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REVISION OF THE SPOTTED DOLPHINS, *STENELLA* SPP.

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ABSTRACT

The taxonomy of the spotted dolphins has been confused. Two apparent species exist, one endemic to the Atlantic and the other pantropical. They have sharply different color patterns and non-overlapping vertebral counts. However, the holotype specimens for most of the names that have been applied to the spotted dolphins (including *S. attenuata, S. frontalis, S. plagiodon* and others) are skulls only, with no information on coloration or number of vertebrae. The two species overlap in all skull characters; geographical variation in both is pronounced. We used a discriminant analysis based on tooth counts and three skull measurements (standardized to skull width) to identify the type specimens to the two species. We used other criteria for assignment of nominal species for which holotype specimens do not exist. We propose that *Stenella frontalis* (G. Cuv., 1829) be used for the Atlantic endemic species and *Stenella attenuata* (Gray, 1846) for the pantropical species and here redescribe the species. Proposed common names are Atlantic spotted dolphin and pantropical spotted dolphin. *S. frontalis* now includes *Delphinus froenatus* F. Cuv., 1829, *D. doris* Gray,

1846 and *D. plagiodon* Cope, 1866. *S. attenuata* (a *nomen conservandum*) includes *D. velox* G. Cuv., 1829, *D. pseudodelphis* Wiegmann, ≤1840, *D. brevimanus* Wagner, 1846, *D. microbrachium* Gray, 1850, *D. albirostratus* Peale, 1848, *Steno capensis* Gray, 1865, *Clymene punctatus* Gray, 1866, *Steno consimilis* Malm, 1871 and *Prodelphinus graffmani* Lönnberg, 1934. Unidentifiable to either of the two valid species are *D. dubius* G. Cuv., 1812, *D. pernettensis* de Blainville, 1817 (suppressed), *D. malayanus* Lesson, 1826 and *D. Rappii* Reichenbach, 1845; these must remain *incertae sedis*.

Key words: *Stenella*, dolphins, taxonomy, *Delphinus*, osteology, geographical variation.

The taxonomy of the spotted dolphins has long been confused (True 1889, Fraser 1950, Perrin 1975, Mitchell 1975, Honacki *et al.* 1982). It is generally recognized that at least two species exist in the Atlantic, one pantropical and the other endemic to the Atlantic (Hershkovitz 1966, Caldwell, Caldwell, Rathjen and Sullivan 1971, Perrin 1975, Perrin *et al.* 1978, Honacki *et al.* 1982). These have been distinguished primarily on the basis of differing color patterns (Fig. 1; Perrin 1975; Leatherwood *et al.* 1983). The nomenclature of these apparent species has been unsettled because the holotype specimens of the several nominal species are skulls associated with no information on the external appearance of the animals in life. In addition, there is pronounced geographical variation in the skulls of both species (described below), leading to the confusing situation of markedly different skulls belonging to the same species in some cases and very similar skulls belonging to different species in others. The name *Stenella attenuata* (Gray, 1846) has been most commonly applied to the pantropical species in the Indian and Pacific Oceans, following True (1903), although Ogawa (1936) used *Prodelphinus froenatus* for a specimen from Japan and Zhou *et al.* (1980) assigned specimens from China to *S. frontalis* (F. Cuvier, 1829). Based on his (Nishiwaki *et al.* 1965) collection and Ogawa's report, Nishiwaki (1967, 1972) listed both *S. attenuata* and *S. frontalis* from Japan, but illustrations for the two species in his 1967 review were drawn after different photographs of the same specimen (published in the 1965 paper). The names most commonly used for spotted dolphins in the Atlantic in recent years (*see* references cited above) have been *S. attenuata, S. frontalis, S. plagiodon* (Cope, 1866) and *S. dubia* (G. Cuvier, 1812). The purposes of this paper are to assign the holotype skulls to the two valid species, redescribe the species and present what is known of their geographical variation.

Materials and Methods

Varying combinations of external and skeletal data were available for 210 spotted dolphins from the Atlantic Ocean, 255 from the Indian and Pacific Oceans and 5 from unknown localities. The specimens examined are listed below in the species accounts. Published locality records (in addition to those listed below for specimens) for the Atlantic came from Pernety (1769), F. Cuvier (1829), True (1885, 1889), Lütken (1889), Cuní (1918), Nichols

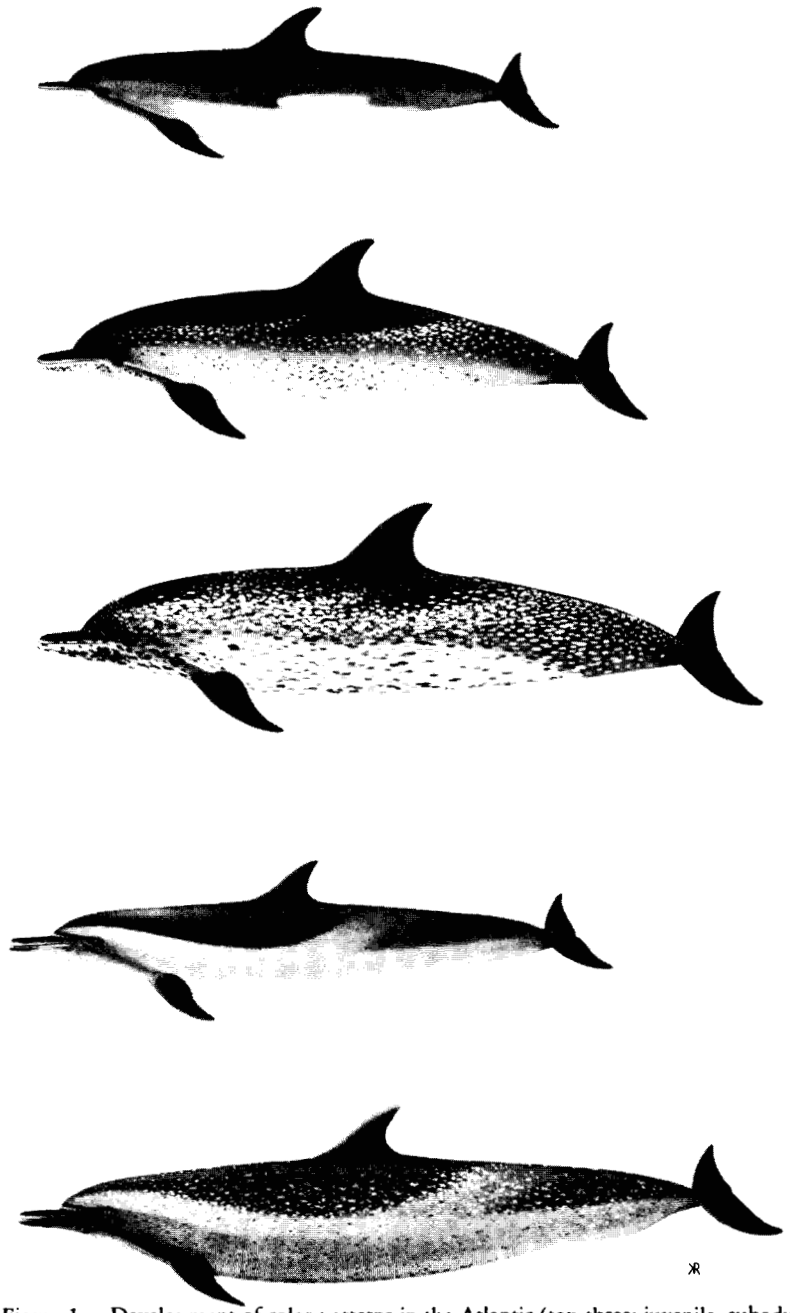


Figure 1. Development of color patterns in the Atlantic (top three: juvenile, subadult and adult) and pantropical (bottom two: juvenile and adult) spotted dolphins.

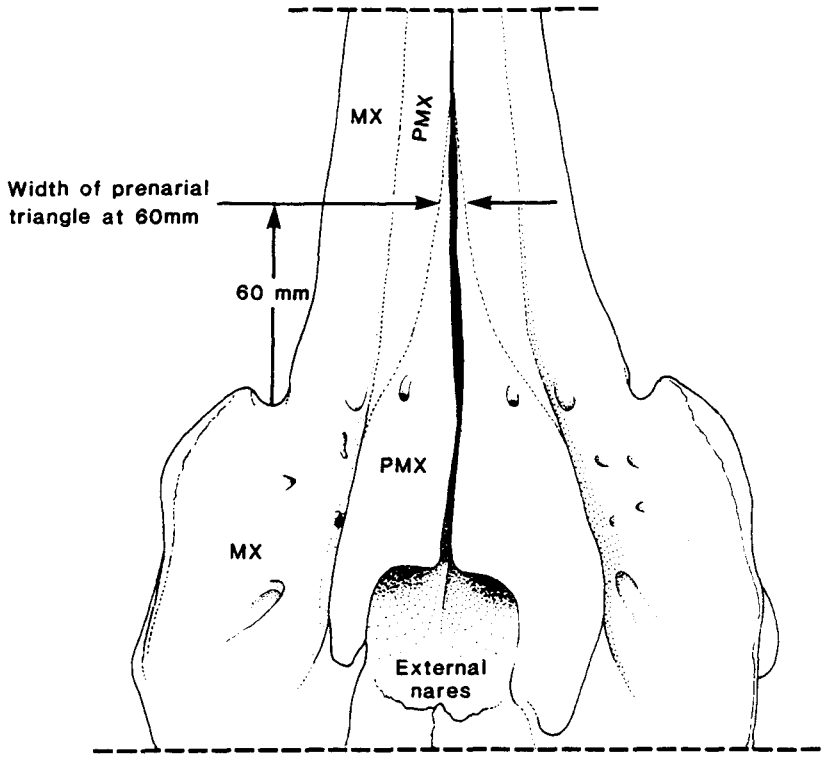


Figure 2. The measurement Width of Prenarial Triangle at 60 mm.

(1920), Allen (1925, 1931), Gunter (1941), Brimley (1946), R. Murphy (1947), Fraser (1950, 1966), Moore (1953), Caldwell (1955, 1960), Kellogg (1955), Cadenat (1956, 1959), Miller and Kellogg (1955), Springer (1957), Cadenat and Lassarat (1959), Mahnken and Gilmore (1959), Schevill and Watkins (1962), Caldwell and Caldwell (1966), Mitchell (1970), van Bree (1971a, 1975), Mörzer Bryns (1971), Caldwell *et al.* (1971), G. Murphy (1979), Schmidly (1972, 1981), Erdman *et al.* (1973), Mercer (1973), Lowery (1974), Brownell and Praderi (1976), Scientific Event Alert Network (1975–1982), Dupuy and Maigret (1976, 1978), Taruski and Winn (1976), Shane (1977), Sutherland and May (1977), Schmidly and Shane (1978), Pinedo and Castello (1980), Fritts and Reynolds (1981), Winn (1982), Fritts *et al.* (1983), Lagendijk (1984), Minasian *et al.* (1984), de Oliveira Gomes (1984), and Best *et al.* (1985). Contributors of unpublished specimen and locality data in addition to the data in the authors' files are listed in the acknowledgments below. All sightings of spotted dolphins were treated as unidentified unless accompanied by description or photographs documenting diagnostic characters. Other records were considered to be of unidentified spotted dolphins (listed below).

External measurements (in cm) follow Norris (1961). Skeletal characters

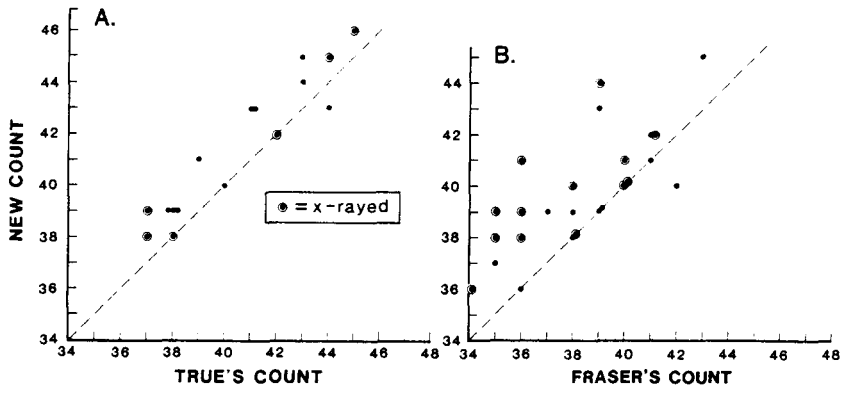


Figure 3. Comparison of highest rostral tooth counts in spotted dolphin skulls made by authors and by True (A) and Fraser (B).

(measured in mm) follow Perrin (1975), with the addition of the character Width of the Prenarial Triangle at 60 mm (Fig. 2). Distal fusion of maxillaries and premaxillaries was used as a criterion for inclusion of skulls in adult series (Perrin 1975). Where this information was not available, sexual maturity was used as a criterion of cranial maturity where possible. Specimens were adjudged physically mature (for inclusion in adult series of postcranial skeletons) if all vertebral epiphyses were fused to the centra.

It is often difficult to count the teeth in a dolphin skull accurately because of dried tissue adhering to the tip of the rostrum or mandible and because the anterior-most teeth are very small and may be lost or buried in the bone. We found that it was frequently necessary to carefully dissect the tips of the rostrum and mandible to expose the anterior-most teeth or alveoli. When this would cause significant damage or when the curator in charge would not allow it, where feasible we made anterior tooth counts from x-rays of the jaw tips. Counts obtained in these ways were often higher than those obtained by earlier workers for the same skulls (Fig. 3). We encountered difficulty in obtaining accurate counts for the mandibular toothrows because the first one or two teeth were often completely buried in the bone. We therefore used the rostral counts in our analyses. To minimize the biasing effect of loss of the first upper tooth or two in preparation, we used highest rostral tooth count regardless of whether it was the left or right. For some skulls, some rostral teeth were obviously missing at the tip of the rostrum, and the original number could not be estimated with confidence. In these cases, the minimal count was used (*e.g.*, for a tooth count of "more than 38," a value of 39 was used). The expected effect on the analyses would be to decrease the precision of a discriminant function based on the speciments but not inject a bias, as the numbers of such skulls were about the same for the two species.

Similar problems were encountered with vertebral counts. The total number of vertebrae proved to be diagnostic for the two species (*see* below), but many

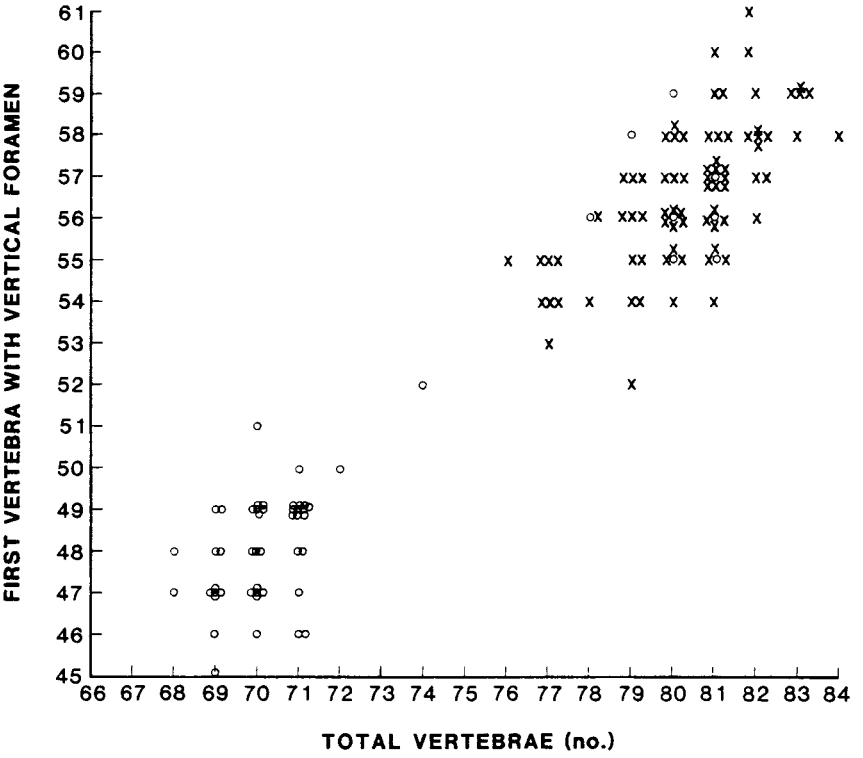


Figure 4. Scatterplot of position of first vertebra with vertically perforating foramen on total number of vertebrae for Atlantic (dots) and Pacific and Indian Ocean (×'s) spotted dolphins.

museum specimens lack one or more terminal vertebrae. The terminal caudal series tapers rapidly, and we were sometimes able to estimate confidently the number of missing vertebrae by comparison with an intact specimen. Other specimens had too many vertebrae missing to allow this estimation. We identified these specimens to the two species by referring to the position of the first caudal vertebra bearing a vertically perforating foramen; this character is highly correlated with total number of vertebrae (Fig. 4).

The skull character Width of the Prenarial Triangle at 60 mm was developed only after most of the museum material had been examined. In some cases it was feasible to re-examine the skulls; in others the measurement was made from a photograph taken perpendicular to the long axis of the skull.

The computer programs used in our multivariate analyses were from the BMDP package (Dixon 1985); these were P4M (factor analysis) and P7M (stepwise discriminant analysis). The factor analysis was performed on standardized data (for each character, mean = zero and standard deviation = one). The number of factors was limited to the number of eigenvalues greater than

1.0. The initial unrotated factors (which were the principal components) were rotated orthogonally, optimizing the distribution of the variance between the two factors (patterning). The convergence criterion for rotation was 0.00001. Kaiser's normalization was employed. In the stepwise discriminant analysis, the F-to-enter at step 0 for a variable was computed from a one-way analysis of variance on the variable for the groups used in the analysis. A variable was removed from the analysis if its F-to-remove was less than the initial F-to-enter. Maximum forced level was set at 1 for all variables.

Specimens examined but not identified as to species—Massachusetts: 1 (USNM 7071—mandible). Florida: 2 (USNM 218344—damaged juvenile cranium, USNM 23414—partial postcranial skeleton). St. Helena: 1 (GM 969—scrimshawed ramus).

Previously unpublished sighting records for unidentified spotted dolphins in the Atlantic (in addition to those from specimens listed above; sources, when other than authors, listed in ACKNOWLEDGMENTS): western North Atlantic, 1 (42°58'N latitude, 59°11'W longitude—EDM); Azores, 1 (37°46'N, 24°44'W—EDM); off New York, 5 (41°00'N, 71°43'W; 40°50'N, 71°47'W; 40°53'N, 71°29'W; 40°54'N, 71°27'W; 40°58'N, 71°38'W); North Carolina and offshore, 3 (Rodanthe; 36°00'N, 74°39'W; 35°17'N, 74°15'W); Florida and offshore, 2 (Destin; 30°48'N, 78°28'W—EDM); Caribbean, 8 (near St. Croix; 20°21'N, 84°40'W; 19°42'N, 84°10'W; 18°22'N, 83°09'W; 17°38'N, 63°35'W—EDM; 14°38'N, 70°53'W; 14°22'N, 71°16'W; Santa Margarita Island); off Panama, 1 (9°51'N, 79°22'W); near Canary Islands, 1 (28°05'N, 63°35'W).

RESULTS OF THE DISCRIMINANT ANALYSIS

The two apparent species differ in the total number of vertebrae as well as in color pattern (*see* redescriptions below). Where vertebral count is available, all specimens with the Atlantic endemic color pattern have about 70 vertebrae and all those with the pantropical pattern have about 80. There is no overlap (Table 1, Fig. 5). Based on this finding, we assigned all specimens with no coloration data but with 74 or more vertebrae to the pantropical species and all those with 72 or fewer to the Atlantic endemic species. This yielded a comparative base of 60 Atlantic specimens of the former and 87 of the later.

Skulls of the two species overlap in every character (*see* below in species redescriptions). We were able to separate the two series, however, by considering several characters simultaneously. Four characters were sufficient to provide separation: Width of Rostrum at ½ Length, Width of Rostrum at ¾ Length, Width of Prenarial Triangle at 60 mm, and Highest Rostral Tooth Count. Because of the considerable geographic variation in size in both species (described below), we standardized the three width measurements through division by Postorbital Width.

The endemic species tends to have a proportionately wider rostrum tip, a shorter prenarial triangle (narrower at 60 mm) and fewer teeth. Discriminant analysis using the four characters correctly identified all of the specimens (Table

Table 1. Specimens of spotted dolphins from Atlantic for which both color pattern and vertebral count are known. Values in parentheses are estimates for specimens with one or more terminal vertebrae missing.

Locality	Specimen number	Color pattern	Vertebrae	Reference
Mid-North Atlantic				
1. Azores	EDM 760	Endemic	68	Mitchell 1970
2. Azores	AMNH 239111	Endemic	69	Mitchell 1970
3. Near Azores	UZMC *Prodelphinus* no. 4	Endemic	(71)	Lütken 1889
4. 46°20'N, 38°44'W	EDM 786	Endemic	70	—
5. 38°40'N, 49°W	UZMC *Prodelphinus* no. 11	Endemic	70	Lütken 1889
Western North Atlantic				
6. Massachusetts	USNM 550016	Pantropical	81	—
7. New York	USNM 550353	Endemic	71	—
8. Off New Jersey	MCZ 51074	Endemic	(70)	—
9. Off New Jersey	MCZ 51294	Endemic	(71)	—
10. Virginia	USNM 504758	Endemic	71	—
11. Off North Carolina	AMNH 239117	Endemic	70	—
12. Off North Carolina	EDM 694	Endemic	69	—
13. Off North Carolina	EDM 695	Endemic	(71)	—
14. Off North Carolina	USNM 22017	Endemic	(69)	True 1889
15. North Carolina	USNM 504321	Endemic	71	—
16. North Carolina	USNM 504322	Endemic	70	—
17. North Carolina	USNM 504736	Endemic	70	—
18. North Carolina	USNM 504748	Endemic	70	—
19. North Carolina	USNM 504762	Endemic	(70)	—
20. North Carolina	USNM 504876	Endemic	70	—
21. North Carolina	USNM 504901	Endemic	68	—
22. North Carolina	USNM 550024	Endemic	69	—
23. North Carolina	USNM 550025	Endemic	69	—
24. North Carolina	USNM 550098	Endemic	71	—
25. North Carolina	USNM 550102	Endemic	71	—
26. Off South Carolina	EDM 696	Endemic	(71)	—
27. Off South Carolina	EDM 697	Endemic	(71)	—
28. South Carolina	USNM 500858	Endemic	69	—

Table 1. Continued.

Locality	Specimen number	Color pattern	Vertebrae	Reference
29. Off Georgia	EDM 844	Endemic	70	—
30. Off Georgia	USNM 261364	Endemic	69	—
31. Off Georgia	Fetus of 261364	Endemic	71	—
32. Off Florida	EDM 700	Endemic	(71)	—
33. Off Florida	EDM 701	Endemic	(71)	—
34. Florida	UF R-1-SF	Pantropical	(77–81)	—
35. Florida	UF R-2-SF	Pantropical	80	—
36. Florida	UF R-4-SF	Pantropical	(80)	—
Gulf of Mexico				
37. Florida	UF R-G-2-SF/SP	Endemic	67	—
38. Florida	USNM 21915	Endemic	70	True 1885
39. Texas	USNM 292070	Endemic	69	Caldwell and Caldwell 1966
Caribbean				
40. Off Haiti	UZMC *Prodelphinus* no. 14	Endemic	70	Lütken 1889
41. Off Puerto Rico	EDM 808	Endemic	69	—
42. Off Puerto Rico	AMNH 239116	Endemic	69	—
43. Lesser Antilles	EDM 803	Endemic	70	—
44. Off Venezuela	AMNH 239113	Endemic	71	—
45. Off Venezuela	EDM 706	Endemic	71	—
46. Off Venezuela	EDM 710	Endemic	(70)	—
47. Off Venezuela	AMNH 239114	Endemic	70	—
48. Off Venezuela	AMNH 239112	Endemic	72	—
Mid-Tropical Atlantic				
49. 6°46′N, 24°35′W	AMNH 39092	Pantropical	(80)	Murphy 1947
50. 2°44′N, 29°W	UZMC *Prodelphinus* no. 8	Pantropical	79	Lütken 1889
Africa				
51. Ivory Coast	ZMA 13.546	Endemic	(70)	van Bree 1971
52. Ivory Coast	ZMA 22.964	Endemic	(~66)	Cadenat and Lassarat 1959
53. Gulf of Guinea	BMNH Atlantide	Pantropical	81	Fraser 1950

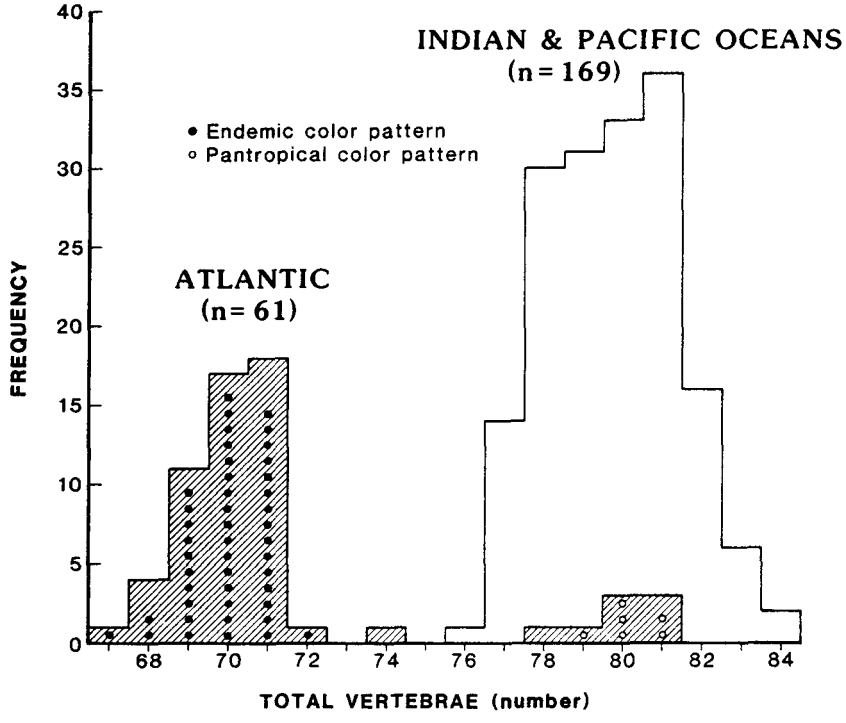


Figure 5. Number of vertebrae in spotted dolphins. Atlantic specimens (hatched) superimposed on Indian and Pacific Ocean specimens. Dot = Atlantic endemic color pattern; open circle = pantropical pattern (all Indopacific specimens had pantropical pattern). Indopacific data from Nishiwaki *et al.* (1965), Ross (1984) and Lütken (1889) and from specimens included in Perrin (1975) and Perrin *et al.* (1979).

2, Fig. 6), including juvenile specimens (CB length 305–414 mm). The holotype specimens are each clearly associated with one of the two species with high probability ($P < 0.01$). The holotypes of *Steno attenuatus* Gray, 1846; *S. capensis* Gray, 1865 and *Delphinus brevimanus* Wagner, 1846 belong to the pantropical species, and those of *Delphinus doris* Gray, 1846; *D. froenatus* F. Cuvier, 1829; *D. frontalis* G. Cuvier, 1829 and *D. plagiodon* Cope, 1866 belong to the endemic species.

All specimens of spotted dolphins from the Indian and Pacific Oceans for which color pattern and/or vertebral count are known are of the pantropical species. Application of the discriminant function based on the Atlantic material to a series of Indopacific skulls resulted in correct classification of all but two of the 115 specimens (lower panel in Fig. 6). The Indopacific specimen with a value of 0.3 for the canonical variable is an aberrant skull. The rostrum is extremely blunt and broad (36 mm at ¾ length; Perrin 1975, fig. 41) and has a highest rostral tooth count of only 38, the lowest value for the specimens of the pantropical species included in the analysis. The dolphin was captured

Table 6. Statistics for skull and postcranial measurements (mm) of geographical series of *Stenella frontalis*. Standard deviations included for samples ≥25. Characters showing sexual dimorphism (*t*-test, M or F sample ≥25, $\alpha = 0.05$) presented separately for males

		A N.W. Atlantic Coast & Gulf of Mexico				
		Range	(*n*)	Mean	SD	CV
Condylobasal length		396–461	(62)	427.6	15.37	3.59
Length of rostrum		222–274	(63)	247.2	11.82	4.78
Width of rostrum at base		86–107	(66)	96.9	4.53	4.67
Width of rostrum at 60 mm	M	67–78	(20)	72.4	—	—
	F	60–82	(35)	69.5	3.91	5.63
Width of rostrum at ½ length	M	53–63	(20)	57.8	—	—
	F	48–63	(34)	55.9	3.48	6.23
Width of pmx's at ½ length	M	27–35	(20)	31.2	—	—
	F	24–34	(34)	29.5	2.65	8.98
Width of rostrum at ¾ length	M	38–50	(20)	43.7	—	—
	F	34–48	(34)	41.2	3.11	7.55
Rostrum tip to external nares		260–319	(63)	289.0	12.86	4.45
Rostrum tip to internal nares		264–329	(59)	295.5	13.93	4.71
Greatest preorb. width		160–188	(65)	176.8	6.16	3.48
Greatest postorb. width	M	187–210	(20)	201.3	—	—
	F	183–207	(35)	197.9	6.17	3.12
Greatest width of ext. nares		41–52	(65)	46.5	2.24	4.82
Zygomatic width	M	185–210	(20)	201.5	—	—
	F	184–208	(35)	196.7	6.10	3.10
Greatest width of pmx's		70–87	(65)	78.6	3.52	4.48
Parietal width	M	141–171	(20)	157.5	—	—
	F	141–164	(35)	153.3	4.99	3.26
Height of braincase	M	103–118	(20)	112.4	—	—
	F	100–120	(35)	109.1	4.49	4.12
Int. length of braincase		114–141	(65)	129.6	4.74	3.66
Length of temporal fossa		61–89	(66)	79.3	4.99	6.29
Height of temporal fossa		45–72	(66)	60.7	4.87	8.02
Length of orbit		50–60	(65)	55.9	2.33	4.17
Length of preorb. process		39–50	(65)	44.4	2.62	5.90
Width of internal nares		46–59	(62)	53.1	2.94	5.54
Length of upper toothrow		191–238	(63)	211.7	10.31	4.87
Length of lower toothrow		181–228	(59)	205.7	9.90	4.81
Length of ramus		332–399	(59)	365.6	14.68	4.02
Height of ramus		61–75	(58)	68.3	3.20	4.69
Diameter of tooth (at mid-length of lower row, transverse at alveolus)		3.5–5.3	(39)	4.50	0.390	8.67
Width of prenarial triangle at 60 mm		0.6–7.3	(54)	3.77	1.834	48.65
Atlas: width		79–98	(27)	87.7	4.21	4.80
height		52–60	(29)	55.3	2.13	3.85
length of lat. process		25–40	(29)	30.1	3.89	12.92

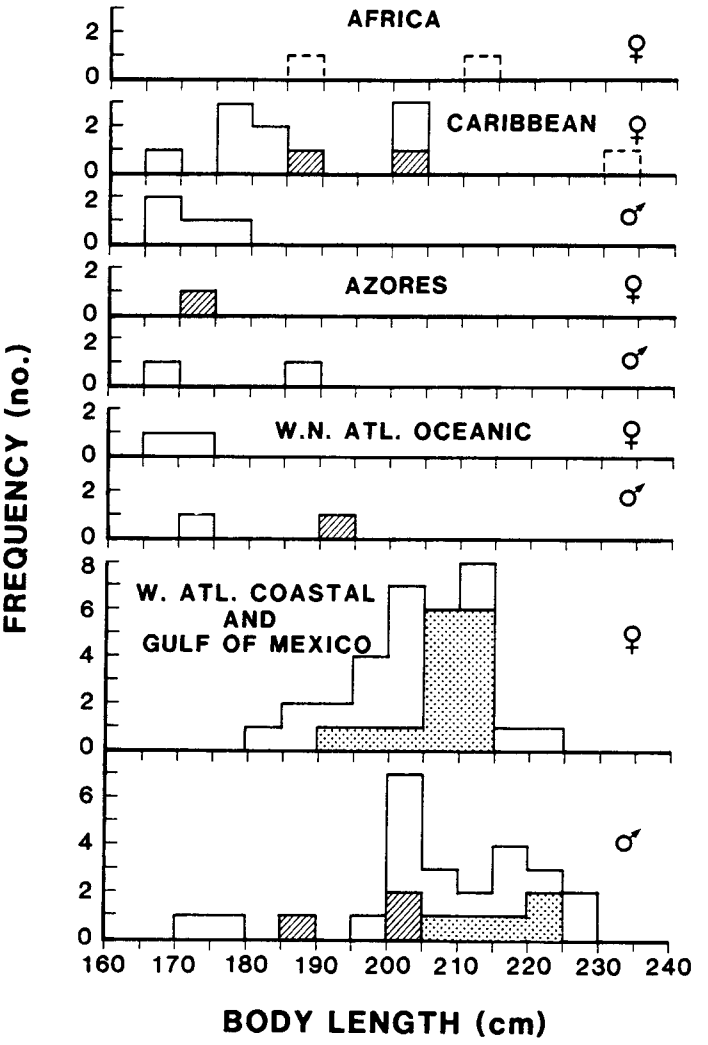


Figure 12. Frequency distributions of body length for five geographical samples of cranially adult specimens of *Stenella frontalis*. Shaded portions represent physically mature specimens; dashed portions are specimens of unknown degree of physical maturity.

The largest Caribbean skull (USNM 254447) was collected on the coast of Panama (inside the 100-fathom [183-m] curve). Spotted dolphins along the coast of Central America may be larger than animals in the Caribbean proper to the east.

The western North Atlantic coastal form is also larger in all postcranial skeletal dimensions, the differences being greatest for the transverse processes of the vertebrae, the sternum and the scapula. The bones of the manus show

Table 5. Statistics for meristic osteological characters for *Stenella frontalis* and *S. attenuata*. Standard deviations and coefficients of variation (CV) included for samples of 25 or more.

		S. frontalis					*S. attenuata*									
							Atlantic					All oceans				
		Range	Mean	SD	CV	*N*	Range	Mean	SD	CV	*N*	Range	Mean	SD	CV	*N*
Tooth counts:	highest rostral	33–42	36.4	1.90	5.2	109	37–48	40.9	2.07	5.2	68	37–48	41.4	2.11	5.1	316
	lowest rostral	32–41	35.7	1.74	4.9	109	35–47	40.3	2.12	5.3	67	35–47	40.6	2.08	5.1	315
	highest mandibular	31–40	34.8	2.25	6.5	103	36–45	39.9	2.10	5.3	69	34–47	40.4	2.04	5.0	315
	lowest mandibular	30–40	34.1	2.29	6.7	101	35–45	39.3	1.92	4.9	69	34–45	39.6	1.99	5.0	315
Vertebrae:	total number	67–72	70.0	1.07	1.5	52	74–81	79.3	—	—	9	74–84	79.7	1.55	1.9	175
	thoracic[a]	13–15	14.2	0.47	3.3	46	14–16	15.1	—	—	9	13–17	15.8	0.73	4.6	184
	lumbar	15–20	17.0	1.19	7.0	30	17–23	20.3	—	—	7	17–24	19.8	1.45	7.3	154
	caudal	28–35	31.8	1.65	5.2	32	34–41	36.4	—	—	7	32–42	37.0	1.65	4.5	155
	first with vert. for.	45–51	48.0	1.23	2.6	49	52–59	56.0	—	—	9	52–61	56.6	1.74	3.1	125
	last with trans. proc.	50–55	53.0	0.90	1.7	49	56–62	60.4	—	—	9	56–66	62.3	1.45	2.3	123
	last with neur. proc.	56–60	58.1	0.96	1.7	49	61–68	66.1	—	—	8	61–71	67.6	1.44	2.1	120
	first with chev. bone	38–41	39.0	0.90	2.3	28	41–46	43.5	—	—	6	41–47	43.5	1.40	3.2	94
	last with chev. bone	60–65	62.2	1.43	2.3	25	66–72	70.0	—	—	5	66–77	72.1	1.63	2.3	85
	number of chev. bones	21–26	23.9	—	—	21	26–33	27.4	—	—	5	24–33	29.7	1.74	5.9	73
Manus:[b]	digit 1, highest no. of phalanges	1–3	2.2	0.67	30.4	31	2–3	2.7	—	—	6	0–3	1.8	0.51	28.3	118
	II	7–10	8.7	0.78	9.0	31	9–10	9.4	—	—	5	7–10	8.5	0.70	8.2	110
	III	6–8	6.7	0.55	8.2	30	6–7	6.4	—	—	5	4–7	6.1	0.55	9.0	110
	IV	2–4	3.1	0.53	17.1	29	3	3.0	—	—	5	2–4	2.9	0.48	16.6	105
	V	0–2	1.5	0.63	42.0	30	2	2.0	—	—	5	0–2	1.6	0.37	23.1	105
	carp. & metacarp., highest number	4–7	5.3	0.65	12.3	31	5–6	5.5	—	—	6	5–8	6.2	—	—	131

[a] Equals highest vertebral rib count.
[b] Some variation in phalanges may be caused by confusion with metacarpals (as pointed out by True 1894).

Table 4. Continued.

	Stenella frontalis	*Stenella attenuata*	
		Atlantic	All oceans[a]
Length of ramus	292–399 (97)	312–375 (30)	296–393 (167)
Height of ramus	55–74 (97)	53–61 (30)	50–75 (170)
Diameter of tooth (at mid-length of lower row, transverse at alveolus)	3.2–5.3 (68)	3.0–4.1 (24)	2.6–4.1 (42)
Width of prenarial triangle at 60 mm	0.6–9.9 (93)	2.1–13.4 (28)	2.1–15.6 (160)
Atlas: width	68–97 (26)	73–83 (6)	73–90 (30)
height	49–60 (26)	45–49 (6)	46–61 (29)
length of lat. process	22–40 (26)	24–26 (6)	18–28 (29)
Length of last thor. neur. spine	72–98 (25)	73–81 (5)	55–81 (28)
First thor. vert.: height	30–57 (26)	42–45 (6)	44–60 (28)
width	75–98 (26)	72–79 (6)	63–86 (29)
First lumbar vert: height	50–71 (25)	45–52 (6)	46–67 (28)
width	179–222 (25)	175–202 (6)	165–207 (28)
Length of first vert. rib	120–151 (26)	113–133 (6)	100–143 (29)
Length of longest vert. rib	242–314 (26)	234–286 (6)	232–313 (29)
Length of first stern. rib	75–99 (25)	73–84 (6)	66–88 (29)
Width of manubrium	88–112 (24)	73–94 (6)	63–106 (30)
Length of longest chev. bone	40–60 (23)	44–56 (6)	40–66 (26)
Scapula: height	116–155 (25)	105–127 (6)	101–135 (30)
length	113–143 (25)	109–132 (6)	99–132 (29)
Humerus: length	59–74 (16)	50–56 (6)	43–62 (30)
width	38–52 (22)	32–36 (6)	32–44 (30)
Length of radius	72–90 (22)	60–72 (6)	56–77 (30)
Length of ulna	66–80 (22)	54–61 (6)	48–65 (29)

[a] From specimens listed below and from Perrin 1975, Perrin *et al.* 1979, Zhou *et al.* 1980, Ross 1984, Best 1969, Nishiwaki *et al.* 1965, Pinedo and Castello 1980.

Table 4. Minimum and maximum skull and postcranial skeletal measurements (mm) for *Stenella frontalis* and *S. attenuata*. Skull measurements are for cranially adult specimens; postcranial measurements are for physically mature specimens. Sample sizes in parentheses.

	Stenella frontalis	*Stenella attenuata*	
		Atlantic	All oceans[a]
Condylobasal length	356–461 (103)	369–437 (31)	356–460 (183)
Length of rostrum	194–274 (105)	208–268 (31)	208–287 (176)
Width of rostrum at base	76–107 (108)	80–95 (31)	74–100 (186)
Width of rostrum at 60 mm	55–82 (108)	55–70 (31)	46–77 (184)
Width of rostrum at ½ length	44–63 (105)	39–49 (31)	35–60 (185)
Width of pmx's at ½ length	22–36 (103)	19–28 (31)	17–32 (170)
Width of rostrum at ¾ length	30–50 (105)	25–36 (31)	23–43 (177)
Rostrum tip to external nares	230–319 (105)	248–312 (31)	245–321 (182)
Rostrum tip to internal nares	236–329 (95)	257–320 (31)	243–329 (171)
Greatest preorb. width	146–188 (106)	147–165 (31)	134–178 (184)
Greatest postorb. width	165–210 (107)	165–185 (31)	151–196 (183)
Greatest width of ext. nares	40–52 (105)	39–48 (31)	37–52 (175)
Zygomatic width	164–210 (107)	163–182 (31)	148–198 (183)
Greatest width of pmx's	65–87 (106)	64–73 (31)	57–76 (186)
Parietal width	130–171 (107)	130–150 (31)	129–161 (185)
Height of braincase	93–121 (106)	89–109 (31)	87–113 (170)
Int. length of braincase	108–141 (105)	110–122 (31)	107–136 (160)
Length of temporal fossa	57–89 (107)	58–73 (31)	53–97 (184)
Height of temporal fossa	45–72 (107)	43–59 (31)	33–79 (184)
Length of orbit	45–60 (106)	45–53 (31)	43–59 (172)
Length of preorb. process	36–50 (105)	31–44 (31)	30–51 (173)
Width of internal nares	40–59 (102)	46–54 (31)	40–61 (171)
Length of upper toothrow	171–238 (104)	175–235 (30)	175–248 (180)
Length of lower toothrow	168–228 (99)	182–222 (31)	177–242 (175)

males and females differ in eight skull measurements and one postcranial measurement (*t*-test, at $\alpha = 0.05$): widths of the rostrum at 60 mm, ½ length and ¾ length; width of the pmx's at ½ length of the rostrum; postorbital, zygomatic and parietal widths; height of the braincase; and height of the first thoracic spine. Adult males are larger in all of these characters. Statistics for the several geographic series described below are presented separately for males and females for the dimorphic characters.

Tooth counts and postcranial meristics are presented in Table 5. Rostral tooth counts range from 32 to 42; lower counts range from 30 to 40. Total number of vertebrae ranges from 67 to 72; the typical formula is C7,T14,L17,Ca32 = 70.

Geographic variation—While very large portions of the range of the species are represented by only one or a very few specimens (*e.g.*, the coasts of South America and Africa), some patterns of variation are evident or at least suggested by the available material. The analyses here are based on more or less coherent series from six geographic regions: (1) along the coast and over the continental shelf in the western North Atlantic coast and Gulf of Mexico; (2) the oceanic western North Atlantic (north of Cape Hatteras and east to 35°W in the eastern extension of the Gulf Stream); (3) the Azores; (4) the Caribbean (including some specimens from near the coast of Venezuela); (5) the mid-tropical Atlantic (including St. Helena); and (6) West Africa.

Adult body length is greatest along the western North Atlantic coast and in the Gulf of Mexico, averaging about 200–210 cm (Fig. 12). Very few data are available on adult length for the oceanic western North Atlantic and the Azores, but it would appear that adults there are about 20–30 cm smaller than adults from the coast to the west and south. Except for one specimen from Panama (229-cm female; USNM 254447), the Caribbean specimens were also smaller, centering around 180 cm. The sample from Africa is too small to allow interpretation, and there are no data on adult length available for the mid-tropical Atlantic.

There is marked geographic variation in the size and shape of the skull (Table 6). The skulls from the oceanic western North Atlantic and the Azores closely resemble skulls from the coastal western North Atlantic in shape but are very much smaller. This is correlated with the lesser body size and low-to-medium degree of spotting discussed above. The western North Atlantic coastal/Gulf of Mexico skulls are on the average larger than the Caribbean skulls in all measurements but one (prenarial width) for which sample sizes are large enough for meaningful comparison. The two series differ proportionately the most in rostral widths, dimensions of the temporal fossa and tooth width. The pelagic Caribbean animals have on the average a more slender rostrum, smaller temporal fossa and smaller teeth than do the coastal animals. As has been hypothesized for a similar coastal/pelagic difference in *Stenella attenuata* in the eastern Pacific (Perrin 1975), this may reflect differential feeding habits; the coastal form may feed on larger (perhaps demersal) prey than is taken by the pelagic form. The two series of skulls are least different in length of tooth row and other cranial dimensions that contain the tooth row.

Table 3. Minimum and maximum external dimensions (cm) and weights (kg) of cranially adult specimens of *Stenella frontalis* and *S. attenuata*. Males and females presented separately for measurements known to vary with sex in *S. attenuata* (Perrin 1975). Sample sizes in parentheses.

