Evidence for Two Species of Common Dolphins (Genus *Delphinus*) from the Eastern North Pacific

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ABSTRACT. Two forms of common dolphins occur sympatrically in the Southern California Bight: a long-beaked form and a short-beaked form. We re-examined the two forms based on 320 specimens, including only adults in morphometric analyses. Color pattern separates the two forms completely, as do total length and all measures of rostral length, both absolute and relative. Numerous additional features, such as vertebral count and tooth counts, show modal differences. Many of the differences in color pattern between the two forms seem to hold for other ocean basins, with some variation. Other workers have also found short- and long-beaked forms in these other regions. The levels of differences we see in this region of sympatry are equal to or greater than those for some other full species of small oceanic dolphins. Our data strongly suggest there is no gene flow between the two forms in this region of sympatry. Thus, we conclude that these two forms of common dolphins represent two distinct species. We review the nomenclature for *Delphinus* and provide re-descriptions of the two species. The short-beaked form is referable to *Delphinus delphis* Linnaeus. The long-beaked form in the eastern Pacific is the nominal species *Delphinus bairdii* Dall, 1873 for which we designate a neotype, although we note that this species is a junior synonym of *Delphinus capensis* Gray, 1828. Further work should resolve the degree of geographical variation for these two species and whether the nominal *D. tropicalis* is a valid species.

INTRODUCTION

Common dolphins of the genus *Delphinus* have a cosmopolitan distribution in tropical and temperate waters. Due to this wide distribution and because of geographical variation, there are more than two dozen nominal species (Hershkovitz, 1966). Most authorities (Hershkovitz, 1966; Mitchell, 1975; Hall, 1981) recognize only one highly variable species, *Delphinus delphis* Linnaeus, pending further research. However, others recognize a distinct long-beaked species in some regions, such as *D. capensis* Gray, 1828 from South Africa (Ellerman and Morrison-Scott, 1951) and *D. tropicalis* van Bree, 1971 from the Arabian to South China Seas (Honacki et al., 1982).

In the eastern North Pacific, Dall (1873) described the long-beaked species *D. bairdii* based on two female dolphins caught off Point Arguello, California. True (1889) found no consistent differences between the skulls of animals from the North Atlantic and North Pacific and thus considered *D. bairdii* to be synonymous with *D. delphis.* Subsequently, G. Miller (1936) of the U.S. National Museum re-evaluated the material on hand and concurred with Dall (1873) that the Pacific specimens had significantly longer rostra than the Atlantic specimens. Miller (1936) also noted that the specimens from the Pacific available to True (1889) had broken rostra. Banks and Brownell (1969) examined a larger series of specimens and recognized two forms of common dolphins from the northeastern Pacific based on the ratio of zygomatic width to rostrum length. They assigned the long-beaked form to *Delphinus bairdii* and the short-beaked form to *Delphinus delphis.* Using the same rostral ratio for common dolphin specimens from other geographical regions, van Bree and Purves (1972) found a bimodal but continuous distribution of ratios and suggested that the difference did not warrant the recognition of two species. Neither Banks and Brownell (1969) nor van Bree and Purves (1972) stratified their sample by age and sex to evaluate

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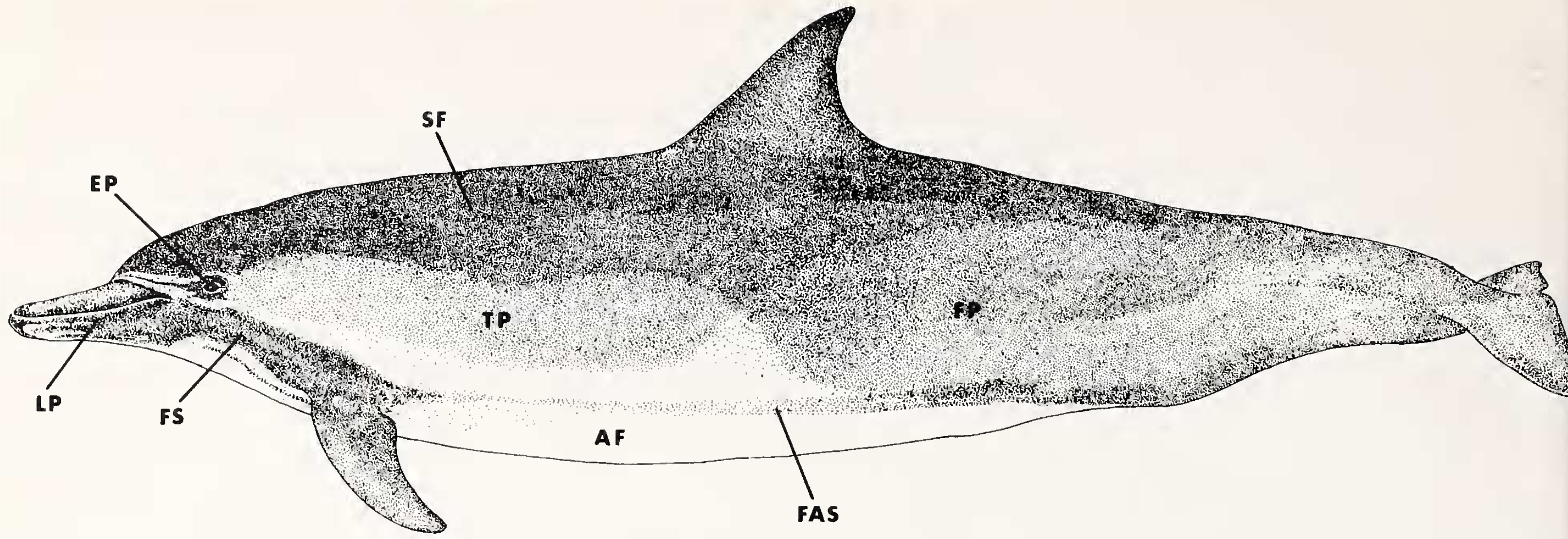

Figure 1. Color pattern terminology for common dolphins as used in text. Abbreviations are as follows; AF = abdominal field, EP = eye patch, FAS = flipper-to-anus stripe, FP = flank patch, FS = flipper stripe, LP = lip patch, SF = spinal field, TP = thoracic patch.

the effects of ontogenetic variation and sexual dimorphism on their results. The relative length of the rostrum to skull length and width is known to increase ontogenetically in other delphinids (Perrin, 1975). Evans (1975, 1982) described some additional differences between the two forms based on multivariate analysis of skull measurements and coloration but did not resolve the taxonomy. In the eastern North Pacific, the common name "Baja-neritic common dolphin" has been applied to the long-beaked form and "Northern temperate offshore common dolphin" to the short-beaked form (Perrin et al., 1985).

Previous morphological studies of species of small oceanic dolphins (Delphinidae) have documented sexual dimorphism and extensive geographical variation (Perrin, 1975, 1984; Perrin et al., 1981, 1985, 1987, 1989; Schnell et al., 1986). This variation in total length, external morphology, skeletal characters, and pigmentation has made it difficult to resolve the taxonomy of these widely distributed species.

We had access to relatively large and well-documented samples of the two nominal forms of *Delphinus* collected from a small geographical region, with nearly complete data on sex and age class. These specimens provided a unique opportunity to assess variation within and between the two forms independent of the effects of ontogenetic development, sexual dimorphism, and geographical variation.

In this paper, we address the following questions: What is the nature of the morphological variation of *Delphinus* in this region? How distinct are the two forms; do they suggest specific or subspecific differences? Can these differences resolve the taxonomy of the genus on a world-wide basis?

MATERIAL AND METHODS

We examined specimens obtained from the southern half of the Southern California Bight from 32°20′N to 34°03′N. This includes less than 300 km of coastline and the adjacent waters less than 50 nautical miles from shore.

The total sample comprised 320 specimens obtained from single strandings, live captures for public display, and animals killed incidental to fishing operations. The last category includes several large samples from single schools. All of the specimens examined in this study are housed in either the Natural History Museum of Los Angeles County, the Southwest Fisheries Science Center, or the San Diego Museum of Natural History. A list of specimens examined is provided in the appendix.

Color patterns of 128 specimens were determined from photographs or high-quality sketches that depict diagnostic features. Animals observed at sea were classified directly in the field or by photographs. The specimens were classified by JEH as having the "long-beak" or "short-beak" pattern; these are markedly distinct and are described below in the Results section. The assignments were made independent of other specimen data. For describing the color patterns (Fig. 1), we use the terminology of Mitchell (1970), Perrin (1972), and Evans (1975).

External measurements were taken for 214 specimens as recommended by Norris (1961), with eight additional measurements (Heyning, 1991). The measurements were collected over several decades by numerous observers. Histograms of all the measures were examined to check for data entry errors. Due to the potential variation in measuring methodologies or recording errors, a few obvious extralimital values (individual records well outside the bell-shaped distribution for that measure) were deleted.

Cranial measurements and meristics were taken for 310 skulls and postcranial measurements and meristics for 126 specimens as described by Perrin (1975), with the addition of the following: width of rostrum at ¾ length, tooth width (measured transversely at midlength of the left mandibular row, at the level of top of the alveolus), length of centrum of first lumbar vertebra, and position of last vertebra with facet for chevron. To eliminate error due to variation in measurement methods among observers, all skull data were taken by WFP and all postcranial data by JEH. When a few (less than 5) terminal vertebrae were missing, the number of missing vertebrae was estimated by comparison with an intact vertebral series. For one specimen for which the number of missing vertebrae were estimated, the missing vertebrae were subsequently located and the estimated number yielded the correct vertebral count. Vertebral and sternal ribs were paired to check for missing ribs. Thoracic vertebrae were defined as any vertebrae associated with ribs, including floating

Table 1. Orthogonally rotated factor loadings for first two factors for male and female cranial variation for common dolphins from southern California with variance explained by factor (VAR).

Measurement	Males		Females	
	Factor I	Factor II	Factor I	Factor II
Condlyobasal length	0.952	0.143	0.957	0.088
Rostral length	0.963	0.121	0.970	0.004
Rostral width				
At base	0.046	0.328	−0.159	0.478
At ¼ length	0.040	0.046	0.004	0.672
At ½ length	−0.013	0.089	−0.020	0.859
At ¾ length	0.030	0.154	0.087	0.764
Premaxillae width at ½ length	0.150	0.273	0.232	0.546
Tip of rostrum to external nares	0.952	0.123	0.973	0.020
Tip of rostrum to internal nares	0.954	0.125	0.968	0.043
Preorbital width	0.082	0.800	−0.039	0.749
Postorbital width	0.289	0.726	0.130	0.697
Zygomatic width	0.402	0.652	0.213	0.640
Width of external nares	0.177	0.456	0.188	−0.062
Greatest width of premaxillae	−0.017	0.790	0.066	0.239
Parietal width	0.308	0.295	0.300	0.219
Height of braincase	0.316	0.169	0.338	0.089
Length of braincase	0.363	0.240	0.526	0.416
Length of temporal fossa	0.461	0.035	0.334	0.145
Height of temporal fossa	0.559	0.020	0.402	0.069
Length of orbit	0.072	−0.112	0.212	0.236
Length of antorbital process	0.151	0.686	0.228	0.564
Width of internal nares	0.366	0.312	0.287	0.293
Length of upper tooth row	0.952	0.101	0.968	−0.008
Length of lower tooth row	0.939	0.152	0.944	0.075
Length of ramus	0.942	0.131	0.947	0.094
Height of ramus	0.770	0.327	0.755	0.267
VAR	8.243	3.619	8.160	4.628

ribs. Caudal vertebrae were defined as the terminal series in the column beginning with the first vertebra articulating with a chevron bone. Counts of the manus bones (carpals, metacarpals, and phalanges) were made only for those specimens for which the manus was intact (all bones connected by cartilage) or for which flipper x-rays were available.

Only adult skulls were included in the analysis of cranial measurements. The primary criterion of adulthood was physical maturity (fusion of all vertebral epiphyses to the centra). If data on physical maturity were not available, specimens were classified as adult if they were known to be both sexually mature (in the case of females, known pregnant or lactating or at least one corpus luteum present in either ovary; in the case of males, testis mass of at least 100 g, following Collet and Saint Girons, 1984; Hui, 1979) and "cranially mature" (exhibiting fusion between the premaxillae and maxillae at the tip of the rostrum; Dailey and Perrin, 1973). The criteria of both sexual and cranial maturity are good estimators of physical maturity for *Delphinus* (Perrin and Heyning, 1993). Only physically mature specimens were used in the analyses of postcranial measurements.

We used principal components analysis with subsequent orthogonal rotation of factors to summarize variation in 26 cranial measurements. The analyses were performed on correlation matrices for males and females separately, using the program Factor Analysis 4M in the BMDP statistical software package (Dixon, 1990), with tolerance limits for matrix inversion = 0.0010, gamma = 1, and the convergence criterion for rotation = 0.00001. Missing variables were estimated with linear regression of the variable in question on the other variables, using the BMDP program, Description and Estimation of Missing Data (Dixon, 1990), with F-to-enter limit = 4.00, missing variable limit per case = 4, eigen value lower limit = 0.001, ridge parameter = 1, method of computing covariance = allvalue, maximum number of iterations for maximum likelihood = 10, and convergence criterion for maximum likelihood = 0.01. The loading coefficients for the factor analysis are given in Table 1.

RESULTS

Adult specimens showed clear concordance in color pattern (Fig. 2), body length, and summarized cranial variation (Figs. 3, 4), sorting into two distinct clusters representing the long-beaked and short-beaked forms. Both forms exhibit sexual dimorphism in both body and skull measures. The two series of skulls are disjunct in rostral length and significantly different in proportionate length of the rostrum (Figs. 5, 6).

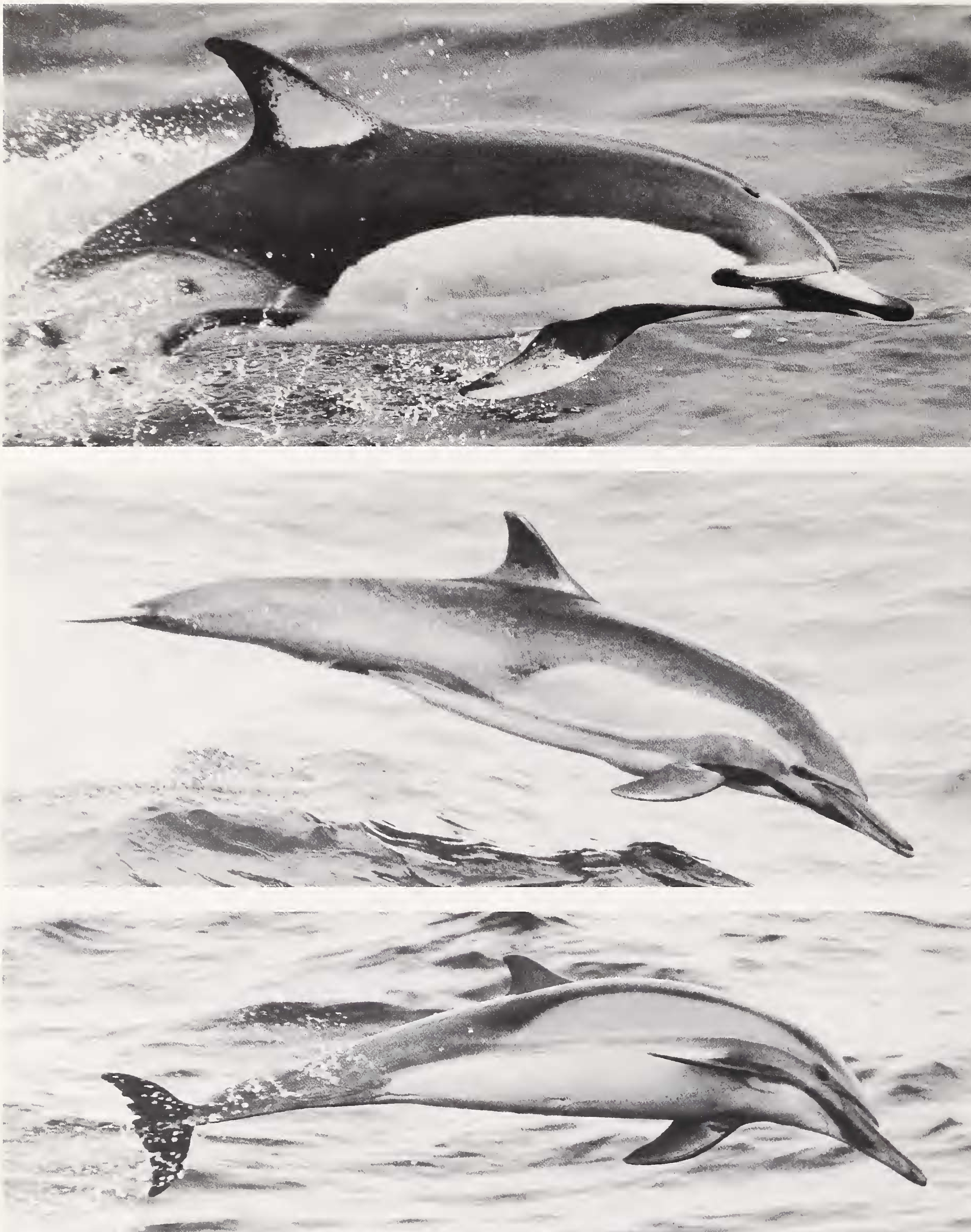

Figure 2. Typical color patterns observed in the field for short-beaked (top) and long-beaked (center, bottom) common dolphins from southern California (top: 9 August 1993, 37°10.4′N, 127°54.1′W, S. R. Benson; middle: 7 August 1993, 29°58′N, 113°32′W, T. Gerrodette; bottom: 13 August 1993, 29°13′N, 112°31′W, J. M. Cotton).

