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VARIATION OF SPOTTED AND SPINNER PORPOISE (GENUS STENELLA) IN THE EASTERN TROPICAL PACIFIC AND HAWAII

BY

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ABSTRACT

Spotted and spinner porpoise occur in coastal and offshore tropical waters of the eastern and central Pacific, as well as elsewhere in world tropical waters. They are important in the tropical yellowfin tuna fishery as indicators and aggregators of tuna. In the eastern Pacific, the range of both is a triangle with the base the coastline from Cabo San Lucas, Mexico to Columbia, and the apex extending seaward to about 10°N latitude, 145°W longitude.

Variation owing to ontogeny, sexual dimorphism, individual variation, and geographical differentiation in coloration, external size and shape, and skeleton are described in qualitative and quantitative terms, and three geographical races of the spotted porpoise, *Stenella attenuata* (Gray, 1846), and four of the spinner porpoise, *S. longirostris* (Schlegel,1841), (nomenclature is provisional) are defined.

SPOTTED PORPOISE

Spotted porpoise are unspotted at birth. During adolescence, dark spots appear on the ventrum, followed by appearance of light spots on the dorsum. The ventral spots enlarge and merge, giving the adult a uniform gray appearance below. There is no sexual dimorphism in the color pattern. Individual variation is greatest in the intensity of dorsal spotting. The dorsal spotting also varies geographically. Animals from the far eastern Pacific are on the average most heavily spotted. The Hawaiian form is nearly unspotted as an adult.

The analysis of ontogeny of external dimensions and shape of the spotted porpoise was based on 214 specimens. Changes in proportions during postnatal development are owing primarily to a disproportionate rate of growth of the section of torso between the umbilicus and anus, combined with an early surge in growth of the snout. The head, dorsal fin, and flippers stop growing at puberty, but total body length and size of the flukes continue to increase into maturity. Adult females are on the average about 10 cm smaller than males, but have relatively longer snouts, greater girth, and greater fluke span. Individual variation is greatest in length of the snout. Of the appendages, the dorsal fin is most variable. Geographical variation is pronounced. Specimens from very near the coast are larger than offshore specimens in all torso dimensions and in fluke span. The offshore animals have longer flippers. The Hawaiian form has a larger head than the offshore form.

The skull of the spotted porpoise was analyzed in terms of groups of functionally related measurements. The functional systems have different patterns of postnatal development. The hearing apparatus is most precocious, followed by the vision apparatus, the braincase, the breathing and sound-producing apparatus, and the feeding apparatus, in that order. Skulls with 5 or more layers in the postnatal dentine can be considered "adult" for purposes of inclusion in taxonomic series. Only the anteriormost elements of the postcranial skeleton develop as rapidly as the skull. The remainder of the skeleton shows protracted growth (until at least 8-10 layers are present in the teeth). In general, males have larger braincases and shorter, broader rostra than females. Individual variation in the skull is greatest in the feeding apparatus. Geographical variation was examined in 147 skeletal specimens. Animals from less than 25 km from the coast in the eastern Pacific (n = 19), including the holotype of *S. graffmani* Lönnberg,1934), have larger skulls and proportionately more robust feeding apparatuses than do specimens from the offshore tuna fishery. Separation in many measurements is complete, but some overlap is to be expected when more specimens of the coastal form become available. Hawaiian specimens have larger skulls than do the offshore animals of the eastern Pacific, but disparity in the proportions of the feeding apparatus is not as great as between the coastal and offshore forms. The differences among the three forms in skull proportions cannot be ascribed to simple heterogenic growth. Selection apparently impinges on a component of the variance of the feeding apparatus which is to some degree independent of a general size factor.

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The coastal, offshore, and Hawaiian forms of spotted porpoise belong to a single species. The name *S. attenuata* (Gray, 1846) – from unknown locality – is provisionally applied, following True's (1906) work on the Hawaiian form. Because of the unsettled state of the taxonomy (especially the nomenclature) of the genus, a trinomial can be applied only to one of the geographical races, namely the coastal form: *S. attenuata graffmani* (Lönnberg, 1934). The offshore and Hawaiian forms are referred to provisionally as *S. attenuata* subsp. A and B, respectively.

SPINNER PORPOISE

Body attenuation in the spinner is less during postpubertal development than in the spotted porpoise. Adults have proportionately larger appendages than do adults of the spotted porpoise. The dorsal fin is canted forward to varying degree in large males. Males and females do not differ in proportionate girth or size of appendages. The eastern Pacific specimens fall into three geographical series based on external size, shape, and coloration. "Costa Rican" spinners (coast of Central America) are longest and most attenuate. "Eastern" spinners (North American coast to about 800 km offshore) are intermediate, and "whitebelly" spinners (>800 km offshore) are greatest in girth and have the least canted dorsal fins. The Hawaiian spinner has a color pattern most like that of the whitebelly form but is larger.

The skeleton of the spinner porpoise develops in the same pattern as in the spotted porpoise, except that cranial development proceeds more rapidly. The adult configuration is reached when 4 layers have been laid down in the dentine, and postpubertal elongation of the axial skeleton is less protracted, rendering overall growth more isogonic. Sexual dimorphism is negligible. Patterns of individual variation are similar to those in the spotted porpoise. Among the geographical forms, the Costa Rican spinner is most divergent, having a very long, attenuate rostrum. Differences between the eastern and whitebelly series are comparatively slight. The Hawaiian spinner has a longer, broader skull than the eastern Pacific forms.

Taxonomy of the spinner porpoise is as confused as that of the spotted porpoise, but again there appears to be but a single species in the Pacific. The name *Stenella longirostris* (Schlegel 1841) is applied provisionally. The Costa Rican, eastern, whitebelly, and Hawaiian spinners deserve subspecific status within *S. longirostris*, but trinomials cannot be assigned until the taxonomy has been adequately reviewed on a worldwide basis. Skulls of unknown provenance can be classified with discriminant functions.

INTRODUCTION

The major objective of this study is to describe the variation among the porpoise of the genus *Stenella* in the eastern tropical Pacific. It is hoped this will contribute to a revision of the genus. For a variety of reasons, such a revision has been difficult to achieve in the past. The taxonomy of the genus is notoriously confused and difficult. As True (1889) stated,

> The genus [*Prodelphinus*, = *Stenella*] comprises a large number of nominal species, for the most part founded upon single skulls. Nearly every large collection contains a considerable number of skulls which may be assigned to this genus. It is found, however, in many cases that when a large number of these skulls is brought together they tend to form continuous series. The differences between the extremes of these series are often striking and perfectly definable, but in the middle they melt away and elude definition. From this fact and from the absence of material the task of revising the species of this genus is a very difficult and disheartening one.

An additional difficulty is that data on external appearance very seldom accompany skeletal specimens in collections, and further, whole specimens are often identified in the field on the basis of external characteristics alone. As Fraser (1966) noted, the situation encountered by the early cetologists still exists.

A primary goal of this study, therefore, was to obtain large series of the spotted and spinner porpoise of the genus *Stenella* occurring in the eastern tropical Pacific, and to describe their variation in coloration, external morphology, and osteology of the cranium and postcranial skeleton owing to development, sexual dimorphism, individual differences within schools, and geographical differentiation.

A complete revision of the genus will require examination of more material than was available to me (for example, the type specimens, most of which are in European collections, have not been examined). I found, however, basis for some comments on the taxonomy of the eastern Pacific forms. I also examined photographs and skeletal material of representatives of the genus from Hawaiian waters and make some comments about the taxonomic positions of those forms.

METHODS

EXTERNAL MEASUREMENTS

To meet logistical constraints imposed by sampling conditions aboard commercial fishing vessels, I reduced the list of standard external measurements for cetaceans compiled by the Committee on Marine Mammals of the American Society of Mammalogists (1961, K.S. Norris ed.) by about half, by (1) deleting those measurements that would be difficult to make accurately, such as maximum girth and length of the anal slit, and (2) deleting further measurements on the basis of intercorrelation, since highly correlated variables produce redundant information. Principal components analysis is a method of summarizing a large number of intercorrelated data in terms of a smaller number of independent axes. I applied principal components analysis to 20 measures of 10 animals in an attempt to evaluate the 20 variates in terms of their relative contributions to the "principal components" of the variance. I used a computer program BMDOIM prepared by the Health Sciences Computing Facility of the University of California Biomedical Center at Los Angeles (Dixon, 1965).

After the deletions, I was left with a list of 14 measurements to be made at sea, which I was confident were the best choices to be made from the original list of 34. All the measurements, including those made only ashore (see below) are listed in table 1 and shown in figure 1. Measurements were made point-to-point on the left side, with a large pair of calipers. The measurement methods proposed by the Committee on Marine Mammals of the American Society of Mammalogists (1961) for several applicable dimensions specify axial projections rather than point-to-point measurements. I feel that the point-to-point method is more precise, is readily applicable for smaller cetaceans, and yields values that are convertible into axial projections, provided that good photographs in several aspects have been made. Girths were measured with a cloth tape. In measuring flipper width, the flipper was pulled out from the body to a position at which the skin was neither depressed nor elevated at the anterior or the posterior insertion, and greatest width parallel to the body axis was then measured.

For specimens examined at sea, the suite of measurements includes the 14 selected as explained above. Measurements taken ashore include 8 additional measurements from those deleted to yield the at-sea list, but do not include measurements of the dorsal fin, flippers, and flukes because of obvious dehydration of these features owing to freezing.

Sample sizes also vary because of occasional mutilated animals.

To allow comparison of my point-to-point measurements with those taken by other workers, in some instances it was necessary to convert them to parallel-to-major-axis equivalents, using conversion coefficients derived from measurements of photographs of typical specimens.

MULTIVARIATE ANALYSIS OF SKELETON MEASUREMENTS

Discriminant analysis was used to study subspecific differences in the skull. This method uses linear compounds of a set of multiple measurements to discriminate between groups. First used by Fisher (1936), the method provides the best linear functions for discrimination, as proved by Rao (1952). The method was first used in analysis of morphology of cetaceans by Ichihara (1957) in his study of fin whales (*Balaenoptera physalus* L.) in the North Pacific and has been employed extensively in the systematics of other vertebrate groups (Jolicoeur, 1959; Jameson, Mackey, and Richmond, 1966).

Multiple discriminant functions are computed as the vectors associated with the latent roots of the determinantal equation

$$|W^{-1}B - \lambda I| = 0$$

where W = pooled within-group variance-covariance matrix, and B = total variance-covariance matrix T - W.

Table 1. External measurements of porpoise

1. Length, total (tip of upper jaw to deepest part of notch between flukes).
2. Length, tip of upper jaw to center of eye.
3. Length, tip of upper jaw to apex of melon (snout length).
4. Length of gape (tip of upper jaw to angle of gape).
5. Length, tip of upper jaw to external auditory meatus.
6. Center of eye to external auditory meatus (direct).
7. Center of eye to angle of gape (direct).
8. Center of eye to center of blowhole (direct).
9. Length, tip of upper jaw to blowhole along midline.
10. Length, tip of upper jaw to anterior insertion of flipper.
11. Length, tip of upper jaw to tip of dorsal fin.
12. Length, tip of upper jaw to midpoint of umbilicus.
13. Length, tip of upper jaw to midpoint of genital aperture.
14. Length, tip of upper jaw to center of anus.
15. Girth, on a transverse plane intersecting axilla.
16. Girth, on a traverse plane intersecting the anus.
17. Length, flipper (anterior insertion to tip).
18. Length, flipper (axilla to tip).
19. Width, flipper (maximum).
20. Height, dorsal fin (fin tip to base).
21. Width, flukes (tip to tip). [referred to below as "span of flukes"]
22. Distance from nearest point on anterior border of flukes to noth [referred to below as "width of fluke"]

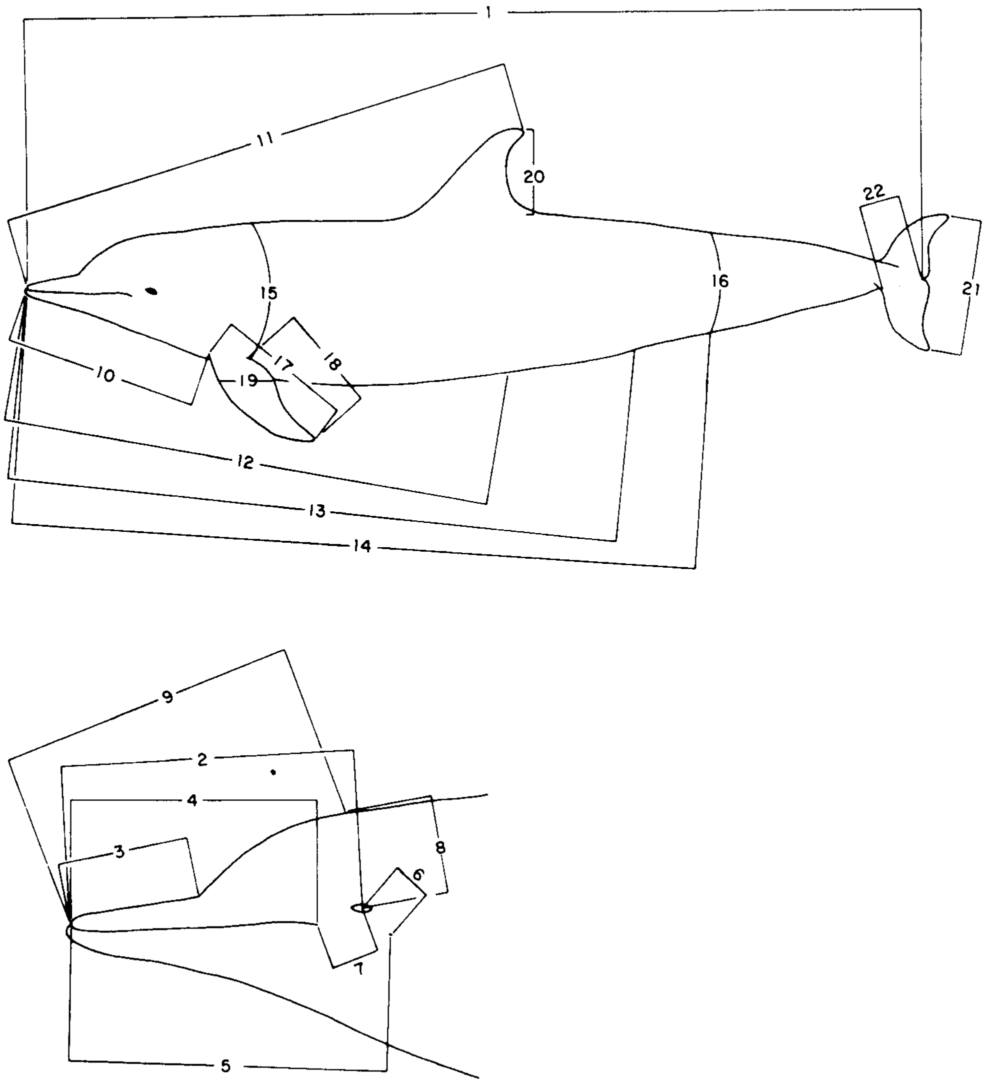


Figure 1. Point-to-point external measurements. Numbers refer to table 1.

The approach effectively accomplishes separation of "between" variance from "within" variance, standardizes it by "within variance," and then throws orthogonal axes through it in such a way that as much of it as possible is accounted for by the first axis, as much as possible of the remainder by the second axis, and so on. Excellent expositions of discriminant analysis have been presented by Cooley and Lohnes (1962) and Seal (1964). UCLA Biomedical Computing Program BMD07M, Stepwise discriminant analysis (Dixon, 1965) was used in this study.

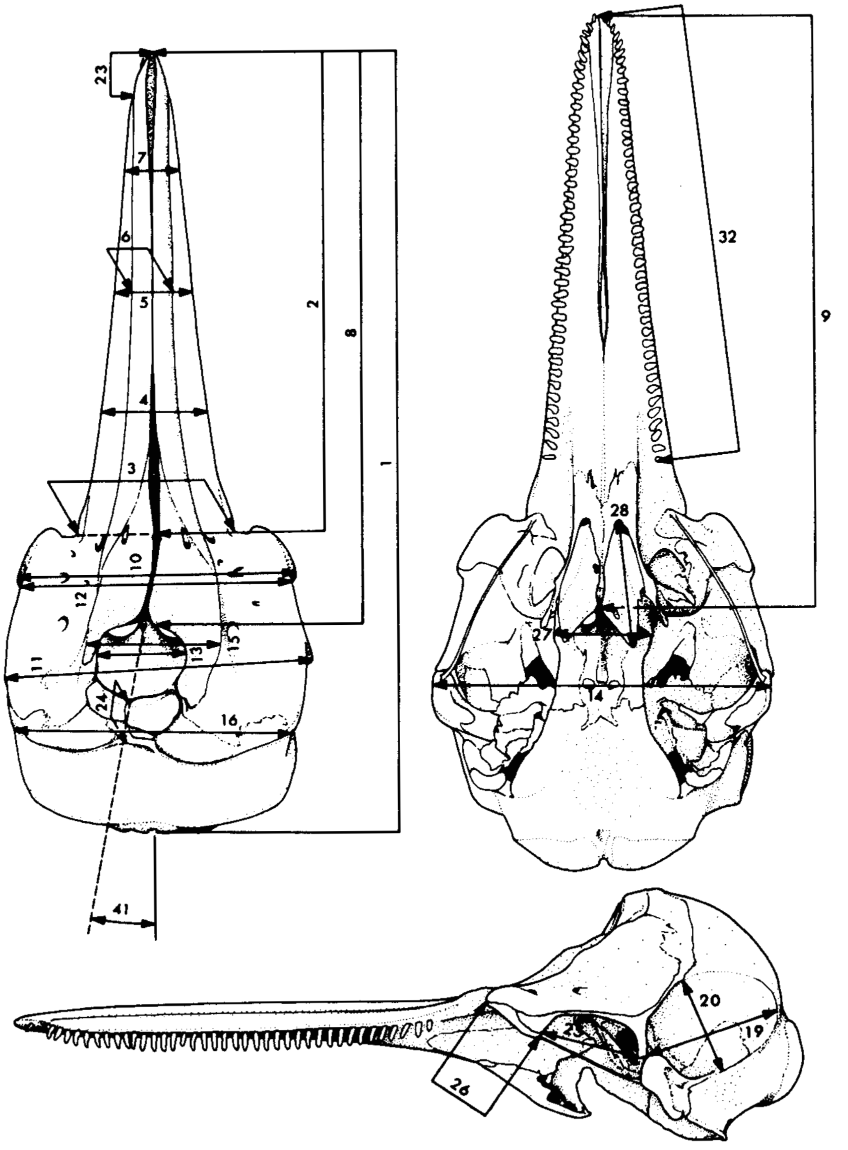


Figure 2. Measurements of the cranium. Numbers refer to table 2 (continued).

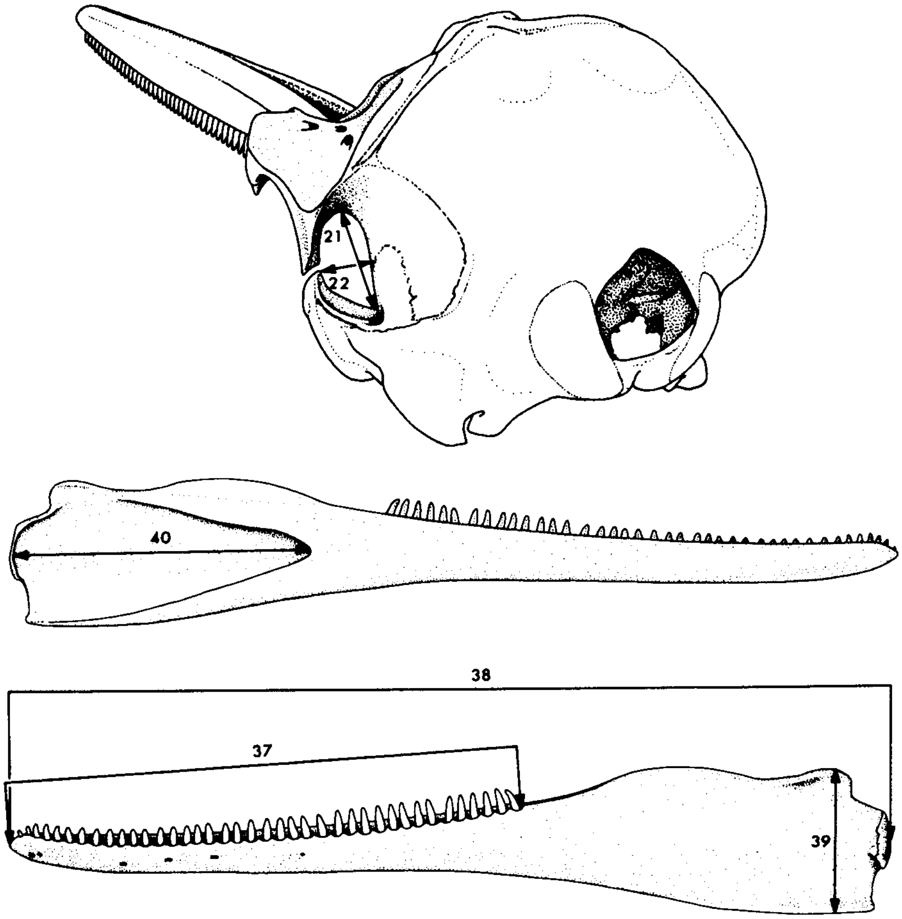


Figure 2 (continued). Measurements of the temporal fossa and mandible. Numbers refer to table 2 (continued).

SKELETON MEASUREMENTS AND MERISTICS

One hundred and nineteen (119) measurements and meristic observations were employed (table 2, fig. 2). The cranial measurements comprise those used by Fraser (1950 and 1966) plus several devised by me. The list of postcranial measurements and meristics is an amalgam of those used previously by Fraser and other workers in the taxonomy of *Stenella*, including Lütken (1889), Flower (1884), True (1889), and others. To facilitate automatic data processing, each was assigned a number and treated independently in lists and tables.

All linear measurements were taken with calipers and read to the nearest millimeter. Internal length of the braincase was measured with the interior extension of a set of dial calipers. Angle of asymmetry was measured with a flexible protractor. Additional observations were made on the state of fusion of the epiphyses of the manus and of the hyoid bones, on the degree of closure of cranial sutures, and on various qualitative aspects of the skeleton.

EXAMINATION OF LAYERS IN TEETH

To inspect layering, teeth were cut longitudinally with a diamond saw into sections 12/1000-inch (0.31 mm) thick. The sections were cleared in glyercine and alcohol, mounted under cover slips in balsam, and examined with transmitted light under a compound microscope. Postnatal dentinal layers were counted to the nearest half layer. The layering has not yet been securely calibrated but is certainly correlated with age. Neonatal animals have only the neonatal tooth with no evidence of layering in the dentine. Accumulation of layers is correlated with external and skeletal growth and the progress of skeletal fusion (described below) and with accumulation of corpora of ovulation in females (unpublished data). The layers are often difficult to read, and the values used here are the averages of several counts for each specimen. The several readings for each tooth were separated by days or weeks and teeth read each time without referring to the specimen numbers or the values obtained previously. Average accuracy is estimated at ± 1 layer for teeth with less than 5 layers, and ± 2 layers for teeth with more than 5 layers.

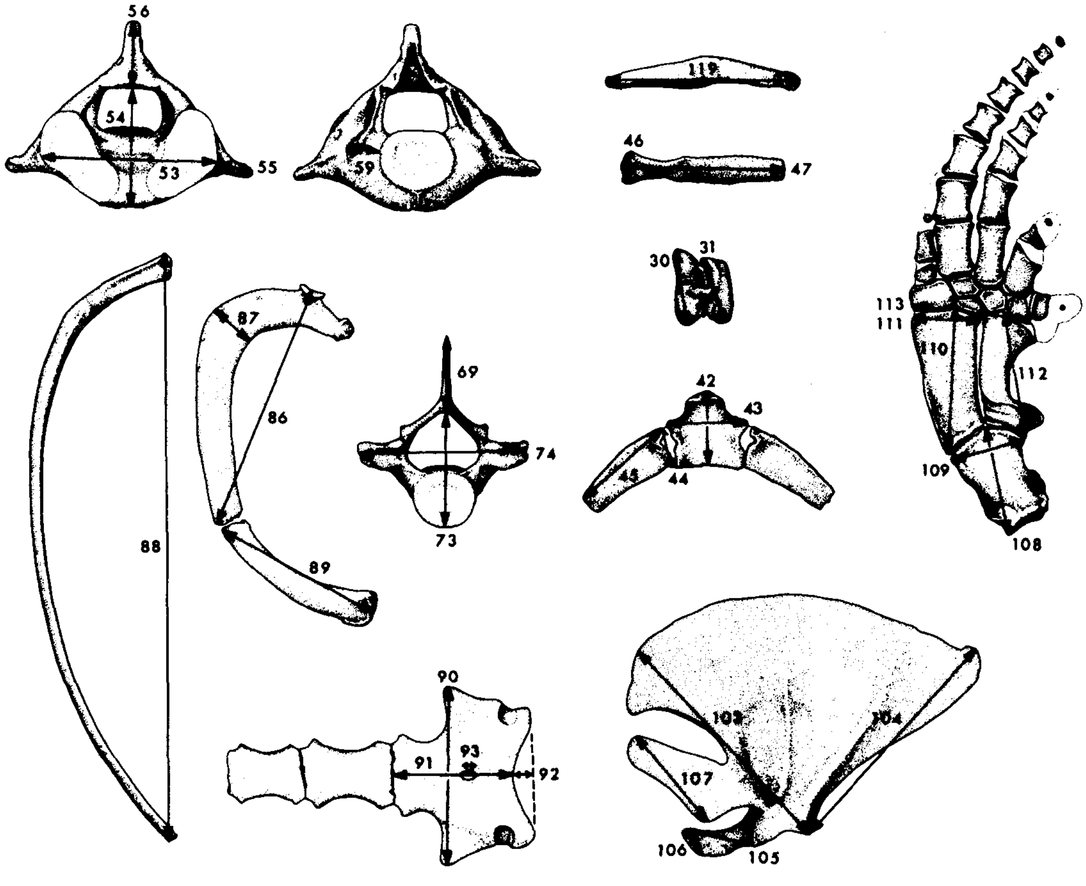


Figure 2 (continued). Postcranial skeletal measurements. Numbers refer to table 2.

Table 2. Skeletal measurements and meristics (continued)

1. Condylobasal length – from tip of rostrum to hindmost margin of occipital condyles.
2. Length of rostrum – from tip to line across hindmost limits of antorbital notches.
3. Width of rostrum at base – along line across hindmost limits of antorbital notches.
4. Width of rostrum at 60 mm anterior to line across hindmost limits of antorbital notches.
5. Width of rostrum at midlength.
6. Width of premaxillaries at midlength of rostrum.
7. Width of rostrum at 3/4 length, measured from posterior end.
8. Distance from tip of rostrum to external nares (to mesial end of anterior transverse margin of right naris).
9. Distance from tip of rostrum to internal nares (to mesial end of posterior margin of right pterygoid).
10. Greatest preorbital width.
11. Greatest postorbital width.
12. Least supraorbital width.
13. Greatest width of external nares.
14. Greatest width across zygomatic processes of squamosal.
15. Greatest width of premaxillaries.
16. Greatest parietal width, within postemporal fossae.
17. Vertical external height of braincase from midline of basisphenoid to summit of supraoccipital, but not including supraoccipital crest (not illustrated).
18. Internal length of braincase from hindmost limit of occipital condyles to foremost limit of cranial cavity along midline (not illustrated).
19. Greatest length of left posttemporal fossa, measured to external margin of raised suture.
20. Greatest width of left posttemporal fossa at right angles to greatest length.
21. Major diameter of left temporal fossa proper.
22. Minor diameter of left temporal fossa proper.
23. Projection of premaxillaries beyond maxillaries measured from tip of rostrum to line across foremost tips of maxillaries visible in dorsal view.
24. Distance from foremost end of junction between nasals to hindmost point of margin of supraoccipital crest.
25. Length of left orbit-from apex of preorbital process of frontal to apex of postorbital process.
26. Length of antorbital process of left lacrimal.
27. Greatest width of internal nares.
28. Greatest length of left pterygoid.
29. Greatest width of anterior overhang of supraoccipital crest (not illustrated).
30. Greatest length of bulla of left tympanoperiotic.
31. Greatest length of periotic of left tympanoperiotic.
32. Length of upper left tooth row – from hindmost margin of hindmost alveolus to tip of rostrum.
33. Number of teeth – upper left.
34. Number of teeth – upper right.

Table 2 (continued). List of skeletal measurements and meristics (continued)

35. Number of teeth – lower left.
36. Number of teeth – lower right.
37. Length of lower left tooth row – from hindmost margin of hindmost alveolus to tip of mandible.
38. Greatest length of left ramus.
39. Greatest height of left ramus at right angles to greatest length.
40. Length of left mandibular fossa, measured to mesial rim of internal surface of condyle.
41. Deviation of skull from symmetry in dorsal view, in degrees.
42. Length of basihyal along midline.
43. Greatest width of basihyal.
44. Greatest width of left thyrohyal proximally.
45. Greatest length of left thyrohyal.
46. Greatest width of left stylohyal.
47. Greatest length of left stylohyal.
48. Number of thoracic vertebrae, defined as equal to number of ribs on side with greatest number.
49. Number of lumbar vertebrae.
50. Number of caudal vertebrae. The very small segment at the tip of the column was counted as a vertebra. If this segment was missing, the column was considered to be damaged, and the count was not made.
51. Total number of vertebrae.
52. Number of fused cervical vertebrae.
53. Greatest width of articulating surface of atlas.
54. Height of atlas – from internal anterodorsal margin of neural canal to bottom of anterior face of body.
55. Length of lateral process of atlas – from margin of anterior articulating surface to farthest point at end of process.
56. Greatest length of neural spine of atlas.
57. Height of dorsal ridge of atlas in anterior view (not illustrated).
58. Length of right dorsolateral spine of atlas (not illustrated).
59. Length of left lateral process of axis – from margin of posterior articulating surface to distal end of process.
60. Number of cervical vertebrae with incomplete neural arches.
61. Cervical vertebra on which left ventrolateral process reaches greatest development.
62. Vertebra on which first vertical perforating foramen appears.
63. First vertebra with greatly reduced metapophyses.
64. Last vertebra with distinct transverse processes.
65. Last vertebra with distinct neural process.
66. First vertebra with unfused epiphysis.
67. Last vertebra with unfused epiphysis.
68. First caudal vertebra with vertical neural spine.
69. Length of neural spine of first thoracic vertebra – from anterodorsal margin of neural canal to tip of spine.

Table 2 (continued). List of skeletal measurements and meristics (continued)

70. Length of neural spine of second thoracic vertebra.
71. Length of neural spine of tenth thoracic vertebra.
72. Length of neural spine of last thoracic vertebra.
73. Height of first thoracic vertebra – from internal anterodorsal margin of neural canal to bottom of anterior face of body.
74. Greatest width of first thoracic vertebra – across lateral processes.
75. Height of first lumbar vertebra (not illustrated).
76. Greatest width of first lumbar vertebra (not illustrated).
77. Length of 23d centrum, exclusive of epiphyses, along ventral midline (not illustrated).
78. Number of vertebral ribs – left.
79. Number of vertebral ribs – right.
80. Number of two-headed ribs – left.
81. Number of two-headed ribs – right.
82. Number of floating ribs – left.
83. Number of floating ribs – right.
84. Number of sternal ribs – left.
85. Number of sternal ribs – right.
86. Greatest length of first left vertebral rib.
87. Width of first left vertebral rib at apex of proximal curvature.
88. Greatest length of longest left vertebral rib.
89. Greatest length of first left sternal rib.
90. Greatest width of manubrium.
91. Length of manubrium along midline.
92. Depth of anterior notch of manubrium.
93. Length of foramen in manubrium.
94. Number of mesosternal elements.
95. Number of mesosternal elements fused.
96. Number of chevron bones.
97. Number in foremost series of fused chevron bones.
98. Vertebra bearing first chevron bone.
99. Vertebra bearing last chevron bone.
100. Greatest length of left half of first chevron bone (not illustrated).
101. Greatest length of left half of largest chevron bone (not illustrated).
102. Greatest length of left half of last chevron bone (not illustrated).
103. Height of scapula – from posterior margin of glenoid fossa to coracovertebral angle.
104. Length of scapula – from posterior margin of glenoid fossa to glenovertebral angle.
105. Greatest length of coracoid process – from anterior margin of glenoid fossa.
106. Greatest width of coracoid process.
107. Greatest width of metacromion process – from apex of ventral curvature to vertebral apex.
108. Greatest length of humerus, measured on ventral side of flipper.
109. Greatest width of humerus distally.
110. Greatest length of radius.
111. Greatest width of radius distally.
112. Greatest length of ulna

Table 2 (continued). List of skeletal measurements and meristics

113. Transverse breadth of proximal row of carpals.
114. Number of ossified phalanges in first digit.
115. Number of ossified phalanges in second digit.
116. Number of ossified phalanges in third digit.
117. Number of ossified phalanges in fourth digit.
118. Number of ossified phalanges in fifth digit.
119. Greatest length of left pelvic rudiment.

The spotted porpoise is of great economic importance in the eastern tropical Pacific. A spotted porpoise is the form most sought after by American fishermen in their quest for tuna associated with porpoise schools (Alverson, 1963; Perrin, 1968, 1969, 1970*b*; Perrin and Hunter, 1972).

American fishing vessels range the entire eastern Pacific in their search for tuna. Logbooks maintained by the tuna captains show that thousands of net sets made in the Commission Yellowfin [tuna] Regulatory Area (CYRA) in the period 1963-1970 were noted as made on fish associated with schools of spotted porpoise (fig. 3, unpublished data, Inter-American Tropical Tuna Commission). Logbook data are not available for the portion of the eastern Pacific outside the CYRA. Figure 4 shows all confirmed locality records for spotted porpoise in the eastern Pacific, including the area outside the CYRA. This includes published records, localities of museum specimens, localities of material collected during government studies, and sighting records collected by government scientists aboard research vessels and tuna seiners. The distribution appears to be bounded on the north by the southwestward extension of the cold California Current and on the south by the northwestward extension of the cold Peru Current (South Equatorial Current). There is an apparent gap between the westernmost limits of the recorded range (at about 145°W) and Hawaiian waters, where a spotted porpoise occurs (referred to *S. attenuata* [Gray, 1846] by True [1906] and subsequent authors). Despite extensive exploratory fishing by commercial tuna vessels and considerable activity in and through the area by government research vessels based on the West Coast and in Hawaii, there have been no recorded sightings of spotted porpoise in this region. The break in distribution, if real, is approximately 700 miles wide. Spotted porpoise also occur to the south of Hawaii in the Phoenix Islands (Peale, 1848) and in the Marquesas (personal communication from K. S. Norris), but the extent of continuity, if any, of these populations is unknown.

HISTORICAL REVIEW

Atlantic Ocean

Linnaeus (1758) described the genus *Delphinus* ("*Dentes in maxilla utraque. Fistula in capite*") and the species *D. delphis* ("*D. corpore oblongo subtereti, rostro attenuato acuto*") from "Oceano Europaeo," based on illustrations by earlier workers. The first indication that more than one species of long-snouted toothed cetacean exists in the Atlantic came when A. J. Pernetty (1769), in an account of a voyage to the Falkland Islands, described a spotted porpoise captured 27 days after his vessel had passed Boa Vista in the Verde Cape Islands [16°44'S, 35°10'W fide Fraser, 1950], as follows (from the 1773 translation):

> On the 20th of November [1763] at eight in the morning we took a porpoise of about a hundred weight. I painted him from the life, but without preserving any proportion to his bulk. For the figure of him see the plate annexed . . . . The porpoise, which I am describing here (and all those we took were of the same kind) is, as I apprehend, of that species, which are called *moines der mer* [monks of the sea]. The fore part of the head terminates in a roll

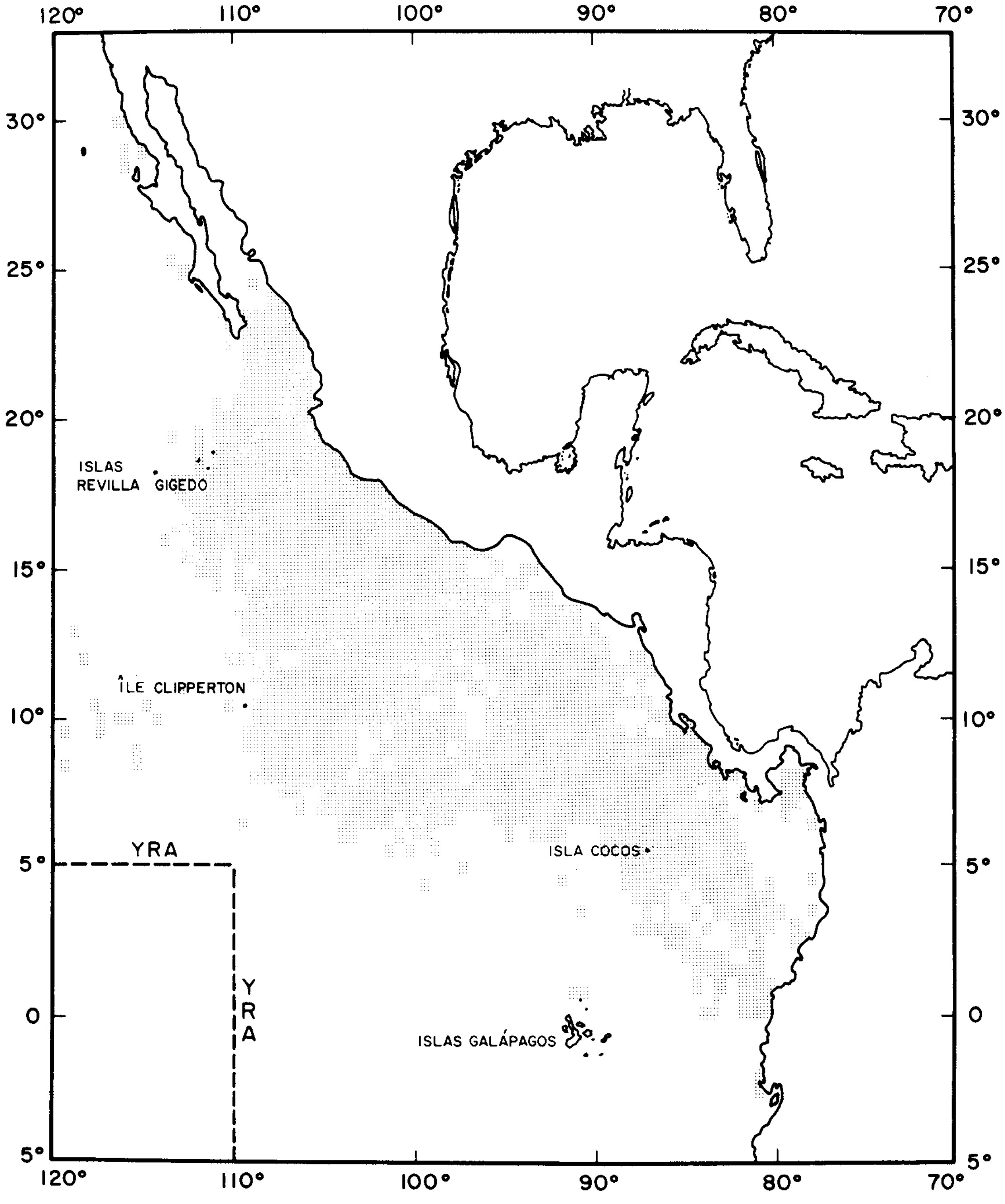


Figure 3. Distribution of purse-seine sets on spotted porpoise in the Commission Yellowfin (tuna) Regulatory Area, 1963-1970, by 1/2-degree squares. From tuna boat logbook data provided by the Inter-American Tropical Tuna Commission.

> near the beginning of the snout or beak, answering to the border of the cowl. The black is blackish, and the belly of a grey, consisting of a pearl colour, somewhat inclining to yellow, interspersed with black and iron-grey spots.

Pernetty's figure shows a spotted porpoise much resembling a large subadult of the offshore spotted porpoise of the eastern Pacific in shape of dorsal fin and in size, density, and distribution of spots, with a band of pigment extending from flipper to gape (see Perrin, 1970*a*). Bonnaterre (1789) considered the spotted animal to be merely a variety of *D. delphis.* Blainville (in Desmarest, 1817) described *Delphinus Pernettensis* on the basis of Pernetty's description and figure. Desmarest later (1820-1822) emended the name to *D. Pernettyi.*

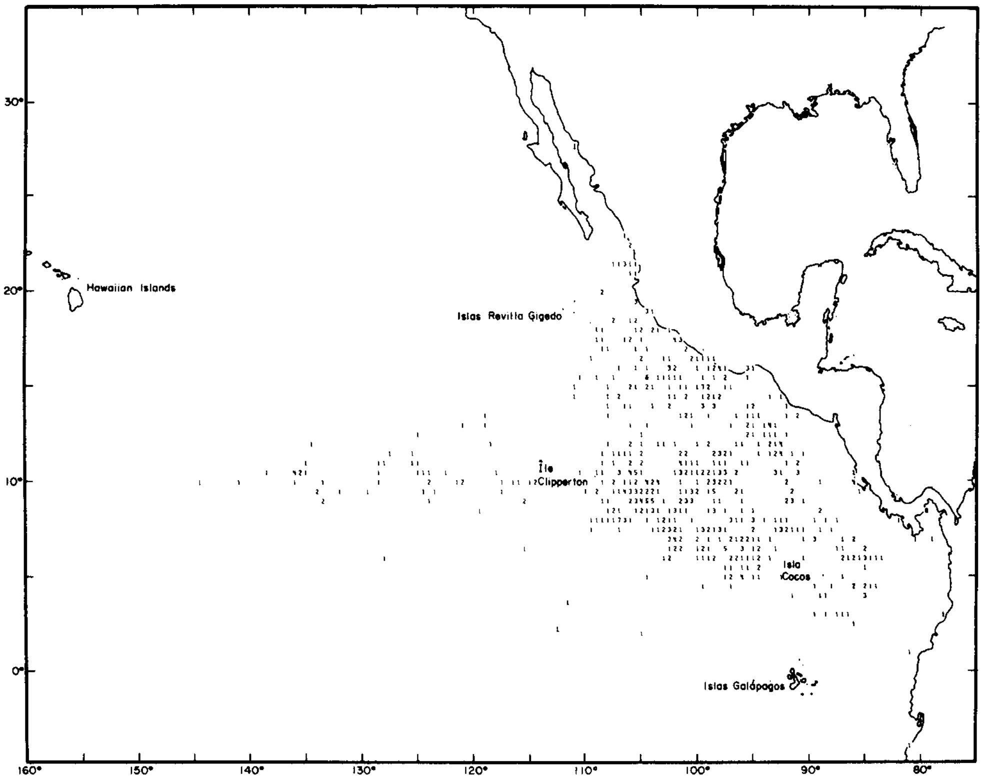


Figure 4. Distribution of locality records of spotted porpoise in the eastern tropical Pacific, from museum specimens, sightings from research vessels, and sightings by scientific observers aboard commercial fishing vessels. Numbers represent records per 1/2-degree square.

Pernetty probably observed two species of porpoise on his voyage. Six days out of the Cape Verde Islands, he observed a school of "some hundred porpoises" that "leaped at least three or four feet high, and turned round not less than three times in the air, as if they had been on a spit." Such gyrations on a longitudinal axis are typical of the spinner porpoises and not of the spotted porpoises. Thus, it appears that despite Pernetty's thinking the contrary, the animal he painted was almost certainly not of the same species as those seen 21 days before and a thousand miles to the north. All authors who have since discussed Pernetty's animal, including Hershkovitz (1966), have assumed that a single species was involved and that Pernetty saw spotted animals at the first position mentioned in his account (near Cape Verde) as well as at the second (some 750 miles off Brazil at 16°S). Van Bree (1970a), however, has determined that Pernetty in the second edition of his work (1770) stated that the specimen was taken between the islands Boa Vista and Maio of the Cape Verde Islands and that only a seabird was taken off Brazil. Van Bree also moved that the specific names *pernettensis* de Blainville 1817 and *pernettyi* Desmarest 1820 be suppressed by the International Commission in Zoological Nomenclature, as *nomina oblita.*

Following Pernetty's account, the next published mention of a long-snouted porpoise distinct from *D. delphis* was by G. Cuvier (1812) who, in a report on cetaceans taken on the coast of France, stated (p.9): *"Or, le Muséum possède plusiers tètes de deux vrais dauphins à museau grèle, differentes de celles du delphis et du tursio.*

Les uns ont les mêmes dents grèles et pointues que le delphis, mais seulement au nombre de 35 partout, en totalité 140. Leur museau est déprimé comme celui du delphis, mais un peu plus court à proportion. Nous n'avons acune notion de l'animal entier.

And on p. 14:4°. *Le dauphin vulgaire à 180 dents, D. delphis, et 5°. cet autre dauphin dont nous avons parlé ci-dessus à 140 dents ou environ, que nous appellerons provisoirement D. dubius."*

These two brief paragraphs constitute the description of *D. dubius.* G. Cuvier neither figured the species nor designated type specimens. Such was not the usual practice in his time. The identity of the skulls examined by him remains in question. The type locality also remains unknown, since Cuvier stated only that the skulls were in possession of the Paris Museum, implying but not stating explicitly (seemingly because of ignorance of their origin) that they had come from the coast of France. In the 1817 edition of his *Le Règne Animal* G. Cuvier appended a footnote to the account of *Delphinus delphis L.: "J'ai plusiers têtes de dauphin qui ont constamment trente-sept dents partout, et qui appartiennent probablement à une espèce particulière."*

Desmarest (1817) treated *D. dubius,* apparently after having personally examined G. Cuvier's material and stated that the tooth count was 37 to 38 in each side of each jaw for a total of 148. It can be assumed that he examined the same skulls described by Cuvier, because Cuvier specified "140 dents ou environ" and later amended his tooth count to 37. He also noted that the skulls were in general smaller than those of *D. delphis,* with a finer, more pointed and conical rostrum not inflated in the middle.

In the second edition of *Ossemens Fossiles* (1823), G. Cuvier supplemented his description of *D. dubius* by stating that the rostrum is narrower and flatter underneath than that of *D. delphis* and that the vomer is slightly exposed longitudinally between the premaxillaries and maxillaries (the latter condition, however, sometimes is also present in *D. delphis).* He also included cranial measurements for *D. dubius.*

Lesson (1828) stated that *D. dubius* lives on the coasts of Europe, presumably on the basis of Cuvier's inclusion of the description in a report on cetaceans taken on the coast of France. In the 1829 edition of *Le Règne Animal*, G. Cuvier again asserted, without specification, that the form occurs in European waters. He also stated that it resembles *D. delphis* in coloration.

F. Cuvier in 1829 (in St. Hillaire) published a color plate and description of a specimen from Cape Verde that he referred to *D. dubius*, but it is not known whether G. Cuvier concurred in the decision. The animal shown ("*quatre pieds six pouces*" long) very much resembles a young subadult or large calf of the spotted porpoise of the eastern Pacific, yet unspotted, with a definite flipper stripe to the gape. F. Cuvier later (1836) said that this specimen was used by Dussumier as the basis for description of *D. frontalis* (description written by G. Cuvier, 1829) before he knew of the existence of *D. dubius*, and that the skull corresponded with *D. dubius* in tooth count (36 vs. 35-38). With this statement, F. Cuvier in effect placed *D. frontalis* (known to be from Cape Verde) in the synomymy of *D. dubius* (unknown locality). His brother apparently did not agree with this, because when he presented Dussumier's description (G. Cuvier, 1829), he stated that *D. frontalis* is similar to *D. dubius* but differs in tooth count and coloration.

Pucheran (1856*a*) published external measurements of the type specimen of *D. frontalis*. The total length (144 cm) agrees well with the idea that the animal was a subadult. True (1889) measured a single skull in the Paris Museum (no. a3035), presumably the type of *D. frontalis*.

F. Cuvier (1829), in the same paper in which he described the specimen from Cape Verde which he referred to *D. dubius*, published a plate of another, similar animal from near the Cape Verde Islands, harpooned by Dussumier, which he called "*dauphin bridé No. 5*," describing the color pattern as follows,

> *Il est nôiratre sur le dos: cette couleur pâlit vers les flancs, et le ventre est blanc. Sa tete est noire en dessus; ces côtés ont une teinte cendrée, et une bande plus sombre forme sur les joues une moustache qui s'étend de l'angle de la gueule jusqu'au-delá des yeux.*

The plate, subsequently often reprinted, does not jibe very well with the description; later (1836) F. Cuvier stated that only the description was accurate. If, however, the lower margin of the dark field anteriorly can be taken to represent the "band on the chops," the pattern can be construed to match that of the spotted porpoise of the eastern Pacific, with a stripe from flipper to gape passing below the eye. This feature, according to F. Cuvier, prompted Dussumier to give the animal the name *Froenatus* ("*bridé*"). Length was "*4-1/2 pieds*," again that of an unspotted small subadult or large calf of the eastern Pacific spotted porpoise. The type specimen of *D. froenatus* (F. Cuvier) may be the second skull in the Paris Museum labeled *P. froenatus* (no. a3033) and measured by Gray (1850) and True (1889).

Gray (1866*b*) described still another species, *Clymene punctata*, from the Cape Verde Islands (16°40'N, 21°W), including a figure of the external appearance of the type specimen, with external and skull measurements. The animal was 6 feet long and spotted. The flipper band is not apparent in the figure, but the other elements of the color pattern are a close match to the spotted porpoise of the eastern Pacific (compare with fig. 5). The tooth counts ($\frac{40}{38}\Big|\frac{40}{38}$) and skull measurements given by Gray also correspond closely. Unfortunately, the holotype was destroyed during World War II (fide Fraser, 1950).

Gray (1865) based *Steno capensis* on a skull from the South African Museum that presumably came from the Cape of Good Hope region and possibly from the South Atlantic. He stated that the skull was "somewhat like that of *Steno attenuatus* [described by Gray in 1846 from a skull from an unknown locality]." In the same paper he referred another skull from the South African museum to *Delphinus doris*, Gray (1846), described from an unknown locality.

Gervais in van Beneden and Gervais (1868-1880), erected the genus *Prodelphinus* to include all the species with *Delphinus delphis*-like skulls but with flat palates, including the forms with spots and 35 to 45 teeth under discussion here and subsumed by Flower (1884) in a section "D" of *Clymenia* Gray, 1868*a* (= *Clymene* Gray, 1864).

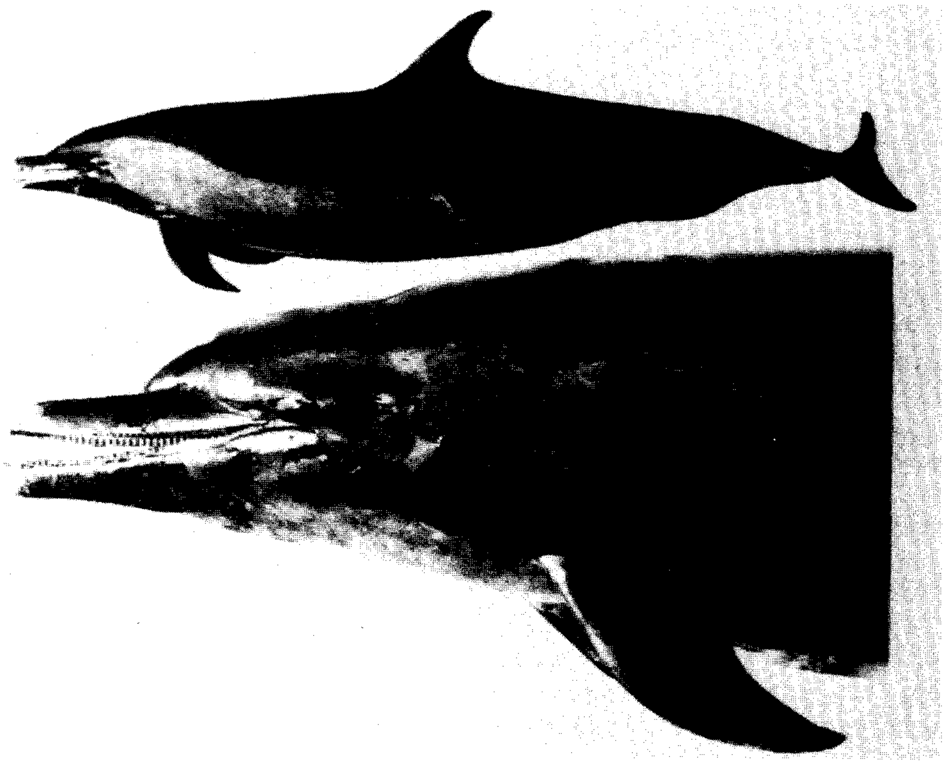


Figure 5. Two spotted porpoise from the far-offshore portion of the range of the spotted porpoise in the eastern Pacific: (top) field no. WFP 49 (USNM no. 396028), adult male, 197 cm, from 3°20′ N latitude, 110°44′ W longitude; (bottom) no. WFP 48 (USNM no. 396027), adult male, 190 cm, from 9°28′ N, 129°18′ W. Specimens photographed after having been frozen for several months and thawed in water. Note mottled appearance below and strong contrast between cape and lateral field.

True (1885) described a spotted porpoise from off Pensacola, Florida, in the Gulf of Mexico and referred it to *Prodelphinus doris* (Gray). He stated that the skull was "identical" with that of *D. palgiodon* Cope, 1866, described from an unknown locality, but that *D. plagiodon* should be a synonym of *P. doris.* True later (1889) reversed himself and separated *P. plagiodon* from *P. doris* on the basis of larger size of the skull and teeth and difference in color. In this paper he also described an individual captured off Hatteras, North Carolina. The plate of the 1884 specimen shows a very heavily spotted animal (216 cm long) with large dorsal fin and rather massive snout. A photograph of the same specimen was reproduced in the 1889 paper. In neither illustration is the position of the flipper stripe clearly discernible, although a slight increase in spot density suggests that it ran from flipper to eye.

Lütken (1889) reported on the skeletons of 16 animals, referred variously to *P. clymene* (Gray, 1850), *P. alope* (Gray, 1846), *P. doris*, and *P. attenuatus*, mostly from the tropical Atlantic. Of the six from known localities, the northernmost specimen (erroneously referred to *P. alope*, a spinner species) came from the mouth of the Bay of Biscay, lending credence to G. Cuvier's (1812) claim that *D. dubius* occurs on the coast of France. Another specimen was from outside the Azores and the remaining four were from between Africa and South America. He illustrated two varieties of "*Prodelphinus doris*." One is heavily spotted, and if a ground pattern is present it is obscure. The other is unspotted and corresponds in pattern, including presence of flipper band to gape, to a subadult or calf of the eastern Pacific spotted porpoise, to the species descriptions of *D. frontalis* and *D. froenatus* F. Cuvier (in St. Hillaire, 1829) and to the description of an animal from Cape Verde referred by F. Cuvier (in St. Hillaire, 1829) to *D. dubius* G. Cuvier.

I mention True's (1889) review of the *Delphinidae* here in the section on the Atlantic because his worldwide coverage of the spotted porpoise includes very complete review, summary, and synthesis of all the above and constitutes a landmark in the taxonomy of the group. He recognized three species from the Atlantic: *P. plagiodon* (Cope), *P. froenatus* (F. Cuvier), and *P. attenuatus* (Gray), "conjointly" considered with *P. malayanus* (Lesson 1828).

The next significant paper dealing with the taxonomy of the spotted porpoises in the Atlantic, that of Fraser (1950) appeared more than 60 years after True's work. Beddard's (1900) account and Fraser's earlier review (in Norman and Fraser, 1937) were based on True's findings. Oliver in 1922 revived *Stenella*, a subgenus of Gray (1866), as a generic designation to replace *Prodelphinus* Gervais.

Fraser reported on a spotted animal taken off the coast of Gabon (0°15′N, 8°44′E). The 2-meter animal did not differ in color pattern from spotted porpoises of the eastern tropical Pacific. Fraser thought the specimen to be unique in its white snout tip. As I have demonstrated (Perrin, 1970*a*), this feature is an aspect of individual and/or among-school variation and occurs in spotted porpoises around the world. Other discrepancies noted by Fraser between the color patterns of this animal and those of *Stenella frontalis, S. froenata, Clymene punctata,* and various specimens from the eastern Atlantic referred to these and other species on the basis of coloration and/or skeleton, can be laid to ontogenetic variation (see Perrin, 1970*a*) and/or inadequacy of early descriptions and illustrations.

Fraser classified the specimen on the basis of cranial characters, in the process accomplishing an exhaustive review of relevant museum materials. He eliminated the types of *Delphinus plagiodon* and *Prodelphinus graffmani* Lönnberg from consideration because of large size, and *Delphinus clymene* Gray (= *Clymene normalis* Gray) because of very small posttemporal fossae. This left 31 skulls (15 from known localities), including the types of *Clymenia doris, Delphinus froenatus* (including the skull considered by G. Cuvier to belong to *D. dubius* G. Cuvier), *D. frontalis, Steno attenuatus,* and *S. capensis.* He divided this series of skulls into two groups on the basis of a dichotomy in the ranges of several measurements expressed as percent of condylobasal length. He provisionally assigned the groups to *S. attenuata* (Gray) and *S. frontalis* (G. Cuvier), making the two species sympatric in the eastern Atlantic. This division was close to that arrived at by True (1889); Fraser placed *D. froenatus* in the synonymy of *S. frontalis.* He later, however, obtained 39 skulls "remarkably similar in their general appearance and measured proportions" from Saint Helena (Fraser, 1966) that bridged the dichotomy and threw the situation back into its original long-standing state of confusion (Best, 1969).

Hershkovitz (1966) followed Fraser (1950). But he revived *Stenella dubia* (= *Delphinus dubius* G. Cuvier) on the basis of Fraser's tentative association of skulls labeled as such in the Paris Museum with the *S. frontalis* group. Rice and Scheffer (1968) recognized only a single species of spotted porpoise worldwide, *S. dubia,* on the basis that "Rice has seen in a single school animals showing all described color variations; no consistent cranial differences have been described."

Density and distribution of spots demonstrably vary ontogenetically and geographically within single species (Perrin, 1970*a*, and section below on coloration). Other elements of color pattern, however, are remarkably constant within recognized delphinid species and species groups. In all bottlenose porpoise (*Tursiops* spp.), the flipper band runs from flipper insertion to eye. In all "common dolphins" (*Delphinus* spp.), the flipper band runs to the gape, and there is a distinctive crisscross effect on the midlateral body, induced by overlap of the cape and ventral field (Perrin, 1972*b*). In the spinner porpoises the band runs to the eye as in *Tursiops* (Perrin, 1972*b*), and section on spinners below). Based on this state of affairs in better-known animals, there would seem to be two species of spotted porpoise in the Atlantic. First, there is a large form of relatively low variability in the western Atlantic, Gulf of Mexico, Caribbean, and possibly eastern Atlantic (Cadenat, 1959). In this species, the flipper band runs to the eye, as in *Tursiops* and the spinners, and there is a spinal blaze (terminology of Mitchell, 1970). This form has commonly been referred to *S. plagiodon* (Cope), on the basis of True's 1889 decision. Second, a form more variable in size and spotting occurs throughout the tropical and sporadically in the warm temperate Atlantic. In this species the flipper band runs to the gape, as in the eastern Pacific spotted forms (Perrin, 1970*b* and above) and in the types of *S. pernettyi* (Desmarest), *S. frontalis* (Dussumier, in G. Cuvier, 1829) and *S. froenata* (F. Cuvier in St. Hillaire, 1829). All clear illustrations and unpublished photographs that I have seen of spotted porpoise from other parts of the world show the flipper band extending to the gape, indicating that first species mentioned above may be limited to the Atlantic. Both these distinct forms may be seen in Mitchell (1970), as "*Stenella plagiodon*" and "*Stenella* sp.," respectively. There are indications that the forms overlap in their geographical ranges but are found in different habitats (Caldwell and Caldwell, 1966; Caldwell et al., 1971). Schmidly, Beleau, and Hildebran (1972) referred animals from the same area of the Gulf of Mexico to both *S. plagiodon* and *S. frontalis.*

Indian and Pacific Oceans

The first notice of spotted porpoise from the Indian and Pacific Oceans was a publication by Lesson in 1826 of the description of the species *Delphinus malayanus* from the area between Java and Kalimantan. He described a harpooned specimen as uniformly ashy gray with a deep furrow at the base of the snout. The figure of the 5′11″ specimen is extremely crude and appears to have been the basis for the written description. The figure is distorted, in that the caudal dorsal ridge (present in all delphinids) if extended anteriorly would run to the gape. The written description compounds this clumsy distortion by saying, "*Une forte carêne, comme celle de certains scombres, occupait les parties latérales et postérieures du corps.*" Despite the general low quality of the account and the (in my opinion) nonidentifiable figured specimen, subsequent workers (True, 1889, and Trouessart, 1898, among others) have considered the description valid and held the name to be the senior synonym for animals of the spotted type from the area. Lesson repeated the written description in his 1828 book but added no new details. G. Cuvier in 1829 published his suspicion that *D. plumbeus* G. Cuvier is the same as *D. malayanus.* Schlegel (1841) referred four specimens from Southeast Asia (a young specimen from Kalimantan, the skull of an old animal from Sulawesi, and two incomplete skulls from Java) to *D. malayanus* and concurred with G. Cuvier about *D. plumbeus.* He also stated that in his opinion *D. dubius* G. Cuvier should also be considered the same animal, making the range of tooth count 30 to 40. The illustrated skull, with $\frac{37}{38}$ teeth and without the "für *D. delphis so charakteristischen tiefen Hohlkehlen auf beiden Seiten der unteren Fläche des Oberkiefers*" is certainly very similar to that of the described species from the Atlantic (and the offshore spotted porpoise of the eastern Pacific). Whether this is the same species dealt with by Lesson, of course, must remain unknown.

Pucheran (1856*a*, 1856*b*) later separated *D. plumbeus* (= *Sotalia plumbea*) from the spotted porpoise.

The "female dolphin No. 2" captured by Dussumier on April 4, 1828, at 32°S lat, 51°E long (about 400 miles south of the Malagasy Republic), and depicted by him in a watercolor sketch that was unpublished until very recently (Arvy, 1972) appears to have been a spotted porpoise, with a stripe from flipper to gape.

G. Cuvier (1829) described *D. velox* from Sri Lanka, with "*le museau un peu plus alongé* [than *D. dubius*], *et partout quarante-une dents.*" F. Cuvier (1829, in St. Hillaire) expanded the description of "*le Dauphin Leger No. 2,*" stating that it was collected by Dussumier between Sri Lanka and the Equator, that it had 40 teeth in each jaw, was 4′ 9″ long and was thus colored "*noir en dessus, et d'une teinte verdâtre très-foncée en dessous, avec des marbrures noires* [black mottling]." His figure shows a dark gray animal with long, well-defined snout and falcate dorsal fin. These features, the tooth count, and ventral mottling connect the specimen with the spotted porpoise.

Hombron and Jacquinot (1842-1853) described and figured an animal from the Straits of Banda, Singapore (fide Gray, 1850) that they called "*dauphin à petits pectorals.*" Wagner (in von Schreber and Wagner, 1846) published an external figure of the animal and labeled it *Delphinus brevimanus*, with no explanation in the text. Gray (1950) based

Delphinus ? *microbrachium* on the skull in the Paris Museum of what presumably was the same specimen, citing Hombron and Jacquinot. Jacquinot and Pucheran in Hombron and Jacquinot (1853), redescribed the species (as *D. brevimanus* Wagner), illustrating external appearance and skull. As True (1889) noted, in the figure the flippers are entirely too small. Their shriveled appearance and the presence of wrinkles in several places suggest that the illustration was prepared from the stuffed skin in the Paris Museum, perhaps accounting for the complete lack of color pattern. The skull is that of a spotted porpoise. Flower (1884) stated that it is "not distinguishable from others [in the Paris Museum] marked *D. dubius*."

Peale (1848) reported on a specimen from the Phoenix Islands (2°47′5″S, 174°13′W) and described the species *Delphinus albirostratus.* The figure and description of external appearance and the tooth counts ($\frac{40}{40?}\big|\frac{40}{40?}$) identify the animal as a spotted porpoise. The specimen was 6′7 1/2″ long, with a stripe from flipper to gape, and "covered with small vermicular white spots." The specimen was not saved. Cassin (1858) republished Peale's figure and placed *D. albirostratus* in the synonymy of "*Lagenorhynchus caeruleoalbus* (Meyen)" [= *D. coeruleo-albus* Meyen, 1833, definitely not a spotted species]. Dall (1874) reported on a specimen taken between Tahiti and San Francisco at latitude 13°N (if the route between Tahiti and San Francisco was a straight line or nearly so, the animal was captured in an area today part of the offshore tuna "porpoise grounds"). The animal was "gray, lighter below and darker above." He referred it tentatively to *L. albirostratus,* stating that Cassin's referral of the species to *Lagenorhynchus* was probably erroneous. The specimen is no longer in the collection of the California Academy of Sciences and was probably lost in the 1906 fire and earthquake.

True in his review of the Delphinidae (1889), included all the species and specimens of spotted porpoise known from the Indian and Pacific Oceans under *Prodelphinus malayanus* (Lesson), except Dall's specimen of *Lagenorhynchus* ? *albirostratus* which he referred to *P. doris* Gray on the basis of skull measurements. He left Peale's specimen in a list of species *incertae sedae.* Later (1894), however, True referred five specimens from the Indian Ocean (two from the Amirante Islands, and one each from Alphonse, Providence, and Johanna Islands, in the Seychelles) to *Prodelphinus attenuatus* (described by Gray in 1846 from a specimen from an unknown locality) on the basis of the spotted coloration that linked them to *Clymene punctata* Gray (described from Cape Verde), which species he had earlier placed in the synonymy of *P. attenuatus* on the basis of cranial characters. True in 1906 referred two specimens of spotted porpoise from Hawaii to *P. attenuata.* These two specimens are included below in the sample of Hawaiian specimens compared to the eastern Pacific series.

Hector (1885) referred a skull and mandible from New Zealand waters to *Clymene attenuata* Gray. Oliver (1922) later referred the specimen to "*Stenella pseudodelphis* Schlegel, 1841" [= *Delphinus pseudodelphis* Wiegmann in von Schreber and Wagner, 1846]. True had considered *D. pseudodelphis* a nomen nudum. Weigmann (loc. cit.) published only a figure of a skull, with no description, antedating *Steno attenuata* Gray. Baker and Stephenson (1972) subsequently referred the New Zealand specimen to *S. dubia* (G. Cuvier, 1812).

In recent years, several authors have reported on spotted porpoise from Japanese waters, each referring the animal to a different species. Ogawa (1936) described a specimen from Nagasaki and referred it to *Prodelphinus froenatus* (F. Cuvier). The photograph shows an animal with a distinct band from flipper to gape and a cape pattern similar to that of the eastern Pacific animals. Spots are not evident in a photostat of the published photograph. Mizue and Yoshida (1962) described three specimens, called *madara iruka,* from Goto Island, Nagasaki Prefecture, and stated they were the same as Ogawa's specimen but probably not *"Prodelphiuus froeuatus* [*sic*]." Again, the color pattern as shown in the photographs differs from that of the eastern Pacific animals only in intensity of spotting. Nishiwaki, Nakajima, and Kamiya (1965) very thoroughly documented a school of about 50 spotted porpoise captured by "oikomi drive" at Arari. They felt that they, "although most resembling *Stenella attenuata*" belonged to an "independent species." In the title of the paper, and in Nishiwaki (1966), the animals were referred to *S. attenuata.* The excellent photographs of these specimens show an animal with color pattern nearly identical to that of far offshore eastern Pacific animals (compare with figure. 5), again differing only slightly in density and size of spots. In his 1965 book (with Yabuuchi) and 1972 review, Nishiwaki recognized both *S. attenuata* and *S. frontalis* (Ogawa's and Mizue and Yoshida's specimens) from Japan.

Dawbin (1966) reported spotted porpoise from the Solomon Islands and referred them to the *"frontalis-attenuata* group." Best (1969) reported on a specimen from off Durban, South Africa, in the Indian Ocean. He referred it to *S. attenuata.*

Prior to studies begun in 1968 by the United States government on the tuna-porpoise association, knowledge of the distribution of spotted porpoises in the eastern Pacific was very scanty. The supposedly endemic spotted *Prodelphinus* (= *Stenella*) *graffmani* Lönnberg, 1934, had been described from off Acapulco. Van Gelder (1960) reported on single skulls from the Tres Marias Islands and from "8 miles southwest of Maldonado Point, Oaxaca, " Mexico. Hershkovitz (1966) listed the range of *S. graffmani* as "eastern Pacific, from Acapulco, Guerrero, Mexico, south, following the coast to Panama and Isla Gorgona off the western coast of Colombia" (localities listed in addition to the type locality are of specimens in the U.S. National Museum). Nishiwaki (1967) published a chart showing *S. graffmani* having an offshore distribution extending from approximately 28°N latitude to the equator and west to approximately 150°W longitude. This chart was based in part on sight observations by crews of Japanese longline fishing vessels (personal communication from M. Nishiwaki).

In the Indian and Pacific Oceans, then, are populations of spotted porpoise off South Africa, in the Seychelles, probably near Sri Lanka, in Malaysian waters, in the Solomons, in Japanese waters, in the South Pacific, in Hawaiian waters, and in the eastern tropical Pacific. All are very similar to each other and to Atlantic specimens in cranial features, all having a flipper-to-gape stripe (like one of the two apparent species in the Atlantic), and differing between each other mainly in intensity of spotting. Most workers have followed True's (1894 and 1906) lead and referred the central and western Pacific animals to *S. attenuata.* Hershkovitz (1966) referred them to *S. dubia,* with *S. attenuata* in synonymy. Rice and Scheffer (1968) placed all spotted porpoise everywhere in *S. dubia.* This move was ill advised, because, as discussed above, there would appear to be at least two species in the Atlantic.

VARIATION

Coloration

Very few accurate descriptions or photographs of color pattern exist for any cetacean, including the species of *Stenella.* Two photographs of spotted porpoise from the eastern tropical Pacific were published before 1968. A photograph included in Lönnberg's (1934) description of *Prodelphinus graffmani* showed the skin of the type specimen, mounted after preservation by salting. A photograph in Walker (1964) under *Stenella graffmani* is of a dead specimen from an unspecified location in the eastern Pacific. In both specimens, postmortem darkening has obviously progressed to the point of obliteration of most of the color pattern.

My direct knowledge of coloration of the spotted porpoises in the eastern Pacific is limited the form involved in the tuna fishery. I have previously documented and discussed variation owing to development, individual variation, and differences among schools (Perrin, 1970*a*).

Sexual Dimorphism

Spotted porpoise of the eastern Pacific are not sexually dimorphic in coloration. In describing the color pattern of *Stenella attenuata,* a nominal form very similar in coloration to spotted porpoise in the eastern Pacific (Perrin, 1970*a*), Nishiwaki (1972) stated that in females "the skin around the mamilla is slightly lighter in color" than in males. In an effort to ascertain whether such a dimorphism exists in spotted porpoise from the eastern Pacific, I examined photographs of 20 specimens (10 males and 10 females), five harpooned inshore and 15 from the tuna fishery. Of these, five females and two males had noticeable mottling or lightening of the skin in the genital region. Nishiwaki did not state his sample size, but there seems to be no consistent difference between males and females in this feature in the eastern Pacific. Nor does inspection of photographs reveal dimorphism in any other element of the color pattern.

Geographical Variation

Dorsal spotting varies widely among adult individuals (Perrin, 1970*a*) and diminishes as one moves westward within the eastern Pacific. This continuum can be broken up into arbitrary increments, as follows:

1. Heavy spotting – Spots so large and numerous as to give mottled or nearly white appearance in dorsal view. Extensive merging of spots over eye and on posterior half of peduncle, with some merging overall.
2. Medium spotting – Spots numerous and obvious. Some spots merge above the eye and on dorsal side of posterior half of peduncle.
3. Sparse spotting – Spots so small and so few as to make spotting almost obscure. All spots discrete.

I rated 107 specimens by these criteria (table 3). Ten were animals observed or harpooned within a few miles of the coast of southern Mexico, of which I examined only photographs. The remaining 97 were from the tuna fishery, and I examined them fresh at sea or in a frozen state ashore. Ninety were taken from 50 to 500 miles offshore, and seven are from farther offshore, to 133°W longitude (generally outside a line joining the Revilla Gigedo Islands, Clipperton Island, and Cocos Island.

Table 3. Intensity of spotting in three geographical series of spotted porpoise

Area	Sample	Dorsal Spotting		
		Heavy	Medium	Sparse
Coastal	10	6(60%)	3(30%)	1(10%)
Offshore	90	61(68%)	61(68%)	13(14%)
Far offshore	7	0	4(57%)	3(43%)

Spotting tends to be heaviest in the easternmost, coastal animals (Perrin, 1970*a*) and sparsest in the westernmost, most offshore animals (fig. 5). Compared to the coastal animals, the offshore animals also are lighter and more mottled in the ventral area below the cape, yielding a sharp contrast with the cape.

The coloration of the Hawaiian form continues the east-west trend. The best published photograph of a Hawaiian spotted porpoise, or "Keiko," is in a *National Geographic* article by Conly and Nebbia (1966:414). Comparison of this photograph with that of an animal (fig. 5) from the westernmost part of the offshore range of the spotted porpoise in the eastern Pacific demonstrates the essential identity of the two forms. The pattern on the head is not apparent in young animals (fig. 6 and photograph on p. 40 of Stenuit, 1968; compare with photographs in Perrin, 1970*a*). The differences in coloration among the spotted porpoises from Hawaii and the offshore and inshore eastern Pacific are of degree, not of kind (fig. 7). Contrast between cape and lateral field is greatest in the Hawaiian animals and least in some of the animals from the far eastern Pacific. Spotting is most intense in the far eastern Pacific and least in Hawaii. Discrete ventral dark spots are present temporarily on the snout and between the gape and flippers during development (fig. 6, and drawing and description of animal in True, 1906); but ventral mottling in adults owing to convergence of the spots, while present, is in most animals so obscure as to appear nearly absent. Dorsal light spots are absent or sparse in all specimens and photographs that I have seen of Hawaiian animals. Animals to the south and west of Hawaii are spotted dorsally (Peale, 1848; Dawbin, 1966; personal communication from K.S. Norris). In all other features of the color pattern there are no differences among the forms.

External Morphology

Few data have been published on the external proportions of spotted porpoise from the eastern Pacific. Lönnberg (1934) included a set of external measurements in his description of the type specimen of *S. graffmani* (2245 mm total length) from a stuffed, salted skin. Other workers (Boice, Swift, and Roberts, 1964; Daugherty, 1966; Harrison, Boice, and Brownell, 1969*b*; Pilson and Waller, 1970) have published measurements of total length ranging from 75 cm to "8-foot[244 cm]."

Figure 6. Young Hawaiian spotted porpoise.

Development

Body proportions change markedly during ontogeny. The analyses are based on measurements of 214 spotted porpoise collected in the tuna fishery.

Growth is heterogonic (fig. 8). Changes in proportions during early postnatal development result primarily from a decreasing rate of growth of the head (snout excepted) relative to that of the torso, combined with an early surge in growth of the snout. Later change in proportion results from continued growth of the torso between the umbilicus and anus. Changes in proportions between birth and maturity are similar to those in *Globicephala* as determined by Sergeant (1962), except that the flippers and dorsal fin become proportionately smaller rather than larger.

To analyze developmental patterns and to provide criteria for deciding which specimens should be included in a consideration of variation in the adults and near adults, the measurements were plotted against total length. