottlenose dolphin (*Tursiops aduncus*) have a similarly long rostrum, they have the clear demarcation that is absent in *S. bredanensis*. The bottlenose dolphin (*T. truncatus*) has a much shorter rostrum and a dorsal fin that is less erect but may still be confused with *S. bredanensis* (Jefferson and Leatherwood 1993; Perrin et al. 2007).

The color pattern appears to vary according to geographic location and age of the individual (Miyazaki and Perrin 1994). *S. bredanensis* is gray in color with a slightly darker gray cape and often has distinctive white lips (Baker 1987; Jefferson and Leatherwood 1993). The darker cape is apparent from above the eye to the dorsal fin, gradually widening, and extending down the sides of the animal (Miyazaki and Perrin 1994; Fig. 1). The sides of the animal are typically a lighter gray color, and there may be white, pink, or yellow splotches or scarring on the tip of the rostrum, along the lower jaw, and in the ventral region. The mottled appearance is more frequently seen in older individuals, whereas uniform shades of gray are common in younger animals (Miyazaki and Perrin 1994).

The skull (Fig. 2) may be confused with that of the Indo-Pacific humpback dolphin (*Sousa chinensis*) or *Stenella* but the skull of *S. bredanensis* is generally longer than those of *Stenella* (condylbasal length > 472 mm—Miyazaki and Perrin 1994). The rostrum of *S. bredanensis* is also long, approximately 60% of the condylbasal length, similar to the ratio between condylbasal length and rostrum in the spinner dolphin (*Stenella longirostris*), Pantropical spotted dolphin (*Stenella attenuata*), and striped dolphin (*Stenella coeruleoalba*—Perrin and Gilpatrick 1994; Perrin and Hohn 1994; Perrin et al. 1994). The mandibular symphysis of *S. bredanensis* is about one-third the length of the mandible, whereas the mandibular symphysis does not generally exceed 30% of the mandibular length in *Sousa* (Ross et al. 1994). The orbits of *S. bredanensis* also are relatively large (> 13% of condylbasal length) compared to *Sousa*. There are 19–26 teeth on each side in the upper jaw and 19–28 teeth in the lower jaw (Miyazaki and Perrin 1994). Tooth counts also can be used to distinguish between *S. bredanensis* and *Sousa* because *S. chinensis* has 30–38 teeth in each jaw and alveoli

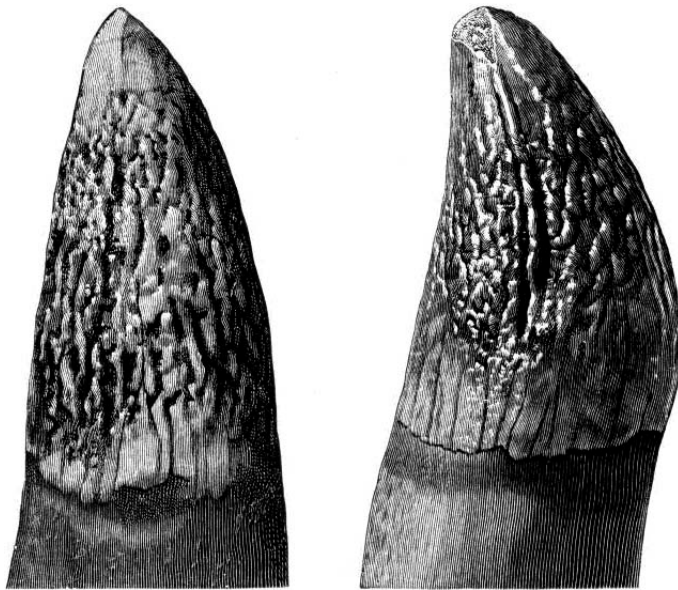


Fig. 3.—Magnified diagram of teeth ridges of *Steno bredanensis* reprinted from Neuville (1928), illustrating the fine tooth ridges that are characteristic of *S. bredanensis*. The tooth is from the middle of the upper jaw; lingual aspect on the left, medial aspect on the right.

that are larger and more widely spaced (Van Waerebeek et al. 1999). The common name comes from fine, longitudinal ridges apparent on the surface of the teeth (Fig. 3). This character can be diagnostic when comparing teeth from *S. bredanensis* side by side with teeth from other delphinids.

GENERAL CHARACTERS

Steno bredanensis is sexually dimorphic, with males larger than females (Miyazaki and Perrin 1994; West 2002). The total length of 64 male and female adult specimens compiled from the Pacific and Atlantic oceans and the Mediterranean Sea ranged from 209 to 265 cm (Miyazaki and Perrin 1994). Larger specimens are reported from Brazil, where maximum length for a male is 283 cm and for a female 270 cm (Siciliano et al. 2007).

Average body mass for *S. bredanensis* is reported as 130 kg (Watson 1981). Fourteen specimens ranged from 90 to 155 kg (Miyazaki and Perrin 1994). The total body length (L)—total body weight (W) relationship for a combination of 15 males and females is estimated as $L = 3.123 + 2.805 \log W$ ($r = 0.999$ —Miyazaki and Perrin 1994).

Selected external measurements of adult specimens compiled from the Pacific and Atlantic oceans and the Mediterranean Sea were as follows (cm): tip of upper jaw to apex of melon, 10–14 ($n = 15$); tip of upper jaw to end of gape, 22–37 ($n = 35$); tip of upper jaw to umbilical scar, 79–121 ($n = 25$); tip of upper jaw to tip of dorsal fin, 129–131 ($n = 2$); girth at axilla, 100–110 ($n = 17$); anterior length of flipper, 36–49 ($n = 36$); width of

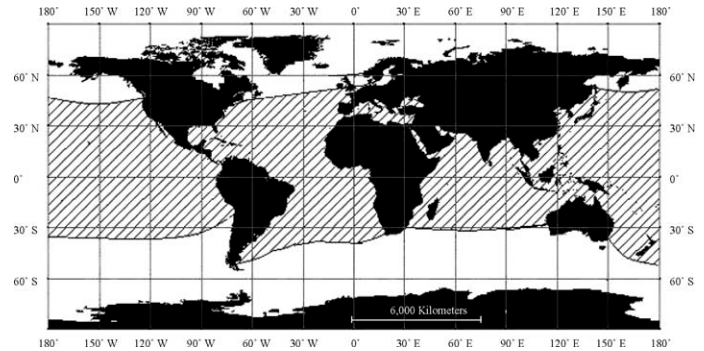


Fig. 4.—Geographic distribution of *Steno bredanensis*.

flipper, 13–17 ($n = 33$); span of flukes, 46–65 ($n = 35$); width of fluke, 14–23 ($n = 27$); and height of dorsal fin, 18–28 ($n = 23$ —Miyazaki and Perrin 1994).

The characteristically long rostrum of *S. bredanensis* is apparent in the skull and mandible (Fig. 2). Cranial measurements compiled from a number of sources for adult specimens from the Atlantic and Pacific oceans and the Mediterranean Sea were as follows (mm): condylobasal length, 472–555 ($n = 66$); length of rostrum, 274–343 ($n = 59$); width of rostrum at base, 87–119 ($n = 58$); width of rostrum at one-half its length, 38–64 ($n = 58$); preorbital width, 169–196 ($n = 6$); postorbital width, 202–239 ($n = 6$); greatest width of premaxillaries, 75–89 ($n = 10$); parietal width, 162–184 ($n = 7$); length of temporal fossa, 86–119 ($n = 40$); height of temporal fossa, 80–105 ($n = 40$); number of teeth in each side of upper jaw, 19–26 ($n = 81$); and number of teeth in each side of lower jaw, 19–28 ($n = 82$ —Miyazaki and Perrin 1994). Cranial measurements obtained by 2 of the authors (KLW and JGM) from another 23 adults from the Atlantic and the Pacific oceans are almost entirely within these ranges except for the following (mm): preorbital width, 163–185; postorbital width, 192–215; greatest width of premaxillaries, 72–85; and parietal width, 133–160.

DISTRIBUTION

Steno bredanensis is found worldwide with reports from the Atlantic, Pacific, and Indian oceans, typically in warm temperate, subtropical, or tropical waters (Fig. 4). In the southwestern Atlantic the most southerly report of the species is from Patagonia in Argentina but is based on a solitary skull at the Academy of Natural Sciences (Philadelphia, Pennsylvania) collected in the late 1800s (catalog number ANSP 23360). The species is reported on many occasions from Brazil (Pinedo and Castello 1980; Rice 1998; Siciliano et al. 2007). In the Caribbean Sea, *S. bredanensis* is reported throughout the Gulf of Mexico and along the coastal United States north to Virginia (Miyazaki and Perrin 1994).

The most northerly records from the northeastern Atlantic are from the Scheldt estuary, Belgium, in the North Sea (Booij 2004), and from a stranded specimen in Paimpol, France (Cuvier 1812; Van Beneden 1889). *S. bredanensis* also is reported from Portugal (Busnel and Dziedzic 1966), Spain (Hashmi and Adloff 1991), the Mediterranean Sea (Watkins et al. 1987), Macronesia (Bronner et al. 2003; Steiner 1995), and the western coast of Africa from Mauritania to Namibia (Addink and Smeek 2001; Bronner et al. 2003; Perrin and Van Waerebeek 2007; Ross et al. 1985; Steiner 1995).

A stranding of *S. bredanensis* is reported off the coast of southeastern Africa near the Zambesi River (Best 1971; Brownell 1975). However, this may have been a mistake, because it appears that this same specimen was later described as a junior synonym for *Sousa plumbea* (Brownell 1975; *plumbea* is currently considered a synonym of *Sousa chinensis*). *S. bredanensis* is reported from Tanzania and Kenya, but not enough detail is provided to evaluate the validity of this report (Davies and Vanden Berghe 1994). It is also found offshore of Somalia, the Aden District, and the Red Sea (Anderson 1891; Ballance et al. 1996; Best 1971; Frazier et al. 1987). The species is found in the Arabian Sea from the Gulf of Oman throughout the Indian Ocean to the Nicobar Islands (Alling 1986; Anderson 1891; Anderson et al. 1999; R. M. Baldwin et al., in litt.; Ballance et al. 1996, 2001; Ballance and Pitman 1998; International Whaling Commission 1994; Leatherwood and Reeves 1989; Van Waerebeek et al. 1999). Strandings are reported from Java, Indonesia (Chasen 1940; Kahn 2001), throughout the South China Sea (Beasley and Jefferson 1997; Chantrapornsy et al. 1996; Corkeron et al. 2003; Heaney et al. 1998; Parsons 1998; Smith et al. 1997; Yang 1976), to the East China Sea (Wenji 1980).