		Stenella frontalis	*Stenella attenuata*	
			Atlantic	All oceans
Total length	M	166–226 (33)	193–231 (6)	166–257 (>1,650)
	F	167–229 (46)	185–194 (4)	163–240 (>4,345)
Tip of upper jaw to:				
Apex of melon		9–14 (60)	9–12 (7)	8–13 (139)
Center of blowhole		23–35 (61)	28–32 (9)	24–33 (170)
Center of eye		25–35 (67)	29–32 (9)	25–33 (155)
End of gape		20–28 (58)	23–27 (7)	21–29 (161)
Ext. aud. meatus	M	30–39 (20)	36 (3)	31–37 (16)
	F	31–38 (31)	34–37 (3)	32–37 (18)
Ant. insert. of flip		38–53 (57)	40–45 (8)	34–45 (153)
Umbilical scar		81–105 (49)	87–103 (8)	80–107 (131)
Center of gen. slit	M	106–145 (24)	129–144 (3)	120–144 (16)
	F	112–158 (33)	130–133 (3)	124–162 (25)
Center of anus	M	119–162 (24)	140–166 (5)	135–166 (18)
	F	123–162 (39)	137–139 (3)	130–171 (25)
Tip of dorsal fin	M	100–137 (23)	113–118 (4)	100–120 (45)
	F	104–136 (39)	107–113 (3)	97–120 (83)
Girth at axilla	M	82–117 (22)	76–90 (3)	76–99 (42)
	F	82–111 (25)	79–85 (2)	71–94 (88)
Girth at anus	M	48–78 (22)	61–95 (4)	53–95 (18)
	F	47–72 (29)	49–56 (2)	49–66 (22)
Eye to:				
Ext. aud. meatus		5–7 (50)	5–6 (7)	5–7 (41)
End of gape		5–7 (54)	5–6 (6)	4–6 (29)
Center of blowhole		12–21 (51)	14–15 (6)	11–17 (109)
Flipper:				
		26–37 (57)	23–27 (9)	23–30 (32)
Ant. length		18–29 (55)	15–20 (8)	14–21 (121)
Post. length	M	9–14 (25)	8–12 (6)	8–12 (12)
Width	F	9–13 (34)	9–10 (3)	9–10 (15)
Flukes:				
Span		35–66 (64)	38–46 (8)	36–49 (120)
Width		10–17 (52)	10–13 (5)	10–15 (17)
Height of dorsal fin		16–25 (66)	13–17 (8)	12–20 (111)
Weight	M	50–143 (14)	87 (1)	max 119 kg
	F	39–127 (22)	— —	—

et al. 1985) could be expected to be negligible compared to the considerable geographic variation in skull size and shape. The series of specimens from the U.S. Atlantic coast and Gulf of Mexico is large enough to allow meaningful assessment of dimorphism (20 adult males and 35 adult females). In this series,

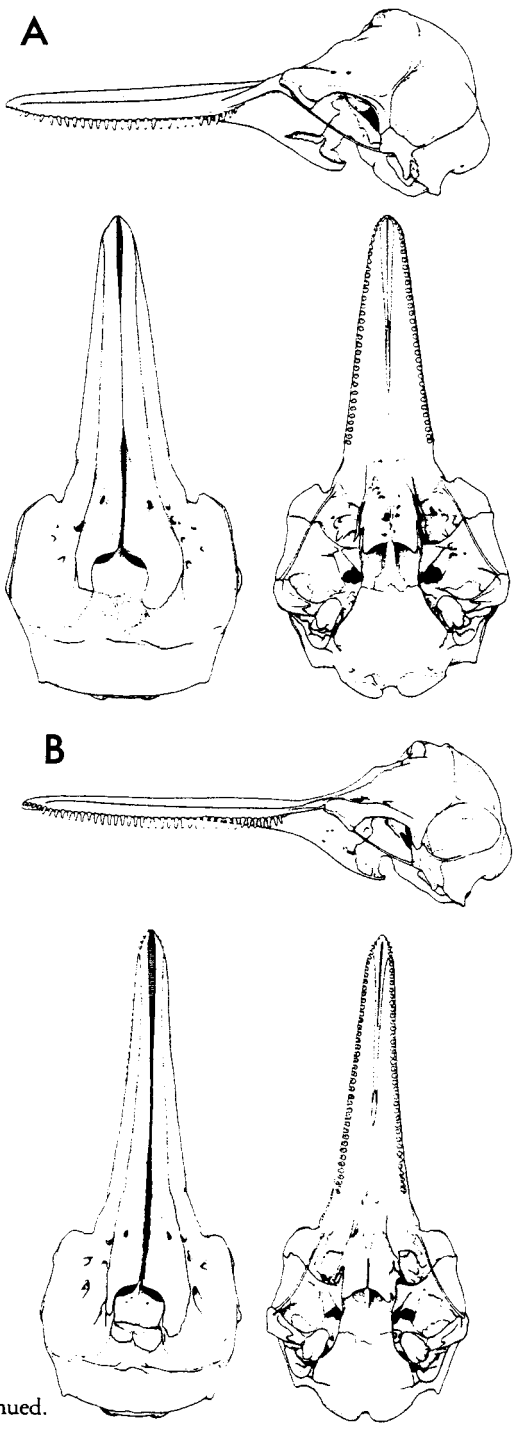


Figure 11. Continued.

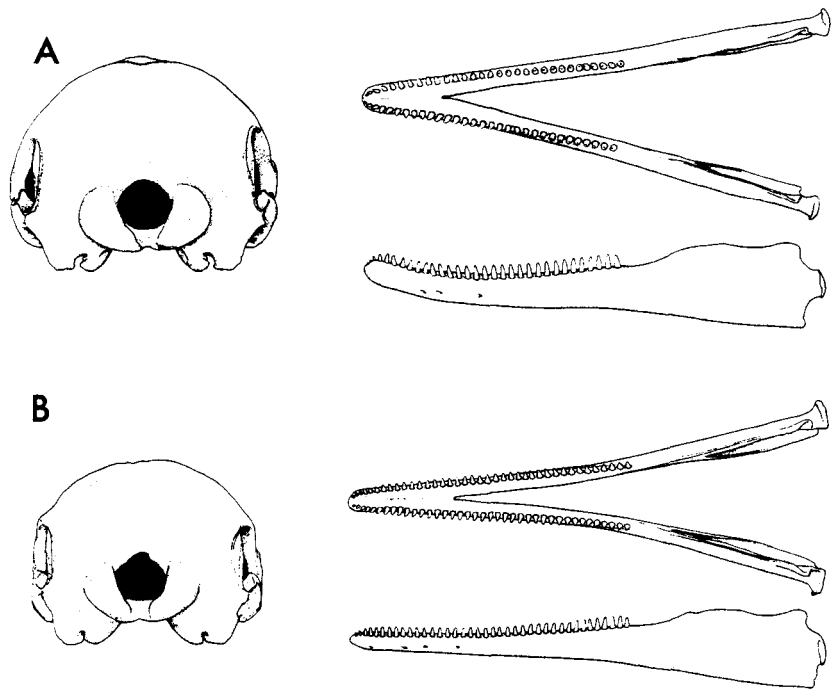
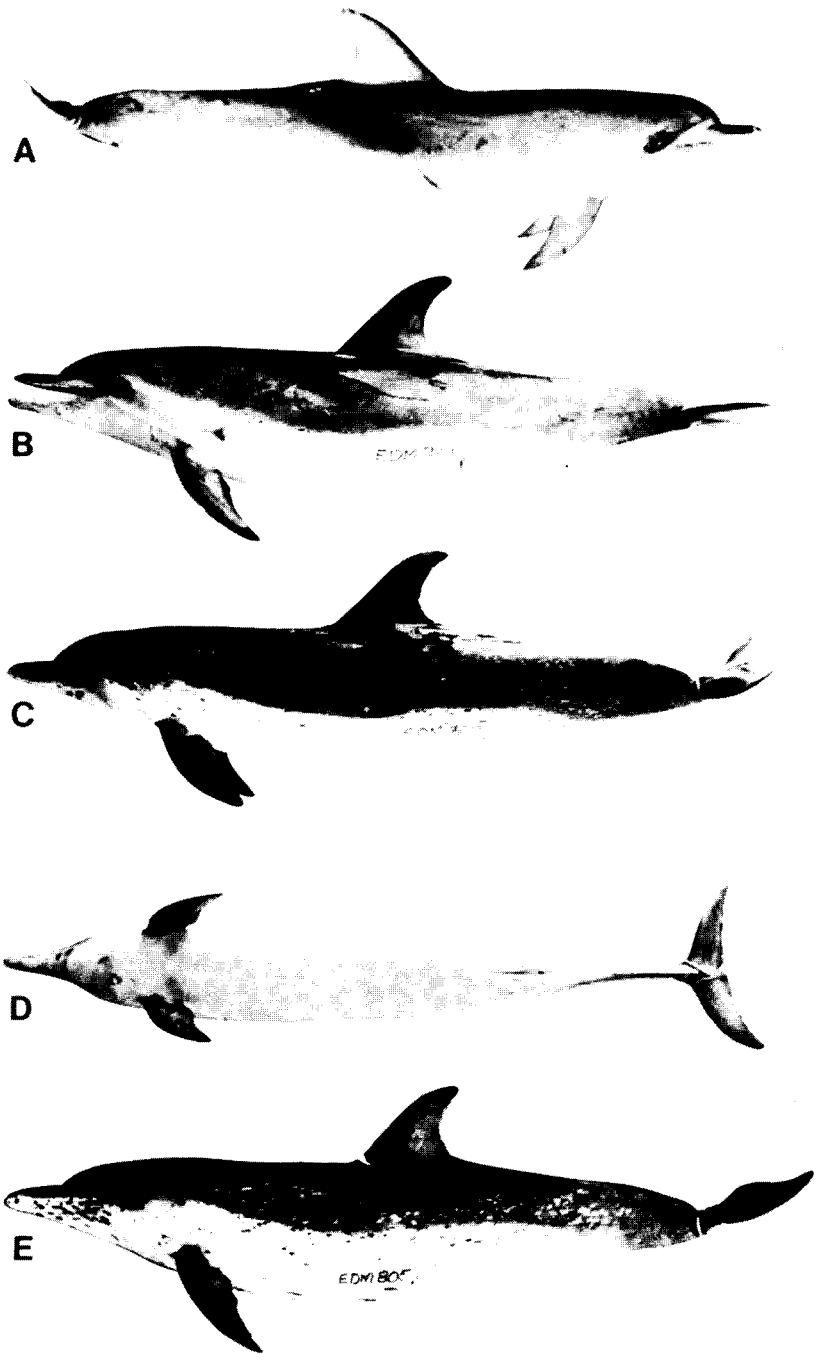


Figure 11. Typical adult skulls of A) *Stenella frontalis* (drawn from USNM 257833) and B) *S. attenuata* (drawn from R-1-SF), both from the Atlantic coast of Florida.

recorded length for males is 226 cm (a physically immature specimen from North Carolina; USNM 22017) and for females 229 cm (a specimen of unknown degree of physical maturity from Panama; USNM 254447). The smallest known cranially adult specimens were a 166-cm male (AMNH 239111 from the Azores, not physically mature) and a 167-cm female (UZMC *Prodelphinus* no. 2 from off Cape Verde, not physically mature). The smallest specimens known to have been physically mature were a 188-cm male from the Azores (UZMC *Prodelphinus* no. 4) and a 186-cm female from off Venezuela in the Caribbean (AMNH 239112). Geographical variation in size is discussed below.

A typical skull from the coastal western North Atlantic is illustrated in Figure 11. Ranges of skull measurements for cranially adult specimens and postcranial measurements for physically mature specimens are in Table 4. The largest known skull is of a 205-cm cranially immature male from off South Carolina (EDM 697). The smallest is of a 191-cm male from west of the Azores (UZMC *Prodelphinus* no. 11, CB length 356 mm). Ranges of the osteological measurements are not presented in Table 4 separately for males and females because many of the skulls in the overall sample are not identified to sex. In any case, the slight sexual dimorphism of the sort known for *Stenella attenuata* (Schnell


A
B
C
D
E

teriorly. The dorsal margin of this mark intersects the ventral margin of the eye stripe several centimeters anterior to the angle of the gape. The flipper stripe consists of two parts: a narrow (less than 5 mm) light line dorsally bordering a wider (about 25–50 mm) darker band with indistinct ventral margin. The flipper stripe may end anteriorly at the eye, between the eye and the gape, or at the angle of the gape; this feature varies both individually and geographically (Fig. 9). When the flipper stripe abuts anteriorly on the gape mark, the junction is delineated with a faint light line. This region of complex interaction of flipper stripe, gape mark and eye stripe is highly variable. All of the dark marks are more or less obscure in heavily spotted adults.

Adult size and intensity of spotting both vary geographically; therefore, body length at the onset of spotting also varies. Spots typically appear before the onset of puberty. The following is a description of the development of spotting to its extreme expression, as in some individuals from the Atlantic coast of the United States. Spots (dark gray to black) appear first in the gular and abdominal regions. Soon after appearance of dark ventral spots, light dorsal spots begin to develop. Both dark and light spots occur in the lateral field. The ventral spots enlarge and begin to coalesce, and the dorsal light spots spread ventrad, overlying the fused dark spots. Finally, the dorsal spots enlarge and coalesce in some areas, especially above the eyes, in the area of the spinal blaze and on the dorsal side of the peduncle. The light spots extend to the appendages. Portions of the original white ventral field remain uncovered in the gular and genital regions, peppered and bordered with dark spots. Thus, the most heavily spotted individuals appear uniformly dark gray with dorsal and ventral light spots and patches. The point to which the development of spots progresses varies both individually and geographically. Dolphins from the U.S. Atlantic coast, Gulf of Mexico and coasts of Central and South America have medium to heavy spotting (Figs. 1 and 8). In the Caribbean, they have medium spotting, with the underlying ground pattern clearly evident in mature adults (Fig. 1). Those from the offshore western North Atlantic (north of Cape Hatteras in the eastern extension of the Gulf Stream) have few if any spots (Fig. 10). This neotenoid coloration is correlated with small adult body size (described below). In the Azores, spotting is light to medium and the ventrum is typically unspotted (Fig. 10). On the coast of West Africa, spotting is again medium to heavy.

Minimum and maximum external dimensions and weights for cranially adult specimens (pmx fused to mx distally) are presented in Table 3. Maximum

→

Figure 10. Geographical variation in intensity of spotting in *Stenella frontalis*: A) unspotted cranially adult male (170 cm) from off Nova Scotia (EDM 786), B) lightly spotted subadult male (166 cm) from the Azores (AMNH 23911, EDM 761), C) and D) lateral and ventral views of a cranially adult female (175 cm) with medium dorsal and lateral sporting but white ventrum from the Azores (captured with B), E) a cranially adult female (179 cm) with lateral mixed dark and light spots, from off Venezuela (AMNH 239114). Heavily spotted condition illustrated in Fig. 8 and medium spotting in Fig. 1.

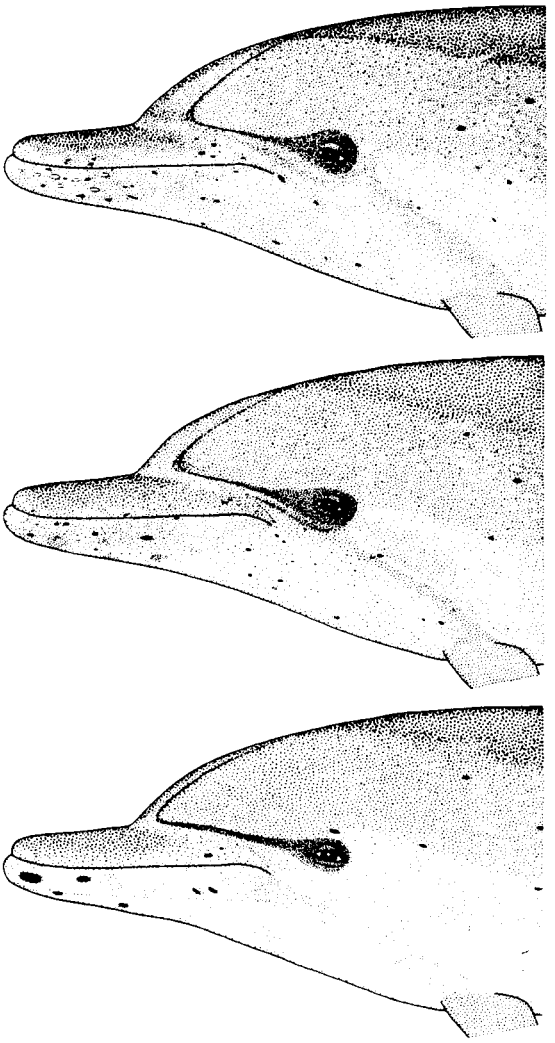


Figure 9. Variation in position of anterior end of flipper stripe in *Stenella frontalis*: (top) behind eye, (middle) lower edge of eye, (bottom) angle of gape. Drawn from photos of (top to bottom) a 205-cm subadult male (EDM 697) from off South Carolina, a 197-cm cranially adult female (EDM 696) from off South Carolina, and a cranially adult 166-cm male (AMNH 239111) from the Azores.

and stripe is present. The blowhole and eye stripes may consist of two or more parallel darker and lighter sub-elements. In young calves there is an irregularly defined extension of the white ventral field up into the lateral field starting at about the level of the anterior insertion of the dorsal fin, giving the animal a blotched appearance. A sharply defined dark gray mark borders the gape pos-

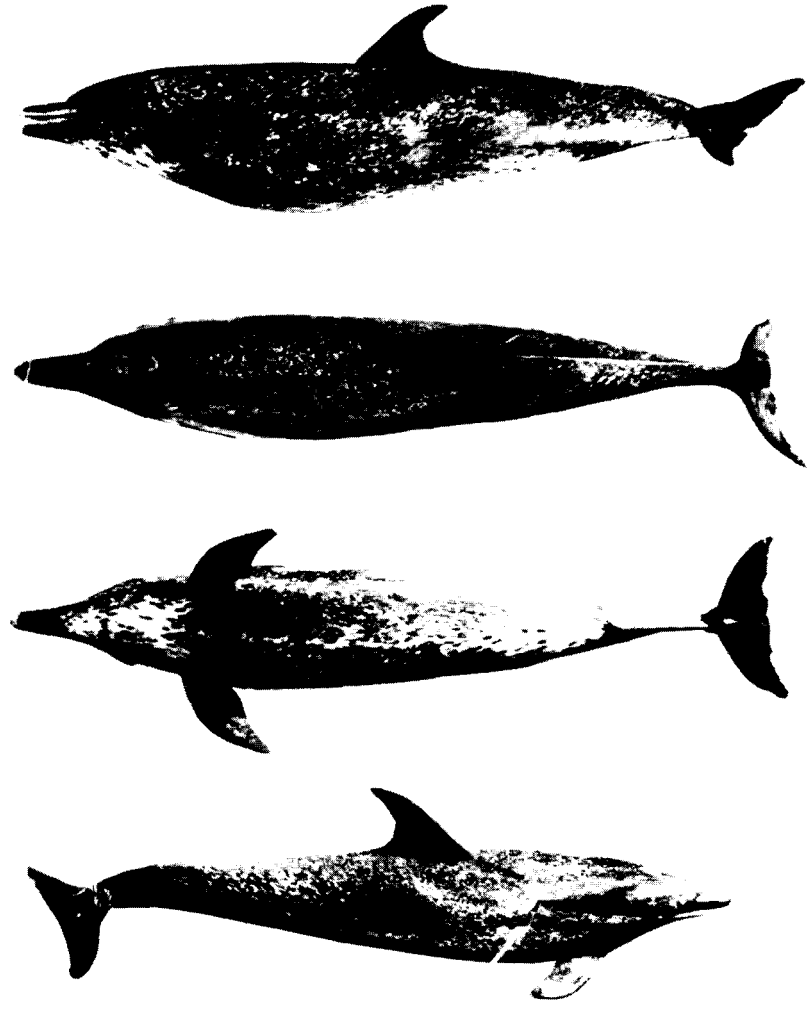


Figure 8. Heavily spotted specimens of *Stenella frontalis*: (top 3) a 206-cm physically mature male (EDM 695) from off the coast of North Carolina and (bottom) a 224-cm male (USNM 253598) from off South Carolina (note spinal blaze).

dorsal fin. The blaze varies individually in length, width and intensity of expression. The combination of spinal blaze and dorsal spotting is unique to this species. The spinal blaze may be nearly obscured by light dorsal spots in mature individuals in some geographical areas, but it is usually at least faintly visible in dorsal view (Fig. 8). The ventral margin of the light gray lateral field begins behind the eye and ends indistinctly in the anal region; it too may be obscured in mature adults in some regions by dark ventrolateral spotting (Fig. 8). The basic delphinid "bridle" of dark-gray-to-black blowhole stripe and eye patch