We here describe the color pattern, external morphology, and skeleton of the two forms in detail. Specimens not entered into the analysis depicted in Figures 3 and 4 (because they were juveniles or because data on body length and skull dimensions were missing or partial) were classified as long-beaked or short-beaked based on association with other, identified specimens from the same school

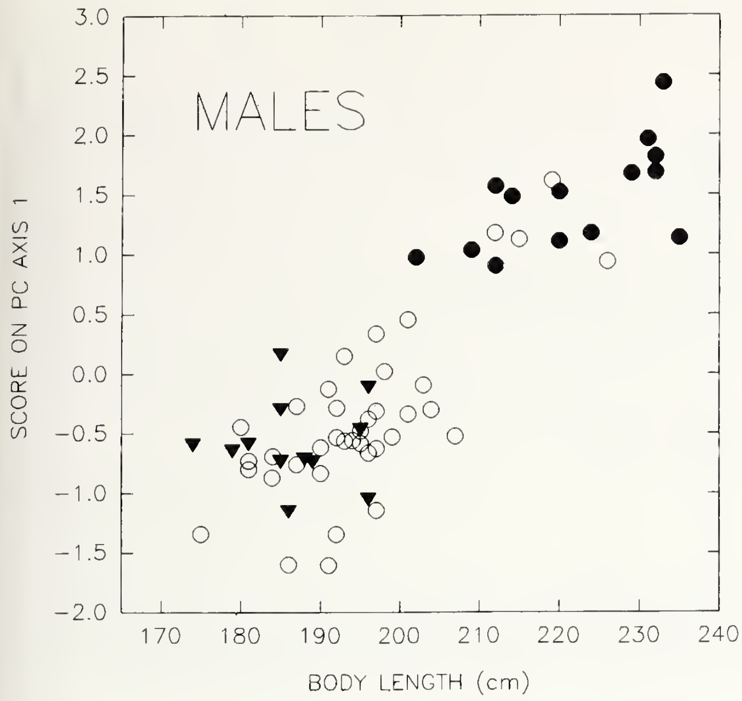

Figure 3. Scatter plot of principal component axis 1 of skull measurements vs. body length for male common dolphins. Symbols indicate color pattern: Triangles represent the short-beaked pattern; solid circles, the long-beaked pattern; and open circles, no color pattern available.

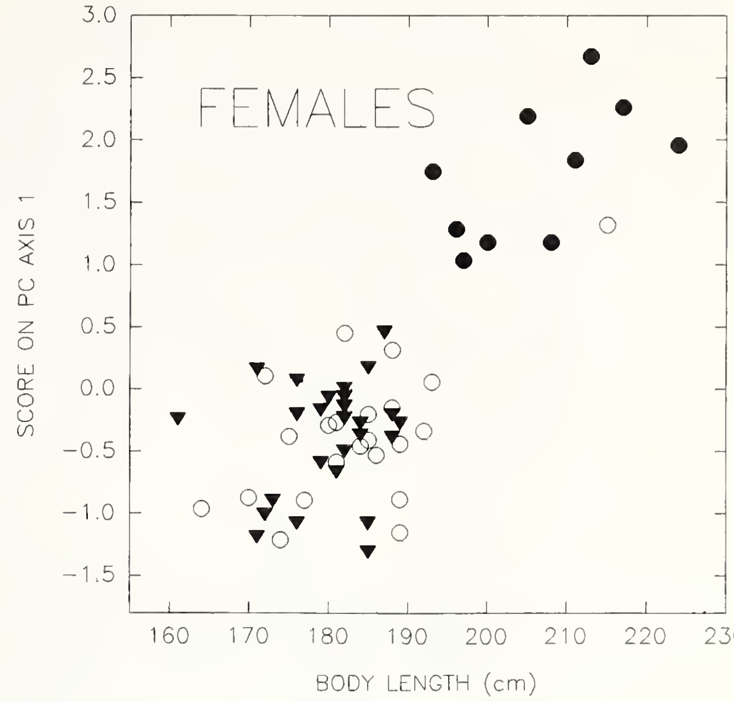

Figure 4. Scatter plot of principal component axis 1 of skull measurements vs. body length for female common dolphins. Symbols indicate color pattern: Triangles represent the short-beaked pattern; solid circles, the long-beaked pattern; and open circles, no available pattern.

or based on possession of characteristics (skull length, body length, color pattern) within the exclusive range of one or the other of the two forms.

COLOR PATTERN

Specimens could be categorized into two distinct groups based on the following diagnoses.

Group 1, Short-Beaked Form (Figs. 7, 9)

Thoracic patch relatively light in color, often with a golden-yellow hue, contrasting sharply with the very dark gray to black spinal field (= cape plus dorsal overlay of Perrin, 1972); flipper-to-anus stripe weakly formed or absent in most animals; flipper stripe does not approach corner of the gape, fusing with lip patch one-third to one-half of the gape length anterior to the corner of the mouth; flipper stripe narrowing distinctly anterior to the eye; eye patch very dark gray or black contrasting sharply with adjacent thoracic patch; white of abdominal field extending forward above the flipper stripe to at least under the eye; light gray to white patches with diffuse edges on dorsal fin and flippers of older adults.

Group 2, Long-Beaked Form (Figs. 8, 10)

Thoracic patch relatively darker, sometimes with a dull ocher hue, not contrasting as sharply with the dark gray spinal field as in the short-beaked form; flipper-to-anus stripe weakly to strongly formed; flipper stripe angling toward corner of mouth and fusing with lip patch at corner of gape to one-third anterior along gape; flipper stripe narrowing moderately anterior to eye; eye patch not contrasting strongly with adjacent thoracic patch; white of abdominal field rarely extending above flipper stripe to eye; rarely only a very slight lightening of the dorsal fin and flippers of some adults.

Specimens that were not calves (over 150 cm) were easily categorized into these two groups based on the above criteria. Although one or more character states may not clearly distinguish between the two forms for every individual, the overall suite of characters made identification relatively easy.

EXTERNAL MORPHOLOGY

External measurements were available for 90 sexually mature specimens. Total length was sexually dimorphic and differed significantly between the long- and short-beaked forms in the study area (Table 2). In both forms, males averaged 5% longer than females. In the short-beaked form, sexually mature males ranged from 172 to 201 cm, whereas sexually mature females ranged from 164 to 193 cm. In the long-beaked form, sexually mature males ranged from 202 to 235 cm, and sexually mature females from 193 to 224 cm.

Due to the size difference, most measures were larger for the long-beaked form. Some exceptions are noteworthy. The means for two of the head width measures (head diameter and rostral width at melon apex) were either equal or the short-beaked form was actually slightly wider in this dimension than the long-beaked form in both sexes (Table 2). This is in spite of the fact that the long-beaked form was larger and the length measures including the beak, such as tip of upper jaw to melon apex, exhibited no overlap between the two forms. Thus,

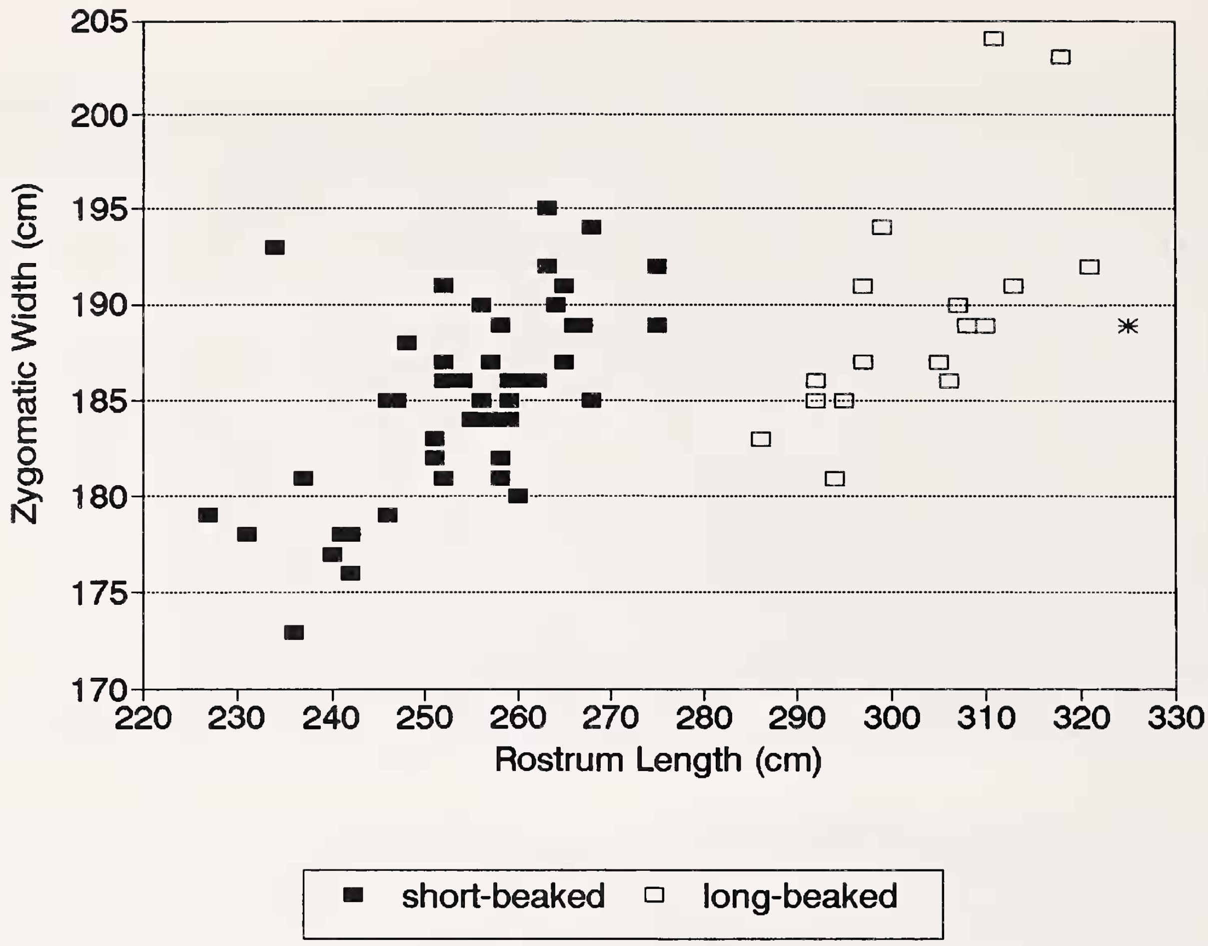

Figure 5. Zygomatic width vs. length of rostrum for adult male common dolphins from southern California. Filled squares represent the short-beaked form; open squares, the long-beaked form; and *, the type specimen of *Delphinus capensis.*

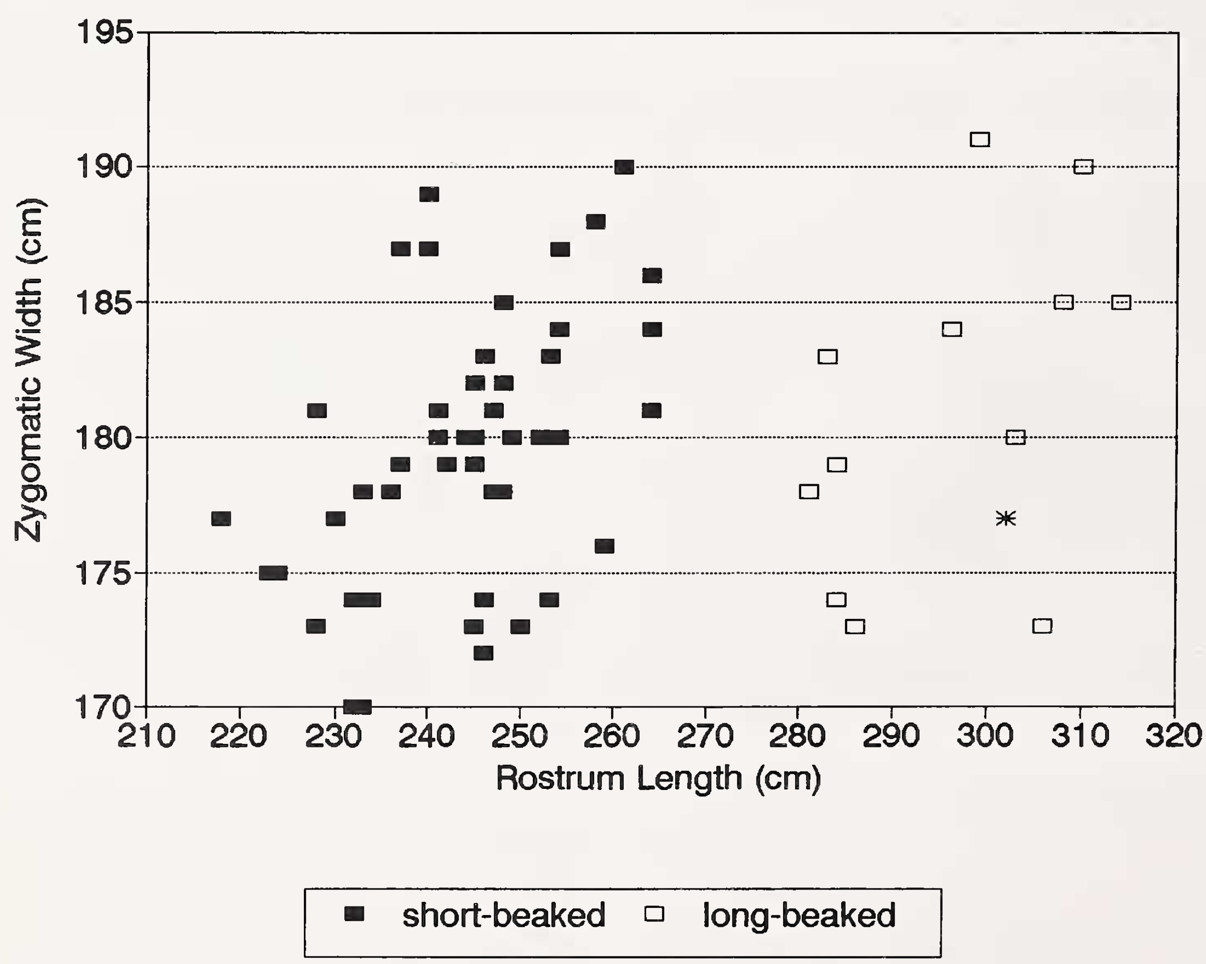

Figure 6. Zygomatic width vs. length of rostrum for adult female common dolphins from southern California. Filled squares represent the short-beaked form; open squares, the long-beaked form; and *, the type specimen of *Delphinus bairdii* based on measurements from the literature.

the head in the long-beaked form was absolutely longer but relatively narrower than in the short-beaked form. The relatively shorter but broader head in the short-beaked form gives the melon a more round, full appearance in profile (Figs. 9, 10). Also, the insertion of the melon onto the beak is at a more acute angle in the short-beaked form (Figs. 9, 10).

In addition, although the sample sizes are small, girth at eye was about equal for the two forms in both sexes, but axillary girth is slightly greater for the long-beaked form; the difference increases at the level of maximum girth. Thus, the short-beaked form tended to be relatively stouter anteriorly than the long-beaked form, giving the short-beaked form a more deep-bodied appearance.

Body mass data suggest that the short-beaked form was heavier for a given body length than the long-beaked form (Fig. 11). Although some masses for stranded animals are biased by emaciation, we know no reason for this to be biased more so for one or the other form. When only fisheries-killed animals are included, the trends appear the same; however, the sample size of adult long-beaked animals is small (n = 4).

Several measures were analyzed as a percentage of total length to account for size differences (Table 3). The length of the flipper and height of the dorsal fin tend to be relatively greater in the short-beaked form, whereas the flukes are relatively equal in size. The dorsal fin also tends to be sexually dimorphic, being larger in adult males than females. The snout-to-melon apex measure is significantly longer in the long-beaked form, with some overlap of this relative measure in males of the two forms.

SKELETAL CHARACTERS

Cranium

Length of the skull was sexually dimorphic, with males of both forms having significantly larger skulls than females (Table 4). The skulls of long-beaked animals were larger than those of short-beaked animals; there was no overlap in our sample. All measures that include the length of the rostrum showed no overlap between the two forms (length of rostrum, tip of rostrum to external nares, tip of rostrum to internal nares). When rostrum length vs. zygomatic width is plotted, two discrete clusters representing the two forms are represented (Figs. 5, 6). The mean length of the braincase differed only slightly between the two forms; the range of long-beaked specimens fell almost entirely within the range of short-beaked specimens for this variable. The means of the rostral width measures for the two forms were almost identical, although males were larger in this dimension than females in both forms.

The means of the cranial width measures (preorbital width, postorbital width, zygomatic width, parietal width) differed less than 5 mm between the two forms. Within sexes, the lengths of the orbits and the length of the antorbital processes were virtually identical in the two forms.

There was no overlap in the length of the upper tooth row and little overlap for the lower tooth row between the two forms. There was almost no overlap in the measures of ramus length. The teeth were also significantly wider in the long-beaked form.

The tooth counts were not sexually dimorphic. There were significantly more teeth in the long-beaked form (Table 5, Figs. 12, 13).

Postcranial Characters

Sixty-one specimens were physically mature and included in our analysis of postcranial morphometric data. Meristic data were analyzed for 105 specimens (Tables 6, 7).

Total vertebral count was bimodally distributed (Fig. 14); this was due to a slightly higher number of caudal and thoracic vertebrae in the long-beaked form. Vertebral characteristics such as the positions of the first vertical foramen, last transverse process, last neural arch, last facet for a chevron, widest vertebra, and first chevron tended to be more posteriorly located along the vertebral column in the long-beaked form. There was no difference observed in any meristic variables associated with the flippers.

Within each sex, the means for all measures of the postcranial skeleton were greater in the long-beaked form. The two forms overlapped in all measurements when both sexes were considered, but the overlap was slight in the height of the first lumbar vertebra, length of longest rib, manubrium width, and both measures of the scapula. In both forms, mean length of the pelvic bone was about 20 mm greater in males than the females.

SIGHTINGS

Identification of the two forms at sea, based on pigmentation differences, is possible at close range (Leatherwood et al., 1988). We have never observed mixed schools of the two forms in southern California waters. One of us (JEH) has seen on several occasions distinct schools of the two forms within a few kilometers of each other on the same day. Evans (1975) also observed no mixed schools. In a recent survey of Californian waters, only four of the 170 sightings of common dolphins assignable to form were thought to be mixed schools of long- and short-beaked animals (Hill and Barlow, 1992). Size of schools for both forms can range from less than 10 to several thousand individuals in the study area. Hill and Barlow (1992) reported an average group size of 183.8 for the long-beaked form and 97.9 for the short-beaked form in the waters off California.