In the western Pacific there are reports from Japan, the Northern Mariana Islands, and Kiribati (Hobbs and Jones 1993; International Whaling Commission 1994; Jefferson et al. 2006; Miller 2006; Miyazaki 1980). A specimen also was obtained from the Marshall Islands (*Smithsonian Cetacean Distributional Database*, available at http://www.cms.int/reports/WAFCET/WAFCET2/WAFCET2_Report.htm, accessed 25 May 2011).

In the central North Pacific, *S. bredanensis* is commonly sighted throughout the Hawaiian Archipelago (Baird et al. 2008). In the eastern Pacific this species is described as part of the fauna in the Bering Sea; however, this report is not substantiated by a positively identified specimen (Collins et al. 1945). The most northerly reports on the west coast of the United States are from Washington and Oregon, but these strandings are thought to represent vagrants outside of normal species range (Ferrero 1994; Norman et al. 2004). *S. bredanensis* is reported from California (Daugherty and Schuyler 1979; Woodhouse 1991), down the coast of Mexico (Estrella 1994; Heyning 1986; Perrin and Oliver 1982; *Smithsonian Cetacean Distributional Database* [[\[cms.int/reports/WAFCET/WAFCET2/WAFCET2_Report.htm\]\(http://www.cms.int/reports/WAFCET/WAFCET2/WAFCET2_Report.htm\), accessed 25 May 2011\]\) through Central America \(Perrin and Kashiwada 1989\), from the Pacific coast of Colombia \(Holt and Jackson 1987; Mora-Pinto et al. 1995; Rodriguez 1989\), and from the Galapagos Islands \(Orr 1965\). The most southerly report along the South American coast is from Chile at 24°S \(Van Waerebeek and Guerra 1988\). *S. bredanensis* is commonly sighted in the eastern tropical Pacific but not in high abundance \(Au and Perryman 1985; Hewitt 1985; Wade and Gerrodette 1993; Wahlen et al. 1986\). *S. bredanensis* is relatively abundant in the Society Islands, French Polynesia, and is occasionally sighted about 1,440 km to the north in the Marquesas, French Polynesia \(Gannier 2000, 2002; Gannier and West 2005; Laran and Gannier 2001\). There are also reports from New Zealand waters \(Baker 1983\), the Solomon Islands, Papua New Guinea \(Brownell et al. 1978\), and Australia \(Baker 1983; Bannister et al. 1996; Ogawa 1938\).](http://www.</p>
</div>
<div data-bbox=)

FOSSIL RECORD

Steno fossils are uncommon but they are reported from the lower and middle Pliocene in Europe (Marcuzzi and Pilleri 1971). Fossil records for cetacean history extend back 50 million years and odontocetes most likely originated approximately 34–35 million years ago (Fordyce 2002). Fossil records for the Delphinidae date back to the late Miocene, possibly 11 million years ago, in both Europe and North America (Barnes et al. 1985; Fordyce 2002).

FORM AND FUNCTION

Form.—The vertebral formula of *Steno bredanensis* is 7 C, 13 T, 15–16 L, 30–31 Ca, total 65–67, with atlas and axis fused (Miyazaki and Perrin 1994; Tinker 1988). A reduced number of vertebrae is reported for 1 adult specimen with a vertebral formula of 7 C, 12 T, 15 L, 28 Ca, total 62 (Buchholtz and Shur 2004; Buchholtz et al. 2005). There are 21 or 22 chevron bones, and phalangeal count is I (3), II (8–9), III (6–7), IV (3), and V (2—Tinker 1988). We have observed 0–1 floating ribs, 6–7 single-headed ribs, and 5–7 double-headed ribs.

Much of what is known of the anatomy comes from a monograph by Neuville (1928). He described the soft anatomy of the thyroid, thymus, lymphatic system, lungs, stomach, spleen, and pancreas. The liver of *S. bredanensis* is bell shaped with 2 surfaces, a convex facies diaphragmatica and a facies visceralis that is divided into 2 lobes (Hojo and Mitsuhashi 1975). There is coronal duplication in teeth (Neuville 1928). Emmetropia, a state of perfect vision where the eye is relaxed while focused on distant objects, and movability of the operculum were observed in air for captive *S. bredanensis* (Dral and Duok van Heel 1974). A diagram of the tympanic bones is provided in Pilleri et al. (1989). The

nasal sac system is described as similar to that of other delphinids (Mead 1975; Purves 1966).

Masses of selected organs are available from Japanese specimens that ranged between 112.4 and 154.7 kg in total body weight: brain, 1,170–1,602 g ($n = 14$); heart, 605–1,080 g ($n = 15$); lungs, 1,640–3,934 g ($n = 15$); liver, 1,720–3,432 g ($n = 15$); left kidney, 489–826 g ($n = 14$); right kidney, 500–830 g ($n = 15$); spleen, 34–178 g ($n = 15$); pancreas, 110–191 g ($n = 14$); and intestines, 1,922–3,480 g ($n = 15$ —Miyazaki and Perrin 1994).

Function.—A physiological study of a captive *Steno bredanensis* compared renal function at 4 and 18 h after a meal. At 4 h after a meal, a higher urine flow rate (2.8 ml/min at 4 h compared to 1.3 ml/min at 18 h), glomerular filtration rate (169 ml/min at 4 h compared to 131 ml/min at 18 h), and urea concentration (82.4 ml/min at 4 h compared to 53.1 total body weight at 18 h) were observed (Malvin and Rayner 1968). Body temperature of an individual in Hawaii monitored with telemetry over 29 hours was 36.5–37.6°C and mean respiration rate was 2.8 breaths per minute (Whittow et al. 1978).

Hemoglobin of *S. bredanensis* is categorized as type V, having 2 distinct hemoglobin bands (Baluda et al. 1972). Blood chemistry and hematology parameters from 17 *S. bredanensis* were compared according to health status (sick versus healthy). Sick dolphins have higher levels of aspartate aminotransferase, alanine aminotransferase, lactate dehydrogenase, bicarbonate, and globulins than healthy ones, whereas healthy individuals have higher levels of alkaline phosphatase and protein than sick *S. bredanensis* (Baluda et al. 1972). Total white blood cell counts are lower in healthy than in sick *S. bredanensis*, and averaged $7.57 \times 10^3/\text{mm}^3$ in 157 samples collected from 8 healthy individuals (C. A. Manire et al., in litt.). A stranded calf in Brazil that died had a white blood cell count of $4.4 \times 10^3/\text{mm}^3$ and low values of aspartate aminotransferase, alanine aminotransferase, creatinine, and glucose (Bastos et al. 2003). Hematocrit from a single individual is reported at 50% (Malvin and Rayner 1968) and averaged 47.8% in 170 samples collected from 8 healthy individuals (C. A. Manire et al., in litt.). Immunoglobulin classes also have been identified from sera (Nash and Mach 1971).

ONTOGENY AND REPRODUCTION

Length at birth is probably about 100 cm; the largest reported fetus measured 93 cm and a stranded calf measured 106 cm (Bastos et al. 2003; Miyazaki and Perrin 1994; West 2002). Growth is rapid during the first 5 years of life, with individuals reaching at least 200 cm by 5 years of age (Miyazaki and Perrin 1994; West 2002). Asymptotic body lengths are reached at about 231–258 cm, depending on geographic region. In Japan, *Steno bredanensis* reaches asymptotic lengths at 231 cm and in Florida at 239 cm

(Miyazaki 1980; M. K. Stolen, in litt.). We observed asymptotic lengths of 210–231 cm ($n = 62$) in a group of specimens from the Atlantic and Pacific oceans. In Brazil, asymptotic length is greater, estimated at 258 cm ($n = 14$ —Siciliano et al. 2007).

In Brazil, a large *S. bredanensis* aged at 6 years old was pregnant (Siciliano et al. 2007). Females sampled from the Atlantic and Pacific oceans begin a gradual process of sexual maturation between 3 and 6 years of age (with age determined from undecalcified dentinal layers) and reach sexual maturity by 8–9 years (West 2002). Females attain sexual maturity at a body length of 212–219 cm and a body mass of 101–108 kg (West 2002). Our observations confirm data suggesting that females reach sexual maturity at about 10 years of age and at 210 cm in length in Japan (unpublished data cited in Miyazaki and Perrin 1994).

Males sampled from the Atlantic and Pacific reach sexual maturity between 5 and 10 years of age, at a body length of 211–216 cm and a body mass of 83–102 kg (West 2002). A stranded male estimated at 7 years of age was considered immature because of small testes mass of 23.3 g (Ferrero 1994), and 2 males 14 and 21 years of age (determined from both decalcified and undecalcified dentinal layers) were sexually mature with testes that contained sperm (Miyazaki 1980). Immature males have testes masses ≤ 54.3 g, whereas sperm-producing testes of mature males have masses of 66–1,500 g (Miyazaki 1980; West 2002).

Females generally attain physical maturity at a younger age and smaller size than males. In females sampled from the Atlantic and Pacific, physical maturity, as defined by fusion of the vertebral epiphyses, is attained at about 9–12 years of age, at a body length of 210–217 cm, and a body mass of 85–101 kg ($n = 13$ —West 2002). Males attain physical maturity (vertebral epiphyseal fusion) at a wide range of ages. One male was physically mature at only 5 years of age, whereas a 14-year-old individual was still immature (in a sample of 15 males—West 2002). A previous report suggested epiphyseal fusion in males at 16 years of age (Miyazaki and Perrin 1994). Males sampled from the Atlantic and Pacific reach physical maturity at 227–231 cm and 119–130 kg (West 2002). No information is available regarding reproductive seasonality or the duration of gestation or lactation.

ECOLOGY

Steno bredanensis may be solitary but is often found in groups of various sizes. The largest report of group size was estimated at 160 individuals in the Mediterranean (Watkins et al. 1987). Group size averaged 10.8 individuals in French Polynesia where solitary sightings and group sizes between 2 and 35 individuals were observed (Gannier and West 2005). Group size averaged 10 individuals from 44 sightings in Hawaii with a range of 2–90 dolphins (Baird et al. 2008). In the Canary Islands, groups are most commonly composed of

10–20 animals ($\bar{X} = 16.8$), although groups of up to 50 individuals are sighted (Ritter 2002).

Large-scale vessel surveys in the eastern tropical Pacific estimate the abundance of *S. bredanensis* at 145,900 (coefficient of variation [CV] = 0.32—Wade and Gerrodette 1993). Vessel surveys conducted in both oceanic waters and off the outer continental shelf in the northern Gulf of Mexico estimate 2,223 individuals (CV = 0.41—Fulling et al. 2003; Mullin and Fulling 2004; Waring et al. 2005). J. R. Mobley (in litt.) conducted aerial surveys within 25 nautical miles of the main Hawaiian Islands and estimated a population size of 123 individuals (CV = 0.63). This is an underestimate of population size because at least 337 distinct individuals were photographically identified over a 6-year period throughout the Hawaiian Islands. However, this study still suggests a relatively small population size as well as site fidelity because of frequent within and between year resightings (Baird et al. 2008). The estimated abundance of *S. bredanensis* throughout the entire Exclusive Economic Zone of Hawaii, including waters > 25 nautical miles from the main Hawaiian Islands, and those in the northwestern Hawaiian Islands is 8,709 individuals (CV = 0.45—Barlow 2006). It is not known whether the animals occurring around Hawaii are part of the same stock as those in the eastern tropical Pacific.

Steno bredanensis is commonly found in shallow nearshore, deep offshore, and oceanic waters. There are many reports from shallow waters of coastal Brazil and Honduras (Carvalho Flores and Ximenez 1997; Kuczaj and Yeater 2007; Lodi 1992). In French Polynesia, this species is most frequently sighted in 1,000- to 2,000-m depths, 1.8–5.5 km from shore (Gannier and West 2005). Similarly in Hawaii, sightings are most common in depths > 1,500 m and > 3 km from shore (Baird et al. 2008). In the Canary Islands, mean sighting depth is slightly > 500 m and mean distance is 4.4 km from shore (Ritter 2002). In French Polynesia, Hawaii, and the Canary Islands *S. bredanensis* has been identified as relatively abundant. All of these locations are characterized by steep volcanic islands that are surrounded by deep oceanic waters close to the coast.

Steno bredanensis is reported to form mixed schools with bottlenose dolphins, melon-headed whales (*Peponocephala electra*), false killer whales (*Pseudorca crassidens*), Fraser's dolphins (*Lagenodelphis hosei*), humpback whales (*Megaptera novaeangliae*), short-finned pilot whales (*Globicephala macrohynchus*), spinner dolphins, and Atlantic spotted dolphins (*Stenella frontalis*—Baird et al. 2008; Gannier and West 2005; Leatherwood and Reeves 1983; Perrin and Walker 1975; Ritter 2002; Scott and Chivers 1990; Watson 1981).

There are no confirmed reports of predation but it is likely, based on anecdotal evidence, that sharks and killer whales (*Orcinus orca*) prey on *S. bredanensis*. An attack by a group of sharks is theorized as the reason why an individual beached itself in Texas (Schmidly and Melcher 1974). In

Hawaii, a captive *S. bredanensis* left trainers in the midst of open ocean experiments when several small sharks, including a 4-m shark, were observed in the area (Norris et al. 1965). Scarring from bites of the cookie-cutter shark (*Isistius brasiliensis*) is common (Addink and Smeenk 2001; Baker 1987).

Diet has been inferred from stomach contents or from field observations of suspected foraging. In most cases, stomach contents are from stranded individuals and may not be representative of the diet of healthy *S. bredanensis*. Stomach contents from strandings in Hawaii consisted primarily of nearshore species, including silverside fish (*Pranesus insularum*), saury (*Cololabis adocetus*), houndfish (*Tylosurus crocodilus*), and an unidentified squid (Shallenberger 1981). We observed head and tail of a houndfish in separate stomach samples from this same stranding. Stomach contents from 3 individuals stranded off Oregon and Washington included top smelt (*Atherinops affinis*), jack smelt (*Atherinops californiensis*), and 2 species of squid (*Ommastrephes bartrami* and *Onychoteuthis borealijaponia*—Ferrero 1994). Stomach contents of stranded specimens in Florida include the blanket octopus (*Tremoctopus violaceus*) and, in a few cases, a significant amount of algae (*Sargassum filipendula*—Layne 1965). The slender inshore squid (*Loligo plei*) was reported as the primary cephalopod prey from Brazilian specimens (dos Santos 2001). A cutlass fish (*Trichiurus lepturus*) and an unidentified bone fish also were reported among solid food remains from Brazil (Di Benedetto et al. 2001; Ott and Danilewicz 1996). Remains include mollusks and fish from the eastern tropical Pacific (Perrin and Walker 1975).

Foraging by *S. bredanensis* has been observed in the field on a number of occasions. In the Azores underwater snipefish (*Macrorhamphosus scolopax*) were fed upon simultaneously by both *S. bredanensis* and Cory's shearwaters (*Calonectris diomedea borealis*—Steiner 1995). The dolphins were observed taking turns feeding from an aggregation of the snipefish that formed a ball about 0.5 m in diameter. However, no dolphins were observed keeping the fish ball together (Steiner 1995). In the southwestern Atlantic off the Brazilian coast, in the Abrolhos Bank breeding ground, *S. bredanensis* was observed catching a diskfish (Echeneidae—Wedekin et al. 2004). In both Hawaii and in the eastern tropical Pacific adult-sized mahi-mahi (*Coryphaena hippurus*) were reported in the mouth of *S. bredanensis* (Brower 1979; Pitman and Stinchcomb 2002). We observed mahi-mahi among the stomach contents of a specimen incidentally caught in the eastern tropical Pacific.

Helminths described in *S. bredanensis* include cestodes, nematodes, trematodes, and acanthocephalans. Cestodes include *Tetrabothrius forsteri*, *Strobilocephalus triangularis*, and *Trigonocotyle prudhoei* (Arvy 1982; Delyamure 1955; Forrester and Robertson 1975; Gibson and Harris 1979;

Layne 1965). We observed the cestodes *Phyllobothrium* and *Monorhynchus* in stranded specimens from both Hawaii and Virginia. Trematodes found in *S. bredanensis* include *Campyla palliata*, *Pholeter gastrophilus*, *Synthesium tursionis*, and *Braunina cordiformis* (Forrester and Robertson 1975; Ott and Danilewicz 1996), and we observed trematodes of the genus *Nasitrema*. Nematodes reported from *S. bredanensis* include *Anisakis* and *Crassicauda* (Forrester and Robertson 1975). The only acanthocephalan reported in *S. bredanensis* is *Bolbosoma capitatum* (Gibson and Harris 1979). An isopod ectoparasite of a fish, *Nerocila*, was found in the stomach of a stranded *S. bredanensis* in southern Brazil (Ott and Danilewicz 1996).

Solitary and mass strandings have occurred in most regions of the world where this species is found. In a mass stranding in Cap Vert, Senegal, 25 of 28 animals were males, indicating an extremely unbalanced sex ratio (Cadenat 1949). We examined specimens at the National Museum of Natural History, Washington, D.C., from a mass stranding in 1976 of 17 individuals from Hawaii and 16 from Virginia Beach, Virginia, that had beached later that same year. In 2002, 14 animals were found dead at Wreck Island, Virginia (West 2002). Historical and recent mass strandings have been reported for Florida, including 16 near Rock Island in 1961 (Layne 1965). Recent strandings have occurred along both the Gulf of Mexico and the Atlantic coasts, as well as in the Florida Keys (C. A. Manire, in litt.; H. L. Rhinehart et al., in litt.). Chronic progressive viral arteritis is a suspected cause behind some of the Florida strandings (H. L. Rhinehart et al., in litt.).

HUSBANDRY

Steno bredanensis has been held in captive facilities around the world, including in the United States, Hong Kong, Japan, Europe, and French Polynesia (Collet 1984; Miyazaki 1980; Parsons 1998; Reeves and Leatherwood 1984; West 2002). In the 1950s, *S. bredanensis* was captured in the Mediterranean Sea and near the Madeira Archipelago, Portugal, for a physiological laboratory (Collet 1984). In the 1960s and 1970s in Japan, individuals of this species were captured and held in a captive facility for at least 4 months (Miyazaki 1980; Nishiwaki 1967). As of 1981, 23 individuals had been collected near Hawaii and held at Sea Life Park (Waimanalo, Hawaii). Five of these either escaped or were released. One of the individuals had initially stranded and then survived in captivity for at least 6 years (Reeves and Leatherwood 1984; Tomich 1986). In 1971, a viable hybrid of a bottlenose dolphin and *S. bredanensis* was born at Sea Life Park, Hawaii (Dohl et al. 1974). At least 5 *S. bredanensis* were held in captivity on the island of Moorea in French Polynesia for up to 6 years during the 1990s. One was a stranded calf that lived for at least 3 years in captivity (West 2002). *S. bredanensis* also has been rehabilitated in

Florida, where 14 individuals were treated following several separate stranding events (C. A. Manire et al., in litt.). A stranded specimen in China was cared for at Ocean Park Hong Kong (R. E. Kinoshita; in litt.).

BEHAVIOR

Steno bredanensis commonly forms subgroups that may be a part of a larger group (Kuczaj and Yeater 2007; Ritter 2002). These tight but dynamic subgroups are often composed of 2–8 individuals involved in synchronous behavior. The social organization may be of fission–fusion type (Kuczaj and Yeater 2007; Ritter 2002). Association patterns have demonstrated strong social bonds, especially between mothers and calves or juveniles (Kuczaj and Yeater 2007). Skimming along at the surface is a common behavior (Jefferson 2002; Jefferson and Leatherwood 1993; Leatherwood and Reeves 1983). Surface swimming has been categorized in Honduras and the Canary Islands as traveling (21–27%), resting (4–10%), or milling (9–24%—Kuczaj and Yeater 2007; Ritter 2002). Play with objects (7%) and sexual behavior (4%) were less commonly observed (Kuczaj and Yeater 2007). In other locations, *S. bredanensis* is known for a propensity to associate or play with marine life or flotsam such as logs, plywood, and plastic bags (Brower 1979; Jefferson 2002; Leatherwood et al. 1982; Pitman and Stinchcomb 2002; Ritter 2002; Steiner 1995). Reports of cooperative feeding among group members also are common; they have been observed engaging in cooperative fish-herding techniques (Addink and Smeenk 2001) and appeared to take turns approaching a small aggregation of snipefish (Steiner 1995). Group feeding has been frequently observed in the Canary Islands and Honduras (Kuczaj and Yeater 2007; Ritter 2002).

Captive individuals of *S. bredanensis* have earned a reputation as being highly trainable, creative, sociable, and easy for humans to work with (Pryor et al. 1969; Tomich 1969). Many of the behaviors elicited by individuals at Sea Life Park (Waimanalo, Hawaii) were new and unreinforced behaviors that led to complex training sessions (Pryor et al. 1969).

Diving capabilities may be more extreme than observed. *S. bredanensis* is reported to dive as deep as 70 m, where a few individuals rubbed against a hydrophone at this depth (Watkins et al. 1987). The deepest dive of a trained *S. bredanensis* in open water is 30 m. However, this training session ended because the animal became agitated due to the presence of sharks (Norris et al. 1965). This specific individual was able to dive frequently, because it made 51 dives in < 2 h during open-water experiments (Norris et al. 1965). *S. bredanensis* may remain submerged for up to 15 min (Jefferson 2002; Miyazaki and Perrin 1994). While bow-riding (riding the waves produced off the bow or front of a moving vessel) *S. bredanensis* has attained swim speeds of up

to 16 km/h (Watkins et al. 1987). Although described as only an occasional bow-rider (Leatherwood and Reeves 1983; Leatherwood et al. 1982), there are reports of bow-riding from the Mediterranean Sea, the Azores, the Canary Islands, French Polynesia, Hawaii, and Honduras (Baird et al. 2008; Kuczaj and Yeater 2007; Ritter 2002; Steiner 1995; Watkins et al. 1987; West 2002).

Some observations of mothers, calves, or mother–calf pairs of *S. bredanensis* have been noted from various regions of the world. Twenty-nine percent of the groups sighted in French Polynesia and 16% of those sighted in the Canary Islands include at least 1 calf (Gannier and West 2005; Ritter 2002). Echelon swimming occurs, where calves swim very close to the dorsal fin of the mother and gain a hydrodynamic boost (Addink and Smeenk 2001). Off the coast of Mauritania, in North Africa, a mother provided her calf with assistance during feeding by encouraging the calf to pick up a fish it had dropped (Addink and Smeenk 2001). A stranded calf of *S. bredanensis* in Moorea, French Polynesia, induced lactation in an adult bottlenose dolphin held in the same lagoon (Gaspar et al. 2000). Epimeletic behavior (care-giving behavior by a healthy individual to a compromised or dead individual) has been described in Brazil and the Canary Islands (Lodi 1992; Ritter 2007). In the Canary Islands, a large adult female, which was presumed to be the mother, supported a dead calf at the surface. This mother and dead calf were resighted over several days, and 2 other adults also were observed providing support to the body of the calf (Ritter 2007).

At sea *S. bredanensis* produces extremely brief echolocation clicks in bursts of only 0.1–0.2 s in duration (Watkins et al. 1987). Echolocation clicks have both low- and high-frequency components ranging between 2.7 kHz and 256 kHz. The maximum peak frequency of echolocation clicks is approximately 25 kHz (Norris 1969). This value is low compared to maximum peak frequencies that have been described for other species of delphinids such as the false killer whale (40 kHz), the Risso's dolphin (*Grampus griseus*—50 kHz), the spinner dolphin (60 kHz), and the bottlenose dolphin (110–130 kHz—Au 2000; Ketten 1984; Madsen et al. 2004). Whistles have been recorded with sound frequencies of 3–12 kHz where sequences are approximately 0.5 s in duration (W. E. Evans, in litt.; Watkins et al. 1987). *S. bredanensis* has emitted stereotyped calls during stressful situations (W. E. Evans, in litt.). Based on recordings from 6 sightings, other individuals of *S. bredanensis* remain silent while a member of the group echolocates, suggestive of eavesdropping (Gotz et al. 2005).

GENETICS

Both mitochondrial and nuclear variation indicate that *Steno bredanensis* is a highly distinctive species. Studies using mitochondrial cytochrome-*b* sequences indicate that *S. bredanensis* differs considerably from other closely related species, a finding consistent with placement of this species in

a separate genus (Agnarsson and May-Collado 2008; LeDuc et al. 1999; May-Collado and Agnarsson 2006). *Steno* and *Sotalia* are sister taxa, according to Bayesian phylogenetic, maximum-parsimony, maximum-likelihood, and neighbor-joining analyses of cytochrome-*b* sequence variation within family Delphinidae, and they are currently retained in the subfamily Steninae (Agnarsson and May-Collado 2008; LeDuc et al. 1999; May-Collado and Agnarsson 2006). However, recent relationships described from a combination of mitochondrial and nuclear DNA phylogenies suggest that *Steno* and *Sotalia* are not sister taxa and that Steninae may be an artificial grouping. Instead, the combination of mitochondrial and nuclear DNA indicate that *Steno* should be allied with the subfamily Globicephalinae or retained as the sole member of Steninae, and that further study is needed to resolve this issue (Caballero et al. 2008).

Isoenzyme analysis of protein variation indicates a low proportion of polymorphic loci (5.3%) from an analysis of 19 loci from 12 enzymes in a population of *S. bredanensis* in waters off Taiji, Japan (Shimura and Numachi 1987). Average heterozygosity of this same population was $0.007 \pm 0.024 SE$, which was the lowest of 12 species of odontocetes examined (Shimura and Numachi 1987). Within family Delphinidae, average coefficient of genetic distance for isoenzyme analyses between *S. bredanensis* and 7 other delphinids is 0.379, compared to the distance of 1.004 between *S. bredanensis* and an average of 4 species of phocoenids (Shimura and Numachi 1987). Differentiation among microsatellite results indicates distinct populations of *S. bredanensis* at 2 different island groups in French Polynesia, which supports site fidelity in this region (Oremus 2008).

CONSERVATION

Population size and status of *Steno bredanensis* is poorly known from most regions of the world. The Convention on International Trade in Endangered Species of Wild Fauna and Flora (2011) lists *S. bredanensis* in Appendix II, as a species that is not necessarily now threatened with extinction but that may become so unless trade is closely controlled. The International Union for Conservation of Nature and Natural Resources (2011) considers *S. bredanensis* a species of “Least Concern.” Despite this, a number of potential threats have been identified, including fisheries that target *S. bredanensis*, the occurrence of this dolphin as incidental catch, and other types of fishery interactions. Additionally, *S. bredanensis* has been live-captured in small numbers for public display, and it may be vulnerable to the negative effects of contaminant burdens and oceanic debris (Kucklick et al. 2002; Leatherwood and Reeves 1989; Miyazaki 1983; Nishiwaki 1967; Oliveira de Meirelles and Duarte do Rego Barros 2007; Schlais 1984).

Fisheries that target *S. bredanensis* directly are reported from Japan, the Solomon Islands, Papua New Guinea, Sri Lanka, the Caribbean, and West Africa. In Japan, schools of

S. bredanensis in nearshore waters have been targeted by drive fisheries (those that drive the dolphins into shore and kill them—Nishiwaki 1967). *S. bredanensis* is occasionally present in the fish market in Shiogama, Japan (Whitehead et al. 2000). A group of 23 animals was taken in an Okinawan drive fishery in 1976, but none were taken between the years of 1977 and 1981 (Miyazaki 1983; Nishiwaki and Uchida 1977). In the calendar year 1985, Japanese drive fisheries reported a take of 60 *S. bredanensis* throughout Japan (Anonymous 1987). Although drives of dolphins are reported as rare events, when they do occur, tens of animals may be killed in a single drive (Whitehead et al. 2000). Similarly, native fishermen in the Solomon Islands and Papua New Guinea target entire schools of *S. bredanensis* in drive fisheries (Takekawa 1996; Young and Iudicello 2007). Various dolphin species, including *S. bredanensis*, are caught in Sri Lanka and sold as either dolphin or “dugong” meat in local fish markets (Leatherwood and Reeves 1989). At least 7 *S. bredanensis* were confirmed at the main fish market in Trincomalee, Sri Lanka, between 1983 and 1986 (Leatherwood and Reeves 1989). On the Caribbean island of St. Vincent, dolphin fishermen pursue all odontocete species encountered, including *S. bredanensis*, but the total take is unknown (Caldwell and Caldwell 1975; Van Bree 1975). A small fishery that targets *S. bredanensis* was reported from the western coast of Africa (Mitchell 1975). Local fishermen from the Atlantic island of St. Helena have harpooned *S. bredanensis*, but this activity is rare, because the animals are known to be difficult to subdue (Perrin 1985).

Steno bredanensis has been indirectly taken as incidental catch from several locations around the world. These include coastal and offshore Japan (drift-net fishery), Sri Lanka (gill-net fishery), the eastern tropical Pacific (purse-seine fishery), Brazil (gill-net fishery), and the Mediterranean Sea (gill-net fishery—Alling 1986; Anonymous 1987; Hobbs and Jones 1993; International Whaling Commission 1994). The annual number of *S. bredanensis* incidentally caught from any of these locations is generally very low, with the highest report being 18 animals caught in the high seas of Japan in 1990 (Hobbs and Jones 1993; International Whaling Commission 1994). Despite only 6 animals being reported from Brazilian gill-net fisheries in 1990, the magnitude of bycatch for *S. bredanensis* is considered higher than for other small cetaceans in Brazil (International Whaling Commission 1994; Monteiro-Neto et al. 2000; Siciliano 1994).

Steno bredanensis has been captured and subsequently held captive in facilities around the world. However, there are no reports of recent collections of this species for captivity, and it is unknown if past collections had a significant impact on local populations.

Bait stealing by *S. bredanensis* has been reported as a problem for fisheries in Hawaii and may also occur in other regions of the world (Schlais 1984). Fishermen have reported losing 20–50% of bait they set, and this species is blamed for all offshore losses in Kona, Hawaii (B. A. Kuljis, in litt.).

There are anecdotal reports of illegal activities (poisoning and shooting) by local fishermen to mitigate their losses. This may have an effect on population numbers of *S. bredanensis* in Hawaiian waters (Schlais 1984).

Chemical contamination of the oceans is a widespread problem and may be particularly threatening to high-level consumers such as dolphins. Low concentrations of dichlorodiphenyltrichloroethane (DDT), dieldrin and trans-nonachlor, and polychlorinated biphenyl levels up to 39 ppm were detected in the blubber, brain, or muscle tissues in 6 of 7 *S. bredanensis* that mass-stranded in Hawaii (O’Shea et al. 1980). In the Gulf of Mexico, levels of persistent organic pollutants in *S. bredanensis* were similar to or lower than those reported from other odontocetes (Kucklick et al. 2002; Struntz et al. 2004). However, *S. bredanensis* has higher percentage ratios of 4,4’-DDT to 4,4’-DDT + 4,4’-dichlorodiphenyldichloroethylene (4,4’-DDE) when compared to those measured in bottlenose dolphins (Kucklick et al. 2002; Struntz et al. 2004). High concentrations of contaminant persistent organic pollutants found in immature dolphins suggest an off-loading of the contaminant from mothers to calves (Kucklick et al. 2002).

Oceanic debris represents an additional threat to *S. bredanensis*. An emaciated individual that was live-stranded in Brazil had ingested 2 plastic bags (Oliveira de Meirelles and Duarte do Rego Barros 2007). Plastic bags also have been found in the stomachs of stranded individuals from Hawaii and Virginia (Walker and Coe 1990).

ACKNOWLEDGMENTS

We are grateful to C. Potter and A. Heilman for assisting with skull measurements. We would like to acknowledge S. Courbis and A. Brittain for assistance with the genetics section and A. Pacini for assistance with the echolocation section. We also express thanks to M. Kuprijanova and R. Brownell.

LITERATURE CITED

- ADDINK, M. J., AND C. SMEENK. 2001. Opportunistic feeding behavior of rough-toothed dolphins *Steno bredanensis* off Mauritania. *Zoologische Verhandelingen Leiden* 334:37–48.
- AGNARSSON, I., AND L. J. MAY-COLLADO. 2008. The phylogeny of Cetartiodactyla: the importance of dense taxon sampling, missing data, and the remarkable promise of cytochrome *b* to provide reliable species-level phylogenies. *Molecular Phylogenetics and Evolution* 48:964–985.
- ALLING, A. 1986. Small cetacean entanglement: a case study of the incidental entrapment of cetaceans in Sri Lanka’s gillnet fishery. *Report of the International Whaling Commission* 36:505.
- ANDERSON, J. 1891. *Steno*. Pp. 324–325 in *Catalogue of Mammalia in the Indian Museum, Calcutta part II. Rodentia, Ungulata, Proboscidea, Hyracoidea, Carnivora, Cetacea, Sirenia, Marsupialia, Monotremata*. Government of India Central Printing Office, Calcutta, India.
- ANDERSON, R. C., A. SHAAN, AND Z. WAHEED. 1999. Records of cetacean ‘strandings’ from the Maldives. *Journal of South Asian Natural History* 4:187–202.
- ANONYMOUS. 1987. United States. Progress report on cetacean research, June 1985 to May 1986. *Report of the International Whaling Commission* 37:183–190.

- ARVY, L. 1982. Phoresies and parasitism in cetaceans. *Investigations on Cetacea* 14:265–316.
- AU, D. W. K., AND W. L. PERRYMAN. 1985. Dolphin habitats in the eastern tropical Pacific. *Fishery Bulletin* 83:623–643.
- AU, W. W. L. 2000. Echolocation in dolphins. Pp. 364–408 in *Hearing by whales and dolphins* (W. W. L. Au, A. N. Popper, and R. R. Fay, eds.). Springer-Verlag, New York.
- BAIRD, R. W., D. L. WEBSTER, S. D. MAHAFFY, D. J. MCSWEENEY, G. S. SCHORR, AND A. D. LIGON. 2008. Site fidelity and association patterns in a deep-water dolphin: rough-toothed dolphins (*Steno bredanensis*) in the Hawaiian Archipelago. *Marine Mammal Science* 24:535–553.
- BAKER, A. N. 1983. Rough-toothed dolphin: *Steno bredanensis*. Pp. 106 in *Whales and dolphins of New Zealand and Australia: an identification guide*. Victoria University Press, Wellington, New Zealand.
- BAKER, M. L. 1987. Rough-toothed dolphins, *Steno bredanensis*. Pp. 84–85 in *Whales, dolphins, and porpoises of the world*. Doubleday, Garden City, New York.
- BALLANCE, L. T., ET AL. 2001. Cetacean sightings around the Republic of the Maldives, April 1998. *Journal of Cetacean Research and Management* 3:213–218.
- BALLANCE, L. T., AND R. L. PITMAN. 1998. Cetaceans of the western tropical Indian Ocean: distribution, relative abundance, and comparisons with cetacean communities of two other tropical ecosystems. *Marine Mammal Science* 14:429–459.
- BALLANCE, L. T., R. L. PITMAN, S. B. REILLY, AND M. P. FORCE. 1996. Report of a cetacean, seabird, marine turtle and flying fish survey of the western tropical Indian Ocean aboard the research vessel *Malcolm Baldrige*, March 21–July 26, 1995. National Oceanic and Atmospheric Administration Technical Memorandum, National Marine Fisheries Service SWFSC 224:1–133.
- BALUDA, M. C., D. D. KULU, AND R. S. SPARKES. 1972. Cetacean hemoglobins: electrophoretic findings in nine species. *Comparative Biochemistry and Physiology, B. Comparative Biochemistry* 41:647–653.
- BANNISTER, J. L., C. M. KEMPER, AND R. M. WARNEKE. 1996. The action plan for Australian cetaceans. Australian Nature Conservation Agency, Canberra, Australia.
- BARLOW, J. 2006. Cetacean abundance in Hawaiian waters estimated from a summer/fall survey in 2002. *Marine Mammal Science* 22:446–464.
- BARNES, L. G., D. P. DOMNING, AND C. E. RAY. 1985. Status of studies on fossil marine mammals. *Marine Mammal Science* 1:15–53.
- BASTOS, B. L., R. MAIA-NOGUEIRA, G. O. NORBERTO, S. BOROCCHO, AND J. E. GUIMARAES. 2003. Hemograma e determinação de ALT, AST, creatinina e glicose em golfinho-de-dentes-rugosos, *Steno bredanensis* (Lesson, 1828), encalhado em Salvador, Bahia. *Arqs Veterinaria* 20:207–211.
- BEASLEY, I., AND T. A. JEFFERSON. 1997. Marine mammals of Borneo—a preliminary checklist. *Sarawak Museum Journal* 51:200–210.
- BEST, P. B. 1971. Order Cetacea. Pp. 1–10 in *Mammals of Africa: an identification manual* (J. A. J. Meester and H. W. Setzer, eds.). Smithsonian Institution Press, Washington, D.C.
- BOOL, J. 2004. Improving the Dutch part of the North Sea as a cetacean habitat. North Sea Foundation, Utrecht, The Netherlands.
- BRONNER, G. N., ET AL. 2003. A revised systematic checklist of the extant mammals of the southern African sub region. *Durban Museum Novitates* 28:56–106.
- BROWER, K. 1979. *Wake of the whale*. Friends of the Earth, New York.
- BROWNELL, R. L., JR. 1975. Taxonomic status of the dolphin *Stenopontistes zambezicus* Miranda-Ribeiro, 1936. *Zeitschrift für Säugetierkunde* 40:173–175.
- BROWNELL, R. L., C. SCHONEWALD, AND R. R. REEVES. 1978. Preliminary report on world catches of marine mammals 1966–1975. National Technical Information Service, Marine Mammal Commission Report PB290713.
- BUCHHOLTZ, E. A., AND S. A. SCHUR. 2004. Vertebral osteology in Delphinidae (Cetacea). *Zoological Journal of the Linnean Society* 140:383–401.
- BUCHHOLTZ, E. A., E. M. WOLKOVICH, AND R. J. CLEARY. 2005. Vertebral osteology and complexity in *Lagenorhynchus acutus* (Delphinidae) with comparison to other delphinoid genera. *Marine Mammal Science* 21:411–428.
- BUSNEL, R. G., AND A. DZIEDZIC. 1966. Caractéristiques physiques de certains signaux acoustiques du Delphinidé *Steno bredanensis*, Lesson. *Comptes Rendus de l'Academie des Sciences, Paris* 262:143–146.
- CABALLERO, S., ET AL. 2008. Molecular systematics of South American dolphins *Sotalia*: sister taxa determination and phylogenetic relationships, with insights into a multi-locus phylogeny of the Delphinidae. *Molecular Phylogenetics and Evolution* 46:252–268.
- CADENAT, J. 1949. Notes sur les cétacés observés sur les côtes du Sénégal de 1941 à 1948. *Bulletin de Institut Français d'Afrique Noire* 11:1–14.
- CALDWELL, D. K., AND M. C. CALDWELL. 1975. Dolphin and small whale fisheries of the Caribbean and West Indies: occurrence, history, and catch statistics—with special reference to the Lesser Antillean Island of St. Vincent. *Journal of the Fisheries Research Board of Canada* 32:1105–1110.
- CARVALHO FLORES, P. A., AND A. XIMENEZ. 1997. Observations on the rough-toothed dolphin *Steno bredanensis* off Santa Catarina Island, southern Brazilian coast. *Biotemas* 10:71–79.
- CHANTRAPORNISYL, S., K. ADULYANUKOSOL, AND K. KITTIVATHANAWONG. 1996. Records of cetaceans in Thailand. *Phuket Marine Biological Center Research Bulletin* 61:39–63.
- CHASEN, F. N. 1940. A handlist of Malaysian mammals: a systematic list of the mammals of the Malay Peninsula, Sumatra, Borneo and Java, including adjacent small islands. *Bulletin of the Raffles Museums, Singapore, Straits Settlement, Issue* 15:110.
- COLLET, A. 1984. Live capture of cetaceans for European institutions. Report of the International Whaling Commission 34:603–607.
- COLLINS, H. B. J., A. H. CLARK, AND E. H. WALKER. 1945. The Aleutian Islands: their people and the natural history (with keys for the identification of the birds and plants). Smithsonian Institution, War Background Studies 21:1–131.
- CONVENTION ON INTERNATIONAL TRADE IN ENDANGERED SPECIES OF WILD FAUNA AND FLORA. 2011. Appendices I, II, and III. www.cites.org/eng/app/appendices.shtml accessed 20 May 2011.
- CORKERON, P. J., C. LEH, P. ANDAU, AND S. LEATHERWOOD. 2003. Cetaceans of northern Borneo. *Brunei Museum Journal* 10:55–64.
- CUVIER, F. 1833. Dauphin a long bec. in: Geoffroy Saint-Hilaire, E. and Cuvier, F. (1824–1842). *Histoire naturelle des mammifères: avec figures originales, coloriées, dessinées d'après des animaux vivans*. Livraison LXVI, 2 pp., 1 pl. A. Belin, Paris, France.
- CUVIER, G. 1812. Description des cétacés échoués dans la baie de Paimpol. *Nouveau Bulletin des Sciences, par la Société Philomatique de Paris, Vol. 3, Year* 5:69–91.
- CUVIER, G. 1823. Recherches sur les ossements fossiles, où l'on rétablit les caractères de plusieurs animaux dont les révolutions du globe ont détruit les espèces. Tome cinquième. Chez G. Dufour et E. d'Ocagne, Libraire, Paris, France.
- CUVIER, F. 1836. De l'histoire naturelle des cétacés, ou recueil et examen des faits dont se compose l'histoire naturelle de ces animaux. Librairie Encyclopedique de Roret, Paris, France.
- DAUGHERTY, A. E., AND P. SCHUYLER. 1979. Rough-toothed dolphin. *Marine Mammals of California* 3:28.
- DAVIES, G., AND E. VANDEN BERGHE. 1994. Check-list of mammals of East Africa. East Africa Natural History Society, Nairobi, Kenya.
- DELYAMURE, S. L. 1955. Helminthofauna of marine mammals (ecology and phylogeny). Pp. 1–522 in *Izdatel'stvo Akademiia Nauk SSSR* (Skrjabin, K. I., ed.), Moscow, Russia. Translated by Israel Program for Scientific Translation, Jerusalem, Israel.
- DESMAREST, A. 1817. Dauphin. *Nouveau dictionnaire d'histoire naturelle, appliqué aux arts, à l'agriculture, à l'économie rurale et domestique, à la médecine, etc.* Par une société de naturalistes et d'agriculteurs. Nouvelle édition presque entièrement refondue et considérablement augmentée. Deterville, Paris, France, 9: 146–180.
- DI BENEDITTO, A. P. M., R. M. A. RAMOS, S. SICILIANO, R. A. DOS SANTOS, G. BASTOS, AND E. FAGUNDES-NETTO. 2001. Stomach contents of delphinids from Rio de Janeiro, southeastern Brazil. *Aquatic Mammals* 27:24–28.
- DOHL, T. P., K. S. NORRIS, AND I. KANG. 1974. A porpoise hybrid: *Tursiops* × *Steno*. *Journal of Mammalogy* 55:217–221.

- DOS SANTOS, R. A. 2001. Cephalopods in the diet of marine mammals stranded or incidentally caught along southeastern and southern Brazil. *Fisheries Research* (Amsterdam) 52:99–112.
- DRAL, A. D. G., AND W. H. DUOK VAN HEEL. 1974. Problems in image-focusing and astigmatism in cetacean—a state of affairs. *Aquatic Mammals* 2:22–28.
- ESTRELLA, A. D. 1994. Presencia del delfín de dientes rugosos o esteno (*Steno bredanensis*), en la costa de Tabasco, México. *Anales del Instituto de Biología, Universidad Nacional Autónoma de México, Serie Zoología* 65:303–305.
- FERRERO, R. C. 1994. Recent strandings of rough-toothed dolphins (*Steno bredanensis*) on the Oregon and Washington coasts. *Marine Mammal Science* 10:114–116.
- FLOWER, W. H. 1884. On the characters and divisions of the family Delphinidae. *Proceedings of the Zoological Society of London* 1883:466–513.
- FORDYCE, R. E. 2002. Fossil records. Pp. 453–471 in *Encyclopedia of marine mammals* (W. F. Perrin, B. Wursig, and J. G. M. Thewissen, eds.). Academic Press, San Diego, California.
- FORRESTER, D. J., AND W. D. ROBERTSON. 1975. Helminths of rough-toothed dolphins, *Steno bredanensis* Lesson 1828, from Florida waters. *Journal of Parasitology* 61:922.
- FRASER, F. C. 1966. Comments on the Delphinoidea. Pp. 7–31 in *Whales, dolphins and porpoises* (K. S. Norris, ed.). University of California Press, Los Angeles.
- FRAZIER, J., G. C. BERTMAN, AND G. H. EVANS. 1987. Turtles and marine mammals. Pp. 288–314 in *Red Sea* (A. J. Edwards and S. M. Head, eds.). Fairview Park, Elmsford, New York.
- FULLING, G. L., K. D. MULLIN, AND C. W. HUBARD. 2003. Abundance and distribution of cetaceans in outer continental shelf waters of the United States Gulf of Mexico. *Fishery Bulletin* 101:923–932.
- GANNIER, A. 2000. Distribution of cetaceans off the Society Islands (French Polynesia) as obtained from dedicated surveys. *Aquatic Mammals* 26:111–126.
- GANNIER, A. 2002. Cetaceans of the Marquesas Islands (French Polynesia): distribution and relative abundance as obtained from a small boat dedicated survey. *Aquatic Mammals* 28:198–210.
- GANNIER, A., AND K. L. WEST. 2005. Distribution of the rough-toothed dolphin (*Steno bredanensis*) around the Windward Islands (French Polynesia). *Pacific Science* 59:17–24.
- GASPAR, C., R. LENZI, M. L. REDDY, AND J. SWEENEY. 2000. Spontaneous lactation by an adult *Tursiops truncatus* in response to a stranded *Steno bredanensis* calf. *Marine Mammal Science* 16: 653–658.
- GERVAIS, P. 1859. *Zoologie et paléontologie Françaises. Nouvelles recherches sur les animaux vertébrés dont on trouve les ossements enfouis dans le sol de la France et sur leur comparaison avec les espèces propres aux autres régions du globe*. Deuxième édition, 2nd ed. Arthus Bertrand, Libraire-Editeur, Paris, France.
- GIBSON, D. I., AND E. A. HARRIS. 1979. The helminth-parasites of cetaceans in the collection of the British Museum (Natural History). *Investigations on Cetacea* 10:309–324.
- GOTZ, T., U. K. VERFUSS, AND H.-U. SCHNITZLER. 2005. 'Eavesdropping' in wild rough-toothed dolphins (*Steno bredanensis*)? *Biology Letters* 2:5–7.
- GRAY, J. E. 1843. List of the specimens of Mammalia in the collection of the British Museum, with a list of genera and synonyms. *British Museum (Natural History) Publications*, London, United Kingdom.
- GRAY, J. E. 1846. On the cetaceous animals. Pp. 13–53 in *The zoology of the voyage of the H.M.S. Erebus and Terror, under the command of Capt. Sir J. C. Ross, R. N., F. R. S., during the years 1839 to 1843. Vol. 1, part 3* (Sir J. Richardson and J. E. Gray, eds.), [1844–1875]. 2 vols. Brown, Green and Longmans, London, United Kingdom.
- HASHMI, D. D. K., AND B. B. ADLOFF. 1991. Surface frequency of cetaceans in the Strait of Gibraltar. *European Research on Cetaceans* 5:16–17.
- HEANEY, L. R., ET AL. 1998. A synopsis of the mammalian fauna of the Philippine Islands. *Fieldiana: Zoology (New Series)* 88:1–61.
- HERSHKOVITZ, P. 1966. *Catalog of living whales*. United States National Museum Bulletin 246:1–259.
- HEWITT, R. P. 1985. Reaction of dolphins to a survey vessel: effects on census data. *Fishery Bulletin* 83:187–193.
- HEYNING, J. E. 1986. First record of the dolphin *Steno bredanensis* from the Gulf of California. *Bulletin of the Southern California Academy of Sciences* 85:62–63.
- HOBBS, R. C., AND L. L. JONES. 1993. Impacts of high seas driftnet fisheries on marine mammal populations in the North Pacific. *North Pacific Commission Bulletin* 53:409–429.
- HOJO, T., AND K. MITSUHASHI. 1975. Corrosions-anatomy of the intrahepatic vascular systems of a rough-toothed porpoise, *Steno bredanensis*. *Kaibogaku Zasshi* 50:258–261.
- HOLT, R. S., AND A. JACKSON. 1987. Report of a marine mammal survey of the eastern tropical Pacific aboard the research vessel *McArthur* July 29–December 6, 1986. National Oceanic Atmospheric Administration Technical Memorandum National Marine Fisheries Service SWFC77.
- INTERNATIONAL UNION FOR CONSERVATION OF NATURE AND NATURAL RESOURCES. 2011. International Union for Conservation of Nature and Natural Resources Red list of threatened animals. www.iucnredlist.org, accessed 20 May 2011.
- INTERNATIONAL WHALING COMMISSION. 1994. Report of the workshop on mortality of cetaceans in passive fishing nets and traps. In *Gillnets and cetaceans* (W. F. Perrin, G. P. Donovan, and J. Barlow, eds.). International Whaling Commission, Cambridge, United Kingdom. Special Issue 15:6–57.
- JEFFERSON, T. A. 2002. Rough-toothed dolphin: *Steno bredanensis*. Pp. 1055–1059 in *Encyclopedia of marine mammals* (W. F. Perrin, B. Wursig, and J. G. M. Thewissen, eds.). Academic Press, San Diego, California.
- JEFFERSON, T. A., D. FERTL, M. MICHAEL, AND T. FAGIN. 2006. An unusual encounter with a mixed school of melon-headed whales (*Peponocephala electra*) and rough-toothed dolphins (*Steno bredanensis*) at Rota, Northern Mariana Islands. *Micronesia* 38:239–244.
- JEFFERSON, T. A., AND S. LEATHERWOOD. 1993. *Marine mammals of the world. Food and Agriculture Organization species identification guide*. Food and Agriculture Organization of the United Nations, Rome, Italy.
- KAHN, B. 2001. A rapid ecological assessment of cetacean diversity, abundance and distribution. The Nature Conservancy, Jakarta, Indonesia.
- KETTEN, D. R. 1984. Correlations of morphology with frequency for odontocete cochlea: Systematics and topology. Ph.D. dissertation, Johns Hopkins University, Baltimore, Maryland.
- KUCKLICK, J. R., ET AL. 2002. Persistent organochlorine pollutants and elements determined in tissues of rough-toothed dolphins (*Steno bredanensis*) banked from a mass stranding event. NISTIR 6857. National Institute of Standards and Technology, Gaithersburg, Maryland.
- KUCZAJ, S. A., AND D. B. YEATER. 2007. Observations of rough-toothed dolphins (*Steno bredanensis*) off the coast of Utila, Honduras. *Journal of the Marine Biological Association of the United Kingdom* 87:141–148.
- LARAN, S., AND A. GANNIER. 2001. Distribution of cetaceans in the Marquesas Islands (French Polynesia). *European Research on Cetaceans* 15:426–430.
- LAYNE, J. N. 1965. Observations of marine mammals in Florida waters. *Bulletin of the Florida State Museum* 1964–1965 9:131–181.
- LEATHERWOOD, S., AND R. R. REEVES. 1983. *The Sierra Club handbook of whales and dolphins*. Tien Wah Press, Singapore, Singapore.
- LEATHERWOOD, S., AND R. R. REEVES. 1989. Marine mammal research and conservation in Sri Lanka 1985–1986. *Marine Mammal Technical Report* 56:1–138.
- LEATHERWOOD, S., R. R. REEVES, W. F. PERRIN, AND W. E. EVANS. 1982. Whales, dolphins and porpoises of the eastern North Pacific and adjacent Arctic waters. National Oceanic Technical Report Circular, National Marine Fisheries Service 444:178–183.
- LEDUC, R. G., W. F. PERRIN, AND A. E. DIZON. 1999. Phylogenetic relationships among the delphinid cetaceans based on full cytochrome *b* sequences. *Marine Mammal Science* 15:619–648.
- LESSON, R. P. 1828. *Histoire naturelle, générale et particulière des mammifères et des oiseaux découverts depuis 1788 jusqu'à nos jours*. Vol. 1. Cétacés. Baudouin Freres, Editeurs, Paris, France.
- LESSON, R. P. 1836. *Histoire naturelle générale et particulière des mammifères et des oiseaux découverts depuis la mort de Buffon*. Baudouin, Paris, France.

- LODI, L. 1992. Epimeletic behavior of free-ranging rough-toothed dolphins, *Steno bredanensis*, from Brazil. *Marine Mammal Science* 8:284–287.
- MADSEN, P. T., I. KERR, AND R. PAYNE. 2004. Echolocation clicks of two free-ranging, oceanic delphinids with different food preferences: false killer whales *Pseudorca crassidens* and Risso's dolphins *Grampus griseus*. *Journal of Experimental Biology* 207:1811–1823.
- MALVIN, R. L., AND M. RAYNER. 1968. Renal function and blood chemistry in cetacea. *American Journal of Physiology* 214:187–191.
- MARCUZZI, G., AND G. PILLERI. 1971. On the zoogeography of cetacea. *Investigations on Cetacea* 3:101–170.
- MAY-COLLADO, L., AND I. AGNARSSON. 2006. Cytochrome *b* and Bayesian inference of whale phylogeny. *Molecular Phylogenetics and Evolution* 38:344–354.
- MEAD, J. G. 1975. Anatomy of the external nasal passages and facial complex in the Delphinidae (Mammalia: Cetacea). *Smithsonian Contributions to Zoology* 207:26–72.
- MILLER, C. 2006. Current state of knowledge of cetacean threats, diversity and habitats in the Pacific Islands region. United Nations Environment Programme Report UNEP/CMS/PIC-1/inf/5:1-68.
- MILLER, G. S., AND R. KELLOGG. 1955. List of North American Recent mammals. *United States National Museum Bulletin* 205:657–658.
- MITCHELL, E. D. 1975. Report of the meeting on smaller cetaceans, Montreal, April 1–11, 1974. Pp. 889–983 in *Review of biology and fisheries for smaller cetaceans* (E. D. Mitchell, ed.). *Journal of the Fisheries Research Board of Canada* 32:875–1240.
- MIYAZAKI, N. 1980. Preliminary note on age determination and growth of the rough-toothed dolphin, *Steno bredanensis*, off the Pacific coast of Japan. Report of the International Whaling Commission Special Issue 13:171–179.
- MIYAZAKI, N. 1983. Catch statistics of small cetaceans taken in Japanese waters. Report of the International Whaling Commission 33:621–631.
- MIYAZAKI, N., AND W. F. PERRIN. 1994. Rough-toothed dolphin *Steno bredanensis* (Lesson, 1828). Pp. 1–20 in *Handbook of marine mammals*. Vol. 5 (S. H. Ridgway and Sir R. J. Harrison, eds.). Academic Press, San Diego, California.
- MONTEIRO-NETO, C., ET AL. 2000. Impact of fisheries on the tucuxi (*Sotalia fluviatilis*) and rough-toothed dolphin (*Steno bredanensis*) populations off Ceara State, northeastern Brazil. *Aquatic Mammals* 26:49–56.
- MORA-PINTO, D. M., M. F. MUNOZ-HINCAPIE, A. A. MEIGNUCCI-GIANNONI, AND A. ACERO-PIZARRO. 1995. Marine mammal mortality and strandings along the Pacific coast of Colombia. Report of the International Whaling Commission 45:427–429.
- MULLIN, K. D., AND G. L. FULLING. 2004. Abundance of cetaceans in the oceanic northern Gulf of Mexico, 1996–2001. *Marine Mammal Science* 20:787–807.
- NASH, D. R., AND J. P. MACH. 1971. Immunoglobulin classes in aquatic mammals. *Journal of Immunology* 107:1424–1430.
- NEUVILLE, H. 1928. Recherches sur le genre "*Steno*" et remarques sur quelques autres cétacés. *Archives du Muséum National d'Histoire Naturelle* 3(3):69–240 + I–XII.
- NISHIWAKI, M. 1967. Distribution and migration of marine mammals in the North Pacific area. *Bulletin of the Ocean Research Institute, University of Tokyo*, Issue 1:1–64.
- NISHIWAKI, M., AND S. UCHIDA. 1977. Dolphin fishing in the Ryukyus. *Bulletin of Science and Engineering Division* 23:51–56.
- NORMAN, S. A., ET AL. 2004. Cetacean strandings in Oregon and Washington between 1930 and 2002. *Journal of Cetacean Research and Management* 1:87–99.
- NORRIS, K. S. 1969. The echolocation of marine mammals. Pp. 391–421 in *The biology of marine mammals* (H. T. Andersen, ed.). Academic Press, London, United Kingdom.
- NORRIS, K. S., H. A. BALDWIN, AND D. J. SAMSON. 1965. Open ocean diving test with a trained porpoise (*Steno bredanensis*). *Deep-Sea Research* 12:505–509.
- OGAWA, T. 1938. Studien über die Zahnwale in Japan, insbesondere über die vier bei uns bisher unbekanntten Gattungen *Tursiops*, *Steno*, *Pseudorca*, *Mesoplodon*. Arbeiten aus dem Anatomischen Institut Universität de Sendai 21:173–232.
- OLIVEIRA DE MEIRELLES, A. C., AND H. M. DUARTE DO REGO BARROS. 2007. Plastic debris ingested by a rough-toothed dolphin, *Steno bredanensis*, stranded live in northeastern Brazil. *Biotemas* 20:127–131.
- OREMUS, M. 2008. Genetic and demographic investigation of population structure and social system in four delphinid species. Ph.D. dissertation, University of Auckland, Auckland, New Zealand.
- ORR, R. T. 1965. The rough-toothed dolphin in the Galapagos Archipelago. *Journal of Mammalogy* 46:101.
- O'SHEA, T. J., R. L. BROWNELL, D. R. CLARK, W. A. WALKER, M. L. GAY, AND T. D. LAMONT. 1980. Organochlorine pollutants in small cetaceans from the Pacific and South Atlantic oceans, November 1968–June 1976. *Pesticides Monitoring Journal* 14:35–46.
- OTT, P. H., AND D. DANILEWICZ. 1996. Southward range extension of *Steno bredanensis* in the southwest Atlantic and new records of *Stenella coeruleoalba* for Brazilian waters. *Aquatic Mammals* 22:185–189.
- PARSONS, E. C. M. 1998. Strandings of small cetaceans in Hong Kong territorial waters. *Journal of the Marine Biological Association of the United Kingdom* 78:1039–1042.
- PERRIN, W. F. 1985. The former dolphin fishery at St Helena. Report of the International Whaling Commission 35:423–428.
- PERRIN, W. F., AND J. W. GILPATRICK, JR. 1994. Spinner dolphin *Stenella longirostris* (Gray, 1828). Pp. 99–128 in *Handbook of marine mammals*. Vol. 5 (S. H. Ridgway and Sir R. J. Harrison, eds.). Academic Press, San Diego, California.
- PERRIN, W. F., AND A. A. HOHN. 1994. Pantropical spotted dolphin *Stenella attenuata*. Pp. 71–98 in *Handbook of marine mammals*. Vol. 5 (S. H. Ridgway and Sir R. J. Harrison, eds.). Academic Press, San Diego, California.
- PERRIN, W. F., AND J. V. KASHIWADA. 1989. Catalog of the synoptic collection of marine mammal osteological specimens at the Southwest Fisheries Center. National Oceanic Atmospheric Administration Technical Memorandum, National Marine Fisheries Service 130:1–19.
- PERRIN, W. F., AND C. W. OLIVER. 1982. Time and area distribution and composition of the incidental kill of dolphins and small whales in the United States purse-seine fishery from tuna in the eastern tropical Pacific, 1979–80. Report of the International Whaling Commission 32:429–444.
- PERRIN, W. F., K. M. ROBERTSON, P. J. H. VAN BREE, AND J. G. MEAD. 2007. Cranial description and genetic identity of the holotype specimen of *Tursiops aduncus* (Ehrenberg, 1832). *Marine Mammal Science* 23:343–357.
- PERRIN, W. F., AND K. VAN WAEREBEEK. 2007. The small-cetacean fauna of the west coast of Africa and Macronesia: diversity and distribution. United Nations Environment Programme Report UNEP/CMS-WATCH-INF.6:1-10.
- PERRIN, W. F., AND W. A. WALKER. 1975. The rough-toothed porpoise, *Steno bredanensis*, in the eastern tropical Pacific. *Journal of Mammalogy* 56:905–907.
- PERRIN, W. F., C. E. WILSON, AND F. I. ARCHER, II. 1994. Striped dolphin *Stenella coeruleoalba* (Meyen, 1833). Pp. 129–159 in *Handbook of marine mammals*. Vol. 5 (S. H. Ridgway and Sir R. J. Harrison, eds.). Academic Press, San Diego, California.
- PETERS, W. 1877. Mittheilung über die von S. M. S. Gazelle gesammelten Säugethiere aus den Abtheilungen der Nager, Hufthiere, Sirenen, Cetaceen und Beutelthiere. *Monatsberichte der Königlich Preussischen Akademie der Wissenschaften Jahre 1876:355–366*, plates 2–3.
- PILLERI, G., M. GIHR, AND C. KRAUS. 1989. Organ of hearing in Cetacea. II. Paleobiological evolution. *Investigations on Cetacea* 22:5–185.
- PINEDO, M. C., AND H. P. CASTELLO. 1980. Primeiros registros dos golfinhos *Stenella coeruleoalba*, *Stenella* cfr., *plagiodon* e *Steno bredanensis* para o sul do Brasil, com notas osteológicas. *Boletim do Instituto Oceanografico Sao Paulo* 29:313–317.
- PITMAN, R. L., AND C. STINCHCOMB. 2002. Rough-toothed dolphins (*Steno bredanensis*) as predators of mahimahi (*Coryphaena hippurus*). *Pacific Science* 56:447–450.
- PRYOR, K. W., R. HAAG, AND J. O'REILLY. 1969. The creative porpoise: training for novel behavior. *Journal of the Experimental Analysis of Behavior* 12:653–661.
- PURVES, P. 1966. Anatomical and experimental observations on the cetacean sonar system. Pp. 197–270 in *Animal sonar systems: biology and bionics* (R. G. Busnel, ed.). Plenum Press, New York.

- REEVES, R. R., AND S. LEATHERWOOD. 1984. Live-capture fisheries for cetaceans in USA and Canadian waters 1973–1982. Report of the International Whaling Commission 34:497–507.
- RICE, D. W. 1998. Marine mammals of the world: systematics and distribution. Special publication number 4 (D. Wartzok, ed.). Society of Marine Mammalogy, Lawrence, Kansas.
- RITTER, F. 2002. Behavioral observations of rough-toothed dolphins (*Steno bredanensis*) off La Gomera, Canary Islands (1995–2000), with special reference to their interactions with humans. *Aquatic Mammals* 28:46–59.
- RITTER, F. 2007. Behavioral responses of rough-toothed dolphins to a dead newborn calf. *Marine Mammal Science* 23:429–433.
- RODRIGUEZ, M. P. 1989. Reporte de algunos cetáceos del Caribe Colombiano. *Boletín Facultad de Biología Marrina* 8:30–40.
- ROSS, G. J. B., V. G. COCKCROFT, AND G. CLIFF. 1985. Additions to the marine mammal faunas of South Africa and Natal. *Lammergeyer* 35:36–40.
- ROSS, G. J. B., G. E. HEINSOHN, AND V. G. COCKCROFT. 1994. Humpback dolphins *Sousa chinensis* (Osbeck, 1765), *Sousa plumbea* (G. Cuvier, 1829) and *Sousa teuszii* (Kukenthal, 1892). Pp. 23–42 in *Handbook of marine mammals*. Vol. 5 (S. H. Ridgway and Sir R. J. Harrison, eds.). Academic Press, San Diego, California.
- SCHÉVILL, W. E. 1987. Note. P. 78 in *Steno bredanensis* in the Mediterranean Sea by Watkins, W. A., P. Tyack, K. E. Moore, and G. Notarbartolo-di-Sciara. *Marine Mammal Science* 3:78–82.
- SCHLAIS, J. F. 1984. Thieving dolphins: a growing problem in Hawaii's fisheries. *Sea Frontiers* 30:293–298.
- SCHLEGEL, H. 1841. *Abhandlungen aus dem Gebiete der Zoologie und vergleichenden Anatomie*. Vol. 1. Beiträge zur Charakteristik der cetaceen. Vol. 2. Weitere Beiträge zur Naturgeschichte der Cetaceen. Vol. 3. Beschreibung einiger neuen grossen Edelfalken, aus Europa und dem nördlichen Afrika. A. Arnz & Co., Leiden, The Netherlands.
- SCHMIDLY, D. J., AND B. A. MELCHER. 1974. Annotated checklist and key to the cetaceans of Texas waters. *Southwestern Naturalist* 18:453–464.
- SCOTT, M. D., AND S. J. CHIVERS. 1990. Distribution and herd structure of bottlenose dolphins in the eastern tropical Pacific. Pp. 387–402 in *The bottlenose dolphin* (S. Leatherwood and R. Reeves, eds.). Academic Press, San Diego, California.
- SHALLENBERGER, E. W. 1981. The status of Hawaiian cetaceans. United States Department of Commerce Report MMC-77/23:1–79.
- SHAW, G. 1801. *General zoology or systematic natural history*. Vol. 2, part 2. G. Kearsley, London, United Kingdom.
- SHIMURA, E., AND K. NUMACHI. 1987. Genetic variability and differentiation in the toothed whales. *Scientific Reports of the Whales Research Institute Tokyo* 38:141–163.
- SICILIANO, S. 1994. Reviews of small cetaceans and fishery interactions in coastal waters of Brazil. Report of the International Whaling Commission Special Issue 15:241–250.
- SICILIANO, S., ET AL. 2007. Age and growth of some delphinids in southeastern Brazil. *Journal of the Marine Biological Association of the United Kingdom* 87:293–303.
- SMITH, B. D., T. A. JEFFERSON, S. LEATHERWOOD, D. T. HO, C. V. THUOC, AND L. H. QUANG. 1997. Investigations of marine mammals in Vietnam. *Asian Marine Biology* 14:145–172.
- STEINER, L. 1995. Rough-toothed dolphin, *Steno bredanensis*: a new species record for the Azores, with some notes on behavior. *Arquipélago—Life and Marine Sciences* 13A:125–127.
- STRUNTZ, W. D. J., J. R. KUCKLICK, M. M. SHANTZ, P. R. BECKER, W. E. McFEE, AND M. K. STOLEN. 2004. Persistent organic pollutants in rough-toothed dolphins (*Steno bredanensis*) sampled during an unusual mass stranding event. *Marine Pollution Bulletin* 48:164–173.
- TAKEKAWA, D. 1996. Ecological knowledge of Fanalei villagers about dolphins: dolphin hunting in Solomon Islands I. Osaka: National Museum of Ethnology. *Senri Ethnological Studies* 42:55–64.
- TINKER, S. W. 1988. *Whales of the world*. Best Press, Inc., Honolulu, Hawaii.
- TOMICH, P. Q. 1969. *Mammals in Hawaii: a synopsis and national bibliography*. Bishop Museum Press, Honolulu, Hawaii.
- TOMICH, P. Q. 1986. *Mammals in Hawaii: a synopsis and national bibliography*. 2nd ed. Bishop Museum Press, Honolulu, Hawaii.
- VAN BENEDEN, P.-J. 1889. *Histoire naturelle des cétacés des mers d'Europe*. F. Hayez, Brussels, Belgium.
- VAN BREDÁ, J. G. S. 1829. Aanteekening omtrent eene nieuwe soort van dolfinj. *Nieuwe Verhandelingen der Eerste Klasse van het Koninklijk—Nederlandsch Instituut van Wetenschappen, Letterkunde en Schoone Kunsten te Amsterdam* 2:235–238.
- VAN BREE, P. J. H. 1975. Preliminary list of cetaceans of the southern Caribbean. *Studies on the Fauna of Curacao and other Caribbean Islands* 48:79–87.
- VAN WAEREBEEK, K., M. GALLAGHER, R. BALDWIN, V. PAPASTRACROU, AND S. M. AL-LAWATI. 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. *Journal of Cetacean Research Management* 1:167–177.
- VAN WAEREBEEK, K., AND C. G. GUERRA. 1988. A southern record of the rough-toothed dolphin, *Steno bredanensis*, in the eastern Pacific. *Estudios Oceanológicos* 7:75–79.
- WADE, P. R., AND T. GERRODETTE. 1993. Estimates of cetacean abundance and distribution in eastern tropical Pacific. Report of the International Whaling Commission 43:477–493.
- WAGNER, J. A. 1846. *Die Ruderfüsser und Fischzitzthierre*. Pp. viii + 1–427 pp., pls. 81–86, 329–385 in *Die Säugthiere in Abbildungen nach der Natur, mit Beschreibungen* (von Schreber, J.C.D., ed.). 7 volumes. Erlangen, West Germany.
- WAHLEN, B. E., G. J. WALKER, R. B. MILLER, AND C. W. OLIVER. 1986. Composition of the incidental kill of small cetaceans in the US purse-seine fishery for tuna in the eastern tropical Pacific, 1982–1984. Report of the International Whaling Commission 36:369–374.
- WALKER, W. A., AND J. M. COE. 1990. Survey of marine debris ingestion by odontocete cetaceans. Proceedings of the Second International Conference on Marine Debris, 2–7 April 1989, Honolulu, Hawaii (R. S. Shomura and M. L. Godfrey, eds.). United States Department of Commerce, National Oceanic Atmospheric Administration Technical Memorandum, National Marine Fisheries Service 154:747–774.
- WARING, G. T., E. JOSEPHSON, C. P. FAIRFIELD, AND K. MAZE-FOLEY. 2005. United States Atlantic and Gulf of Mexico marine mammal stock assessments—2005. United States Department of Commerce, National Oceanic Atmospheric Administration Technical Memorandum, National Marine Fisheries Service 194:1–346.
- WATKINS, W. A., P. TYACK, AND K. E. MOORE. 1987. *Steno bredanensis* in the Mediterranean Sea. *Marine Mammal Science* 3:78–82.
- WATSON, L. 1981. *Sea guide to whales of the world*. Elsevier-Dutton Publishing Co., Inc., New York.
- WEDEKIN, L. L., A. FREITAS, M. H. ENEGAL, AND I. SAZIMA. 2004. Rough-toothed dolphins (*Steno bredanensis*) catch diskfishes while interacting with humpback whales (*Megaptera novaeangliae*) off Abrolhos Bank breeding ground, southwest Atlantic. *Aquatic Mammals* 30:327–329.
- WENJI, H. 1980. A rough-toothed dolphin, *Steno bredanensis* from the East China Sea. *Acta Zoologica Sinica* 26:280–285.
- WEST, K. L. 2002. The ecology and biology of the rough-toothed dolphin, *Steno bredanensis*. Ph.D. dissertation, University of Hawaii, Honolulu.
- WHITEHEAD, H., R. R. REEVES, AND P. L. TYACK. 2000. Science and the conservation, protection, and management of wild cetaceans. *Cetacean Societies: Field Studies of Dolphins and Whales* 12:308–332.
- WHITTOW, G. C., I. F. G. HAMPTON, AND C. A. OHATA. 1978. Body temperature of the rough-toothed dolphin. *Journal of Wildlife Management* 42:184–185.
- WOODHOUSE, C. D. 1991. Marine mammal beachings as indicators of population events. National Oceanic Atmospheric Administration Technical Reports 98:111–115.
- YANG, H. 1976. Studies on the whales, porpoises and dolphins of Taiwan. *Annual Report of Science Museum Taiwan* 19:131–178.
- YOUNG, N. M., AND S. IUDICELLO. 2007. An evaluation of the most significant threats to cetaceans, the affected species and the geographic areas of high risk, and the recommended actions from various independent institutions. National Oceanic Atmospheric Administration Technical Memorandum, National Marine Fisheries Service NMFS-OPR-36:1-275.

Associate editor of this account was BARBARA BLAKE. Editor was MEREDITH J. HAMILTON.