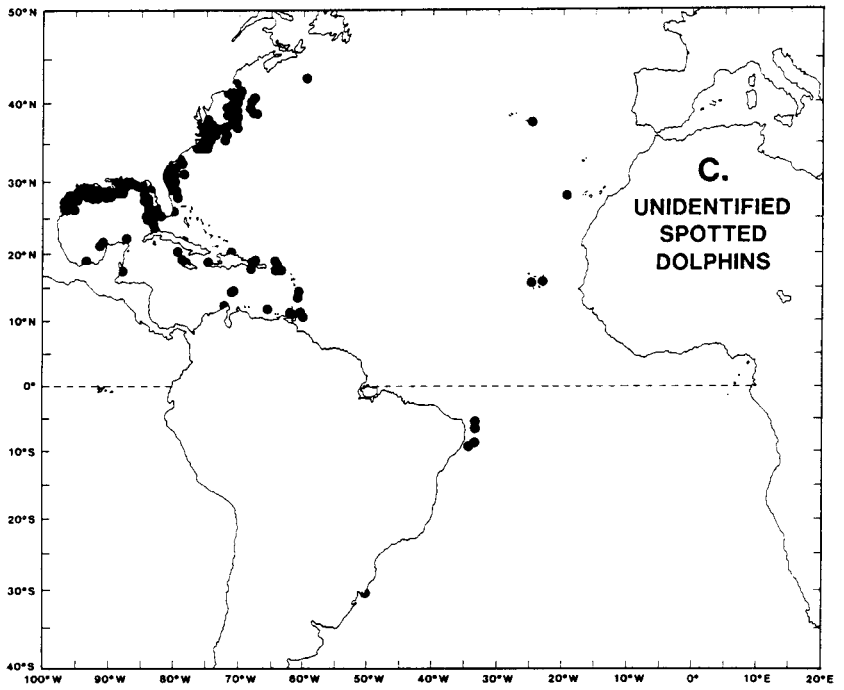
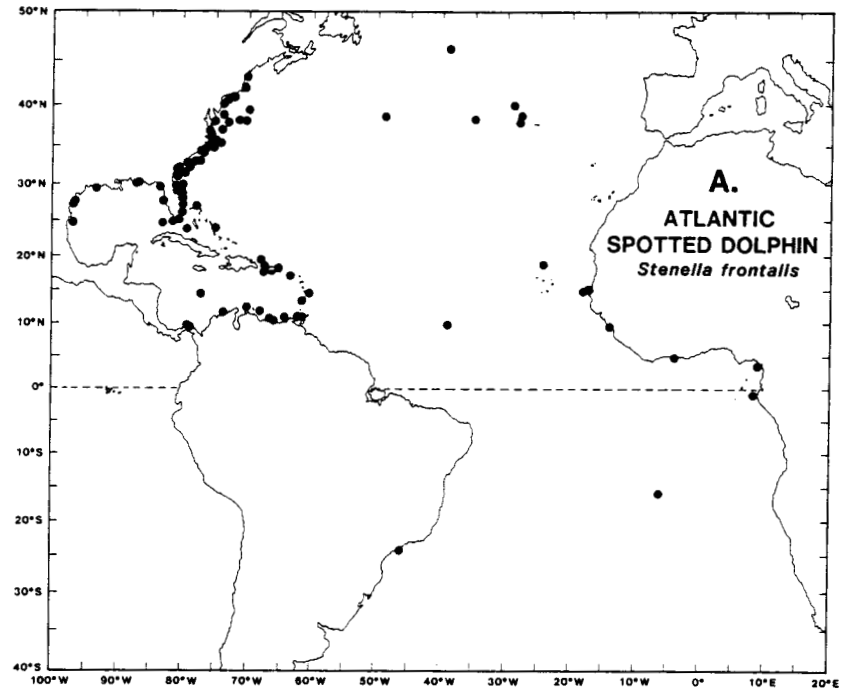
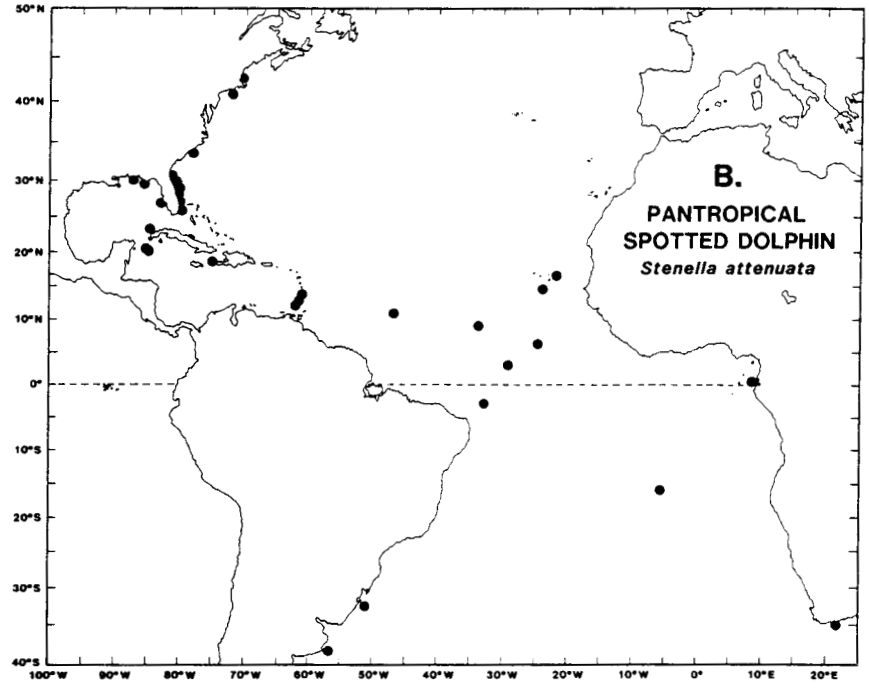


Figure 7. Locality records in the Atlantic for A) *Stenella frontalis,* B) *S. attenuata* and C) unidentified spotted dolphins. Note: the latitude for "*Prodelphinus* no. 2" in Lütken (1889) should be 19°03'N, not 13°03'N (based on original field data sheets in UZMC).

Prodelphinus no. 1 in the Copenhagen Museum and MNHN A-3031 in the Paris Museum), both collected in the 19th century. All records of spotted dolphins from St. Helena in this century are of the pantropical species, and the fishermen presently living on the island have no knowledge of a second type of spotted dolphin (Perrin 1985*a,* Perrin and Perrin 1985). As was probably the case for a record of the southern right whale dolphin, *Lissodelphis peronii,* a coldwater species (Perrin 1985*a*), it is possible that the two early specimens were collected by ships on the way to or from St. Helena. It was common practice aboard whalers and some other vessels to harpoon dolphins for use as food for the crew. It is, of course, also possible that the species formerly occurred at the island or that it visits the island's waters only rarely. The two skulls closely resemble specimens from West African and mid-tropical Atlantic waters (discussed below).

Diagnosis—The color pattern consists of an underlying ground pattern present at birth and superimposed dark ventral and light dorsal spots that develop with maturation (Fig. 1). In the ground pattern, the ventral margin of the dark gray cape (terminology of Perrin 1972) is obscured anteriorly by a spinal blaze (terminology of Mitchell 1970) that sweeps up and back, its apex below the


A.
ATLANTIC
SPOTTED DOLPHIN
Stenella frontalis
50°N
40°N
30°N
20°N
10°N
0°
10°S
20°S
30°S
40°S
100°W
90°W
80°W
70°W
60°W
50°W
40°W
30°W
20°W
10°W
0°
10°E
20°E


B.
PANTROPICAL
SPOTTED DOLPHIN
Stenella attenuata
50°N
40°N
30°N
20°N
10°N
0°
10°S
20°S
30°S
40°S
100°W
90°W
80°W
70°W
60°W
50°W
40°W
30°W
20°W
10°W
0°
10°E
20°E

1846. *Delphinus frenatus.* Gray, Zoology of the voyage of *H.M.S. Erebus* and *Terror,* 1, p. 39.
1866. *Tursio fraenatus.* Gray, Catalogue of seals and whales in the British Museum, p. 256.
1880. *Prodelphinus fraenatus.* H. Gervais, *in* van Beneden and Gervais, Ostéographie des Cétacés, p. 605, pl. 38, fig. 4.
1884. [*Clymenia*] *fraenata.* Flower, Proc. Zool. Soc. London, 1883, p. 512.
1889. *Prodelphinus froenatus.* True, Bull. U.S. Nat. Mus., 36, p. 68, 70, 73, 166, pl. 19, fig. 1 & 2, pl. 20, fig. 1.
1900. *Prodelphinus fraenatus.* Beddard, Book of whales, p. 261.
1846. *Delphinus Doris* Gray, Zoology of the voyage of *H.M.S. Erebus* and *Terror,* 39, pl. 20.
1866. *Tursio Doris.* Gray, Catalogue of seals and whales in the British Museum, p. 255.
1866. *Clymene doris.* Gray, Proc. Zool. Soc. London, 1866, p. 214.
1868. *Clymenia doris.* Gray, Synopsis of the whales and dolphins in the British Museum, p. 6, pl. 20.
1885. *Prodelphinus doris.* True, Rep. U.S. Nat. Mus., 1884, p. 317, pl. 1–6.
1885. *Prodelphinus doris.* Flower, List of specimens of Cetacea in the Zoological Department of the British Museum, p. 26.
1866. *Delphinus plagiodon* Cope, Proc. Acad. Nat. Sci. Philadelphia, 18, p. 296.
1885. *Prodelphinus plagiodon.* True, Rep. U.S. Nat. Mus., 1884, p. 323, pl. 4, 6.
1940. *Stenella plagiodon.* Kellogg, Nat. Geogr. Mag., 77, p. 83, pl. 19.
1889. *Prodelphinus obscurus* Lütken (not Gray), Vid. Selsk. Skrift., Copehagen, Nat. Mat. 5(1), p. 43.
1981. *Stenella pernettensis plagiodon* (Cope) of Hall, Mammals of N.A., p. 883.

Holotype and type locality—Adult skull, Muséum National d'Histoire Naturelle, Paris (MNHN) no. A-3035, and mounted skin (no. 25 of the Catalogue de la Galerie de Zoologie) off Cape Verde, West Africa (approximately 15°N, 18°W).

Distribution—Tropical, subtropical and warm temperate Atlantic (Fig. 7a). Not known to occur in Indian or Pacific Oceans. Perrin *et al.* (1978) noted the possible existence of endemic tropical dolphins in the Atlantic and speculated that they may represent forms that arose during Pleistocene isolation of the tropical Atlantic from the Indopacific.

G. Cuvier (1829) stated that *D. dubius* (probably = *S. frontalis*) occurs in European waters. There is a skull of *S. frontalis* in the British Museum (BMNH 1948.5.1.1, acquired from the Rothschild collection and accessioned in 1948) labeled "coast of Europe," but we could find no other record of the species from the eastern Atlantic north of the Cape Verde Islands. Unidentified spotted dolphins reported from the Canary Islands may be of this species (Fig. 7c).

There are two skulls of *S. frontalis* labeled as from St. Helena (UZMC

combinations: *Prodelphinus plagiodon* (True, 1885), *Stenella plagiodon* (Kellogg, 1940).

Steno consimilis Malm, 1871

Hershkovitz (1966) placed this species in the synonymy of the spinner dolphin, *Stenella longirostris* (Gray, 1828). We did not examine the holotype skull (in the Technological Institute, Norrkoping, Sweden), which is from Madagascar, but as illustrated by Malm it is a typical skull of the pantropical spotted dolphin, with 45 rostral teeth and 40 mandibular on each side.

Prodelphinus graffmani Lönnberg, 1934

The type specimen (in the State Museum of Natural History, Stockholm) consists of the mounted skin and damaged skull of a large spotted dolphin harpooned near Acapulco, Mexico, in the eastern tropical Pacific. Perrin (1975) found all spotted dolphins in the eastern Pacific to be conspecific and placed *P. graffmani* in the synonymy of *Stenella attenuata* as a subspecies, *S. a. graffmani*. *Stenella graffmani* (Kellogg, 1940) is a later combination.

Name Priority

For the pantropical spotted dolphin, the valid synonyms *Delphinus velox* G. Cuvier, 1829, *D. pseudodelphis* Wiegmann, 1840 (or earlier) and possibly *D. brevimanus* Wagner, 1846 antedate *Steno attenuatus* Gray, 1846. However, because of the long and continuous use of the latter and its emended forms and binomial recombinations, as well as because none of the first three names has had currency in this century, we are proposing that *Stenella attenuata* be used for this species, as a *nomen conservandum* (under Article 23b of the International Code of Zoological Nomenclature).

The senior synonym for the Atlantic spotted dolphin is *Delphinus frontalis* G. Cuvier, 1829. The name in various forms has also been in continuous use since its appearance, and we propose that *Stenella frontalis* be used for this species.

REDESCRIPTION OF *STENELLA FRONTALIS*

1829. *D[elphinus] frontalis* G. Cuvier, Règne Animal, 1, p. 288.
1880. *Prodelphinus frontalis*. Gervais, *in* van Beneden and Gervais, Ostéographie des Cétacés, p. 605, pl. 38, fig. 3.
1884. *[Clymenia] frontalis*. Flower, Proc. Zool. Soc. London, 1883, p. 512.
1950. *Stenella frontalis*. Fraser (in part), Atlantide Rep., 1, p. 61.
1829. *[Delphinus] froenatus* F. Cuvier, *in* Geoffroy Saint-Hilaire and F. Cuvier, Histoire Naturelle des Mammifères, 3, Sect. 58 (unpaginated).
1836. *Delphinus fraenatus*. F. Cuvier, Histoire Naturelle des Cétacés, p. 155, pl. 10, fig. 10.

belonged "to the same group as the styx [and] euphrosyne" (now in the synonymy of the striped dolphin, *Stenella coeruleoalba*). We have examined the two syntype skulls of *D. asthenops* (PANS 2595 and 2956 in the Museum of the Peabody Academy) and agree with Cope. The holotype specimen of *D. crotaphiscus,* formerly at the MCZ, has been lost. In any case, it is clear from Cope's description that the skull was not of a spotted dolphin. (Skull characters separating spotted dolphins from other species in *Stenella* are summarized in Perrin *et al.* 1981). Other combinations and emended forms: *Clymenia esthenops* (Gray, 1871), *Clymenia aesthenops* (Dall *in* Scammon, 1874), *Stenella asthenops* (Hershkovitz, 1966), *Clymenia crotaphiscus* (Gray, 1871), *Prodelphinus crotaphiscus* (Trouessart, 1898), *Stenella crotaphiscus* (Hershkovitz, 1966) and [*Stenella*] *crotaphyscus* (Honacki *et al.*, 1982).

Delphinus clymene Gray, 1850

True (1889) placed this species (and its later forms *Delphinus normalis* Gray, 1866 and *Clymenia normalis* Gray, 1868) in synonymy with *Prodelphinus froenatus* (F. Cuvier); this was followed by Hall (1981) in his synonymy of *Stenella frontalis*. Later workers, however, recognized the species as distinct and valid, as *Stenella clymene* (Hershkovitz 1966, Perrin *et al.* 1981).

Steno capensis Gray, 1865

The holotype skull (BMNH 1519.a.), from the Cape of Good Hope, represents the pantropical species (C in center panel of Fig. 6). Other combinations: *Clymenia Capensis* (Flower, 1884) and *Prodelphinus capensis* (Trouessart, 1898).

Clymene punctata Gray, 1866

The holotype skull of this species, from Cape Verde, West Africa, was destroyed in Berlin during World War II (Fraser 1950), but upper tooth counts (42) obtained by True (1889)—which are likely to be low (*see* MATERIALS AND METHODS)—and the color pattern as depicted by Gray (1866) identify this specimen as a pantropical spotted dolphin. Gray's illustration shows an animal with a well-defined cape, no spinal blaze, a "chevron" blaze between dorsal fin and flukes, and division of the peduncle into dark upper and light lower halves; all of these are features of the pantropical species' pattern. *Delphinus punctatus* (Gray, 1866) is a later combination.

Delphinus plagiodon Cope, 1866

This species was based on a skull (USNM 3884) from an unknown locality. The discriminant analysis identifies it as a specimen of the endemic species (P1 in Fig. 6). It very closely resembles large skulls of the species from the U.S. Atlantic Coast (discussed below) and may have been collected there. Other

attenuatus Gray, 1843 appeared earlier but without description or figure and therefore is a *nomen nudum*. Later combinations: *Clymenia attenuatus* (Flower, 1884), *Clymenia attenuata* (Hector, 1885), *Prodelphinus attenuatus* (Flower, 1885), *Stenella attenuata* (Iredale and Troughton, 1934).

Delphinus brevimanus Wagner, 1846
Delphinus? microbrachium Gray, 1850

These two species were based on the same specimen of the pantropical spotted dolphin collected near Singapore and figured (external appearance only) by Hombron and Jacquinot (1842–1853) under the name "*dauphin à petites pectorales.*" The skull of the holotype specimen (MNHN 1882-113; B in Fig. 6) was described by Jacquinot and Pucheran in Hombron and Jacquinot (1853). Neither name has been used in this century, and therefore we consider each to be a *nomen oblitum*. Other combinations: *Steno brevimanus* (Gray, 1866), *Prodelphinus brevimanus* (H. Gervais *in* P. J. van Beneden and P. Gervais, 1880).

Delphinus Doris Gray, 1846

The holotype specimen of this species is a skull (BMNH 352.a.) from an unknown locality that conforms well with the endemic Atlantic species (D in center panel of Fig. 6). Other combinations: *Tursio Doris* (Gray, 1866), *Clymene doris* (Gray, 1866), *Clymenia Doris* (Gray, 1868) and *Prodelphinus doris* (True, 1885 and Flower, 1885).

Delphinus albirostratus Peale, 1848

The holotype specimen of this species was collected in the Phoenix Islands in the Pacific but subsequently lost. As noted by Perrin (1975), the figure in Peale is of a pantropical spotted dolphin. For a time the species was placed in *Lagenorhynchus* (Dall 1874, True 1889). The figure for *D. albirostratus* in Cassin (1858) is in plate 6 (fig. 2), not Plate 7 as stated in Cassin's text.

Delphinus mediterraneus Loche, 1860

Hershkovitz (1966) placed this species in synonymy with *Stenella frontalis* (G. Cuvier), but Loche's description of the color pattern identifies the type specimen as a striped dolphin, *Stenella coeruleoalba* (Meyen, 1833), a fact recognized by Hall (1981). *D. delphis mediterranea* (Nobre, 1900) is a later combination.

Delphinus asthenops Cope, 1865
Delphinus crotaphiscus Cope, 1865

Honacki *et al.* (1982), following Hall (1981), stated that [*Stenella*] *dubia* includes these two nominal species. Cope (1865), however, believed that they

an unknown locality) thought by Schlegel (1841) to be the holotype was probably a different skull. We have examined photographs of it and agree; either the figures are extremely inaccurate, or a different skull is involved. The maxillary foramina and the nasal bones in particular are of different configurations in the two specimens. The highest rostral and mandibular tooth counts in the Leiden skull are only 41 and 39, respectively, as opposed to 44 and 46 in Wiegmann's figure. The skull figured by Wiegmann, however, (like the ZMB specimen—P2 in Fig. 6) does conform well with the skull of the pantropical species. The rostrum is narrow distally, the prenarial triangle long, and tooth counts very high, above the range for the endemic species. We therefore believe the name *D. pseudodelphis* to be a valid synonym for the pantropical species. It has been used in a substantive manner only once in this century, by Oliver (1922), as *Stenella pseudodelphis,* and we therefore propose that it be considered a *nomen oblitum*. *Prodelphinus pseudo-delphis* (True, 1889) was a later combination.

Delphinus loriger Wiegmann, 1841(?)

Hershkovitz (1966), followed by Hall (1981), included this species in the synonymy of *Stenella dubia,* but the figure of external appearance that comprises the description is clearly of a common dolphin, *Delphinus delphis* Linnaeus.

Delphinus Rappii Reichenbach, 1846

The holotype specimen of this species (from the Cape of Good Hope and in the Stuttgart Museum) has 20–30 teeth in the lower jaw and 22 in the upper. It was described earlier by Rapp (1837) under "*Delphinus capensis* Gray" but is not of the same species as the holotype of *D. capensis* Gray, 1828, which was a specimen of *D. delphis* (Hershkovitz 1966); the tooth counts as given by Rapp are too low. We have not examined the specimen but believe that Hershkovitz (1966) was not justified in including the name in the synonymy of *Stenella dubia*. Rapp noted a similarity to *Delphinus malayanus* Lesson (discussed above), but this was likely based on external appearance. The crude illustration appended to his description indeed resembles the (equally crude) illustration in Lesson's description, but neither much resembles a spotted dolphin. Until the holotype skull can be critically examined, the species should remain *incertae sedis*. In any case, the name has not been used since 1846 and should be considered a *nomen oblitum*.

Steno attenuatus Gray, 1846

This nominal species was based on a juvenile skull from an unknown locality (BMNH 347.b.). The skull is clearly a specimen of the pantropical species (Fig. 6), possibly from India (Gray 1843). The name has been in continuous use for spotted dolphins in the Indian and Pacific Oceans since True (1894) applied it to several specimens from the Indian Ocean. The name *Delphinus*

D[elphinus] velox G. Cuvier, 1829

G. Cuvier based *D. velox* on a specimen captured by Dussumier between Ceylon and the Equator. The holotype specimen is a mounted skin in the Paris Museum (No. 17 of the Catalogue de la Galerie de Zoologie). Pucheran (1856) reported measurements of the mounted skin. He also noted that, while F. Cuvier (1836) had reversed himself and stated that the animal was uniformly dark-gray below rather than spotted, he (Pucheran) could still see traces of dark ventral spots on the stuffed skin. As noted by Perrin (1975), the shape, coloration (mottled below) and tooth counts as described by F. Cuvier (1829) from notes by Dussumier, who collected the specimen, indicate that it was a pantropical spotted dolphin. Trouessart (1898) placed the species tentatively in the synonymy of *Delphinus malayanus* Lesson but dropped it from the subsequent edition of his list (1904–1905). Other than in the reiteration of Trouessart's (1898) synonymy by Ellerman and Morrison-Scott (1951), the name has not been applied to spotted dolphins in this century and therefore should be considered a *nomen oblitum.*

Delphinus frontalis G. Cuvier, 1829
Delphinus froenatus F. Cuvier, 1829

The respective holotype specimens of these two species were both harpooned by Dussumier off Cape Verde, West Africa. Perrin (1975) suggested that they were pantropical spotted dolphins, based on position of the flipper stripe (running below the eye to the gape, rather than to the eye as in western Atlantic specimens of the endemic spotted dolphin), but it is now apparent that the endemic species varies in this character (*see* discussion of geographical variation below). The holotype specimens of *D. frontalis* and *D. froenatus* have recently been identified in the Paris Museum (MNHN A-3035 and A-3034, respectively, D. Robineau, pers. comm.), and they conform with the endemic species (F1 and F2 in Fig. 6). The species is known to occur in the area from other evidence (Lütken 1889, specimen no. 2, with 68 vertebrae and upper tooth count of 37). Both names have been used extensively in the literature (Hershkovitz 1966, Honacki *et al.* 1982). *D. frontalis* was published first (Fraser 1950). Other combinations and emendations: *Prodelphinus frontalis* (H. Gervais *in* P. J. van Beneden and P. Gervais, 1880), *Clymenia frontalis* (Flower, 1884), *Stenella frontalis* (Fraser, 1950), *Delphinus fraenatus* (F. Cuvier, 1836), *D. frenatus* (Gray, 1846), *Tursio fraenatus* (Gray, 1866), *Prodelphinus fraenatus* (Gervais *in* van Beneden and Gervais, 1880), *Clymenia fraenata* (Flower, 1884), *Prodelphinus froenatus* (True, 1889) and *P. fraenatus* (Beddard, 1900).

Delphinus pseudodelphis Wiegmann, 1840 or earlier

A plate (no. 38) in von Schreber (1840, as cited by Wagner 1846) consists of three views of a skull with this name as the legend. There is no information on the species in the text. Wagner in the 1846 edition of *Schreber's Saeugthiere* noted that a skull in the Leiden collection (Zool. Mus. Berlin no. 12009, from

Review of the Nominal Species

Many names have been applied to spotted dolphins. Here we review the names and re-assign them to one or the other of the two valid species where possible. We have drawn heavily on the comprehensive work by Hershkovitz (1966). Additional discussion of many of the nominal species was given by Perrin (1975).

D[elphinus] dubius G. Cuvier, 1812

Cuvier did not designate a holotype specimen for this species, but he later (1823) published measurements of a skull under *D. dubius*. A skull of uncertain origin in the Paris Museum (A-3033, labeled *D. froenatus*) conforms precisely to these measurements. Examination of the 19th century material of unknown origin in the Paris Museum, however, indicates that G. Cuvier's (1812) "several skulls" possibly included specimens of both spotted species; it therefore would not be prudent to designate A-3033 as a lectotype for *D. dubius*; the name best remains a *nomen nudum*. Other combinations include *Prodelphinus dubius* (H. Gervais *in* P. J. van Beneden and P. Gervais, 1880), *Clymenia dubia* (Flower, 1884) and *Stenella dubia* (Hershkovitz, 1966).

Delphinus pernettensis de Blainville, 1817

This species was based on a sketch published by Pernety (1769) of a dolphin captured in the Cape Verde Islands off West Africa. The specimen was not saved. Although the strongly defined cape shown in the sketch is evocative of the color pattern of the pantropical spotted dolphin, the identification cannot be certain. The point is moot, as the name has been suppressed by the International Commission of Zoological Nomenclature (Opinion 1067) following van Bree (1971*b*). Other combinations and emended forms: *D. Pernettyi* (Desmarest, 1822), *Delphinorhynchus Pernettyi* (Lesson, 1827), *Delphinus Pernetyi* (True, 1885), *D. pernettyensis* (Philippi, 1893) and *Stenella pernettyi* (Hershkovitz, 1966).

Delphinus malayanus Lesson, 1826

Lesson (in Lesson and Garnot 1826) based this species on a specimen harpooned between Java and Kalimantan (Borneo). There is no holotype specimen. We believe that the dolphin in the crude sketch included in the description (prepared by an artist based on Lesson's field observations) cannot be identified with any confidence. It could be a specimen of the pantropical spotted dolphin, but it could equally well represent a specimen of *Stenella longirostris, Steno bredanensis, Sousa chinensis,* or even a sun-darkened specimen of *Stenella coeruleoalba* or *Delphinus delphis*. Weber (1923) following Schlegel (1841) applied *Prodelphinus malayanus* to spotted dolphins from Indonesia. In our opinion, *D. malayanus* should be considered a *nomen nudum*. Other combinations: *Steno Malayanus* (Gray, 1846), *Prodelphinus malayanus* (True, 1889).

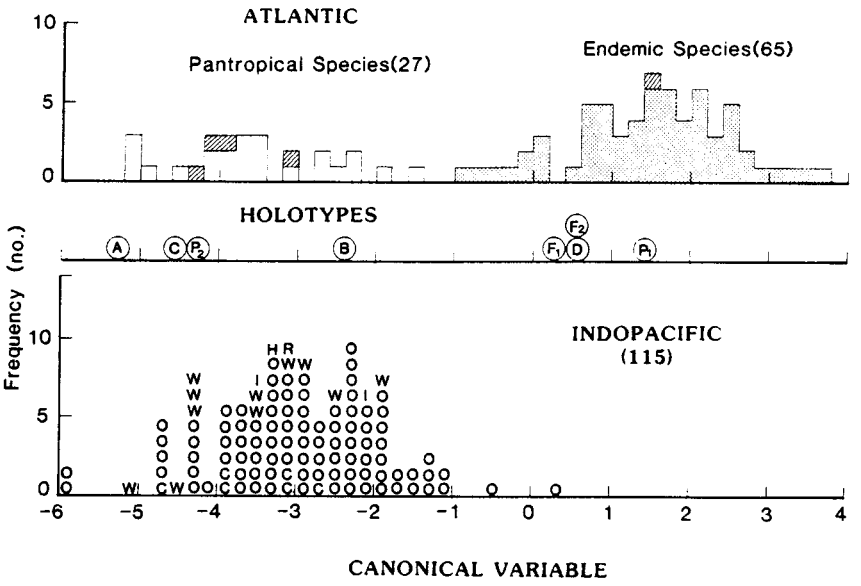


Figure 6. Frequency distributions of specimens of spotted dolphins on first canonical variable. Atlantic specimens (top panel) identified to the endemic and pantropical species based on color pattern and/or number of vertebrae. Juvenile specimens hatched. Holotype specimens (middle panel): A = *Steno attenuatus* (juvenile), B = *Delphinus brevimanus*, C = *S. capensis*, D = *P. Doris*, F1 = *D. froenatus*, F2 = *D. frontalis*, P1 = *D. plagiodon*, P2 = possible holotype of *D. pseudodelphis*. Indopacific specimens (bottom panel) include coastal (C) and oceanic (O) specimens from the eastern Pacific and skulls from Hawaii (H), the western Pacific (W), the Indian Ocean (I) and the Red Sea (R).

with other pantropical spotted dolphins and had the typical pantropical color pattern and 81 vertebrae. The other Indopacific specimen with an anomalously high value for the canonical variable (−0.5) was also an eastern Pacific specimen with a relatively broad rostrum (32 mm at ¾ length) and tooth count at the low end of the range for the species (38). This result indicates that the discriminant function cannot be used to identify skulls with certainty, but it does not affect the conclusions concerning the holotype specimens; the holotypes having values similar to those of the aberrant eastern Pacific specimens are from the Atlantic and are clearly associated with the distribution of Atlantic specimens known to be of the endemic species.

For purposes of the species redescriptions below, an additional 35 Atlantic specimens lacking data on coloration or number of vertebrae were assigned to the two species using the discriminant function; these had data for all four of the skull characters. Another 12 specimens with missing values for one or more of the four characters were identified by comparing the values for the remaining characters with those for the two Atlantic series. If a skull was outside the range for one of the species in any of the characters but within it for the other for all characters, it was assigned to the latter.

Table 2. Statistics for stepwise discriminant analysis of skulls of *Stenella frontalis* and *S. attenuata*.

Character	*F*-value to enter	Order of entry	Coefficients[a]	Classification functions[b]	
				S. frontalis	*S. attenuata*
Wd. of rost. at ¾ ln/po wd.	167.38	1	0.0153	0.0317	−0.0984
Wd. of prenar. triangle at 60 mm/po wd.	58.94	2	−0.0379	−0.3063	0.0158
Highest rostral tooth count	23.03	3	−0.1621	12.7033	14.0818
Wd. of rost. at ½ ln/po wd.	6.85	4	0.0203	1.8991	1.7263
Constant			−2.3379	−500.8247	−494.2775

[a] For discriminant function; standardized by pooled within-group variances.

[b] Used with original proportional measurements and tooth count. Add products of measurement (÷ po width) or tooth count and corresponding function values to constant; classify as *S. frontalis* or *S. attenuata* depending on which results in highest value for classification function.

and females (except specimens from mid-tropical Atlantic, which are of unknown sex and are compared to the pooled sexes for series A).

B N.W. Atlantic Oceanic				C Azores			
Range	(*n*)	Mean	Comparison of A and B	Range	(*n*)	Mean	Comparison of A and C
356–393	(5)	374.6	***	375–384	(3)	380.3	***
194–229	(6)	215.5	***	211–221	(3)	215.3	***
83–88	(6)	85.5	***	81–85	(3)	82.3	***
61–64	(2)	62.5	—	59–60	(2)	59.5	—
61–64	(4)	63.3	**	60	(1)	60.0	*
48–50	(2)	49.0	—	47–50	(2)	48.5	—
47–54	(4)	50.5	**	48	(1)	48.0	*
26–28	(2)	27.0	—	27	(2)	27.0	—
26–31	(4)	28.5	ns	26	(1)	26.0	ns
32–36	(2)	34.0	—	33–38	(2)	35.5	—
32–37	(4)	34.8	***	34	(1)	34.0	*
230–263	(6)	250.5	***	245–256	(3)	250.3	***
236–277	(4)	254.5	***	258–268	(3)	261.7	***
155–162	(5)	157.6	***	150–160	(3)	156.0	***
173–177	(2)	175.0	—	179–181	(2)	180.0	—
175–182	(3)	177.7	***	177	(1)	177.0	*
44–46	(5)	45.4	ns	43–47	(3)	45.0	ns
172–178	(2)	175.0	—	180–183	(2)	181.5	—
172–182	(3)	176.3	***	179	(2)	179.0	**
65–75	(5)	70.6	***	71–72	(3)	71.3	***
141–144	(2)	142.5	—	146	(2)	146.0	—
137–144	(3)	140.7	***	137	(1)	137.0	**
100–101	(2)	100.5	—	102–109	(2)	105.5	—
97–104	(3)	100.7	**	97	(1)	97.0	*
108–118	(5)	114.4	***	114–126	(3)	118.3	***
68–71	(5)	69.2	***	65–68	(3)	66.7	***
46–56	(5)	52.2	***	46–55	(3)	51.0	**
45–51	(6)	48.5	***	47–52	(3)	50.0	***
37–45	(6)	40.0	***	40	(3)	40.0	***
48–52	(5)	49.8	**	47–49	(3)	48.0	**
171–200	(6)	186.2	***	183–188	(3)	185.3	***
168–197	(6)	181.7	***	180–184	(3)	181.7	***
292–332	(6)	315.8	***	315–324	(3)	319.7	***
56–61	(6)	58.5	***	56–61	(3)	59.0	***
3.8–4.3	(6)	4.08	**	3.2–3.8	(3)	3.57	**
3.1–5.2	(6)	3.92	ns	1.8–2.7	(3)	2.13	ns
74–82	(5)	77.6	***	76–79	(3)	77.7	***
48–51	(5)	49.0	***	49–52	(3)	50.3	**
20–28	(5)	23.0	***	22–25	(3)	23.7	**

Table 6. Continued.

	A N.W. Atlantic Coast & Gulf of Mexico				
	Range	(*n*)	Mean	SD	CV
Length of last thor. neur. spine	72–98	(27)	83.6	6.30	7.54
First thor. vert.: height	30–57	(29)	49.0	5.35	10.92
width	77–98	(29)	88.6	5.97	6.74
First lumbar vert.: height	43–71	(28)	55.6	4.89	8.79
width	184–222	(28)	202.9	9.83	4.84
Length of first vert. rib	120–151	(29)	136.8	8.40	6.14
Length of longest vert. rib	253–314	(29)	291.3	15.5	5.32
Length of first stern. rib	74–99	(28)	87.8	5.25	5.98
Width of manubrium	80–112	(27)	103.4	6.89	6.66
Length of longest chev. bone	41–60	(26)	51.9	5.68	10.94
Scapula: height	110–155	(28)	139.1	9.86	7.09
length	99–143	(28)	128.7	10.53	8.18
Humerus: length	62–74	(23)	67.7	—	—
width	39–52	(25)	43.8	3.54	8.08
Length of radius	77–95	(25)	83.9	4.41	5.26
Length of ulna	67–84	(25)	74.6	4.37	5.86

		D Caribbean			Comparison of D and A	
		Range	(*n*)	Mean	*t*-test[a]	Percent difference
Condylobasal length		374–431	(17)	398.3	***	6.85
Length of rostrum		211–261	(17)	233.8	***	5.42
Width of rostrum at base		76–93	(17)	85.9	***	11.35
Width of rostrum at 60 mm	M	59–67	(4)	62.3	—	—
	F	55–69	(11)	62.1	***	10.65
Width of rostrum at ½ length	M	48–53	(4)	50.3	—	—
	F	44–53	(11)	48.7	***	12.88
Width of pmx's at ½ length	M	24–30	(4)	27.5	—	—
	F	23–30	(11)	26.7	**	9.49
Width of rostrum at ¾ length	M	35–38	(4)	36.8	—	—
	F	30–39	(11)	34.7	***	15.78
Rostrum tip to external nares		247–303	(17)	273.1	***	5.50
Rostrum tip to internal nares		259–311	(16)	280.1	***	5.21
Greatest preorb. width		146–172	(17)	159.9	***	9.56
Greatest postorb. width	M	166–189	(4)	177.0	—	—
	F	165–194	(11)	181.0	***	8.54
Greatest width of ext. nares		40–47	(16)	42.9	***	7.96

Table 6. Extended.

B N.W. Atlantic Oceanic				C Azores			
Range	(*n*)	Mean	Comparison of A and B	Range	(*n*)	Mean	Comparison of A and C
65–82	(5)	73.4	**	73–75	(2)	74.0	*
40–47	(5)	43.0	*	43–45	(3)	43.7	ns
71–87	(5)	77.6	***	76–81	(3)	78.7	**
45–53	(5)	47.6	**	45–50	(2)	47.5	*
169–192	(5)	181.2	***	177–179	(2)	178.0	**
107–132	(5)	117.6	***	110–127	(3)	120.7	**
223–243	(5)	236.0	***	234–245	(3)	240.3	***
72–89	(5)	78.2	***	75–80	(3)	78.0	**
73–99	(5)	84.8	***	88–92	(3)	89.7	**
41–50	(5)	44.8	*	40–49	(3)	44.7	*
109–127	(5)	118.2	***	116–123	(3)	119.0	**
96–131	(5)	109.6	**	113–115	(3)	114.3	*
55–60	(3)	58.0	***	57–59	(2)	58.0	**
35–40	(5)	36.8	**	36–38	(3)	37.3	*
69–76	(5)	72.4	***	72–77	(2)	74.5	**
58–72	(5)	64.0	***	66–69	(2)	67.5	*

E Mid-Tropical Atlantic				F Africa			
Range	(*n*)	Mean	Comparison of A and E	Range	(*n*)	Mean	Comparison of A and F
382–406	(3)	390.7	***	368–419	(9)	396.2	***
220–232	(3)	226.3	**	212–248	(9)	230.3	***
81–86	(3)	84.3	***	81–93	(9)	87.1	***
55–62	(3)	59.3	***	67	(1)	67.0	—
				62–70	(2)	66.0	ns
45–48	(3)	46.7	***	56	(1)	56.0	—
				51–55	(2)	53.0	ns
22–27	(3)	24.7	***	30	(1)	30.0	—
				25–33	(2)	29.0	ns
33–35	(3)	33.7	***	38	(1)	38.0	—
				37–41	(2)	39.0	ns
253–272	(3)	262.7	***	249–289	(9)	269.0	***
263–288	(3)	274.7	*	262–297	(8)	279.8	**
150–160	(3)	156.3	***	153–170	(9)	163.3	***
169–179	(3)	175.3	***	188	(1)	188.0	—
				183–188	(2)	185.5	*
43–46	(3)	45.0	ns	42–48	(9)	45.2	ns

Table 6. Continued.

		D Caribbean				
		Range	(*n*)	Mean	*t*-test[a]	Percent difference
Zygomatic width	M	167–184	(4)	174.8	—	—
	F	164–194	(11)	180.2	***	8.39
Greatest width of pmx's		66–78	(17)	71.3	***	9.29
Parietal width	M	131–151	(4)	140.8	—	—
	F	133–151	(11)	142.0	***	7.37
Height of braincase	M	96–106	(4)	100.0	—	—
	F	93–106	(11)	98.3	**	9.90
Int. length of braincase		108–124	(16)	117.5	***	9.34
Length of temporal fossa		57–80	(17)	69.8	***	11.98
Height of temporal fossa		48–62	(17)	54.5	***	10.21
Length of orbit		47–56	(16)	51.4	***	8.05
Length of preorb. process		36–47	(16)	40.9	***	7.88
Width of internal nares		40–55	(16)	48.5	***	8.66
Length of upper toothrow		179–227	(17)	202.8	**	4.20
Length of lower toothrow		184–224	(15)	196.0	**	4.72
Length of ramus		316–372	(15)	337.8	***	7.60
Height of ramus		55–66	(16)	60.4	***	11.57
Diameter of tooth (at mid-length of lower row, transverse at alveolus)		3.3–4.6	(13)	3.94	***	12.44
Width of prenarial triangle at 60 mm		1.0–6.8	(16)	3.23	ns	—
Atlas: width		76–82	(10)	79.8	***	9.01
height		46–54	(10)	49.2	***	11.03
length of lat. process		19–27	(10)	22.4	***	25.48
Length of last thor. neur. spine		62–80	(10)	71.7	***	14.23
First thor. vert.: height		39–48	(9)	44.7	**	8.78
width		66–90	(10)	76.6	**	13.50
First lumbar vert.: height		44–51	(10)	47.7	***	14.21
width		158–207	(10)	175.2	***	13.65
Length of first vert. rib		107–133	(10)	116.0	***	15.20
Length of longest vert. rib		200–274	(10)	244.5	***	16.07
Length of first stern. rib		68–92	(10)	77.0	***	12.30
Width of manubrium		72–92	(10)	83.3	***	19.44
Length of longest chev. bone		38–54	(10)	43.2	***	16.76
Scapula: height		102–138	(8)	115.8	***	16.75
length		88–123	(8)	105.3	***	18.18
Humerus: length		54–62	(4)	57.0	—	—
width		35–42	(9)	39.1	**	10.73
Length of radius		70–82	(9)	74.9	***	10.73
Length of ulna		60–73	(9)	67.6	***	9.38

[a] A *t*-test, based on pooled variance (homogeneity assumed); ns, $P < 0.05$; *, $0.05 \leq P > 0.01$; **, $0.01 \leq P > 0.001$; ***, $P \leq 0.001$. Blank indicates that larger sample < 25.

Table 6. Extended.

E Mid-Tropical Atlantic				F Africa			
Range	(*n*)	Mean	Comparison of A and E	Range	(*n*)	Mean	Comparison of A with F
167–179	(3)	175.0	***	189	(1)	189.0	—
				184–186	(2)	185.0	*
66–73	(3)	69.0	***	68–76	(9)	72.7	***
130–149	(3)	142.0	***	140	(1)	140.0	—
				143–152	(2)	147.5	ns
94–103	(3)	99.3	***	97	(1)	97.0	—
				102–105	(2)	103.5	ns
111–121	(3)	116.7	***	112–131	(9)	122.4	***
67–69	(3)	68.0	***	67–74	(9)	70.4	***
53–59	(3)	56.7	ns	47–61	(9)	54.4	***
48–50	(3)	49.3	***	47–54	(9)	50.4	***
39–45	(3)	41.3	ns	37–46	(8)	41.4	**
44–53	(3)	49.0	*	46–56	(8)	49.9	**
187–203	(3)	193.6	**	118–216	(9)	198.1	***
178–197	(3)	186.0	**	181–209	(8)	195.3	**
321–345	(3)	329.3	***	316–352	(8)	335.1	***
58–61	(3)	59.0	***	56–66	(8)	60.0	***
3.3–3.5	(3)	3.37	***	35–38	(2)	36.5	**
1.5–2.1	(3)	1.90	ns	0.8–9.9	(8)	3.64	ns
74	(1)	74.0	*	—	—	—	—
45	(1)	45.0	***	—	—	—	—
17	(1)	17.0	**	—	—	—	—
64	(1)	64.0	**	—	—	—	—
44	(1)	44.0	ns	—	—	—	—
70	(1)	70.0	**	—	—	—	—
43	(1)	43.0	•	—	—	—	—
168	(1)	168.0	**	—	—	—	—
109	(1)	109.0	**	—	—	—	—
221	(1)	221.0	***	—	—	—	—
74	(1)	74.0	*	—	—	—	—
66	(1)	66.0	***	—	—	—	—
37	(1)	37.0	*	—	—	—	—
109	(1)	109.0	**	—	—	—	—
90	(1)	90.0	**	—	—	—	—
59	(1)	59.0	*	—	—	—	—
37	(1)	37.0	ns	—	—	—	—
69	(1)	69.0	**	—	—	—	—
62	(1)	62.0	**	—	—	—	—

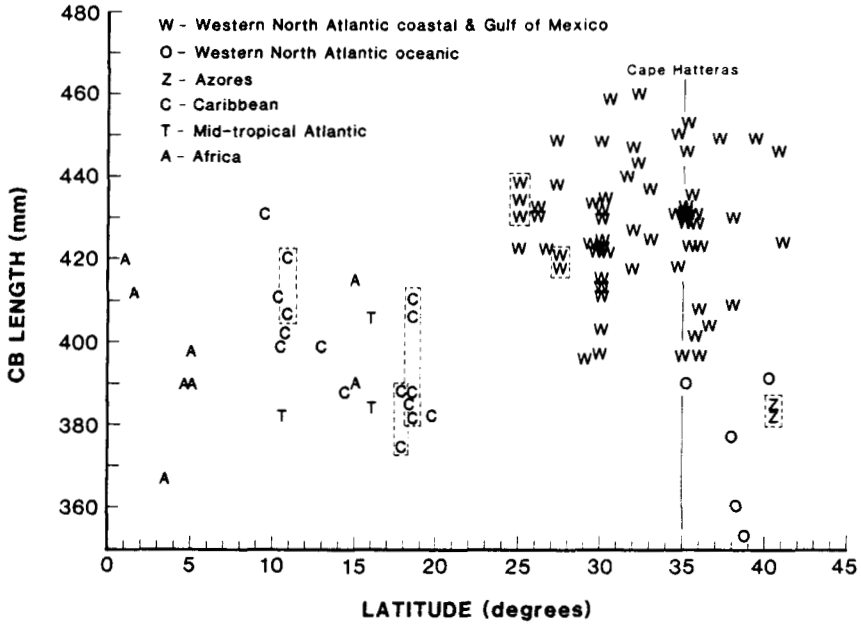


Figure 13. Scatterplot of CB length on latitude (absolute) for six geographical series of *Stenella frontalis*. Specimens enclosed in dashed rectangles captured or stranded together.

less difference in size between the two series than do nearly all of the other postcranial elements, although the differences are large relative to those in most of the skull characters.

The specimens from the mid-tropical Atlantic are also smaller than the coastal specimens in nearly all cranial and postcranial dimensions. The African series appears intermediate; the specimens came from localities scattered from Cape Verde to the eastern Gulf of Guinea, and it is possible that more than one population is involved. For example, the specimens from the Cape Verde Islands could be from an oceanic population and others from one or more coastal populations.

The variation in skull size exhibits a latitudinal pattern (Fig. 13). The Caribbean offshore and mid-tropical Atlantic specimens form a group of smaller skulls from between 10° and 20° (north and south) (but note the 431-mm skull from Panama), and the western North Atlantic oceanic and Azores series comprise a group of very small high-latitude skulls, all smaller than any other skulls from north of 20°N. This reflects the apparent circular distribution in the Atlantic (Fig. 7), with coastal animals at mid-latitudes and small oceanic animals at low and high latitudes. The circular pattern of distribution could be an artifact of sampling effort.

In a factor analysis based on 22 skull measurements considered simultaneously (Table 7), the several series exhibit a similar pattern (Fig. 14). The

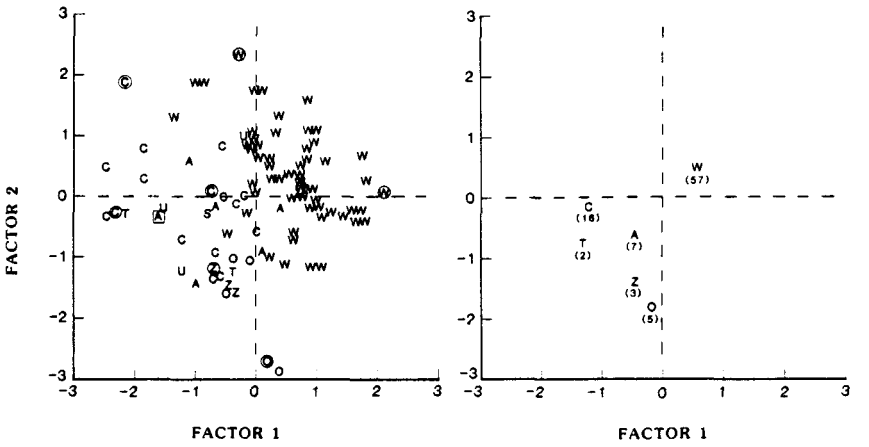


Figure 14. (*Left*) Skulls of six geographical samples of *Stenella frontalis* plotted on first two orthogonally rotated factors. U = unknown locality; *see* Figure 13 for other symbols. Holotype (from Africa) in box. Circled specimens illustrated in Figure 15. (*Right*) Group means of the geographical series.

Table 7. Loadings of othogonally rotated factors for 22 skull measurements of 94 specimens of *Stenella frontalis*. Factors sorted so that variables appear in decreasing order of variance explained by factors. Rearranged so that for each successive factor, loadings greater than 0.5000 appear first. Loading less than 0.25 indicated by dash. Proportion of total variance explained by Factors 1 and 2 = 0.79.

	Component	
	I	II
Width of rost. at 60 mm	0.846	0.414
Width of rost. at ½ length	0.835	0.374
Width of rost. at ¾ length	0.820	0.425
Width of rost. at base	0.810	0.459
Zygomatic width	0.807	0.540
Width of pmx's at ½ length	0.803	—
Postorbital width	0.796	0.555
Preorbital width	0.765	0.569
Width of int. nares	0.762	—
Height of braincase	0.748	0.431
Parietal width	0.707	0.476
Greatest width of pmx's	0.692	—
Int. length of braincase	0.640	0.600
Greatest width of ext. nares	0.639	—
Length of temporal fossa	0.619	0.597
Length of preorb. process	0.580	0.474
Length of rostrum	0.271	0.939
Length of upper toothrow	—	0.919
Rost. tip to external nares	0.324	0.917
Condylobasal length	0.482	0.863
Length of orbit	0.458	0.737
Height of temporal fossa	0.481	0.587

loadings for Factor 1 are highest (and account for most of the variance) for the measurements that involve skull widths (*i.e.*, the rostral widths, facial widths and cranial widths), while they are highest for Factor 2 for the length measurements (CB, rostral and tooth-row lengths, *etc.*). The western North Atlantic skulls are both long and relatively broad, the skulls from the offshore western North Atlantic, the Azores and the mid-tropical Atlantic are small and relatively broad, and the Caribbean skulls are of intermediate size and narrow (Fig. 14). The African sample is heterogenous but closest to the Caribbean sample. Specimens at or near the extreme values for the two factors and modal specimens for the western North Atlantic coastal series, the Caribbean series and the (small) series from the Azores are illustrated in Figure 15.

There is significant geograpahical variation in number of teeth; the range of the series means is 3 or 4 teeth in each jaw, or 12–16 overall. Tooth counts are lowest in the western North Atlantic coastal series and the specimens from the Azores (Table 8). The mid-tropical Atlantic specimens have the highest counts, and the western North Atlantic oceanic, Caribbean and African series are intermediate.

There is little geographical variation in postcranial meristic characters (Table 8). Total number of vertebrae is remarkably constant (CV = 1.40). Only the positions of the first vertebra with a vertically perforating foramen and the last vertebra with a neural process vary among the series; the values for the former are greater in the western North Atlantic oceanic and Caribbean series and the latter greater in the Caribbean series than in the western North Atlantic coastal series.

Comparisons—Stenella frontalis differs in coloration from the other spotted dolphin, *S. attenuata,* in having a spinal blaze and lacking a division of the peduncle into upper dark and lower light halves. The background of dark ventral spots is white, rather than gray as in *S. attenuata.* The ground pattern is very similar to that of the bottlenose dolphin *Tursiops truncatus* (Montagu); similar features are broad and complex eye and blowhole stripes, flipper stripe demarcated dorsally by a narrow light line, flipper stripe terminating anteriorly at the eye or between the eye and the angle of the gape (in most specimens of *S. frontalis*), ventral margin of dorsal cape interrupted by spinal blaze, and ventral margin of lateral field terminating in the anal region. The two species differ materially only in possession of dorsal spots (some geographical forms of *T. truncatus* have dark ventral spots—Ross 1977).

Length at birth in *S. frontalis* is between 76 and 120 cm (Caldwell and Caldwell 1966, Perrin and Reilly 1984). The range of adult body length is about the same as in *S. attenuata* (although that species may reach a greater length; Table 3), but *S. frontalis* is heavier bodied (Fig. 16). Adults of the same length weigh 10 to 30 kg more. *Stenella frontalis* also has larger flippers, flukes and dorsal fins (Table 3). In external size and shape, it is intermediate between *S. attenuata* and *T. truncatus,* showing many similarities to the latter in external morphology of the rostrum, melon, flippers and dorsal fin (Fig. 17). Again, the similarity to *T. truncatus* is greatest for the spotted form of that

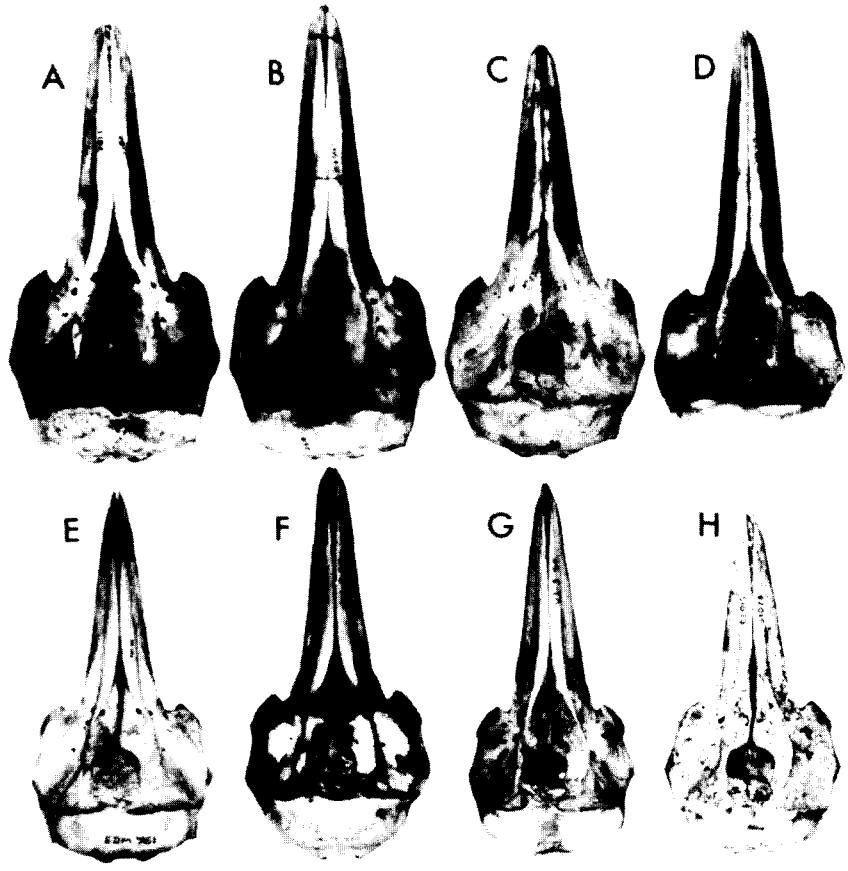


Figure 15. Variation in adult skull size and shape in *Stenella frontalis* (specimens circled in Fig. 14). A) MCZ 1182, sex unknown, South Carolina (western North Atlantic specimen—"C" in Fig. 14, factor scores 2.10, 0.14); B) USNM 21915, sex unknown, Florida Gulf Coast ("W": −0.32, 2.35); C) EDM 694, female, North Carolina ("W": 0.75, 0.03); D) USNM 254447, female, coast of Panama ("C": −0.07, 1.86); E) AMNH 239111 (= EDM 761), male, Azores ("Z": −0.64, −1.16); F) UF VI-2-SF, sex unknown, Virgin Islands "C": −0.74, 0.10); G) UF VI-3-SF, sex unknown, Virgin Islands—stranded with UF VI-2-SF ("C": −2.29, −0.26); H) MCZ 51073, female, off New Jersey ("O": 0.11, 2.75).

species, which has a proportionately slimmer rostrum than do the unspotted forms (Ross 1977).

Stenella frontalis shares with *S. attenuata* and *T. truncatus* a suite of cranial characters that separate the three species from the other small delphinids with dorsal fin and externally well-defined beak (abrupt transition from beak to melon) (*i.e., S. longirostris, S. clymene, S. coeruleoalba, Delphinus delphis* and

Table 8. Statistics and comparisons of tooth counts and vertebral meristics for geographical series of *Stenella frontalis*. Standard deviations included for samples of 25 or more; characters for which largest sample smaller than 25 not included.

	A U.S. East Coast & Gulf of Mexico					B N.W. Atlantic Oceanic				C Azores			
	Range	(*n*)	Mean	SD	CV	Range	(*n*)	Mean	Comparison of A with B	Range	(*n*)	Mean	Comparison of A with C
Tooth counts:													
Highest rostral	33–39	(63)	35.7	1.66	4.65	36–39	(6)	37.2	*	35–37	(4)	36.0	ns
Lowest rostral	32–38	(63)	35.0	1.52	4.34	35–39	(6)	36.8	**	35–38	(4)	36.0	ns
Highest mandibular	31–38	(60)	33.5	1.61	4.81	35–38	(6)	36.3	***	33–37	(4)	34.8	ns
Lowest mandibular	30–37	(59)	32.9	1.60	4.86	33–38	(6)	35.8	***	33–34	(3)	33.7	ns
Vertebrae:													
Total number	68–71	(30)	70.0	0.98	1.40	70–71	(5)	70.4	ns	68–71	(3)	69.3	ns
Thoracic	13–15	(28)	14.1	0.45	3.19	14–15	(5)	14.2	ns	13–14	(2)	13.5	ns
First with vert. for.	45–49	(29)	47.5	1.15	2.42	48–51	(5)	49.2	**	47–49	(3)	48.3	ns
Last with trans. proc.	50–54	(29)	52.8	0.95	1.80	52–55	(5)	53.6	ns	52–53	(3)	52.7	ns
Last with neur. proc.	56–59	(29)	57.8	0.90	1.56	57–59	(5)	58.2	ns	58–60	(3)	59.0	ns

Table 8. Continued.

	D Caribbean				E Mid-tropical Atlantic				F Africa			
	Range	(*n*)	Mean	Comparison of A with D	Range	(*n*)	Mean	Comparison of A with E	Range	(*n*)	Mean	Comparison of A with F
Tooth counts:												
Highest rostral	35–41	(17)	37.7	***	39–40	(3)	39.3	***	36–42	(10)	37.6	**
Lowest rostral	34–41	(17)	37.0	***	37–39	(3)	38.0	**	36–39	(10)	36.7	**
Highest mandibular	34–40	(15)	36.6	***	38	(3)	38.0	***	36–40	(9)	37.3	***
Lowest mandibular	34–39	(15)	36.3	***	37–38	(3)	37.3	***	34–40	(9)	36.3	***
Vertebrae:												
Total number	69–72	(10)	70.3	ns	70	(1)	70.0	ns	68–70	(2)	69.0	ns
Thoracic	14–15	(10)	14.3	ns	14	(1)	14.0	ns	—	—	—	—
First with vert. for.	48–50	(10)	48.8	**	48	(1)	48.0	ns	49	(1)	49.0	ns
Last with trans. proc.	53–54	(10)	53.3	ns	54	(1)	54.0	ns	53	(1)	53.0	ns
Last with neur. proc.	58–60	(10)	58.9	**	58	(1)	58.0	ns	58	(1)	58.0	ns

[a] A *t*-test based on pooled variance; ns, $P > 0.05$; *, $0.05 \leq P > 0.01$; **, $0.01 \geq P > 0.001$; ***, $P \leq 0.001$.

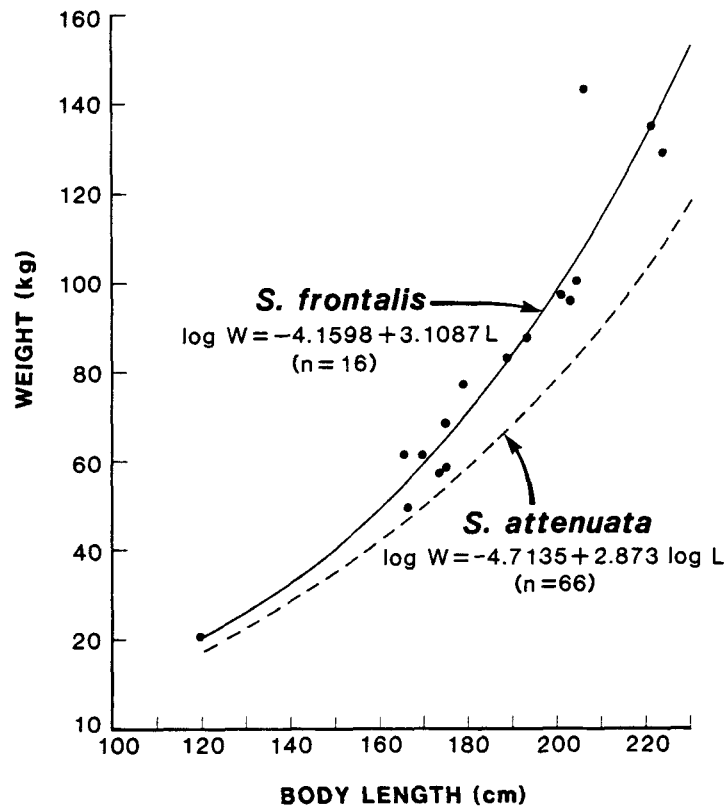


Figure 16. Length-weight relationships for males of *Stenella frontalis* and *S. attenuata* (from Perrin *et al.* 1976).

Lagenodelphis hosei; Perrin *et al.* (1981): (1) a relatively large temporal fossa; (2) typically about 40 or fewer teeth in each row; (3) well developed alveoli in the distal 1 cm or so in upper and lower jaws; (4) proximal halves of upper and lower tooth rows convergent in a continuous curve rather than in a sigmoid curve; (5) a relatively long mandibular symphysis; (6) distal half of the rostrum not markedly flattened dorso-ventrally; and (7) no grooves in the palate. *S. frontalis* and *S. attenuata* overlap in all skull characters, but in the former the rostrum is on the average broader distally, the prenarial triangle shorter and the teeth larger and less numerous. In large specimens, the tip of the mandible usually curves upward (Fig. 11), but in small specimens (*e.g.*, those from the offshore western North Atlantic) it may be straight, as in *S. attenuata*. Large skulls of *S. frontalis* from some regions are similar to small skulls of *T. truncatus* but can be separated from them on the basis of tooth count (more than 30 in each row in *S. frontalis*).

As well as differing in minimum and maximum values for nearly all post-

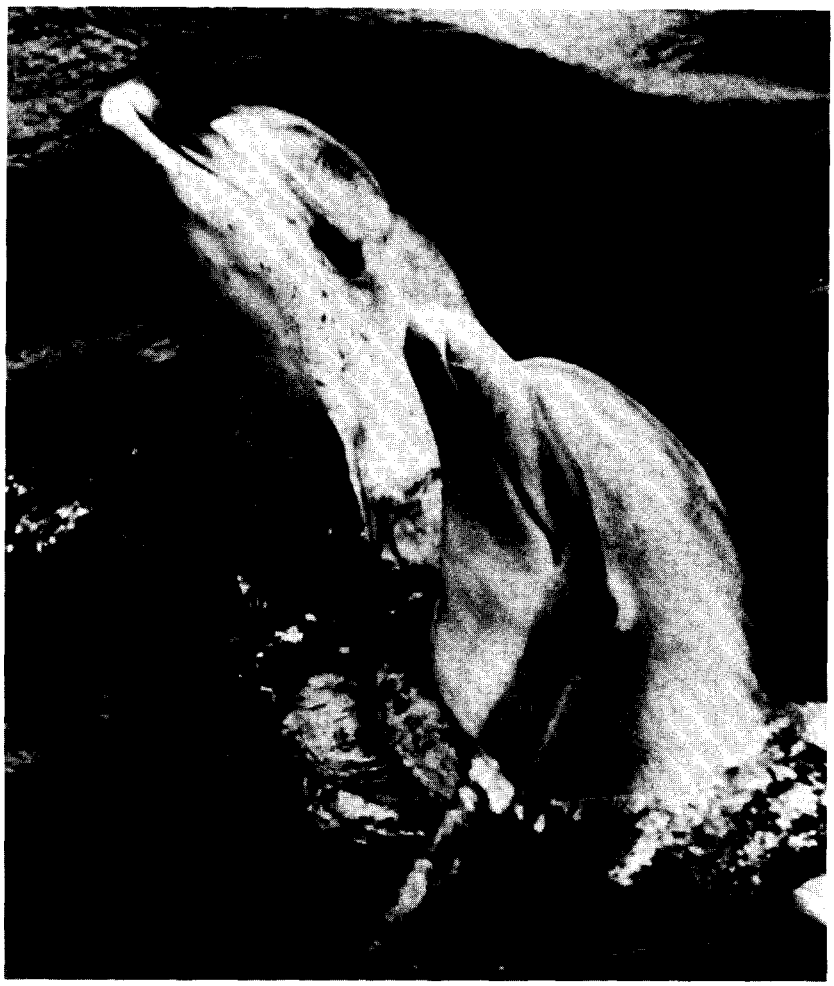


Figure 17. A young specimen of *Stenella frontalis* (top) and a specimen of *Tursiops truncatus*, showing similarities in ground coloration and shape of rostrum and melon.

cranial measures (those for *S. frontalis* being greater), *S. frontalis* and *S. attenuata* are distinct in some of the characters. The present series of physically mature adult specimens (n = 22 and 29, respectively) do not overlap in length of the ulna, and the overlap in length of radius is very slight (Table 4); the osseous flipper in *S. frontalis* is proportionately longer. The two species are also separate in vertebral counts; *S. frontalis* typically has one or two fewer thoracic vertebrae (and ribs), three fewer lumbars and five or six fewer caudals than does *S. attenuata*, for totals of 67–72 and 74–84 in the two species, respectively (Table 5). *T. truncatus* has 65 or fewer vertebrae (Ross 1984).

As in all delphinids for which chromosome number is known, the number of chromosomes is 2N = 44 (Árnason 1974, 1980, Duffield 1977). The G-banded karyotype of *S. frontalis* is not distinguishable from those of *S. clymene* and *Tursiops truncatus* (Árnason 1980). It is similar to that of *S. attenuata,* which is "nearly identical" with that of *S. longirostris* (Worthen 1981). There are slight banding differences between the karyotypes in this group and those of *Lagenorhynchus obliquidens* and *L. albirostris.* The C-banded karyotype of this species exhibits consistent differences from those of *S. longirostris* and *S. attenuata,* which are very similar (Worthen 1981). No clear picture of relationships emerges from these findings.

Ecology—Along the southeastern coast of the United States and in the Gulf of Mexico, the large heavily spotted form of *S. frontalis* inhabits the continental shelf, usually being found inside or near the 100-fathom (183-m) line (within 250–350 km of the coast) but sometimes seasonally coming into very shallow water near the shore, perhaps in pursuit of migratory forage fish (Caldwell and Caldwell 1966, 1973, Schmidly and Shane 1978). It is usually replaced in nearshore shallow waters by *T. truncatus* (Caldwell and Caldwell 1966). The offshore distributions of this form and the other, more oceanic forms in the Caribbean, mid-tropical Atlantic and oceanic western North Atlantic are very poorly known. Recent surveys of small cetaceans in the western North Atlantic, for example, have not distinguished between the two species of spotted dolphins (Erdman *et al.* 1973, Taruski and Winn 1976, Schmidly 1981, Winn 1982, Fritts *et al.* 1983). *S. frontalis* is taken in a subsistence harpoon fishery at St. Vincent in the Lesser Antilles (pers. comm., R. V. Walker). In this area, there is strong morphological convergence with *S. attenuata* (Fig. 18), and the two species may have similar ecologies.

The stomach of a specimen of *S. frontalis* captured off northern Florida contained many small cephalopod beaks, and dolphins of this species have been observed to feed on small clupeoid and carangid fishes and large squid (Caldwell 1955, Caldwell and Caldwell 1966) and to follow trawlers to eat discarded fish (Moore 1953). Of 19 specimens stranded on the U.S. east coast, the stomachs of nine contained only squid remains, six had both fish and squid, and four contained only fish. The otoliths from four of these stomachs were identified to species: a sciaenid *Cynoscion* sp. predominated in one, the sciaenid *Stenotomuschrysops* in two, and a clupeoid *Anchoa* sp. in the fourth; other families represented were Congridae, Gadidae, Trichiuridae and Triglidae (unpublished data, JGM).

Recorded ectoparasites and commensals include the rabbit-eared barnacle *Conchoderma auritum* (van Bree 1971*a*), the pseudo-stalked barnacle *Xenobalanus globicipitis,* an unidentified cyamid crustacean (Caldwell, Caldwell and Zam 1971) and the remora *Remora* (= *Remilegia*) *australis* (Follett and Dempster 1960). Endoparasites include the trematodes *Campula palliata, Pholeter gastrophilus* and *Braunina cordiformis,* and the nematodes *Halocercus delphini* and *Anisakis* sp. (Zam *et al.* 1971).

Life history—Nothing is known of the life history of this species.

Behavior—Pods ususally consist of fewer than 50 individuals and most

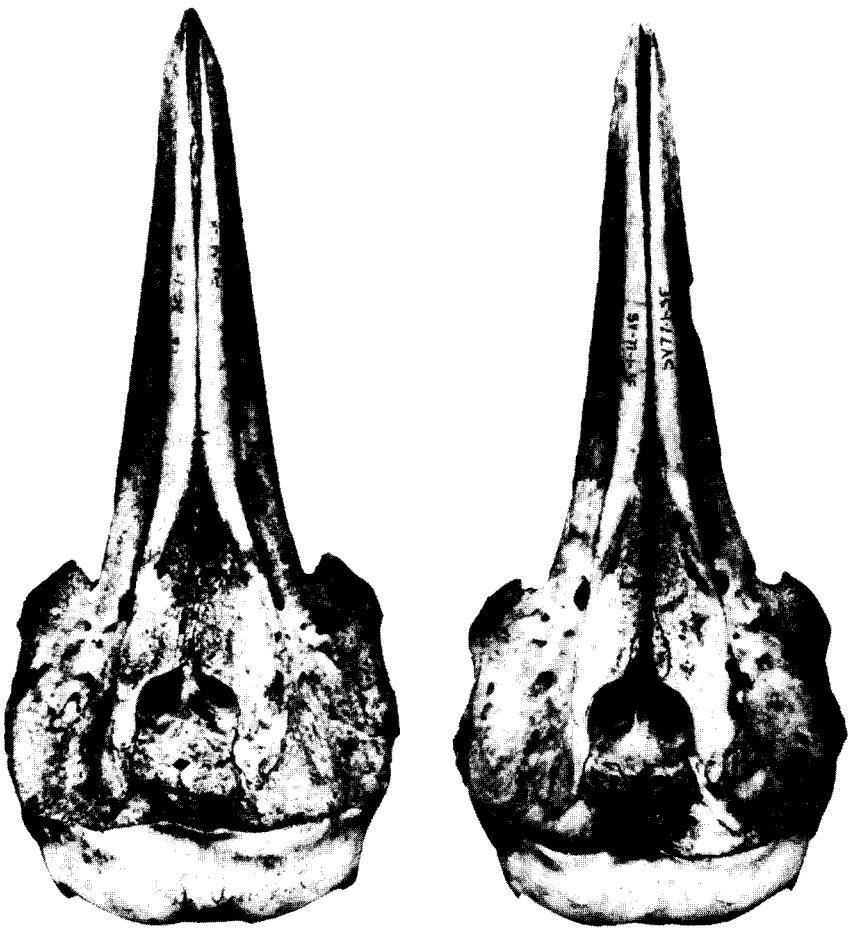


Figure 18. Adult skulls of *Stenella frontalis* (left, UF SV77-1-SP) and *S. attenuata* (UF SV77-1-SF) from St. Vincent in the Lesser Antilles, demonstrating convergence.

typically of 5 to 15 in coastal waters (Caldwell and Golley 1965, Caldwell and Caldwell 1966, Lowery 1974, Leatherwood *et al.* 1976). Three types of underwater sounds are produced in captivity: whistles, burst-pulses of various kinds, and series of sharp clicks presumed to be for echolocation (Caldwell and Caldwell 1966, 1971). A signature whistle has been identified, but it is less distinctive than in *T. truncatus* (Caldwell *et al.* 1973).

Common name—The established vernacular name "Atlantic spotted dolphin" is suitable for this endemic species.

Specimens included (museum acronyms defined in Appendix 1)—oceanic North Atlantic: Azores, 2 (MNHN B2/110, UZMC *Prodelphinus* no. 4); 40°15'N, 29°05'W, 2 (EDM 760, AMNH 239111); 46°20'N, 38°44'W, 1

(EDM 786); 38°40'N, 49°W, 1 (UZMC *Prodelphinus* no. 11); 35°15'N, 74°33'W, 1 (AMNH 239117); 38°05'N, 70°10'W, 1 (MCZ 24800); 38°15'N, 71°17'W, 1 (MCZ 51073); 39°31'N, 69°37'W, 1 (MCZ 51294). Massachusetts: Cape Cod, 1 (USNM 550751, photographs and external measurements only). New York: Amagansett, 1 (USNM 550353). New Jersey: off Cape May, 1 (MCZ 51074); Raritan Bay, 1 (USNM 550099). Maryland: Assateague Island, 2 (USNM 504949 and 550129). Virginia: Lynnhaven Beach, 1 (RAB 030, in possession of R. A. Blaylock); False Cape, 1 (USNM 504758). North Carolina: off Cape Hatteras, 3 (EDM 694 and 695, USNM 22017); Hatteras Island, 1 (USNM 504748); Hatteras, 1 (GWO 020, in possession of Guy W. Oliver); Frisco, 1 (USNM 504736); Buxton, 1 (USNM 550024); Salvo, 1 (USNM 550355); Nags Head, 2 (USNM 504901 and 550101); Bodie Island, 2 (USNM 550098 and 550102); Avon, 1 (USNM 504762); Ocracoke Island, 5 (USNM 504321, 504322, 504862, 504863 and 504876); Topsail Island, 1 (FTI unnumbered, in possession of WFP). South Carolina: off Charleston, 3 (EDM 696 and 697, USNM 253598); Charleston, 1 (MCZ 1182); Bull's Bay, 1 (CM 2555); Hilton Head, 1 (USNM 500858). Georgia: off Georgia, 3 (USNM 261364 and fetus, EDM 844). Atlantic coast of Florida: off St. Augustine, 16 (UF 18727–18739, MLF 294 and stillborn fetus of MLF314, measurements and photographs only of latter two, in possession of DKC); Anastasia Island, 1 (UF 3334); Crescent Beach, 1 (UF 18740); New Smyrna, 1 (UF S-SP-30); Straits of Florida, 2 (EDM 700 and 701); Fort Pierce Inlet, 1 (RSMAS SWF-813); Port Salerno, 1 (RSMAS C-78-3); Miami, 1 (USNM 257833); Hallendale, 1 (RSMAS C-80-5); Upper Matacumbe Key, 1 (RSMAS C-76-12); Content Key, 1 (ANSP 16709). Florida Gulf Coast: St. Petersburg, 2 (UF 18742 and UF R-G-9-SP); off Steinhatchee, 8 (UF 18741 and R-G-2-SP to R-G-8-SP, external measurements and photographs only, in possession of DKC); Eglin Air Force Base, 1 (R-G-10-SP, external measurements and photographs only, in possession of DKC); Destin, 2 (LACM 27057 and 27058); off Pensacola, 1 (USNM 21915); off Boca Grande, 1 (USNM 23414). Louisiana: Johnson's Bayou, Cameron Parish, 1 (MSU 2139). Texas: Port Aransas, 1 (TCWC 1543); off Port Aransas, 3 (USNM 292069-71); Yarborough Pass, Padre Island, 1 (TCWC 25577). Caribbean: St. Thomas, Virgin Islands, 4 (UF VI-1-SF to VI-4-SF); Puerto Rico, 1 (UZMC *Prodelphinus* no. 10); 17°42'N, 67°22'W, 2 (EDM 808 and AMNH 239116); 19°42'N, 67°50'W, 1 (UZMC *Prodelphinus* no. 14); 14°34'N, 60°03'W, 1 (EDM 803); St. Vincent, Lesser Antilles, 1 (UF SV77-1-SP); 11°02'N, 61°54'W; 2 (AMNH 239112 and 239114); 10°57'N, 61°34'W, 1 (EDM 710); 10°52'N, 66°28'W, 2 (EDM 706 and AMNH 239113); 10°41'N, 66°00'W, 2 (ZMA unnumbered A and B); 9°30'N, 79°00'W, 1 (USNM 254447). Mid-tropical Atlantic: 10°N, 39°W, 1 (UZMC *Prodelphinus* no. 31); St. Helena, 2 (UZMC *Prodelphinus* no. 20 and MNHN A-3031). Africa: 19°03'N, 24°24'W, 1 (UZMC *Prodelphinus* no. 2); Cape Verde, 2 (MNHN A-3034–holotype of *Delphinus frontalis*; MNHN A-3035–holotype of *D. froenatus*); Senegal, 1 (IFAN 76-54); off Vridi, Ivory Coast, 4 (IFAN unnumbered–pregnant female, photographs and measurements only in Cadenat and Lassarat 1959–ZMA 22.964, ZMA 13.148

and ZMA 13.546); Fernando Po, 1 (BMNH [18]62.12.2.6); off Conakry, Guinea, 1 (ZMA 22964); off Pointe Noire, Gabon, 1 (ZMA 15.171). Unknown localities: USNM 3884 (holotype of *Delphinus plagiodon*), BMNH 352.a. (holotype of *D. doris*), BMNH 1948.5.1.1 ("coast of Europe").

Previously unpublished locality records (in addition to those from specimens listed above; sources, when other than authors, listed in ACKNOWLEDGMENTS)—Maine, 1 (48°08'N, 70°39'W–JGM); off New York, 1 (40°37'N, 12°00'W); off Delaware, 2 (38°N, 73°W; 37°N, 74°W); off North Carolina, 4 (35°35'N, 75°20'W; 35°17'N, 74°15'W; 34°49'N, 75°36'W, 34°45'N, 76°45'W); off South Carolina, 1 (approx. 32°50'N, 79°30'W); Bahamas, 1 (approx. 24°N, 74°30'W); Caribbean, 10 (25°11'N, 80°08'W; 24°20'N, 82°48'W; 18°43'N, 74°42'W; approx. 17°30'N, 88°W; 17°03'N, 63°05'W; 14°30'N, 77°10'W; approx. 12°30'N, 70°W; approx. 12°N, 68°W; 11°39'N, 73°50'W; approx. 11°N, 64°W); off Brazil, 1 (approx. 24°S, 46°W); Azores, 2 (approx. 38°N, 28°W).

REDESCRIPTION OF *STENELLA ATTENUATA*

1829. [*D*]*elphinus velox* G. Cuvier, Règne Animal, ed. 2, 1, p. 288.
1840. (or earlier). *Delphinus pseudodelphis* Wiegmann, Schreber's Saeugethiere, pl. 358.
1843. *Delphinus attenuatus* Gray, List mamm. Brit. Mus., p. 105 (*nomen nudum*).
1846. *Steno attenuatus* Gray, Zoology of the voyage of *H.M.S. Erebus* and *Terror,* 1 (Mammalia), p. 44, pl. 28.
1884. *C*[*lymenia*] *attenuatus.* Flower, Proc. Zool. Soc. London, 1883, p. 512.
1885. *Clymenia attenuata.* Hector, Trans. N.Z. Inst., 17, p. 211.
1885. *Prodelphinus attenuatus.* Flower, List Cetacea Brit. Mus., p. 30.
1934. *Stenella attenuata.* Iredale and Troughton, Mem. Australian Mus. 6, p. 66.
1975. *Stenella attenuata graffmani* (Lönnberg) of Perrin, Bull. Scripps. Inst. Oceanogr. 21, p. 125.
1981. *Stenella attenuata attenuata* (Gray) of Hall, Mammals of N.A., p. 882.
1841. *Delphinus malayanus* Schlegel (not Lesson), Abhandl. Gebiete. Zool. u. Vergl. Anat., p. 20 and pl. 2(2).
1923. *Prodelphinus malayanus.* Weber (*sensu* Schlegel 1841), Die Cetaceen der Siboga-Expeditie, p. 8.
1846. *Delphinus brevimanus* Wagner, Schreber's Saeugethiere, 7, pl. 361.
1866. *Steno? brevimanus.* Gray, Cat. seals and whales Brit. Mus., p. 236.
1880. *Prodelphinus brevimanus.* H. Gervais, *in* van Beneden and Gervais, Ostéographie des Cétacés, p. 605.
1850. *Delphinus? microbrachium* Gray, Cat. Mamm. Brit. Mus., Cetacea, p. 119.

1848. *Delphinus albirostratus* Peale, U.S. Exploring Expedition, Mammalia, p. 34, pl. 7, fig. 2.
1874. *Lagenorhynchus albirostratus?*. Gill, *in* Scammon, Marine mammals of the north-western coast of North America, p. 293.
1858. *Lagenorhynchus caeruleoalbus*. Cassin, U.S. Exploring Expedition, Mammalogy and Ornithology, p. 31, pl. 6, fig. 2.
1874. *Delphinus ceruleo-albus* of Gill, not Meyen 1833, *in* Scammon, Marine mammals of the north-western coast of North America, p. 293.
1865. *Steno Capensis* Gray, Proc. Zool. Soc. London, 1865, p. 522.
1884. *C[lymenia] Capensis*. Flower, Proc. Zool. Soc. London, 1883, p. 512.
1898. *Prodelphinus capensis*. Trouessart, Cat. Mamm., p. 1035.
1866. *Clymene punctata* Gray, Proc. Zool. Soc. London, 1865, p. 738.
1866. *Delphinus punctatus*. Gray, Cat. seals and whales Brit. Mus., p. 398.
1871. *Steno consimilis* Malm, Kong. Svensk. Vetensk. Handl., 9, p. 104, pl. 6, figs. 53a, b.
1889. *Prodelphinus alope* Lütken (not Flower 1885), Vid. Selsk. Skrift., Copenhagen, 6, Nat. Mat. 5, 1, p. 43.
1922. *Stenella pseudodelphis* Oliver, Proc. Zool. Soc. London 1922, p. 583.
1934. *Prodelphinus graffmani* Lönnberg, Ark. Zool. Stockholm, 26A, 19, p. 1, pl. 1.
1940. *Stenella graffmani*. Kellogg, Nat. Geogr. Mag., 77, 1, p. 85.

Holotype and type locality—Subadult skull (rostrum still growing), British Museum (Natural History), London (BMNH) no. 347.b., from unknown locality, possibly India (Gray 1843).

Distribution—Worldwide in tropical and some subtropical waters. In Atlantic, broadly sympatric with *S. frontalis* except in oceanic western North Atlantic (Fig. 7) and possibly northern coast of South America. A specimen listed by Lütken (1889; *Prodelphinus* no. 6) as from the Bay of Biscay is actually from off Brazil; the coordinates of latitude and longitude (written on the skull by the collector) are transposed in his paper. There is a single extralimital record from Alaska, with credible locality data; a mummified carcass was found on the beach at Cold Bay on 10 September 1983 (USNM 550771).

Diagnosis—This dolphin is unspotted at birth, with strongly defined cape passing high over the eye, flipper stripe terminating anteriorly at the angle of the gape, and peduncle divided into dark upper and light lower portions (Fig. 1; Perrin 1970, 1972). The typical delphinid eye and blowhole stripes and lip mark are present. The eye stripe is relatively narrow (1–2 cm) and encloses a black eye patch and extension of the eye patch as a black line (a few mm wide) forward to the apex of the melon. The entire eye stripe may be bordered by a narrow light line. The blowhole stripe is relatively narrow and may be composed of sub-elements. The intersection of the anterior end of the flipper stripe and lip mark is demarcated by a narrow light line. The ventral margin of the flipper stripe may be bordered by a narrow light line and subtended by a parallel narrow dark line. A light gray band (4–6 cm) may parallel the ventral margin of the cape. Color at birth is dark gray above and ivory below; the extremities are dark gray. The ventrum darkens to light gray, then dark gray spots appear

ventrally, first in the gular and abdominal regions. Subsequently, light dorsal spots appear. The dark ventral spots increase in number and size until they are largely confluent in adults. The light dorsal spots also increase in size and number and may be confluent in some areas, especially at the ventral margin of the cape over the eye and behind the cape on the upper side of the peduncle. In heavily spotted individuals from some regions (*e.g.*, the Pacific coasts of Mexico and Central America), the ground pattern may be nearly obscured dorsally. Spotting may extend to the dorsal fin and flippers. In adults, several cm of the rostrum and lower jaw may be white. The white may extend posteriorly to edge the entire gape (*e.g.*, Fraser 1950). This feature varies individually and geographically; it is especially prominent in specimens from the western Pacific (Nishiwaki *et al.* 1965).

Minimum and maximum external dimensions and weights for cranially adult specimens from the Atlantic and from all oceans are presented in Table 3. Maximum recorded length for males is 257 cm and for females 240 cm (both from the eastern tropical Pacific). The smallest known cranially adult specimens (a male of 166 cm and female of 163 cm) were also from the eastern tropical Pacific. Adult length in the species thus varies about 1 m (roughly 50 percent of midpoint length of about 2 m).

A typical skull from the western North Atlantic is illustrated in Figure 11. Ranges of skull measurements for cranially adult specimens and postcranial measurements for physically mature specimens are in Table 4 for the Atlantic and for all oceans. Development and variation of the complete skeleton were described and illustrated by Perrin (1975). The largest known skull is of the above-mentioned 257-cm male (119 kg) from the Gulf of Panama in the eastern Pacific (USNM 261432). Ranges are not presented separately for males and females in Table 4 because the substantial geographic variation in this species (discussed below) could be expected to obscure sexual dimorphism. Slight sexual dimorphism does exist in several skull dimensions and has been described for samples from the eastern Pacific (Table 9; also Perrin 1975, Schnell *et al.* 1985). Females tend to have a longer rostrum and males a larger braincase, but there is very great overlap in all characters.

Rostral tooth counts range from 35 to 48 and mandibular counts from 34 to 47 and average about 40 in each jaw (Table 5). The number of vertebrae ranges from 74 to 84 (but note that the specimen with the isolated value of 74—UZMC *Prodelphinus* no. 6—may represent a case in which one or more vertebrae were lost during preparation of the specimen; the specimen with 76 vertebrae is also in the Copenhagen Museum—*Prodelphinus* no. 15). The typical vertebral formula is C7, T16, L20, Ca37 = 80.

Geographic variation—The species varies geographically in coloration, body size and cranial and postcranial measurements. This has been demonstrated based on large series of specimens from the eastern tropical Pacific (Perrin 1975, Perrin *et al.* 1979, Douglas *et al.* 1984, Perrin *et al.* 1985, Schnell *et al.* 1986). Material from other parts of the Pacific, from the Indian Ocean and from the Atlantic is still too limited to support more than very tentative conclusions concerning geographic variation involving those areas.

As noted above, degree of spotting varies geographically in the eastern

Table 9. Skull measurements (mm) exhibiting sexual dimorphism in *Stenella attenuata* (from Schnell *et al.* 1985; unweighted means of mixed sample of 543 specimens drawn from two or more populations in eastern Pacific).

Measurement	Mean		P[a]
	Male	Female	
Length of rostrum	239.4	242.5	***
Width of rostrum at base	85.2	83.8	***
Width of rostrum at ¼ length	59.6	57.9	***
Width of rostrum at ½ length	44.4	42.9	***
Width of premaxillaries at ½ length	24.1	22.8	***
Width of rostrum at ¾ length	31.9	30.1	***
Rostrum tip to internal nares	281.6	284.3	**
Greatest preorbital width	152.3	149.5	***
Greatest postorbital width	170.5	167.9	***
Zygomatic width	170.5	167.3	***
Greatest width of pmx's	67.5	66.9	**
Parietal width	141.3	138.0	***
Height of braincase	99.2	96.9	***
Int. length of braincase	120.1	117.9	***
Greatest width of left pmx	26.6	26.1	***
Length of temporal fossa	68.8	67.1	***
Width of temporal fossa	52.9	51.1	***
Length of preorbital process	38.3	37.6	**
Width of int. nares	48.0	47.2	***
Length of upper toothrow	204.7	207.4	***
Length of lower toothrow	199.0	201.8	***
Length of ramus	339.0	342.2	**
Diameter of tooth (at mid-length of lower row, transverse at alveolus)	3.82	3.70	***

[a] **, $P < 0.01$; ***, $P < 0.001$.

Pacific. Dolphins close to the coast are on the average more heavily spotted than those that are more offshore (Perrin 1975). Specimens from the western Pacific (Nishiwaki *et al.* 1965), the southern Indian Ocean (Ross 1984), Africa (Fraser 1950) and the mid-tropical Atlantic (field observations by WFP at St. Helena) are spotted to about the same extent as those in the offshore eastern Pacific, although in some areas (*e.g.*, Hawaii and St. Helena) dorsal spotting in some adults is so weakly developed as to give the animal an unspotted appearance when seen at a distance.

Body size also varies geographically (Table 10). Coastal spotted dolphins from the eastern tropical Pacific are the largest (males and females averaging 223 and 207 cm, respectively), followed closely by those from the coastal western North Atlantic and Gulf of Mexico. Of those regions for which adequate samples exist, the oceanic eastern tropical Pacific is inhabited by the smallest animals; males average 200 cm (n = 1,280) and females 187 cm (n = 3,890). Only single lengths are available for the Caribbean (a 191-cm female; SV77-1-SF) and Africa (a 200-cm male; the BMNH *Atlantide* specimen), values that fall within the ranges for all the large samples from other regions.

Table 10. Geographic variation in body length (cm) in *Stenella attenuata* (sample size in parentheses).

		Eastern Pacific[a,b]										Coastal eastern N. Atlantic & Gulf of Mexico	
			Oceanic (offshore)										
			Northern										
		Coastal	W. of 120°W		E. of 120°W		Southern		Western N. Pacific[c]		S.W. Indian Ocean[c]		
Mean	M	223.2 (47)	198.6	(200)	200.1	(994)	196.6	(86)	204–207	(80)	—	215.8	(5)
	F	206.5 (87)	186.6	(499)	187.8	(3,077)	185.3	(314)	192–195	(251)	—	188.3	(3)
Range	M	197–246 (47)	177–228	(200)	166–240	(994)	175–220	(86)	max 234	(>300)	216–220 (2)	193–231	(5)
	F	179–227 (87)	165–215	(499)	163–215	(3,077)	168–206	(314)	173–220	(>344)	215 (1)	186–194	(3)
SD	M	11.73 (47)	9.10	(200)	9.46	(994)	7.52	(86)	—		—	—	
	F	10.47 (87)	7.34	(499)	7.28	(3,077)	7.12	(314)	—		—	—	

Length also varies geographically within the oceanic eastern Pacific; samples from different latitudinal/longitudinal strata differ by as much as 3 cm in average body length (Table 10). It is not yet known if this reflects the existence of only clinal variation or the existence of more than one breeding population.

Variation in skull size and size of the postcranial skeleton in the eastern Pacific parallels that in body size (Perrin 1975, Douglas *et al.* 1984); the coastal form has a much larger skull and larger postcranial bones than does the oceanic form (Tables 11 and 12). The temporal fossa is especially large; the means for the two measurements of this feature (as well as height of ramus and tooth diameter) in the coastal series lie outside the ranges for the measurements for all 55 specimens from other waters in the Atlantic, Pacific and Indian Oceans. This is also true for the height of the mandibular ramus. The largest skull known for the species (CB length 460 mm; illustrated in Perrin 1975) is in this series.

Geographical variation in the cranium also exists within the oceanic eastern tropical Pacific (Perrin *et al.* 1979, Schnell *et al.* 1986); skulls of dolphins from north of the equator differ from those from south of the equator in being on the average larger and having proportionately larger temporal fossae. Specimens from the far western portion of the range in the eastern Pacific show affinities with those from south of the equator in the east and with specimens from Hawaii. As noted above, it is not yet known if this variation is wholly clinal or if it reflects the existence of two or more breeding populations. Schnell *et al.* (1986) found correlations between the north/south variation and several environmental variables, including annual solar insolation amd sea-surface temperature.

The specimens in the series from the oceanic eastern Pacific and from St. Helena in the Atlantic are on the average smaller than those from other areas, and the specimens in the series from the coastal western North Atlantic, Hawaii, the western Pacific and the Indian Ocean are intermediate.

Virtually nothing is known about the species in the eastern North Atlantic and in the Southern Hemisphere aside from St. Helena. The five specimens from Africa and South America are listed individually in Table 11 because of their broad provenance and diversity. The skull from the Gulf of Guinea is the shortest known for the species from the Atlantic. As noted by Best (1969) and Ross (1984), this is because of its very short rostrum (illustrated in Fraser 1950); in other features it does not differ materially from other Atlantic specimens. The skulls from Cape Verde and Argentina are small and similar to those from St. Helena and the oceanic eastern Pacific, but the two skulls from Brazil are the largest known for the species from the Atlantic. It is evident that much more material must be in hand before geographic variation in the Atlantic can be adequately described. The same is true for the Indian Ocean (as noted by Ross 1984) and the central, southern and western Pacific.

The specimen from Alaska is problematical. The rostrum is extremely long, but in other dimensions it conforms well with the oceanic form in the eastern tropical Pacific.

Stenella attenuata also varies geographically in meristic characters. Douglas

et al. (1984) detected a mean difference of approximately one tooth per row between the coastal and oceanic forms in the eastern Pacific (40.4/39.4 and 41.3/40.2, respectively). Only the series of specimens from St. Helena is large enough to allow comparision with the eastern Pacific series. Average of highest rostral and mandibular counts in that series are 41.0 and 39.9, respectively (n = 42 and 43; SD = 2.12 and 2.19), closest to the eastern Pacific coastal form (when the upwardly biasing effect of using highest count rather than average of left and right counts is considered). Tooth counts for the Atlantic specimens overall are approximately ½ tooth lower than for all specimens pooled (Table 5).

Coastal spotted dolphins in the eastern Pacific have on the average about 78 vertebrae, as opposed to about 80 in the oceanic form (Fig. 19). The series from other regions are too small to allow comparisons (Table 5).

Comparisons—See redescription of *S. frontalis* above for comparisons with that species and with *S. longirostris, S. clymene. S. coeruleoalba, Delphinus delphis, Lagenodelphis hosei* and *Tursiops truncatus.*

Ecology—The species occurs both in coastal waters and in the open ocean. In the eastern tropical Pacific it commonly associates with schools of yellowfin tuna (*Thunnus albacares*) and may be found together with tuna, spinner dolphins (*S. longirostris*) and large numbers of sea birds. This multispecies aggregation is correlated in distribution with certain oceanographic variables, including depth and steepness of the thermocline and sea-surface temperature, and may constitute a symbiotic foraging association involving two or more of the species (Au and Perryman 1985). The existence of greater morphological differences between *S. attenuata* and *S. longirostris* in this region than exist between them in other places where they do not school and forage together (*e.g.*, Hawaii, just to the west) may indicate that ecological character displacement has occurred (Perrin 1985*b*). Large numbers of spotted dolphins are killed incidentally by tuna seining operations in the eastern tropical Pacific and at least two populations there have declined in size (Smith 1983).

Recorded stomach contents include a large number of small epipelagic and mesopelagic fishes and squids and unidentified nemertean worms and crab larvae (Fitch and Brownell 1968, Perrin *et al.* 1973, Shomura and Hida 1965, Ross 1984). Fish families represented are Exocoetidae, Scombridae, Myctophidae, Gonostomatidae, Bregmacerotidae, Gempylidae, Paralepididae, Alepisauridae, Bramidae, Bathylagidae, Trichiuridae, Congridae, Scopelosauridae, Opisthoproctidae, Evermannellidae, Balistidae, Melamphaidae and Stromateidae. Cephalopod remains were of the families Onychoteuthidae, Ommastrephidae, Enoploteuthidae, Histioteuthidae, Chiroteuthidae, Cranchiidae, Lycoteuthidae and Octopoteuthidae. Lactating females may feed more heavily on epipelagic fish than do pregnant females (Bernard and Hohn 1985).

Ectoparasites and commensals include a cyamid amphipod *Syncyamus* sp. (Leung 1970) and the barnacles *Conchoderma auritum* (Perrin 1969) and *Xenobalanus globicipitis* (Ross 1984). Endoparasites include the cestodes *Tetrabothrium forsteri, Strobilocephalus triangularis, Phyllobothrium delphini* and *Monorygma delphini,* the trematodes *Nasitrema globicephalae, N. stenosoma,*

Table 11. Statistics of cranial measurements (mm) for geographical series of cranially adult specimens of *Stenella attenuata* (sample size in parentheses).

	Atlantic								
					Africa[b]		S. America		
	Coastal N.W. Atlantic & Gulf of Mexico		St. Helena (11)[a]		Cape Verde	Gulf of Guinea	Fernando de Noronha	Coast of Brazil	Uruguay
					ZMA-IFAN	BMNW			
	Mean	Range	Mean	Range	no. 32	"Atlantide"	CMNH 2524	MCNRS[c] 026	MACNBA 23–46
Condylobasal length	415.3	403–432 (10)	401.1	387–423	388	369	437	440	389
Length of rostrum	253.3	243–271 (10)	240.0	231–260	232	208	268	270	221
Width of rostrum at base	88.1	78–93 (10)	86.2	82–94	84	85	95	90	92
Width of rostrum at ¾ length	30.6	27–33 (10)	27.6	25–32	28	31	36	46	31
Zygomatic width	175.1	171–182 (10)	171.2	163–178	169	171	182	185	177
Greatest width of pmx's	70.4	65–73 (10)	67.7	65–70	66	69	75	73	69
Parietal width	140.0	131–146 (10)	138.6	131–145	138	146	150	151	142
Length of temporal fossa	68.0	63–73 (10)	65.4	63–70	58	66	64	65	61
Height of temporal fossa	52.1	45–55 (10)	50.0	43–56	45	59	56	56	45
Length of upper toothrow	216.2	200–235 (10)	205.0	194–224	196	175	228	224	196
Length of ramus	356.5	345–375 (9)	341.1	328–362	331	312	370	—	343
Height of ramus	58.0	55–61 (9)	57.9	53–62	57	61	59	—	57
Diameter of tooth (at midlength of lower row, transverse at alveolus)	3.37	3.0–3.5 (6)	3.50	3.3–3.7	—	—	4.1	—	—

Table 11. Continued.

	Pacific Ocean								
	Eastern Pacific[d]		Hawaii[e]		Western Pacific[f]		Alaska (1)	Indian Ocean[g]	
	Coastal (31)	Oceanic (575)	Mean	Range	Mean	Range	USNM 550771	Mean	Range
Condylobasal length	436.7	396.1	413.6	395–440 (12)	412.4	400–433 (12)	435	410.2	345–423 (6)
Length of rostrum	262.3	237.1	250.8	240–269 (12)	249.2	243–258 (12)	270	247.8	233–261 (6)
Width of rostrum at base	90.5	83.0	89.2	86–94 (13)	87.7	78–95 (12)	85	87.6	87–89 (5)
Width of rostrum at ¾ length	35.6	29.6	31.8	28–35 (12)	30.9	28–34 (12)	30	31.2	29–35 (5)
Zygomatic width	180.9	165.3	172.2	164–181 (13)	168.7	159–183 (12)	179	174.7	166–183 (6)
Greatest width of pmx's	72.3	65.8	68.9	65–71 (13)	68.3	61–76 (12)	69	67.8	65–70 (6)
Parietal width	147.8	138.3	141.0	135–150 (13)	140.7	130–152 (12)	144	135.0	131–138 (6)
Length of temporal fossa	81.1	65.8	62.0	57–70 (13)	64.8	61–70 (10)	66	66.8	62–72 (6)
Height of temporal fossa	61.0	50.7	50.2	42–56 (13)	51.8	47–55 (10)	51	50.8	46–56 (6)
Length of upper toothrow	225.6	202.9	215.9	200–232 (12)	214.5	204–232 (13)	226	211.0	199–223 (6)
Length of ramus	370.6	335.5	351.4	339–379 (12)	353.2	340–374 (13)	369	346.7	334–355 (6)
Height of ramus	66.0	57.2	57.5	53–61 (13)	58.4	55–61 (12)	61	57.7	56–61 (6)
Diameter of tooth (at midlength of lower row, transverse at alveolus)	4.73	3.51	—	—	—	—	3.4	—	3.8 (1)

[a] All of unknown sex.
[b] ZMA-IFAN no. 32 is of unknown sex; BMNH "Atlantide" is a male.
[c] From Pinedo and Castello (1980).
[d] From Douglas *et al.* (1984); averages of pooled males and females adjusted for sex to "zwitter" values.
[e] From Perrin (1975).
[f] Eight specimens examined, three from Nishiwaki *et al.* (1965), two from Zhou *et al.* (1980).
[g] Three specimens examined, two from Ross (1984), one from Best (1969).

Table 12. Statistics of postcranial measurements (mm) for geographical series of physically mature specimens of *Stenella attenuata* (sample size in parentheses).

	Atlantic			Pacific						Indian Ocean (1)
	Coastal N.W. Atlantic & Gulf of Mexico (5)		Africa (1)	Eastern Pacific coastal		Eastern Pacific oceanic[a]		Hawaii (2)		
	Mean	Range	BMNH "Atlantide"	Mean	Range	Mean	Range	USNM 395877	UBC 8511	SAM 35515[b]
Atlas: width	77.4	73–83	80	86.8	82–90 (5)	77.8	73–84 (16)	90	82	84
First thor. vert. width	75.4	72–79	74	79.8	77–82 (5)	71.8	63–80 (16)	84	86	—
First lumb. vert. width	189.6	175–202	179	193.5	180–207 (5)	174.8	165–188 (15)	—	200	—
Length of longest vert. rib	261.8	234–286	256	292.0	281–313 (4)	248.9	232–263 (16)	265	270	—
Scapula: height	119.2	112–127	105	130.0	126–135 (5)	108.2	101–123 (16)	124	117	103
Humerus: length	52.0	50–56	50	57.0	53–62 (5)	48.1	43–53 (16)	51	50	51

[a] From Perrin (1975).
[b] From Best (1969).

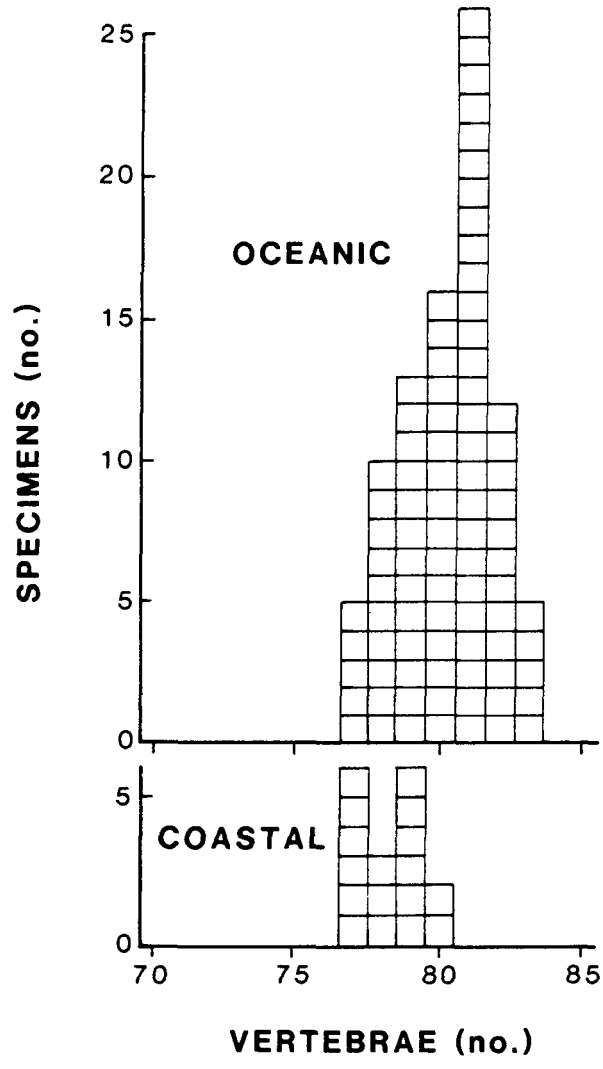


Figure 19. Number of vertebrae in coastal and oceanic specimens of *Stenella attenuata* in the eastern Pacific.

Campula rochebruni, *Orthosplanchnus ? elongatus* and *Zalophotrema pacificum*, the nematodes *Anisakis simplex*, *A. typica*, *A. alexandri*, *Mastigonema stenellae*, *Halocercus delphini* and *Crassicauda* sp. and the acanthocephalans *Bolbosoma vasculosum* and *B. balaenae* (Neiland *et al.* 1970, Dailey and Perrin 1973, Zhou *et al.* 1980, Dailey and Otto 1982, Ross 1984).

Predators include one or more of the carcharinid sharks, the cookie-cutter shark (*Isistius brasiliensis*) and the killer whale (*Orcinus orca*); in addition they

may include other sharks, the false killer whale (*Pseudorca crassidens*), the pygmy killer whale (*Feresa attenuata*) and the short-finned pilot whale (*Globicephala macrorhynchus*) (Leatherwood *et al.* 1973, Perryman and Foster 1980, WFP, unpub. data).

Behavior—Pods range in size from a few dolphins to several thousand (Scott *et al.* 1985). For oceanic populations, home range may be several hundred kilometers or more in diameter, within which seasonal migrations occur (Perrin *et al.* 1979). The species migrates into Japanese waters seasonally, following the northern edge of the warm Kuroshio Current (Miyazaki *et al.* 1974). This dolphin often rides the bow waves of ships (Leatherwood *et al.* 1982). Two trained specimens reached a top speed of 11.03 m/sec (21.4 knots) in 2.0 seconds (Lang and Pryor 1966).

Life history—Average age at sexual maturation in males is 14.7 yr (Hohn *et al.* 1985). Females mature on the average at 10–12 yr (Myrick *et al.* 1986); the range is 10 to 17 yr. Maximum longevity in both sexes may exceed 45 yr (Kasuya 1985). Aged females may become postreproductive (Perrin *et al.* 1976, Myrick *et al.* 1986). Average calving interval in the eastern Pacific is 2 to 3 yr and in the western Pacific 4 to 6 yr, the difference possibly related to differential status of the populations (Kasuya 1985, Myrick *et al.* 1986).

Common name—We propose that the vernacular name "pantropical spotted dolphin" be used for this species.

Specimens included (museum acronyms defined in Appendix 1)—Massachusetts: Revere, 2 (USNM 550016–17). Rhode Island: Charleston, 1 (USNM 550356). North Carolina: Carolina Beach, 1 (NCSM 2564). Atlantic Coast of Florida: Fernandina Beach, 1 (UF R-2-SF); New Smyrna Beach, 1 (UF 18984); Sebastian [?], 1 (MCZ 20584); Port Canaveral, 1 (RSMAS SWF-829); Fort Lauderdale, 1 (RSMAS C-77-9); near Soldier Key (near Miami), 1 (UF R-1-SF); Coconut Grove, 1 (USNM 218344). Gulf Coast of Florida: Pensacola, 2 (USNM 550374; UF R-G-2-SF); Panama City, 4 (external photos only, USNM MME00174); Big Pass (near Sarasota), 1 (UF R-G-1-SF). Caribbean: St. Vincent, 2 (UF SV-77-1-SF and SV-1-SF). Brazil: Isla Fernando de Noronha, 1 (CMNH 2524); Rio Grande, 1 (MCNRS 026—not examined, data from Pinedo and Costello 1980). Uruguay: 1 (MACNBA 23-46—not examined, data from Brownell and Praderi 1976). Mid-tropical Atlantic: 11°N, 47°W, 1 (UZMC *Prodelphinus* no. 6); 9°N, 33–34°W, 1 (UZMC *Prodelphinus* no. 3); 6°46'N, 24°35'W, 1 (AMNH 39092); 2°44'N, 29°W, 1 (UZMC *Prodelphinus* no. 8). St. Helena: 44 (USNM 347651; BMNH 1946.9.10.4, 1956.11.2.1–6, 1957.5.9.1–8, 1958.5.27.1–3, 1959.2.23.1–8, 1959.12.31.1–11, 1960.6.24.1–5, 1961.11.24.1). Africa: Cape Verde, 2 (ZMA 22.962; PML unnumbered—holotype of *Clymene punctata,* not examined, data from Gray 1966 and True 1889); Gabon, 1 (BMNH *Atlantide* specimen). "Southeast Atlantic": 1 (MCZ 7942). "South Atlantic": 1 (MCZ 1187). "Mid Atlantic": 1 (BMNH 1878.2.11.1). "Atlantic Ocean": 2, (UZMC *Prodelphinus* no. 21, 24). Red Sea: Koseir, 2 (ZMB 31975, LIZ 6886). Persian Gulf: Siham, 1 (BMNH 73.1749). Indian Ocean: Seychelles, 2 (BMNH 347.e, f); Amirante Islands, 2 (USNM 36049–50); Alphonse Island, 1 (USNM 36131); Providence Island, 1 (USNM 36051); Île d'Anjouan, 1 (USNM

36048); Madagascar, 2 (MNHN 1928-162, A-3037); 28°20'S, 60°E, 1 (UZMC *Prodelphinus* no. 15); South Africa, 5 (BMNH 1878.2.11.1, SAM 35515—not examined, data from Best 1969—, PEM 1520/84, 1517/68, 1520/85—not examined, data from Ross 1984); "Indian Ocean," 2 (RMNH cat. b no. 19, MNHN A-3029); Djibouti, 1 (MNHN 1981-185—not examined, data from Robineau and Rose 1984). Western Pacific: Indonesia, 4 (MNHN A-3028, 1882-113, 1882-305; USNM 49873); China, 2 (NJNU 7803-4—not examined, data from Zhou *et al.* 1980); Japan, 9 (BMNH 1966.6.14.1, TKO 102–4 and 4 unnumbered—not examined, data from Nishiwaki *et al.* 1965, unnumbered specimen in Ogawa 1936—not examined); Solomon Islands, 12 (BMNH 1966.11.18.2, 3, 5, 8; WHD 278, 289, 440, 444, 451, 452, 456, 459). Hawaii: 16 (15 listed in Perrin 1975, MNHN 1874-642). Alaska: 1 (USNM 550771). Eastern tropical Pacific (in addition to 132 listed in Perrin 1975 and 19 in Perrin *et al.* 1979): 12 km north of Mazatlan, Mexico, 1 (ZMA 16.204); 20°26'N, 106°32'W, 9 (SDMNH 23552-54, 235645-6; SWFC DJT 39, 40, 42, 46); 18°18'N, 103°50'W, 1 (SWFC TCB 36); 16°16'N, 98°52'W, 1 (UZMC *Galathea* CN 1); 11°44'N, 132°26'W (NMNS JOH 14); 9°39'N, 106°17'W, 2 (MNHN 1982-97, 99); 9°27'N, 109°44'W, 1 (NSM BGT 18); 9°00'N, 101°57'W, 4 (MNHN 1982-93, 94, 95, 96); 8°57'N, 102°05'W, 7 (MNHN 1982-84, 87, 88, 89, 90, 92, 117); 8°42'N, 105°20'W, 1 (SWFC AXB 23); 8°29'N, 140°48'W, 1 (LACM 72313); 8°18'N, 138°10'W, 1 (LACM 72312); 8°17'N, 138°33'W, 1 (LACM 72310); 8°16'N, 140°46'W, 1 (SWFC JWG 57); 8°15'N, 132°20'W, 1 (LACM 72314); 8°13'N, 98°32'W, 1 (TCWC TAL 4); 8°13'N, 135°20'W, 1 (NMNS VFC 32); 7°30'N, 130°58'W, 1 (LACM 72315); 7°18'N, 132°57'W, 1 (LACM 72316); 5°54'N, 129°40'W, 1 (LACM 72322); 4°55'N, 107°45'W, 1 (NMNS RMB 24); 4°40'N, 105°15'W, 1 (NMNS RMB 47); 2°55'N, 119°20'W, 1 (NMNS DAA 169); 2°53'S, 98°45'W, 2 (SWFC GCF 7, 10); 6°02'S, 85°46'W, 2 (NMNS SRM 45, 46); 8°48'S, 89°21'W, 1 (SWFC SFG 3); 8°53'S, 90°47'W, 6 (SDMNH 23571 and 23749, WSL 13, 14, 15, 17; SWFC WSL 18); 9°03'S, 84°28'W, 1 (SWFC SRM-A); 9°08'S, 90°34'W, 1 (SDMNH WSL 5); 9°12'S, 91°33'W, 1 (SDMNH 23751); 12°12'S, 83°17'W, 2 (LACM WFP 681, 682). Unknown localities: 2 (BMNH 347.B., ZMUB 12009–only photographs examined, other data from True 1889).

Previously unpublished locality records (in addition to those from specimens listed above; sources, when other than authors, listed in ACKNOWLEDGMENTS)—Florida, 1 (26°55'N, 80°05'W—JGM); Gulf of Mexico, 1 (23°00'N, 84°28'W); Caribbean, 8 (20°14'N, 84°35'W; 20°06'N, 84°29'W; 18°52'N, 74°50'W; 18°43'N, 74°42'W; 14°11'N, 61°W; 13°12'N, 61°27'W; near Grenada, 2 sightings); St. Helena (multiple sightings—WFP).

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Appendix 1

Museum and Collection Acronyms

AMNH, American Museum of Natural History, New York; ANSP, Academy of Natural Sciences of Philadelphia; BMNH, British Museum (Natural History), London; CM, Charleston Museum, Charleston, South Carolina; CMNH, Cleveland Museum of Natural History; FTI, Fayetteville Technical Institute, Fayetteville, North Carolina; IFAN, Institut Fondamental d'Afrique Noire, Dakar, Senegal; GM, Goteborg Museum; LACM, Los Angeles County Museum of Natural History; LIZ, Institute of Zoology, Leningrad; MACNBA, Museo Argentino de Ciencias Naturales, Buenos Aires; MCNRS, Museu de Ciências Naturais, Rio Grande do Sul, Brazil; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Masschusetts; MLF, Marineland of Florida, St. Augustine; MNHN, Muséum National d'Histoire Naturelle, Paris; MSU, McNeese State University, Lake Charles, Louisiana; NCSM, North Carolina State Museum, Raleigh; NJNU, Nanjing Normal University; NMNS, National Museum of Natural Sciences, Ottawa; NSM, National Science Museum, Tokyo; PANS, Philadelphia Academy of Natural Sciences, Pittsburgh; PEM, Port Elizabeth Museum, Port Elizabeth, South Africa; PML, Public Museum of Liverpool; RMNH, State Museum of Natural History, Leiden; RSMAS, Rosenstiel School of Marine and Atmospheric Science, University of Miami; SAM, South African Museum, Cape Town; SDMNH, San Diego Museum of Natural History; SWFC, Southwest Fisheries Center, La Jolla, California; TCWC, Texas Cooperative Wildlife Collection, Texas A & M University, College Station; TKO, Ocean Science Institute, University of Tokyo*; UBC, University of British Colombia, Vancouver; UF, Florida State Museum, University of Florida, Gainesville; USNM, U.S. National Museum of Natural History, Washington, D.C.; UZMC, Zoologisk Museum, Copenhagen; ZMA, Zoologisch Museum, University of Amsterdam; ZMB, Zoologisches Museum, Berlin; ZMUB, Zoologisk Museum, Universitetet i Bergen, Norway.

* All cetacean specimens now at National Science Museum, Tokyo.