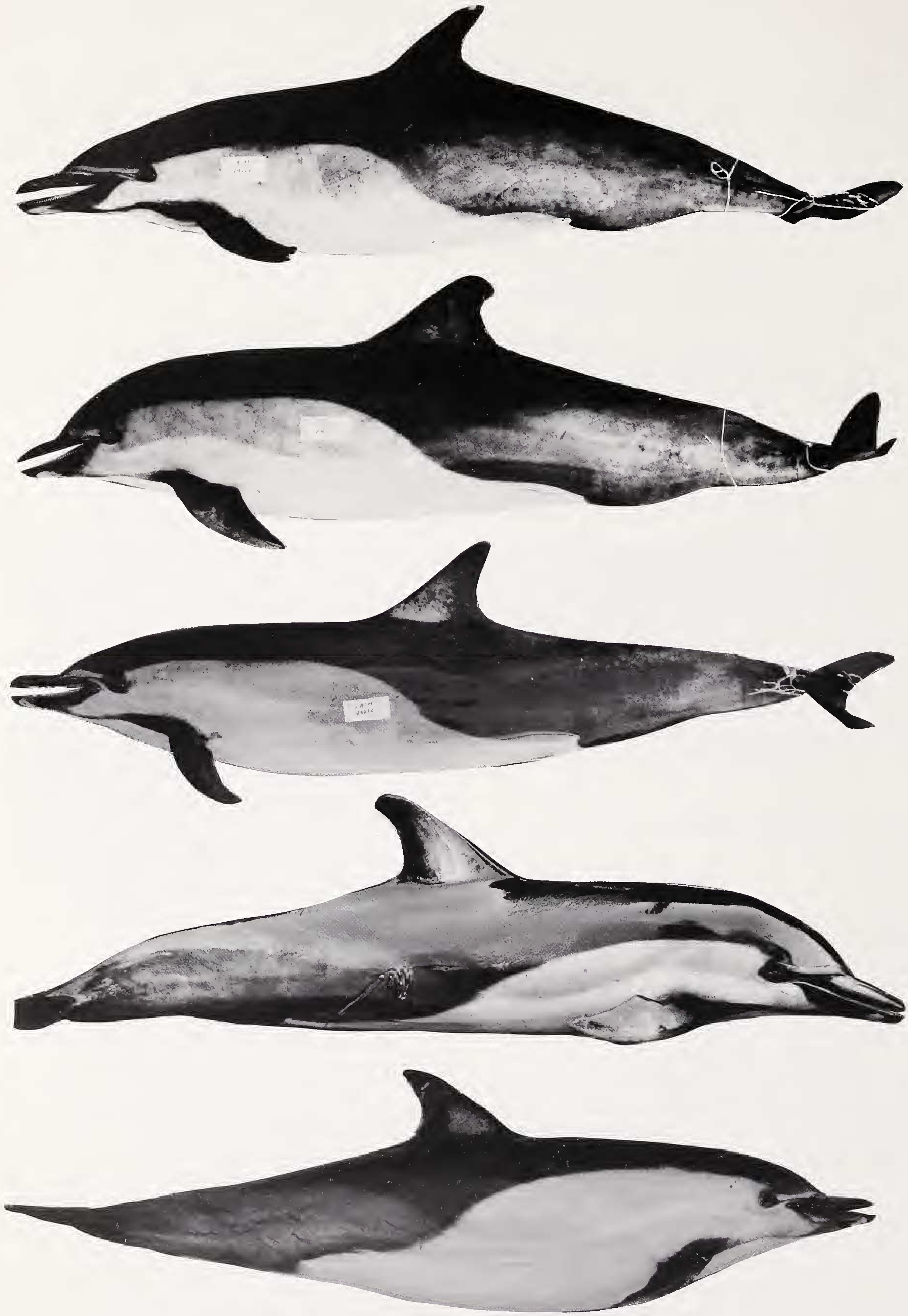

Figure 7. Representative color patterns for adult short-beaked common dolphins from southern California waters to demonstrate individual variation (from top to bottom: LACM 84227, male, 190 cm; LACM 84225, male, 188 cm; LACM 84222, female, 198 cm; LACM 72288, female, 171 cm; LACM 72334, female, 184 cm).

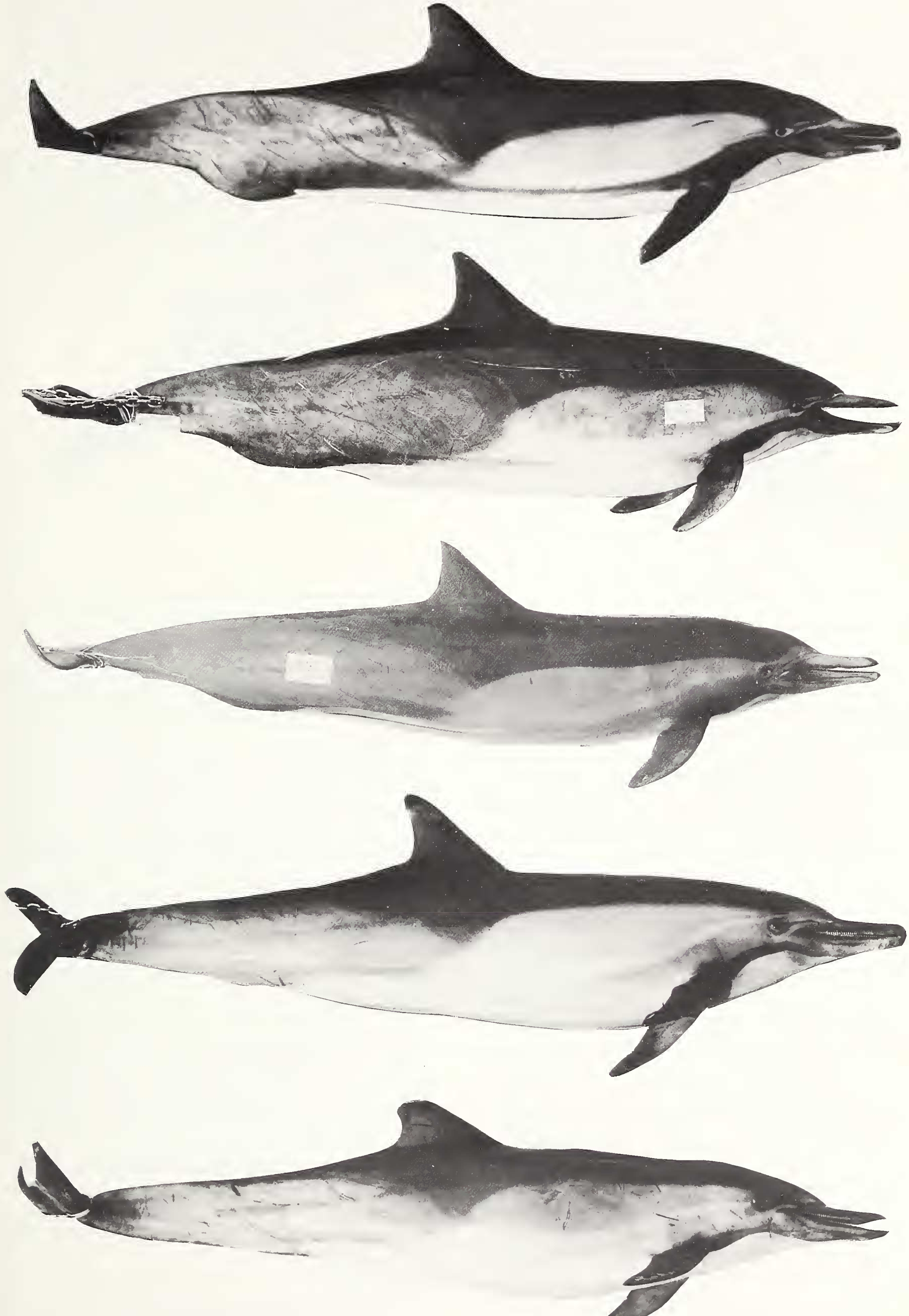

Figure 8. Representative color patterns of long-beaked common dolphins from southern California waters to demonstrate individual variation (from top to bottom: LACM 84240, male, 235 cm; LACM 84220, male, 212 cm; LACM 84254, male, 229 cm; LACM 84021, female, 211 cm; LACM 84223, female, 196 cm). Top specimen is the neotype of *D. bairdii.*

Figure 9. Detail of typical short-beaked color pattern (LACM 84257, female, 187 cm). Note position of flipper stripe and where it meets with lip patch.

DISCUSSION

COLOR PATTERN

The color pattern of common dolphins is among the most complex of any cetacean (Mitchell, 1970) and is extremely variable. This individual variation has limited the use of coloration as a taxonomic tool (Fischer, 1881; True, 1889; Evans, 1975). In the eastern North Pacific, the difference between the two forms in the position of the anterior end of the flipper stripe was first described by Evans (1975). However, he did not note any other coloration differences between the two forms.

The general differences we found for long- and short-beaked common dolphins off California seem to apply fairly well to common dolphins found in other ocean basins. The general pattern of the short-beaked form can be seen in animals from the western North Atlantic off Florida and Virginia (Leatherwood et al., 1976, figs. 130, 133 top) and off Nova Scotia and Newfoundland (Mitchell, 1970, fig. 1, listed as *Delphinus delphis*). Specimens with the short-beaked color pattern are found in the Southwest Pacific off New Zealand (Baker, 1983:112; Robson, 1976:14, 41, 45). Published photographs of specimens from the western Mediterranean (Gihr and Pilleri, 1969) exhibit the short-beaked color pattern. The general pattern of the long-beaked form can be found in the Equatorial Atlantic off the coasts of Venezuela and Senegal (Mitchell, 1970, fig. 3, listed as *Delphinus* sp.).

Along the west coast of Africa, the animals appear to vary somewhat in pigmentation, but specimens similar to our short-beaked form (Cadenat, 1959, figs. 9, 13–15) and other specimens more like our long-beaked form (Cadenat, 1959, figs. 1, 4, 7) have been collected. Okada and Hanaoka (1938) published photographs of specimens exhibiting the long-beaked color pattern (Pl. XXI, fig. 1) and the short-beaked pattern (Pl. XXI, fig. 2) from Japanese waters. These regions could be similar to southern California in that the two forms may occur sympatrically.

The *bairdii*-type coloration pattern may be typical of the long-beaked form found near the Cape of Good Hope, based on illustrations in Smithers (1983:320) and Ross (1984, fig. 23). This region is the locality of the type specimen of *Delphinus capensis*. The type specimen of *D. capensis* was illustrated by Gray (1828) and True (1889). However, either the specimen had lost all its coloration or the color pattern was not illustrated, making it impossible to attribute a coloration type to that specimen.

The color pattern of the short-beaked form can be more complicated, especially on animals from the North Atlantic, by the addition of numerous abdominal stripes between the flipper stripe and the thoracic patch (e.g., Mitchell, 1970, fig. 1 top). Evans (1975) noted that the flank blaze within the flank patch described by Mitchell (1970) in North Atlantic short-beaked common dolphins was absent in all specimens examined from the North Pacific. Thus, some geographical variation within each form is undoubtedly present.

Light gray to white patches were found on the dorsal fins and flippers of many specimens in our sample. These were more often present and more pronounced on the short-beaked form. However, these features demonstrated a high degree of individual variation and seem to increase in contrast with age as young animals lack distinct patches.

Figure 10. Detail of typical long-beaked color pattern (LACM 84254, male, 229 cm). Note the position of the flipper stripe in contrast with the short-beaked form in Figure 9.

Thus, these characters cannot be used to differentiate the two forms with any degree of accuracy.

Evans (1975) noted that the coloration of the long-beaked nominal species from the northern Indian Ocean, *Delphinus tropicalis,* was similar to that of the long-beaked form in the eastern North Pacific. The two papers Evans cited (van Bree, 1971a; Pilleri and Gihr, 1972a) both lack photographs or text regarding coloration of *D. tropicalis,* but another paper (van Bree, 1971b) does contain an illustration of one specimen. This illustration is an oblique view of an animal with a flipper stripe that fuses with the lip patch near the posterior end of the gape. Pilleri and Gihr (1972b) provided photographs of a specimen, darkened by the sun, but with a very similar color pattern. These patterns are similar to that found on long-beaked specimens from the eastern North Pacific and almost identical to photographs of long-beaked animals from the west coast of Africa (e.g., Cadenat, 1959, fig. 1).

EXTERNAL MORPHOLOGY

In the study area, the short-beaked form is significantly smaller than the long-beaked form. In the offshore waters of the eastern tropical Pacific, only the short-beaked form exists based on analysis of skull types and pigmentation (Evans, 1975, 1982). In this region the offshore short-beaked form is significantly larger than the short-beaked specimens found off southern California; males average 207 cm and females 194 cm (Perrin et al., 1985). Thus, the short-beaked form in the eastern tropical Pacific is intermediate in length between the short- and long-beaked forms off California. In the North Atlantic, males reach at least 223 cm (Mitchell, 1970). Thus, the short-beaked common dolphins from these regions are slightly larger than the short-beaked form from Californian waters (Table 2). In the Black Sea, the average length for sexually mature short-beaked males is 178 cm (n = 890) and for females 170 cm (n = 1,809) (Perrin and Reilly, 1984).

Two conclusions can be drawn from these data. One is that in the area of sympatry off California, the short-beaked form is smaller than in other regions of the eastern Pacific, perhaps due to character displacement. The second point is that although size is a useful criterion for distinguishing most adult specimens of the two forms off California, this difference does not hold for other regions.

The maximum length for common dolphins with relatively long beaks from South African waters is 254 cm for males and 222 cm for females (Ross, 1984).

Many of the modal differences we found in external morphology probably show a greater degree of overlap than is actually present, because of interobserver differences. These data were collected over a period of 25 years by numerous observers using slightly different methods.

SKELETAL MORPHOLOGY

Our study corroborates previous works (Banks and Brownell, 1969; Evans, 1975, 1982) that indicated

Table 2. Means, standard deviations (for sample sizes > 24), samples sizes (in parentheses), and minimum and maximum values for external measures for adult specimens of the two forms of common dolphins from California. Snout (= beak) measures are taken from the tip of the upper jaw.

	Males		Females	
	Short-beaked	Long-beaked	Short-beaked	Long-beaked
Total length	189.5 ± 7.37	219.1	180.1 ± 6.5	207.7
	(28) 172–201	(15) 202–235	(37) 164–193	(10) 193–224
Snout to anus	137.7	158.3	130.3 ± 4.3	145.0
	(20) 127–148	(12) 148–174	(27) 120–138	(6) 139–151
Snout to genital slit	121.0	138.8	123.7 ± 4.4	138.0
	(23) 109–128	(12) 129–151	(26) 116–133	(6) 132–145
Snout to umbilicus	89.3	103.1	86.3	95.5
	(18) 83–95	(10) 100–109	(24) 80–90	(4) 94–98
Snout to dorsal fin tip	114.4	125.5	106.9 ± 4.0	122.9
	(18) 105–126	(12) 119–137	(27) 98–115	(7) 113–133
Snout to anterior dorsal fin	84.7	95.3	82.6	94.3
	(7) 80–91	(12) 88–100	(18) 76–86	(7) 88–101
Snout to flipper	44.6	49.3	41.9 ± 2.1	47.5
	(17) 41–49	(10) 47–52	(28) 38–46	(6) 45–50
Snout to ear	35.9	38.6	34.2	38.9
	(15) 32.5–40.0	(9) 37.0–41.	(22) 31.5–37.2	(7) 36.5–43.0
Snout to eye	30.8	34.4	29.3 ± 1.6	33.6
	(20) 27.3–34.3	(12) 31.0–38.0	(33) 26.5–32.7	(7) 31.0–37.0
Snout to gape	26.1	29.1	24.8 ± 1.3	28.4
	(24) 21.7–28.0	(12) 27.0–32.0	(33) 22.0–27.5	(7) 27.0–31.0
Snout to blowhole	31.4	34.8	30.4 ± 1.8	34.7
	(19) 27.7–34.2	(13) 31.1–40.0	(34) 26.4–33.8	(8) 32.5–38.4
Snout to melon apex	12.3 ± 0.89	15.7	11.6 ± 0.7	15.4
	(25) 10.5–14.0	(14) 14.0–17.5	(26) 10.5–13.0	(8) 13.3–17.0
Eye to ear	5.3	5.6	5.2	5.6
	(20) 3.3–8.0	(9) 5.0–6.5	(21) 4.6–6.2	(6) 5.0–6.1
Eye to gape	5.8	6.4	5.8 ± 0.4	5.8
	(20) 4.6–6.6	(12) 5.5–7.0	(25) 4.7–7.0	(7) 4.5–6.9
Right eye to blowhole	18.3	17.4	17.1	16.3
	(2) 18.0–18.5	(7) 16.0–18.5	(10) 16.3–18.5	(5) 16.0–16.5
Left eye to blowhole	14.3	16.2	14.6	15.0
	(15) 10.7–18.0	(9) 15.0–17.5	(19) 13.2–16.0	(7) 14.0–16.0
Blowhole length	1.2	1.3	1.1	1.1
	(11) 0.9–1.5	(12) 1.0–2.0	(21) 0.8–1.5	(8) 0.8–1.3
Blowhole width	2.4	2.5	2.1	2.4
	(13) 1.6–3.0	(12) 2.0–3.0	(21) 1.7–2.9	(8) 1.9–2.8
Head diameter at eyes	20.1	20.1	19.9 ± 1.5	18.9
	(12) 19.0–21.1	(11) 19.0–22.5	(26) 17.2–22.8	(7) 18.0–19.5
Rostral width at melon apex	7.4	7.2	7.9	6.5
	(11) 6.1–8.4	(13) 6.2–8.0	(19) 6.0–11.0	(8) 6.0–7.4
Projection of lower jaw	0.4	0.7	0.4	0.6
	(11) 0.2–0.5	(11) 0.3–1.5	(16) 0.2–1.0	(4) 0.5–1.0
Flipper length, anterior	30.0	31.1	27.1 ± 2.1	29.7
	(22) 25.4–34.3	(12) 28.9–33.0	(27) 24.0–31.0	(8) 28.4–32.0
Flipper length, posterior	21.2	22.7	19.5 ± 1.8	20.4
	(22) 17.2–24.6	(12) 18.9–25.0	(27) 16.2–23.0	(8) 18.0–23.0
Flipper width	9.9	10.2	8.8 ± 0.8	9.7
	(21) 8.5–11.3	(12) 8.8–12.2	(25) 7.1–11.0	(8) 9.0–10.7
Length of genital slit	9.6	9.3	12.1	11.5
	(11) 5.9–12.3	(11) 6.6–12.5	(11) 9.5–16.6	(8) 8.0–13.0
Fluke width	42.9	47.9	38.5 ± 3.9	42.4
	(22) 29.9–52.3	(11) 40.0–58.0	(25) 29.0–46.0	(7) 38.0–49.0
Fluke depth at lobe	(1) 12.5	14.7	12.3	13.1
	12.5	(7) 13.3–16.5	(4) 11.5–13.0	(4) 12.0–14.0

Table 2. Continued.

	Males		Females	
	Short-beaked	Long-beaked	Short-beaked	Long-beaked
Fluke depth at notch	12.0	13.0	11.4	11.7
	(21) 9.9–14.0	(10) 12.0–14.5	(24) 9.6–13.0	(7) 10.5–13.0
Fluke notch depth	2.4	2.4	2.3 ± 0.6	2.5
	(18) 1.8–3.5	(11) 1.5–3.0	(25) 1.0–3.0	(7) 1.5–3.0
Dorsal fin height	20.1	19.9	16.6 ± 1.4	17.4
	(22) 17.0–26.1	(12) 17.0–24.5	(25) 14.0–19.0	(8) 13.0–21.1
Dorsal fin base length	30.1	32.7	27.1	33.0
	(8) 24.9–33.0	(10) 30.0–36.0	(10) 19.0–32.0	(8) 27.0–41.1
Girth at eye	70.5	68.6	67.8	67.7
	(2) 68–73	(8) 66–73	(6) 66–71	(6) 65–70
Girth at axilla	97.5	100.1	91.7 ± 6.1	95.4
	(23) 88–111	(10) 87–110	(26) 73–101	(8) 83–103
Girth, maximum	101.4	112.4	99.2	106.6
	(7) 96–108	(10) 93–133	(15) 86–111	(7) 87–116
Girth at anus	63.1	66.9	54.5 ± 4.5	55.9
	(21) 49–73	(11) 54–80	(26) 47–66	(7) 50–65
Girth midway anus–fluke notch	32.5	34.8	29.6	31.0
	(2) 32–33	(8) 31–38	(5) 28–32	(4) 29–34
Caudal height	15	15.6	13.6	15.8
	(2) 15.0	(8) 14–17	(5) 13–14	(4) 14–19
Caudal thickness	(1) 3.5	(1) 4.9	3.0	4.4
	3.5	4.9	(4) 3–5	(5) 3–6

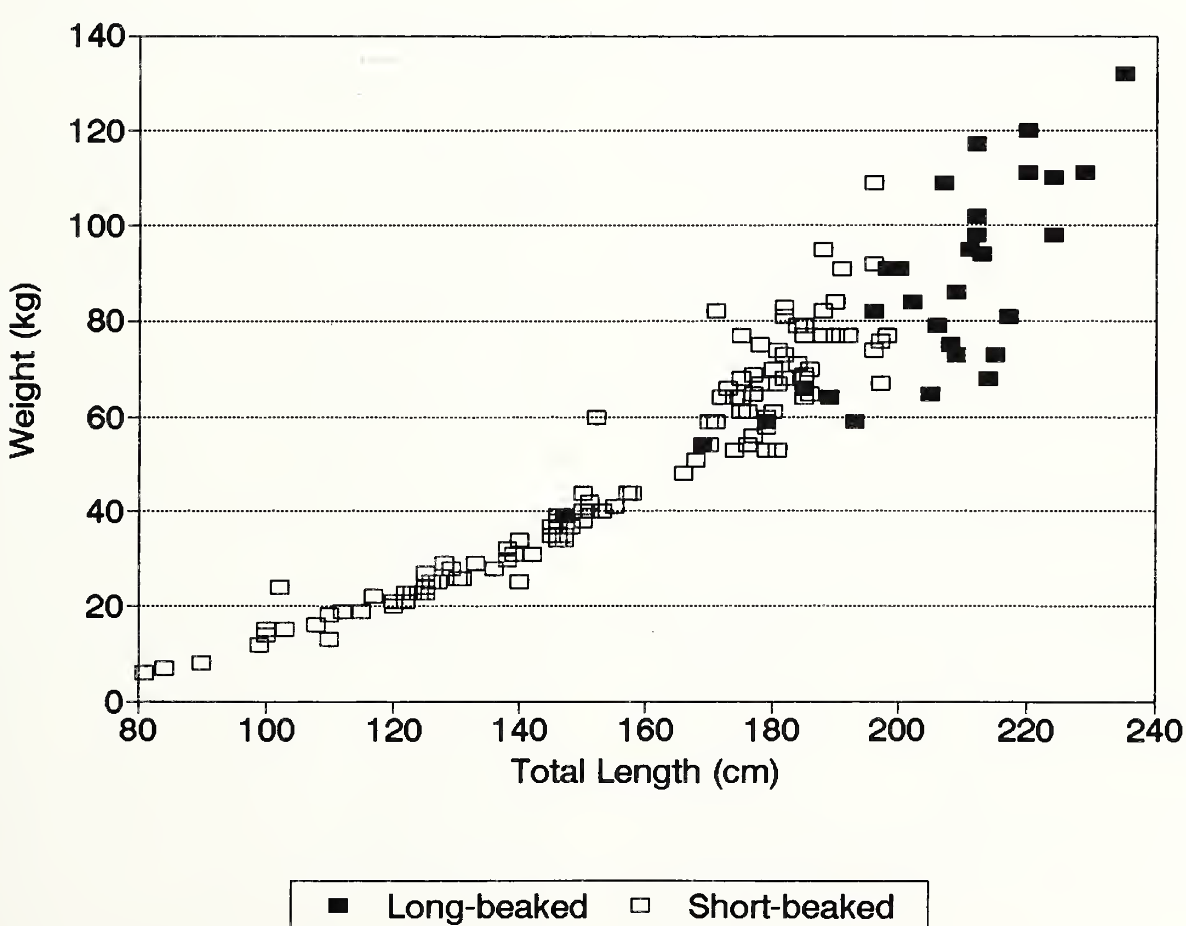

Figure 11. Plot of length and mass data for the two forms of common dolphins off California. Note that for the same body length the short-beaked form tends to be heavier. Open squares represent short-beaked specimens, and filled squares long-beaked specimens.

Table 3. Means, standard deviations (for sample sizes > 20), samples sizes (in parentheses), and minimum and maximum values for selected external measures as percentage of total length for adult specimens of the two forms of common dolphins from California.

	Short-beaked	Long-beaked
Flipper length anterior		
Males	15.8 ± 1.1	14.1
	(24) 13.8–17.4	(12) 13.5–15.1
Females	15.0 ± 1.2	14.4
	(26) 13.3–17.1	(8) 13.9–15.5
Dorsal fin height		
Males	10.2 ± 2.3	9.0
	(24) 8.7–13.6	(12) 7.3–10.4
Females	9.3 ± 0.8	8.4
	(24) 7.6–10.6	(8) 6.0–9.5
Fluke width		
Males	22.9 ± 2.0	21.7
	(22) 17.8–26.5	(11) 18.4–24.7
Females	21.2 ± 2.0	20.5
	(25) 17.6–24.7	(7) 19.0–23.2
Snout to melon apex		
Males	6.4 ± 0.4	7.2
	(27) 5.5–7.1	(14) 6.2–8.0
Females	6.4 ± 0.4	7.6
	(25) 5.6–7.3	(7) 7.3–8.1

that there are two forms of common dolphins in the eastern North Pacific separated completely by rostral length. To take into account size differences, Banks and Brownell (1969) used the ratio of rostral length to zygomatic width to distinguish the two forms. They found that specimens with a ratio above 1.55 could be assigned to *D. bairdii* and below 1.53 to *D. delphis*.

In their response to Banks and Brownell's (1969) study, van Bree and Purves (1972) noted that they found some specimens with intermediate ratios of rostral length to zygomatic width when sampling common dolphins from other ocean basins. However, neither of these two studies separated specimens by sex, nor did they include only mature specimens. This confounded sexual dimorphism, ontogenetic variation, and geographical variation with potential subspecific or specific level differences. Evans (1982) re-plotted rostral length on zygomatic width, incorporating only sexually mature animals, and obtained more discrete clusters than did Banks and Brownell (1969).

We plotted rostrum length on zygomatic width (Figs. 5, 6) using only mature specimens stratified by sex and found that the differences are not just size related; they represent a true shape difference in the skulls of these two forms. We found that adult specimens from California waters were separated by a gap between 1.47 and 1.52 for this ratio (Table 8).

Skull measurements are available for specimens of *Delphinus* sp. from South Africa (Ross, 1984), the type locality of *D. capensis.* We re-analyzed the ratio of rostrum length to zygomatic width, including only specimens considered to be mature based on either age (over 8 growth layer groups; Ross, 1984, table 90) or known reproductive status (Ross op. cit., tables 92, 93). Adult specimens from this region have an average ratio of 1.68 (n = 12) with a range of values from 1.59 to 1.76. These numbers do not include one specimen lacking maturity data with an extremely long beak that has a ratio of 1.87. Based on this small sample, common dolphins from the waters off South Africa have beaks that are modally longer than in the long-beaked form off southern California, with considerable overlap in the range of values. These values are even more distinct from those of the short-beaked form off California.

The ratio of rostrum length to zygomatic width for 10 specimens of *D. tropicalis,* excluding two immature skulls, ranges from 1.89 to 2.22 (Pilleri and Gihr, 1973–1974; van Bree and Gallagher, 1978; Mohan, 1985). One specimen from off the Arabian Peninsula with a ratio of 1.72 was considered to represent a specimen of *D. delphis* by van Bree and Gallagher (1978). This value is well out of the range of the short-beaked form from other regions and within the range of values for the long-beaked form from either California or South Africa. Thus, we believe this specimen does not belong to the short-beaked *D. delphis* form, but with the long-beaked *D. capensis* form (see discussion under Taxonomy). In this same paper, van Bree and Gallagher (1978) presented data from a long-beaked specimen from Taiwan with a rostral ratio of 1.75. Kasuya (1973) noted another specimen from Taiwan with a *bairdii*-type rostral length.

Based on the data in Ross (1984), the long-beaked common dolphins from South Africa have an average upper tooth count of 52 (n = 17) with a range of 47--60 and an average lower tooth count of 51 (n = 13) with a range of 47–57. These values are almost identical to the tooth counts for the long-beaked form from California (Table 7). Tooth counts for 11 *D. tropicalis* were 57–69/54–64 (van Bree and Gallagher, 1978; Mohan, 1985). These values overlap somewhat with the tooth counts for the long-beaked form from South Africa and California. These counts do not include the specimen from the Indian Ocean with a rostral ratio of 1.72. This specimen has upper tooth counts of 57 and 56, within the region of overlap between *D. tropicalis* and the long-beaked form.

Perrin et al. (1987) found that vertebral counts were one of two diagnostic characters useful for distinguishing between two species of spotted dolphins in the Atlantic. In the California sample, we found strong modal differences in several vertebral meristics, but no separation. Thus, some specimens cannot be assigned to a particular form or species based on univariate postcranial characters only. Off South Africa, the range of vertebral formulas in the

Table 4. Means, standard deviations (for sample sizes > 30), samples sizes (in parentheses), and minimum and maximum values for skull measurements for adult specimens of the two forms of common dolphins from the coast of southern California.

	Males		Females	
	Short-beaked	Long-beaked	Short-beaked	Long-beaked
Condylobasal length	421.5 ± 13.04 (48) 392–445	473.6 (19) 446–498	406.3 ± 14.06 (49) 382–442	465.5 (12) 445–486
Rostral length	254.4 ± 10.97 (48) 227–275	302.0 (19) 286–321	244.0 ± 10.99 (49) 218–264	296.2 (12) 281–314
Rostral width				
At base	86.9 ± 4.03 (50) 78–98	85.9 (19) 77–93	84.9 ± 4.10 (51) 73–93	82.7 (13) 78–88
At ¼ length	57.6 ± 2.87 (48) 52–63	57.4 (19) 53–61	55.7 ± 2.59 (49) 49–63	55.3 (12) 52–58
At ½ length	51.3 ± 2.55 (48) 45–57	50.9 (19) 46–55	48.7 ± 2.06 (49) 43–55	48.3 (12) 46–51
At ¾ length	38.1 ± 2.65 (48) 33–44	38.0 (19) 33–47	35.4 ± 2.12 (49) 32–41	35.1 (12) 30–39
Premaxillae width at ½ length	23.6 ± 1.67 (48) 21–27	23.9 (19) 19–28	22.7 ± 1.49 (49) 20–25	23.5 (12) 21–26
Tip of rostrum to external nares	301.9 ± 11.91 (48) 272–321	359.5 (19) 331–375	290.3 ± 12.18 (48) 263–314	343.2 (12) 326–364
Tip of rostrum to internal nares	297.1 ± 11.53 (47) 270–318	344.5 (19) 323–370	285.3 ± 12.64 (49) 258–316	339.5 (12) 322–355
Preorbital width	167.3 ± 4.76 (50) 158–177	167.4 (19) 156–181	161.6 ± 5.06 (51) 150–175	160.3 (13) 150–169
Postorbital width	187.6 ± 4.81 (49) 176–197	190.4 (19) 183–205	182.5 ± 4.81 (51) 174–192	183.1 (13) 173–193
Zygomatic width	184.9 ± 5.27 (49) 173–195	189.1 (19) 181–204	179.6 ± 4.91 (51) 170–190	180.8 (13) 173–191
Width of external nares	45.1 ± 2.26 (50) 39–50	45.6 (19) 41–49	44.3 ± 2.35 (50) 39–50	45.1 (13) 43–50
Greatest width of premaxillae	71.5 ± 2.99 (50) 66–78	71.1 (19) 66–77	71.8 ± 3.19 (50) 63–79	70.8 (13) 68–74
Parietal width	148.9 ± 2.99 (50) 139–162	153.8 (19) 145–162	145.4 ± 5.26 (51) 132–156	149.8 (13) 138–158
Height of braincase	108.0 ± 4.35 (50) 98–116	112.3 (19) 106–126	103.5 ± 15.89 (50) 94–114	108.8 (13) 100–118
Length of braincase	116.1 ± 4.73 (49) 106–124	119.3 (18) 114–129	112.0 ± 4.32 (49) 104–124	116.8 (13) 111–124
Length of temporal fossa	67.6 ± 4.19 (50) 59–84	73.6 (19) 65–81	65.8 ± 4.15 (51) 54–73	69.4 (13) 64–76
Height of temporal fossa	51.0 ± 4.11 (50) 41–60	57.6 (19) 49–63	48.9 ± 3.78 (51) 42–58	55.5 (13) 48–68
Length of orbit	49.3 ± 1.99 (50) 45–54	49.2 (19) 44–55	48.7 ± 2.22 (51) 45–53	48.2 (13) 44–53
Length antorbital process	44.5 ± 2.62 (50) 39–51	44.9 (19) 41–50	42.4 ± 2.52 (51) 36–48	43.8 (13) 38–47
Width of internal nares	54.2 ± 2.15 (49) 48–59	55.8 (19) 53–60	52.1 ± 2.16 (51) 47–57	54.1 (13) 50–60
Length of upper tooth row	214.3 ± 9.90 (47) 188–232	258.8 (19) 241–275	205.0 ± 10.09 (49) 181–226	253.6 (12) 232–271
Length of lower tooth row	208.5 ± 10.77 (49) 184–232	246.4 (20) 228–268	200.5 ± 9.84 (50) 181–218	238.3 (13) 215–255
Length of ramus	354.8 ± 13.34 (49) 323–379	405.0 (20) 384–433	343.0 ± 12.69 (50) 321–372	394.3 (13) 371–419
Height of ramus	64.1 ± 2.52 (50) 57–70	70.8 (20) 66–77	62.2 ± 2.89 (50) 57–69	67.8 (13) 65–71
Tooth width	2.81 ± 0.233 (41) 2.5–3.4	3.71 (15) 3.3–4.0	2.83 ± 0.238 (33) 2.3–3.3	3.57 (11) 3.2–4.0

Table 5. Medians, sample size (in parentheses), and minimum and maximum values for tooth row counts for the two forms of common dolphins from the coast of southern California.

	Short-beaked	Long-beaked
Upper teeth, left	49	53
	(136) 42–54	(45) 48–59
Upper teeth, right	49	53
	(138) 42–54	(45) 47–58
Lower teeth, left	47	51
	(143) 41–53	(46) 47–55
Lower teeth, right	47	51
	(172) 41–53	(47) 47–55

long-beaked form is C 7, T 14–17, L 18–23, Ca 30–34, for a total of 72–76 (n = 11; Ross, 1984). The total counts are below the range of counts for the long-beaked form off California and even below the average vertebral counts for the short-beaked form off California (Table 8). This is due primarily to fewer caudal vertebrae.

In summary, common dolphins from off South Africa are very similar to the long-beaked form in coloration, rostral length, and tooth counts but differ in average total vertebral count.

Casinos (1984) examined specimens of *Delphinus* from the Atlantic Coast of South America. Based on his data, only 6 of the 10 specimens are assignable to form. These all represent the long-beaked form based on rostral ratios (1.55–1.77, n = 5) or tooth counts (60–59/53–55, n = 1). The locality for these specimens ranged from Venezuela to the La Plata region of Argentina.

Ogawa (1936) recognized both the short-beaked form (*D. delphis*) and the long-beaked form (*D. capensis*) in Japanese waters based on the length of the rostrum and tooth count. For *D. delphis*, he found the range of total vertebrae was 74–78 (n = 6) and the ranges of the tooth counts were 44–49/44–50 (n = 8). The pigmentation pattern in Ogawa's (1936) photograph of *D. delphis* agrees with our definition of the short-beaked form. The tooth count ranges listed by Ogawa for *D. capensis* are 54–55/51–55 (n = 3).

Based on a small sample, Kasuya (1973) found that the sigmoid process of the tympano-periotic complex was larger in the short-beaked form (*D. delphis*, n = 6) than in the long-beaked form (*D. bairdii*, n = 2).

ECOLOGY

To occur sympatrically, these two forms must be exploiting the environment in at least subtly different ways. Banks and Brownell (1969) suggested that until the end of the 1800s the long-beaked form was more common, and that in this century the short-beaked form was more prevalent in southern California waters. These authors also suggested that the long-beaked form is more abundant off California during periods of relatively warm water.

We analyzed stranding data from 1970 to 1990 for common dolphins stranded along southern California shores (Fig. 15) to evaluate any potential temporal patterns. A gradual shift in relative abundance of the two forms is evident. From 1970 to 1982 inclusive, 84.4% (n = 109) of the common dolphins strandings were of the short-beaked form. During the years 1983 to 1988, 88.2% (n = 34) of the stranded common dolphins were of the long-beaked form. This shift roughly coincides with the onset of the warm water El Niño event of 1982/1983, which also apparently shifted the distribution

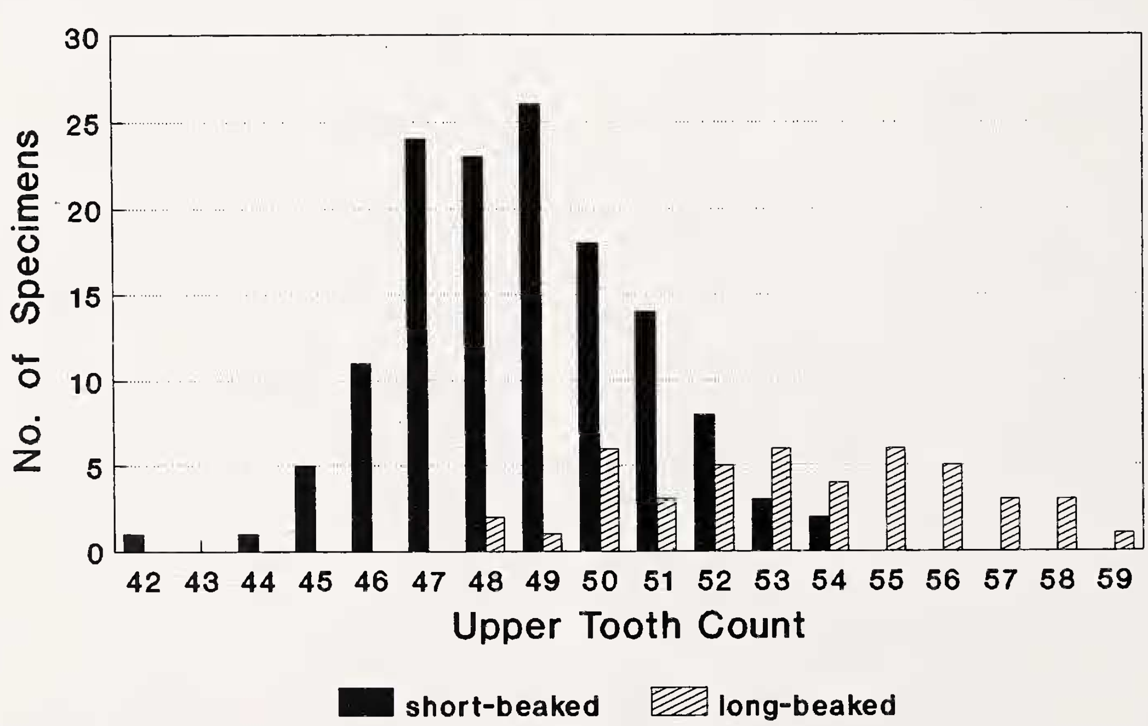

Figure 12. Upper left tooth row counts for common dolphins from waters off southern California. Filled bars are short-beaked specimens, and hatched bars long-beaked specimens.

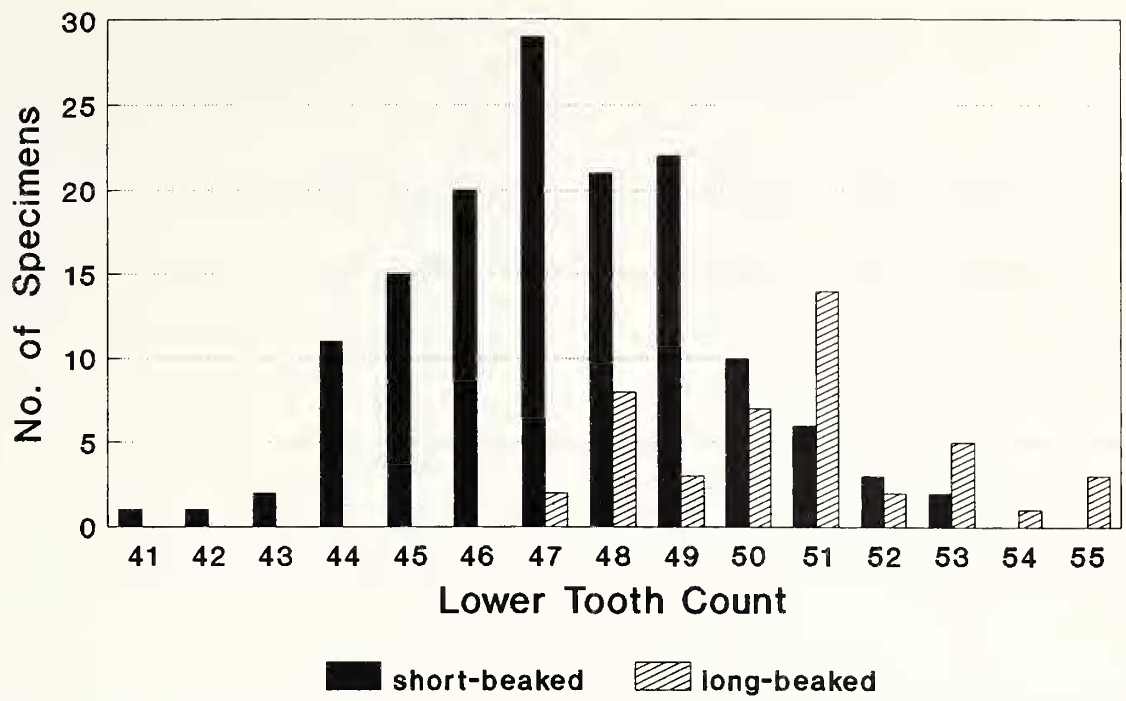

Figure 13. Lower left tooth row counts for common dolphins from waters off southern California. Filled bars are short-beaked specimens, and hatched bars long-beaked specimens.

of coastal bottlenose dolphins (*Tursiops truncatus*) northward along the California coast (Wells et al., 1989). For 1989 and 1990, a less clear pattern is evident, with 37% of common dolphins consisting of the long-beaked and 63% of the short-beaked form.

Banks and Brownell (1969) suggested that during periods when the long-beaked form is less abundant in southern California the short-beaked form moves in from the north or from offshore waters. It is unlikely that the short-beaked form moves in from the north, as both forms are uncommon north of Point Conception (see below).

Common dolphins are capable of travelling long distances in the study area. For example, a radio-tagged female short-beaked animal was resighted 270 nautical miles from its capture point after just 10 days (Evans, 1982).

The tendency of one form or the other to strand with greater frequency during different periods of years indicates that certain environmental factors may be more advantageous to one or the other form at different times. There are undoubtedly fine-scale ecological differences in how these two forms utilize southern California waters.

Differences in feeding habits between the two forms are not as yet characterized. Stomach contents from 10 short-beaked common dolphins from southern California have been analyzed (Fitch and Brownell, 1968; Schwartz et al., 1992). The primary prey were squids of the family Gonatidae and *Loligo opalescens*, followed by Pacific hake (*Merluccius productus*). One specimen had primarily northern anchovies (*Engraulis mordax*) in its stomach. The stomachs from only two long-beaked animals were available (Schwartz et al., 1992). The contents from these stomachs contained almost equal amounts of northern anchovies and Pacific hake. Based on this very small sample, the short-beaked form may feed more extensively on squid than the long-beaked form.

DISTRIBUTION IN THE EASTERN PACIFIC

The northernmost record of a short-beaked common dolphin in the eastern Pacific is that of a stranded animal from British Columbia (Guiguet, 1954). However, at-sea observations and strandings of *Delphinus* north of Point Conception have been reported as uncommon (Evans, 1982; Sullivan and Houck, 1979). Off southern California south of Point Conception, common dolphins are the most abundant species of cetacean seen in surveys (Evans, 1982), but these surveys have not distinguished between the long-beaked and short-beaked forms. More recent surveys made only one sighting of the long-beaked form north of Point Conception; the short-beaked form was found in waters off the length of California but was more abundant off southern California (Hill and Barlow, 1992).

All animals observed at sea and collected as specimens from the offshore eastern tropical Pacific, ranging as far south as northern Peru, have been of the short-beaked form (Evans, 1982; Perrin et al., 1985).

The short-beaked form seems to range from the shallow coastal waters to thousands of nautical miles from shore, at least in the eastern tropical Pacific. Distributions of the two forms overlap in nearshore waters of the eastern Pacific (Perrin et al., 1985).

Central California is the northernmost limit for stranded long-beaked common dolphins (Banks and Brownell, 1969). The majority of specimens collected in the Gulf of California and published to date represent the long-beaked form (Banks and Brownell, 1969; Evans, 1982). All animals observed at sea in the Gulf of California by JEH have been

Table 6. Medians, standard deviations (for sample sizes > 24), samples sizes (in parentheses), and minimum and maximum values for postcranial meristics for the two forms of common dolphins from southern California.

	Short-beaked	Long-beaked
Vertebral count	76 ± 1.48	78 ± 0.64
	(80) 74–80	(25) 77–80
No. of lumbar vertebrae	20 ± 1.12	20 ± 0.96
	(76) 18–24	(25) 19–22
No. of caudal vertebrae	34 ± 1.30	35 ± 1.04
	(75) 30–36	(25) 33–37
First vertebra with vertical foramen	54 ± 1.70	55 ± 1.46
	(76) 49–59	(26) 53–57
Last vertebra with transverse process	58 ± 1.26	59 ± 1.22
	(75) 54–61	(26) 55–60
Last vertebra with neural arch	63 ± 1.45	65 ± 1.03
	(75) 60–68	(25) 63–67
First vertebra with chevron	43 ± 1.19	44 ± 0.83
	(75) 41–46	(25) 42–45
No. of chevrons	25 ± 2.32	27 ± 1.78
	(71) 18–29	(25) 23–30
No. of vertebral ribs	15 ± 0.63	15 ± 0.56
	(78) 13–16	(25) 14–16
No. of sternal ribs	8 ± 0.76	8 ± 0.72
	(77) 6–10	(26) 7–9
Number of carpals and metacarpals	10	10
	(33) 10	(15) 10
Phalanges		
Digit 1	2	2
	(33) 1–2	(10) 1–3
Digit 2	8 ± 0.62	8
	(32) 7–9	(9) 8–9
Digit 3	6 ± 0.45	6
	(33) 5–7	(9) 6–7
Digit 4	2 ± 0.5	2
	(31) 1–3	(10) 1–3
Digit 5	1	1
	(29) 1	(9) 1
Number of cervicals fused	2 ± 0.42	2
	(75) 2–4	(25) 2
Last vertebra with facet for chevron	66 ± 1.56	68
	(65) 61–70	(24) 59–70
Widest vertebra	23 ± 1.42	24 ± 1.46
	(70) 21–26	(25) 22–27

of the long-beaked form. Long-beaked specimens have been collected from coastal central Peru (Banks and Brownell, 1969). The "Guerrero common dolphin" that occurs along the west coast of Mexico could be either the long-beaked form or a large-bodied population of the short-beaked form (Perrin et al., 1985).

In the eastern North Pacific, all sightings of long-beaked animals have been within about 100 nautical miles of shore (Perrin et al., 1985; Hill and Barlow, 1992). The long-beaked form off South Africa also seems to have a nearshore distribution (Ross, 1984).

Nishiwaki (1967), based primarily on the work of Ogawa (1936), described and mapped the distribution of common dolphins in the western Pacific. He stated that the long-beaked form, *D. capensis,* favors warm waters and is only found in the more southern regions of Japan such as the waters off Kyushu during the summer. The short-beaked form, *D. delphis,* avoids cooler waters but during summer may be found offshore north of Honshu in the warm Kuroshio current.

TAXONOMY

For all species of delphinids studied to date, moderate to strong patterns of morphological variation over sometimes short geographical distances seem to be typical (Perrin, 1984). For most species, only small samples are available from restricted localities. The strong geographical variation and small sample sizes have hampered studies regarding alpha-level taxonomy, because samples collected over wide areas are then needed to distinguish between intraspecific (gamma-level taxonomy) and interspecific differences (e.g., Perrin et al., 1981, 1987).

The current study is unique in that the study area is quite small and thus theoretically free from the effects of geographical variation. Also, the samples of both forms are large enough to support statistical analysis, even when stratified by sex and age.

One interpretation is that the above evidence of complete morphological separation of these sympatrically occurring forms suggests that the forms represent two species. Wiley (1981:62) considered such cases of completely distinct phenotypic populations in a region of sympatry *prima facie* evidence for two species. In addition to our morphological data, initial research utilizing molecular data also suggests two species. Based on analyses of mitochondrial DNA sequence data, Rosel et al. (in press) found that the California short-beaked form was more closely related to common dolphins from the Black Sea than to the sympatrically occurring long-beaked form. Based on the ratio of rostrum length to zygomatic width, Banks and Brownell (1969) also found that Black Sea animals clustered with the short-beaked form from the eastern North Pacific.

An alternative hypothesis is that various demes of common dolphins form a Rassenkreis and the two forms we describe are examples of the extremes in a single species that do not interbreed. Although the Rassenkreis phenomenon is considered rare for large vagile vertebrates (Mayr, 1969), one potential delphinid example has been proposed. Ross (1977) examined a small series of bottlenose dolphins from South Africa and distinguished two species, *Tursiops truncatus* and *T. aduncus,* based on differences in size, morphology, and coloration. Subsequently, in evaluating specimens of *Tursiops* sp. from Australia, Ross and Cockcroft (1990) found that the two forms off South Africa appear to represent the extremes of a cline

Table 7. Means, standard deviations (for sample size > 24), sample sizes (in parentheses), and minimum and maximum values for postcranial measures for adult specimens of the two forms of common dolphins from California.

	Males		Females	
	Short-beaked	Long-beaked	Short-beaked	Long-beaked
Width of atlas	126.5 ± 8.1 (26) 110–143	133.3 (6) 125–142	120.0 ± 5.6 (25) 108–129	127.4 (5) 121–135
Height of atlas	51.7 ± 2.7 (26) 46–58	54.5 (6) 53–56	48.1 (24) 42–52	53.8 (5) 50–58
Length of atlas lateral process	24.7 ± 2.4 (26) 19–30	27.8 (6) 27–30	23.4 (24) 20–28	25.4 (5) 24–28
Length of atlas dorsal spine	45.6 ± 4.7 (26) 35–56	50.2 (6) 46–54	44.5 ± 4.2 (25) 38–55	50.2 (5) 47–54
Height of first thoracic vertebra	47.5 (11) 42–52	51.0 (4) 50–52	45.1 (13) 41–49	51.0 (2) 47–55
Width of first thoracic vertebra	88.0 ± 5.8 (26) 77–100	90.3 (6) 85–95	82.6 (23) 74–94	88.6 (5) 79–99
Length of first thoracic spine	33.2 (23) 23–41	39.0 (6) 34–45	28.7 (23) 20–48	30.8 (5) 21–35
Height of first lumbar vertebra	51.0 (23) 48–56	57.4 (5) 55–59	48.3 (23) 41–53	54.2 (5) 50–58
Width of first lumbar vertebra	191.6 ± 9.0 (25) 177–208	204.5 (6) 192–211	184.3 (24) 165–200	200.2 (5) 187–216
Length of first lumbar spine	74.2 (24) 66–84	80.2 (6) 75–84	68.4 (24) 56–78	75.8 (5) 71–82
Length of first vertebral rib	121.5 ± 6.0 (25) 112–131	132.0 (6) 121–142	112.2 ± 4.1 (25) 105–121	121.0 (4) 115–130
Length of longest vertebral rib	269.6 (24) 249–287	298.8 (6) 287–322	256.2 ± 9.0 (25) 241–278	275.5 (4) 268–285
Maximum width of manubrium	102.2 ± 5.7 (26) 91–112	114.8 (5) 105–121	96.6 ± 4.6 (25) 87–109	108.0 (4) 99–122
Height of scapula	126.1 ± 6.1 (25) 117–139	139.0 (5) 136–144	118.2 ± 6.8 (25) 104–130	128.5 (4) 118–143
Length of scapula	122.0 ± 6.6 (25) 112–132	135.0 (5) 133–137	112.6 ± 6.5 (25) 101–123	199.0 (4) 110–129
Maximum length of humerus	56.6 (24) 50–62	62.0 (5) 57–65	52.9 ± 3.3 (25) 47–61	58.3 (4) 57–60
Maximum length of radius	76.7 (23) 70–84	83.8 (5) 81–88	70.6 ± 5.0 (25) 63–82	76.8 (4) 65–86
Maximum length of ulna	66.6 (23) 59–73	73.6 (5) 70–78	61.4 ± 5.1 (25) 54–73	70.0 (4) 68–72
Maximum width of humerus	40.4 (24) 37–43	42.8 (5) 41–44	36.8 (24) 33–40	41.5 (4) 38–46
Length of longest chevron	46.3 ± 4.1 (26) 37–53	51.3 (6) 48–59	41.8 ± 3.8 (25) 34–50	48.0 (5) 41–54
Length of longest pelvic	92.7 (20) 64–111	93.4 (5) 79–101	62.9 (17) 47–76	73.8 (5) 58–84
Width of widest vertebra	193.9 ± 9.6 (25) 174–214	207.4 (5) 200–211	187.3 (23) 169–205	202.8 (5) 187–220
Length of centrum of first lumbar	23.5 ± 1.8 (26) 20–27	25.5 (4) 23–30	21.8 (23) 20–24	24.2 (5) 22–27

found along the coasts of Australia. This cline, particularly relating to body size, is strongly correlated with water temperature. We believe our study does not represent such a pattern and that their study does not represent a Rassenkreis for the following reasons. First, the two forms of *Tursiops* occurring off the coast of South Africa are essentially allopatric, associating with different bodies of waters or currents (Ross, 1977, 1984; Ross and Cockcroft, 1990), and thus are potentially physically isolated from each other. The two forms of common dolphins off the coast of southern California often are seen within minutes and kilometers of each other, so no physical barrier can be invoked as a genetic

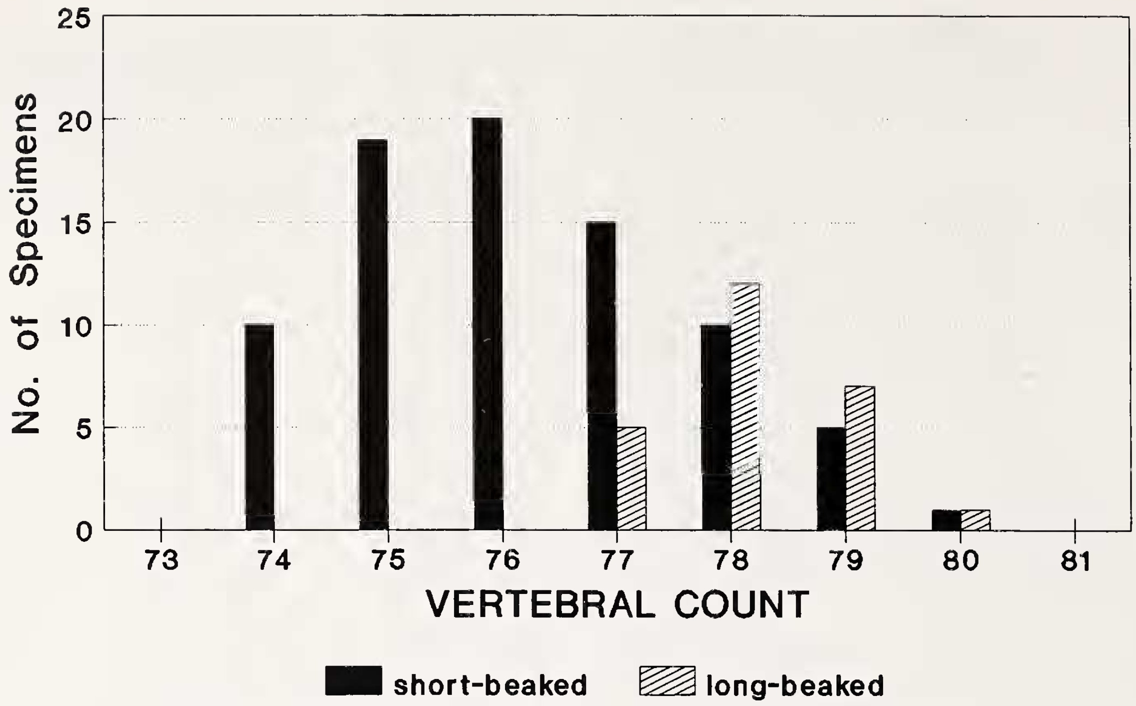

Figure 14. Total vertebral counts for common dolphins from waters off southern California. Filled bars are short-beaked specimens and hatched bars long-beaked specimens.

isolating mechanism. Second, the differences between the Southern African forms of *Tursiops* were based on extremely small samples (n = 5 for adult *T. truncatus;* Ross, 1977, table 1). Intermediates between the two forms may be found when a larger sample is examined. Finally, the two forms of common dolphins are found sympatrically in several distinct regions (e.g., western Pacific, eastern Pacific, eastern Atlantic). A Rassenkreis would not explain this type of pattern.

We conclude that the two forms of common dolphins represent two distinct species. Below, we review the nomenclature for *Delphinus,* provide redescriptions of the two species, and suggest further research.

REVIEW OF *DELPHINUS* NOMENCLATURE

The annotated list of the nominal species of common dolphins provided here is based largely on Hershkovitz (1966). We converted measurements in the original descriptions to metric units (centimeters for external morphometrics and millimeters for cranial morphometrics). Based on the type material, we attempted to assign each nominal species to either the long-beaked or short-beaked form of *Delphinus* as recognized and diagnosed herein.

Table 8. Means, standard deviations (for sample size > 30), sample sizes (in parentheses), and minimum and maximum values for the ratio of rostrum length to zygomatic width for adult specimens from the coast of California.

	Short-beaked	Long-beaked
Males	1.37 ± 0.046	1.60
	(47) 1.21–1.46	(19) 1.52–1.67
Females	1.36 ± 0.055	1.64
	(48) 1.23–1.47	(12) 1.55–1.77

There are numerous problems inherent in such an exercise. Foremost is that most of the type specimens lack data relating to maturity, either sexual or physical. Thus, many type specimens may be unsuitable for comparative studies because they may be juveniles. For the majority of type specimens, not even the sex is recorded. Published tooth counts are also a potential problem. In a previous study of tooth counts in spotted dolphins (*Stenella*), Perrin et al. (1987) found that their tooth counts were typically higher than those listed in previous works. They believed that previous workers overlooked the anteriormost teeth because they are very small and/or buried in remnants of tissue. We found this to be true for specimens of *Delphinus* as well. For example, the published tooth counts for the type of *D. major* (Gray, 1866a) are listed as 46/47, whereas our counts for this specimen are 52/49. Therefore, based upon high tooth counts, we are confident in referring that type to the long-beaked form; the same is true for referring very low-tooth-count specimens to the short-beaked form. For specimens at the upper range of the short-beaked form, we are less confident regarding assignments based on this character. Lastly, description of coloration is often not useful as the pigmentation of cetaceans darkens quickly postmortem (Norris and Prescott, 1961; Mitchell, 1970) and many descriptions and illustrations are obviously not from fresh specimens.

We consulted with the original description for each species and note in the text if we were able to examine any type material. Several of the type specimens are housed in the Natural History Museum, formerly the British Museum (Natural History). These specimens are listed here with the original museum acronym (BM) as found in the literature.

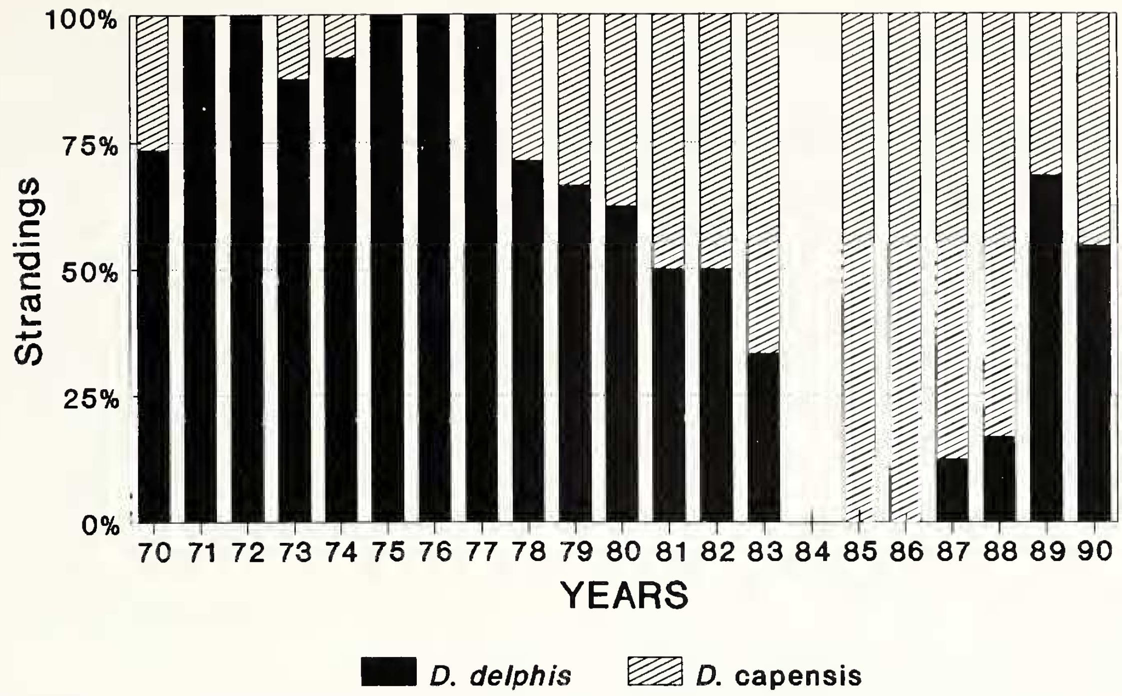

Figure 15. Strandings by year of common dolphins classified to species from southern California. The differences of absolute abundance of strandings reflects, in part, differences in response effort to strandings. Filled bars are short-beaked specimens and hatched bars long-beaked specimens.

We did not include the "varieties" of common dolphins (*variegatus, balteatus, moschatus,* and *marginatus*) listed by Fischer (1881), because they were used to describe color variation. According to the *International Code for Zoological Nomenclature* (Article 45g), such designated varieties published prior to 1961 are considered subspecies. It is beyond the scope of this paper to discuss the validity of subspecies.

Delphinus delphis
Linnaeus, 1758

No type specimen was designated. This species is based on description of an animal from "*Oceano europaeo*" by Artedi (1738).

Delphinus vulgaris
Lacépède, 1804

This species is represented by an illustration of the whole animal and skull. The illustration is an extremely crude rendering of a dolphin that we believe is not referable even to genus. The published tooth count of 42–38/47–47 is well within the exclusive range of the short-beaked form and the type description indicates that Lacépède (1804) intended this species to supplant *D. delphis.*

Delphinus capensis
Gray, 1828

The type specimen (BM 41.1734) was a stuffed whole mount with skull inside collected from the Cape of Good Hope housed in the Natural History Museum (London). The published external measurements are as follows: total length, 206; maximum girth, 107; snout to blowhole, 33; snout to melon apex, 18 cm; snout to dorsal fin, 97 cm; dorsal fin height, 25; fluke width, 46 cm. The tooth counts are reported as 50/50. Gray (1828) noted that this species is distinguished by its relatively short beak. This comment appears to be made in comparison to *Stenella longirostris,* then regarded to be in the genus *Delphinus.* The skull was later removed from the mount. We measured the type and found the rostral ratio to be 1.71 and the tooth counts 54–53/51–52. The maxillae and premaxillae are fused along the entire length of the rostrum, indicating the specimen is an adult animal. The skull measurements and tooth counts of the type specimen associate it with the long-beaked form from California (Banks and Brownell, 1969; van Bree and Purves, 1972).

Delphinus longirostris
G. Cuvier, 1829

This name is preoccupied by *D. longirostris* Gray, 1828, now placed in the genus *Stenella* (Hershkovitz, 1966).

Delphinus novae-zelandiæ
Quoy and Gaimard, 1830

The following external measurements for the type specimen have been published (Quoy and Gaimard, 1830; Gray, 1850): total length, 188; snout to blowhole, 33; snout to eye, 30; snout to flipper, 43; snout to dorsal fin, 83. The tooth counts are reported as 43/47, and the skull measurements are as follows: skull length, 356 mm; nose, 203; length of mandible 305. Gray (1850) also noted that the skull was very much like that of *D. janira.* The low tooth counts associate this nominal species with the short-beaked form.

Delphinus loriger Wiegmann, 1846

This name was published in 1846 in Schreber's *Säugthiere* (Wagner, 1846). Hershkovitz (1966) considered this species to be a junior synonym of *Stenella dubia* (G. Cuvier, 1812). Perrin et al. (1987) stated that based on the published pigmentation pattern this specimen was a common dolphin. This species is only known from a description and illustration of a whole animal (Wagner, 1846, Pl. CCCLXII). The animal had a flipper stripe like that of the short-beaked form. Thus, we consider this species to be a junior synonym of *D. delphis.*

The year this species was named is problematic. Hershkovitz (1966) listed the author and date as "Wiegmann, 1841 (?)" and secondarily listed the 1846 edition of Schreber's *Säugthiere* edited by J. Wagner. This listing has been followed by Hall (1981) and Perrin et al. (1987). This ambiguity may be due to the fact that Wagner (1846) mentioned that the species was based on the papers of A. Wiegmann. We examined the volumes of *Archiv für Naturgeschichte* for the years 1836 through 1847. This series was edited by A. Wiegmann in the late 1830s and early 1840s and includes a supplement that summarized the published biological work of the previous year. There is no mention of *D. loriger* in any volume. Sherborn (1935) considered that Wiegmann had published this species name in the 1846 edition of *Säugthiere.* According to the *Catalogue of the Books, Manuscripts, Maps and Drawings in the British Museum (Natural History)* (1903:1861), A. Wiegmann began editing the 1846 edition of Schreber's *Säugthiere,* but the volume was completed by Wagner; this may explain Wagner's mention of the "papers" of Wiegmann.

Delphinus janira Gray, 1846

The type specimen is a skull collected from Newfoundland and housed in the Museum of the Bristol Institution. The published diagnostic features and measurements are listed as the following: skull length, 453; skull width at orbit, 195; length of mandible, 318; tooth counts 43/42. The very low tooth counts associate this nominal species with the short-beaked form.

Delphinus sao Gray, 1846

The type of this species is a skull from Madagascar that Gray stated was located in the Paris Museum. However, Robineau (1990) does not list this specimen in his list of cetacean types in the Muséum national d'Histoire naturelle, Paris. Measurements and characters published by Gray are as follows: tooth counts, 55/55–60/60; skull length, 430; beak length, 267; tooth row length (upper?), 222. Hershkovitz (1966) erroneously listed this species as authored by Gray (1850). The tooth count is above the range of the short-beaked form and, thus, this nominal species groups with the long-beaked form.

Delphinus forsteri Gray, 1846

This species is based on a description and unpublished illustration of an animal from near New Caledonia by Forster (1844). Gray (1846) published this illustration and noted that there were white patches on the dorsal fin and flippers of this specimen. The tooth count was listed as 44/44. Based on the low tooth count and the distinct light patches on the flippers and dorsal fin, we tentatively refer this species to the short-beaked form.

Delphinus fulvifasciatus Wagner, 1846

The type specimen was collected off Hobart Town, Tasmania and housed in the Muséum national d'Histoire naturelle, Paris (CAC: A.3025). Robineau (1990) published the following skull measurements: condylobasal length, 432; rostrum length, 270; rostral width at base, 90; preorbital width, 173; postorbital width, 191; zygomatic width, 184; length of mandible, 383; height of ramus, 68. The tooth counts are listed as 42+, 45/44, 45. Based on the published skull measurements, the ratio of rostral length to zygomatic width of 1.47 associates this specimen with the short-beaked form.

Delphinus albimanus Peale, 1848

The type originally consisted of a mounted skin with partial mandibles and manus bones within, collected off the coast of Chile. A rather crude illustration of the whole type specimen was published by Cassin (1858). True (1889) examined the type mounted skin, dissected out the partial mandibles, and commented that he believed that this species was like *D. forsteri,* a variety of *D. delphis* with white patches on the flipper. The mounted skin of the type specimen is now lost (Poole and Schantz, 1942), but the mandibles are still available in the National Museum of Natural History. Based on the distinct white patches on the flipper and the comments of True (1889), we tentatively refer this nominal species to the short-beaked form.

Delphinus frithii Blyth, 1859

The type specimen was collected on a voyage from England to India and is represented by a skull in the Calcutta Museum. The published tooth counts are 55/50; the upper count is within the exclusive range of the long-beaked form.

Delphinus algeriensis Loche, 1860

The type consists of a skin with skull and possibly a complete skeleton collected from the coast of Algiers housed in the Natural History Museum of Algiers. The illustration of the type specimen depicts an animal with a mixture of *Stenella coeruleoalba* and *Delphinus* spp. coloration. However, the description of the skull (Loche, 1860:477) clearly mentions the long grooves on the palate, a character unique to the genus *Delphinus*. The published tooth counts of 41–41/41–39 would associate this nominal species with the short-beaked form.

Delphinus major Gray, 1866

The type specimen is a skull in the Natural History Museum (BM 1852.10.5.2) from an unknown locality. The original published measurements (Gray, 1866a) of the type skull are the following: condylobasal length, 533; rostrum length, 318; rostrum width at notches, 106; mandible length, 445; tooth counts, 46/47. We examined the type skull. The published ratio of rostrum length to skull width is 1.73 (van Bree and Purves, 1972), whereas our measurements yield a slightly different ratio of 1.70. We examined the type and report the tooth counts as 52/49. We found almost complete fusion of the maxillae to the premaxillae along the rostrum, suggesting adulthood. Both tooth counts and the rostral ratio place this species with the long-beaked form from the eastern North Pacific. This is in agreement with the conclusions of Banks and Brownell (1969) and Evans (1975).

Delphinus moorei Gray, 1866

The type specimen is represented by a skull in the Liverpool Free Museum, from a 192-cm female collected southwest of the Cape of Good Hope. The original published measurements of the type skull are as follows: skull length, 445; rostrum length, 279; mandible length, 368; rostral width at notch, 91; rostrum width midlength, 49; tooth counts, 44/48. External measurements (in cm) are as follows: 192; beak length, 14.6; snout to eye, 33; snout to blowhole, 33; snout to flipper, 47; snout to anus, 141; snout to genital slit, 138. The published illustration of a whole specimen (Gray, 1866b:736, fig. 1) depicts a nondescript, three-tone dolphin. However, the lack of white below the eye is characteristic of the long-beaked form. For a female of this size, the rostrum tip to eye and rostrum to melon apex measures are above the range of the short-beaked form. Also, the condylobasal length and rostrum length are at the lower ends of ranges of the long-beaked form and above the ranges of the short-beaked form. The lower tooth count is in the region of overlap, but the upper count is in the short-beaked range. However, the published tooth counts are likely to be low. We consider this species referable to the long-beaked form.

Delphinus walkeri Gray, 1866

The type specimen is a skull in the Liverpool Free Museum, from a 202-cm female collected southwest of the Cape of Good Hope. We have not examined it. This species was described by Gray (1866b) as being extremely similar to *D. moorei*, with the following features: skull length, 419; rostrum length, 279; rostrum width at notches, 85; rostrum width midlength, 47; tooth count, 47/49. The external measurements were described as being very similar to those of *D. moorei*. The published illustration (Gray, 1866b:737, fig. 2) does not provide enough details to ascertain which form this species represents.

Delphinus pomeegra Owen, 1866

The type specimen is a skull collected from the Madras coast of India now housed in the Natural History Museum (BM 1478a-66.2.5.5). The tooth counts given in the original description are listed as 42–41/45–46. In Owen's (1866, Pl. 8) illustration, the tip of the rostrum appears somewhat worn. True (1889) remarked that the tip is damaged and estimated that about 7 cm are missing. Based on our examination of the skull, we believe this may be an overestimate of the amount of the rostrum that is missing. Comparing the overall skull morphology to other specimens, we estimate that 2 cm or less are missing. There is no fusion of the maxillae to the premaxillae along the rostrum, indicating that the specimen was not yet sexually mature and the tip of the rostrum was still growing (Perrin and Heyning, 1993). This specimen is from the northern Indian Ocean, where so far only animals with very long rostra have been documented, such as the type specimen and referred specimens of *D. tropicalis*. The published coloration of the type specimen as very dark, almost black above and lighter below, appears to represent postmortem darkening of the coloration, as no form of *Delphinus* that we know of has such a simple color pattern. Because the type specimen is immature and the rostrum is damaged, we regard this species as a *nomen dubium*.

Eudelphinus tasmaniensis Van Beneden and Gervais, 1880

This species is based on a skull in the Muséum national d'Histoire naturelle, Paris (CAC: A.3071) collected in Tasmania. Robineau (1990) was unable to locate this skull in the collection. No type description is provided, only an illustration of the palate and pterygoid region (Van Beneden and Gervais, 1880, Pl. 39, fig. 9). True (1889) reported a condylobasal length of 445 mm and an orbital width of 168 mm. The upper tooth counts (53–50) of the type obtained from the illustration cannot be considered accurate as the counts widely differ bilaterally in other specimens on the same plate. We consider this species to be a *nomen dubium.*

Delphinus dussumieri Blandford, 1891

This name was proposed for *D. longirostris* G. Cuvier, 1829, which is preoccupied by *Stenella longirostris* (Gray, 1828). However, *D. dussumieri* is preoccupied by *D. dussumieri* Fischer, 1829 as a new name for *D. capensis* F. Cuvier, 1829, which in turn is preoccupied by *D. capensis* Gray, 1828. Both *D. dussumieri* Fischer, 1829 and *D. capensis* F. Cuvier, 1829 are considered junior synonyms of *Cephalorhynchus heavisidii* (Hershkovitz, 1966). *Delphinus tropicalis* van Bree, 1971 was proposed as a new name for the species to which the names *D. longirostris* G. Cuvier and *D. dussumieri* Blandford, 1891 had been applied.

Delphinus microps Burmeister, 1866 (not Gray)

This species is based on a short description of three skulls collected from the coast of Brazil. The skulls are all about 460 mm long and have a zygomatic width of about 190 mm with a tooth count range of 47–49/44–48. Burmeister's original description of the types noted that this species appears almost identical to *D. walkeri.* The skull length and width are within the range of the long-beaked form and outside the range for the short-beaked form. The tooth counts are low for the long-beaked form, but, as mentioned previously, the true counts may be higher than given in some of the original descriptions. We therefore consider this type attributable to the long-beaked form.

Delphinus marginatus Lafont, 1868 (not Pucheran, 1868)

Hershkovitz (1966) considered this species to be based on a misidentification and therefore not a new species name.

Delphinus bairdii Dall, 1873

This species was based on two specimens collected by Charles Scammon off Point Arguello, California. The type specimens are lost (Poole and Schantz, 1942). See discussion below.

Delphinus tropicalis van Bree, 1971

This is a new name proposed for *D. longirostris* and *D. dussumieri,* as both names are unavailable. The type specimen is a skull collected from the Malabar coast housed in the Muséum national d'Histoire naturelle in Paris (specimen numbers CAC: A.3065 and CAG: B II/64; Robineau, 1990). We did not examine the skull. The tooth counts of the type are reported as 65–65/57–58 and the ratio of rostral length to zygomatic width as 2.06 (van Bree and Gallagher, 1978). Both the tooth counts and the ratio of rostral length to zygomatic width are above the range of values for the long-beaked form off California.

In reviewing the nomenclature, we find that the senior synonym for the short-beaked form is *Delphinus delphis* Linnaeus, 1758 and for the long-beaked form *Delphinus capensis* Gray, 1828.

The species *Delphinus delphis* is based on the description by Linnaeus (1758) of "*corpore oblongo subtereti, rostro antenuato acuto.*" This diagnosis was used to differentiate the common dolphin from *Orcinus orca* and *Phocoena phocoena,* then considered to be congeneric. No type was designated, and the type locality was listed as "*Oceano Europaeo.*" The lack of a type specimen and detailed diagnosis raises several potential problems of nomenclature.

The first relatively complete description of a common dolphin from European waters is provided by Lilljeborg (1866). This specimen of unknown sex was collected from Kristiania Bay, Norway and housed in the Zoological Museum of the University of Kristiania (Oslo). The total length of the specimen was 181 cm with a snout to melon apex length of 10.5 cm. The ratio of rostral length to zygomatic width is 1.48. Both the external measurement of the snout relative to total length and the rostral ratio of the skull are within the exclusive ranges of values for the short-beaked form.

The next rather detailed description of a common dolphin from European waters is that of Flower (1880). The specimen he described was an immature female 156 cm in length caught off the Cornwall coast of the United Kingdom in 1878. The complete skeleton was collected and housed originally in the Museum of the Royal College of Surgeons, then later transferred to the Natural History Museum, London. This animal was illustrated (Flower, 1880) by a watercolor of moderately good quality that depicts some strong accessory stripes, such as the primary and secondary abdominal stripes and the eye-to-anus stripe of Mitchell (1970). The flipper stripe intersects with the lower jaw about one-third the distance anterior to the hind-end of the gape. Based on the illustrated color pattern, it is not possible to assign this specimen to one or the other of the forms we describe from off California. The tooth counts of Flower's specimen were listed as 46–44/48–47. This is near the mean number of teeth we found for the short-beaked form and just at or below the lower limit for the long-beaked form off California.

Both of the above early described specimens of common dolphins from European waters were of

Figure 16. Illustration from Scammon (1874) of one of the syntypes of *D. bairdii*.

the short-beaked form. Additionally, the range of values for zygomatic width to rostrum length (1.37–1.54) for 31 specimens (albeit not stratified by age or sex) from European waters (van Bree and Purves, 1972) clustered with the short-beaked form. As we are unable to find specimens of the long-beaked species from European waters, we refer the short-beaked form to the species *Delphinus delphis*.

The type of *Delphinus bairdii* was described by W. H. Dall (1873) based on two females caught off Point Arguello, California by Captain Charles Scammon. In the original description, Dall (1873) mentioned that one entire skeleton was sent to the U.S. National Museum. Poole and Schantz (1942) noted that there are no records of the specimen arriving at the museum, nor are there catalog numbers for it. The type specimen has not been found subsequently (J. Mead, National Museum of Natural History, pers. comm.). What is available for the syntypes are the total lengths, a few skull measurements, and tooth counts published in the original description. In addition, Scammon (1874) illustrated the pigmentation of one of the syntypes, which we reproduce here (Fig. 16).

As the type specimens have been lost, it is important to firmly establish which of the two forms present off California was considered *D. bairdii* in order to stabilize the nomenclature. The tooth counts for the type specimen were reported as 53/47 (Dall, 1873). The upper tooth count is at the upper limit of the tooth count we found for the short-beaked form and well within the range of the long-beaked form. The lower tooth count is at the minimal range of tooth counts for the long-beaked form but well within the range of the short-beaked form. However, Dall (1974) mentioned that there was room for four to five additional teeth in each mandibular tooth row. Tooth counts as originally listed are often lower than those obtained by today's methods (see Perrin et al., 1987). Thus, it is possible that the tooth count of the type specimen of *D. bairdii* would be higher and within the exclusive range of the long-beaked form if re-examined today.

The total lengths of the two females mentioned in the type description (Dall, 1873) were 201 and 206 cm. These lengths fall well outside the range of total length for the short-beaked form and are very close to the average length (207.7 cm) of physically mature female long-beaked common dolphins in this region. The condylobasal length and the rostrum length of the type skull are significantly above the range of these measures for female short-beaked specimens and even above the mean condylobasal and rostrum length for the long-beaked specimens we examined. The illustration provided by Scammon (1874) depicts an animal clearly assignable to the long-beaked form based on the criteria we used in our analysis of color pattern, especially the flipper stripe angling toward the corner of the mouth. Therefore, based on total length, skull measures, and pigmentation, the types of *D. bairdii* belong to the long-beaked form.

In order to provide taxonomic stability, we propose a neotype for *Delphinus bairdii*, LACM 84240. This specimen consists of a complete skeleton of a physically mature male. The external measurements and skull and postcranial data are listed in Tables 9–11. A photograph of the whole specimen is found in Figure 8 and a photograph of the skull in Figure 18.

In their analysis of rostral length vs. zygomatic width, Banks and Brownell (1969) found that the type specimens of *D. bairdii* Dall, 1873; *D. major* Gray, 1866; and *D. capensis* Gray, 1828 were included in a cluster with the long-beaked form. In their review of the previous study, van Bree and Purves (1972) noted that there was no reason to call the long-beaked form *D. bairdii*, because there are no described differences between *D. capensis*, *D. major*, and *D. bairdii*, and *D. capensis* is the senior synonym. The published values (van Bree and Purves, 1972) for the ratios of zygomatic width to rostral length for *D. capensis* (1.74) and *D. major* (1.73) clearly group these two nominal species with the long-beaked form from California (see Table 10).

The long-beaked forms from South Africa and California are similar in overall skull shape, including relative rostral length, in general coloration pattern, and in tooth count. The two populations differ significantly in total vertebral count. We believe that this difference alone does not warrant assigning species status to these populations. If they are considered one species, the range of vertebral count is nine (72–80). Perrin et al. (1987) found that the

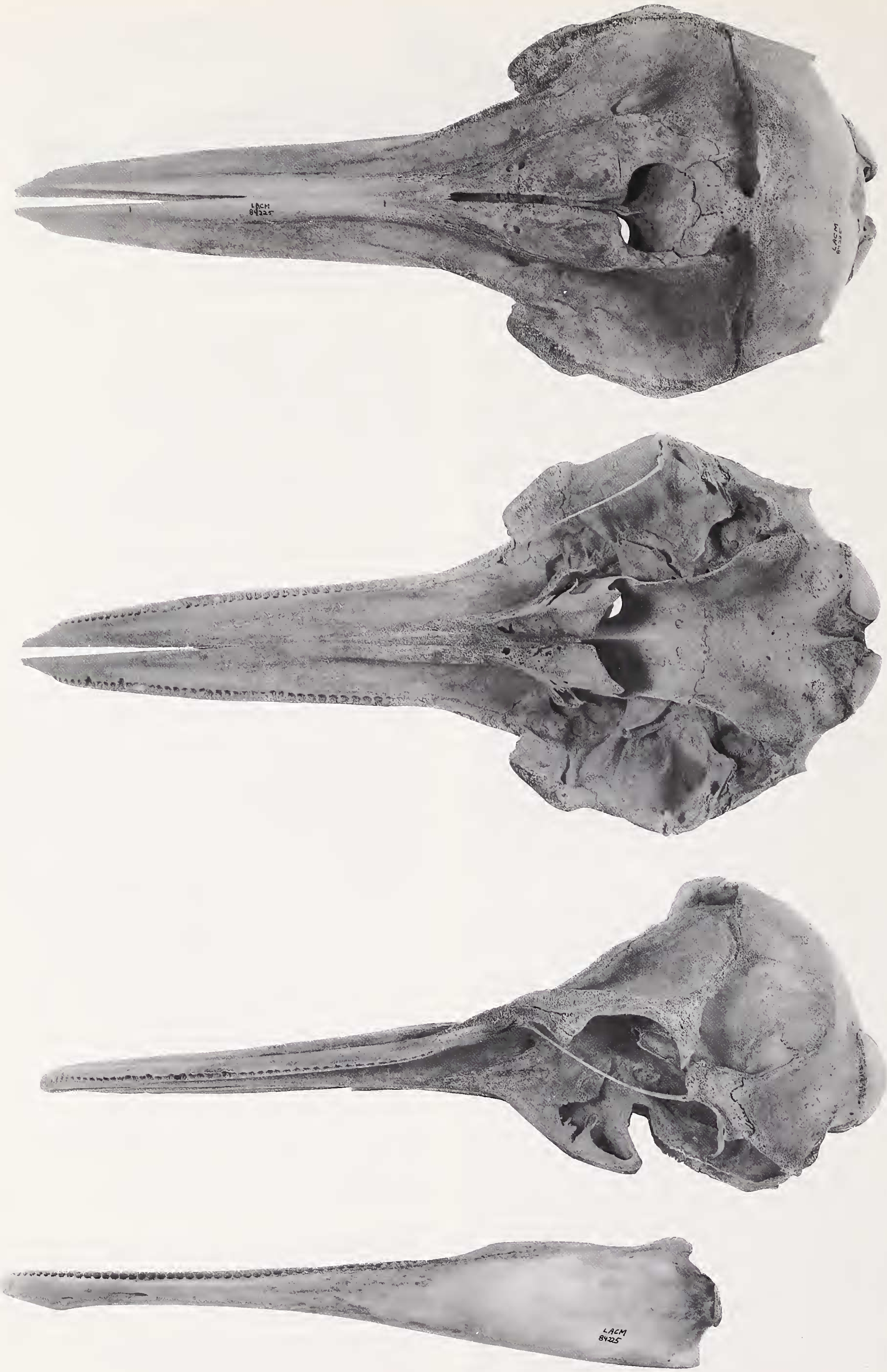

Figure 17. Typical skull of adult *Delphinus delphis* from the waters off southern California (LACM 84225, male, total length 188 cm).

Figure 18. Typical skull of adult *Delphinus capensis* from the waters off southern California (LACM 84240, male, total length 235 cm). This specimen is also designated as the neotype of *Delphinus bairdii,* considered to be a junior synonym.

Table 9. External morphometrics (in centimeters) for the neotype of *Delphinus bairdii* (LACM 84240).

Total length	234.5
Snout to anus	170.0
Snout to genital slit	145.0
Snout to umbilicus	107.0
Snout to dorsal fin tip	133.0
Snout to anterior dorsal fin	99.0
Snout to flipper	46.5
Snout to ear	37.5
Snout to eye	33.0
Snout to gape	27.5
Snout to blowhole	33.5
Snout to melon apex	14.5
Eye to ear	5.5
Eye to gape	5.5
Right eye to blowhole	18.5
Left eye to blowhole	16.5
Blowhole length	1.7
Blowhole width	2.0
Head diameter at eyes	19.5
Rostral width at melon apex	7.5
Projection of lower jaw	1.0
Flipper length, anterior	33.0
Flipper length, posterior	24.0
Flipper width	11.0
Length of genital slit	12.0
Fluke width	58.0
Fluke depth at lobe	16.0
Fluke depth at notch	13.5
Fluke notch depth	3.0
Dorsal fin height	24.5
Dorsal fin base length	33.0
Girth at eye	71.0
Girth at axilla	105.0
Girth, maximum	118.0
Girth at anus	78.0
Girth midway anus–fluke notch	38.0
Caudal height	16.5
Caudal thickness	4.2

Table 10. Skull measurements (in millimeters) and tooth counts for the neotype of *Delphinus bairdii* (LACM 84240).

Condylobasal length	469
Rostral length	295
Rostral width	
At base	93
At ¼ length	60
At ½ length	55
At ¾ length	46
Premaxillae width at ½ length	27
Tip of rostrum to external nares	346
Tip of rostrum to internal nares	339
Preorbital width	167
Postorbital width	190
Zygomatic width	185
Width of external nares	45
Greatest width of premaxillae	70
Parietal width	156
Height of braincase	109
Length of braincase	114
Length of temporal fossa	72
Height of temporal fossa	53
Length of orbit	47
Length of antorbital process	42
Width of internal nares	55
Length of upper tooth row	246
Length of lower tooth row	237
Length of ramus	339
Height of ramus	74
Tooth width	3.7
Upper teeth, left	58
Upper teeth, right	55
Lower teeth, left	51
Lower teeth, right	52

pan-tropical spotted dolphin (*Stenella atennuata*) has a range of nine in total number of vertebrae. Thus, the variation noted in the long-beaked common dolphin is comparable to the range of variation found in another widely distributed delphinid.

Evans (1982) found that sexually mature animals from the eastern Pacific formed two discrete clusters; the few available specimens of *D. tropicalis* formed another cluster, with rostral lengths even greater than in the long-beaked form from the eastern Pacific. The sample size of *Delphinus* sp. specimens from the Indian Ocean is still small. One specimen from this region has a rostrum-to-zygomatic width ratio of 1.72, within the range of *D. capensis.* Another specimen from South African waters has a ratio of 1.87, near the lower range of values for *D. tropicalis.* If *D. tropicalis* is a valid species, then by using our criteria *D. capensis* also occurs in the Indian Ocean. The alternative hypothesis is that rostral length increases clinally in the Indian Ocean. The coloration of specimens of the nominal *D. tropicalis* is very similar to that of *D. capensis* from the west coast of Africa, and thus on this evidence *D. tropicalis* may be a junior synonym of *D. capensis.*

RE-DESCRIPTION OF *DELPHINUS DELPHIS*

Delphinus delphis Linnaeus, 1758
Delphinus vulgaris Lacépède, 1804
Delphinus nova-zealandiæ Quoy and Gaimard, 1830
Delphinus zelandæ [sic] Gray *in* Dieffenbach, 1843
D[elphinus] novae zeelandiæ [sic] Wagner 1846
Delphinus novae zealandiæ [sic] Gray 1850
Delphinus loriger Wiegmann, 1846
Delphinus fulvifasciatus Wagner, 1846
Delphinus janira Gray, 1846
Delphinus foresteri Gray, 1846
Delphinus albimanus Peale, 1848
Delphinus algeriensis Loche, 1860

HOLOTYPE. None.

TYPE LOCALITY. *Oceano Europaeo.*

DIAGNOSIS. The coloration consists of the basic criss-cross pattern with the thoracic patch relatively light gray to a medium golden-yellow in color, contrasting sharply with the very dark gray to black spinal field. The flipper-to-anus stripe is weakly formed or absent in most animals. One or more abdominal accessory stripes may be present. The flipper stripe does not angle toward the corner of the gape and fuses with the lip patch one-third to one-half of the gape length anterior to the corner of the mouth. The flipper stripe narrows distinctly anterior to the eye. There is always a wide, lightly pigmented region between the flipper stripe and the eye which extends anteriorly to the gape region. The eye patch and bridle are black, contrasting sharply with the adjacent thoracic patch. The white of the abdominal field extends above the flipper stripe to at least under the eye. Light gray to white patches with diffuse edges are found on the dorsal fin and flippers of many adults.

This species of common dolphin is relatively heavier and deeper-bodied anteriorly, with a more rounded melon that inserts onto the beak at a sharp angle when viewed in profile. The flippers and dorsal fin are larger than in *D. capensis.* The total length ranges from 172 to at least 223 cm in mature males and from 164 to 215 cm for mature females.

The tooth counts range from 42/41 to 54/53. The vertebral formula range is as follows: total, 74–80; thoracic, 13–16; lumbar, 18–24; caudal, 30–36. The ratio of rostral length to zygomatic width for adults ranges from 1.21 to 1.47 (Fig. 17).

DISTRIBUTION. This species is found in temperate and tropical waters of all major oceans and some seas (Fig. 19). In the North Pacific, *D. delphis* has been found from British Columbia south to Chile and out to 135°W. There are few records from the Gulf of California. In the western Pacific this species is documented from New Caledonia, New Zealand, and Japanese waters. There are records from north of Hawaii. Thus, the range may extend entirely across the tropical and temperate North Pacific. Records from the western North Atlantic range from at least Florida to Newfoundland and in the eastern Atlantic from northern Europe south to the west coast of Africa. This species is found in the Mediterranean and Black Seas.

GEOGRAPHICAL VARIATION. Accessory stripes are more common on animals from the North Atlantic. The distinct flank blaze found on animals from the North Atlantic is less conspicuous or absent on animals from the eastern North Pacific.

RE-DESCRIPTION OF *DELPHINUS CAPENSIS*

Delphinus capensis Gray, 1828
Delphinus sao Gray, 1846
Delphinus frithii Blyth, 1859
Delphinus major Gray, 1866
Delphinus moorei Gray, 1866
Delphinus microps Burmeister, 1866
Delphinus bairdii Dall, 1873
Delphinus bairdi [sic] Norris and Prescott, 1961

HOLOTYPE. Whole mount with skull (BM 41.1734) in the Natural History Museum (London).

TYPE LOCALITY. Cape of Good Hope.

DIAGNOSIS. The overall pigmentation pattern is more muted than that of *D. delphis.* The ground coloration consists of a criss-cross pattern with the thoracic patch relatively darker, not contrasting as sharply with the dark gray spinal field as in *D. delphis.* The flipper-to-anus stripe is weakly to strongly formed. The flipper stripe angles toward the corner of the mouth and fusees with the lip patch at the corner of the gape to one-third anterior along the gape or closely parallels the gape. The flipper stripe narrows moderately anterior to the eye. The eye patch does not contrast strongly with the adjacent

Table 11. Postcranial measurements (in millimeters) and meristics for the neotype of *Delphinus bairdii.*

Vertebral count	79
No. of lumbar vertebrae	22
No. of caudal vertebrae	36
First vertebra with vertical foramen	55
Last vertebra with transverse process	59
Last vertebra with neural arch	66
First vertebra with chevron	44
No. of chevrons	29
No. of vertebral ribs	15
No. of sternal ribs	8
Number of carpals and metacarpals	10
Number of cervicals fused	2
Last vertebra with facet	69
Widest vertebra	22
Width of atlas	138
Height of atlas	54
Length of atlas lateral process	30
Length of atlas dorsal spine	54
Height of first thoracic vertebra	52
Width of first thoracic vertebra	95
Length of first thoracic spine	34
Height of first lumbar vertebra	59
Width of first lumbar vertebra	211
Length of first lumbar spine	82
Length of first vertebral rib	142
Length of longest vertebral rib	294
Maximum width of manubrium	118
Height of scapula	140
Length of scapula	133
Maximum length of humerus	65
Maximum length of radius	84
Maximum length of ulna	73
Maximum width of humerus	44
Length of longest chevron	59
Length of longest pelvic	99
Width of widest vertebra	211
Length of centrum of first lumbar	30

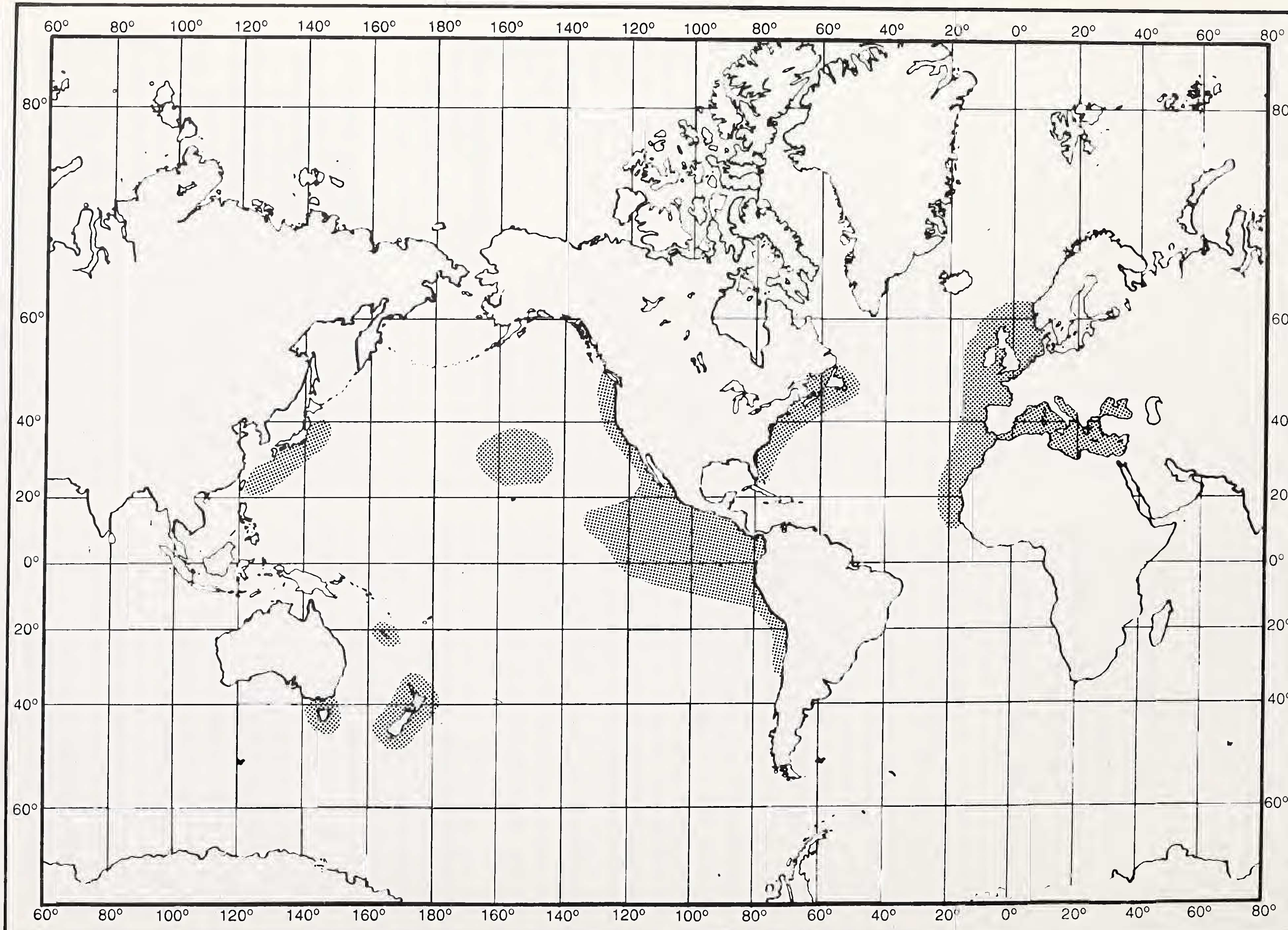

Figure 19. Approximate known distribution of the short-beaked common dolphin, *Delphinus delphis*, based on specimen records or sightings at sea identified by the diagnostic characters listing in this paper.

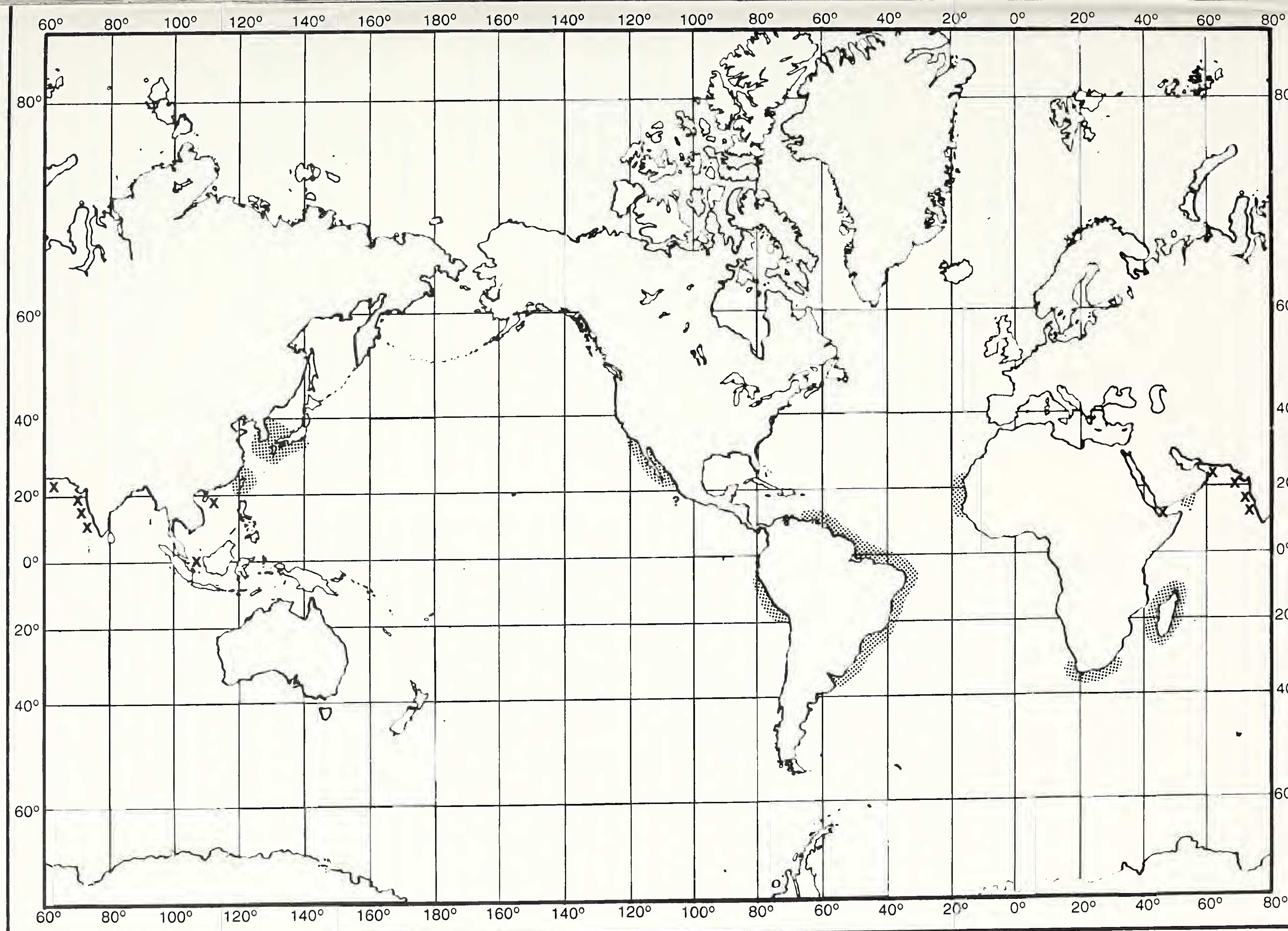

Figure 20. Approximate known distribution of the long-beaked common dolphin, *Delphinus capensis*, based on specimen records or sightings at sea identified by the diagnostic characters listed in this paper. Records of the nominal species *D. tropicalis* are represented by ×'s.

thoracic patch, and the white of the abdominal field rarely extends above the flipper stripe to below the eye. There may be a slight lightening of the flippers and dorsal fin of some adults.

This species is slightly more slender than *D. delphis,* with a flatter melon that inserts onto the beak at a more gradual angle when viewed in profile. Total length for mature specimens ranges from 193 to at least 222 cm for females and from 202 to 254 cm for males.

The tooth counts are 47–60/47–57. The vertebral formula is as follows: cervical, 7: thoracic, 14–17; lumbar, 18–23; caudal, 30–37, for a total of 72–80. The range of ratio of rostral length to zygomatic width is 1.52–1.77 (Fig. 18).

DISTRIBUTION. Restricted to nearshore tropical to temperate waters of some oceans (Fig. 20). In the eastern North Pacific, this species is recorded from Point Conception south to Peru, including the Gulf of California. In the western North Pacific, specimens have been recorded from the coasts of Korea, southern Japan, and Taiwan. In the Atlantic, records are available from coastal Venezuela south to the La Plata region of Argentina. This species is found along the west coast of Africa and in South African and Madagascan waters.

GEOGRAPHICAL VARIATION. Animals from the coast of southern Africa have lower vertebral counts (72–76) than animals from the eastern North Pacific (77–80). The animals from southern Africa also may have relatively longer beaks and an overall larger body size than animals from the eastern North Pacific.

SPECIATION. These two similar species currently have a parapatric distribution pattern. The narrow regions of sympatry seem to be limited to nearshore waters in several ocean basins. One question posed by such a pattern of distribution is whether speciation occurred sympatrically or allopatrically. Allopatric speciation still seems to be the most favored model (Mayr, 1963; Coyne, 1992). For large, vagile marine species, the most likely geographical isolation would involve entire ocean basins. Both the species of common dolphins are found primarily in tropical to moderate temperate waters, avoiding cold temperate zones. The Americas form a significant barrier to marine organisms between the Atlantic and Pacific Oceans, except for cold temperate forms that range around the tip of South America. Common dolphins are not recorded from this region (Goodall, 1978). The tip of southern Africa does not presently seem to be a barrier to temperate species between the Indian and Atlantic Oceans. The long-beaked common dolphin is found in the mixed waters of the Agulhas Current off the southeast coast of southern Africa (Ross, 1984). The cooling of waters during the Pleistocene could have resulted in southern Africa becoming a barrier to tropical and warm temperate species (Davies, 1963). This potential isolation of the Atlantic from the Indo-Pacific waters provides a geographical isolating mechanism for the speciation in common dolphins based on the allopatric model. Unfortunately, our data are not appropriate to test this hypothesis.

COMMON NAMES. Because of the nearshore sympatry, the vernacular names "offshore" to describe the short-beaked species and "neritic" or "Baja-neritic" for the long-beaked species are perhaps misleading. We suggest the common names "short-beaked common dolphin" and "long-beaked common dolphin" for the two species.

FUTURE RESEARCH

Common dolphins are a highly variable, widely distributed group consisting of two or possibly three species. Due to the complexity of this problem, we outline several areas for further research on this genus. First, more molecular-genetic (isozymes and DNA) evidence should be examined over a wide geographical range. Morphological analyses of specimens from other regions could address both interspecific and intraspecific variation of the two species of *Delphinus.* These studies will better define the species characteristics and population structure. Ecological and distributional studies need to be performed to elucidate non-morphological differences between the two species. Such ecological studies should focus on regions where the two species occur sympatrically and compare these to regions where only one species predominates, such as *D. capensis* in the Gulf of California.

The remaining existing type specimens for nominal species not here referred to either of the two species should be examined for maturity, relative rostrum length, and accurate tooth counts so their taxonomic status can be resolved.

Further sampling and a review of *D. tropicalis* is needed to determine whether it is an extremely long-beaked form along a cline of *D. capensis* found in the Indian Ocean or represents a third species of common dolphin.

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APPENDIX

List of specimens examined by catalog number. Museum acronyms are as follows: LACM = Natural History Museum of Los Angeles County, SDMNH = San Diego Museum of Natural History, SWFC = Southwest Fisheries Science Center. Three specimens are not identifiable to species due to a lack of sufficient accompanying data, specimen damage, or immaturity.

Delphinus delphis (n = 263)

LACM: 27088, 27090, 27099, 27100, 27401, 30860, 31491, 40127, 43471, 43474, 47147, 52320, 54065, 54066, 54068, 54070, 54071, 54073, 54074, 54075, 54179, 54180, 54454, 54461, 54558, 54565, 54568, 54619, 54621, 54622, 54625, 54626, 54627, 54628, 54629, 54631, 54632, 54633, 54634, 54635, 54636, 54640, 54641, 54642, 54643, 54644, 54732, 54736, 54738, 54741, 54743, 54744, 54745, 54746, 54747, 54748, 72181, 72278, 72279, 72280, 72281, 72282, 72283, 72287, 72288, 72293, 72299, 72333, 72334, 72335, 72336, 72337, 72338, 72339, 72340, 72341, 72342, 72343, 72344, 72345, 72346, 72347, 72348, 72349, 72350, 72351, 72352, 72353, 72354, 72355, 72356, 72357, 72358, 72359, 72360, 72361, 72362, 72363, 72364, 72365, 72366, 72367, 72368, 72369, 72370, 72371, 72372, 72373, 72374, 72375, 72376, 72377, 72378, 72379, 72380, 72381, 72382, 72383, 72384, 72385, 72386, 72387, 72388, 72389, 72390, 72391, 72392, 72393, 72394, 72395, 72396, 72397, 72398, 72399, 72400, 72401, 72402, 72403, 72404, 72405, 72406, 72407, 72408, 72409, 72410, 72411, 72412, 72413, 72414, 72415, 72416, 72417, 72418, 72419, 72420, 72421, 72422, 72423, 72425, 72426, 72428, 72454, 72468, 72495, 72496, 72497, 72498, 72503, 72505, 72543, 72587, 84007, 84039, 84041, 84042, 84045, 84046, 84050, 84054, 84067, 84074, 84078, 84090, 84094, 84096, 84105, 84106, 84108, 84109, 84118, 84129, 84131, 84132, 84134, 84136, 84137, 84138, 84139, 84140, 84143, 84155, 84170, 84172, 84173, 84177, 84178, 84181, 84196, 84197, 84199, 84207, 84208, 84209, 84216, 84225, 84226, 84227, 84229, 84230, 84231, 84232, 84255, 84257, 84261, 84279, 84280, 84282, 84283, 88904; **SDMNH:** 961, 2591, 19144, 19145, 20140, 20141, 20142, 21204, 21205, 21206, 21207, 21208, 21209, 21210, 21211, 21266, 21269, 22841, 22865, 23017, 23018, 23024, 23582, 23741, 23743, 23744, 23745, 23810; **SWFC:** 39, 40, 43, 44, 45, 48.

Delphinus capensis (n = 54)

LACM: 54067, 54463, 54618, 54735, 72284, 72285, 72286, 72289, 72424, 72427, 72429, 72430, 72469, 72494, 72499, 72500, 72502, 72544, 72593, 72595, 84009, 84021, 84040, 84071, 84077, 84083, 84091, 84092, 84100, 84121, 84125, 84127, 84130, 84135, 84163, 84183, 84184, 84185, 84220, 84221, 84223, 84228, 84233, 84236, 84239, 84240, 84241, 84254, 84256, 84258, 84278, 84281; **SWFC:** 39, 43.

Delphinus sp.

LACM: 72501, 84038, 84171.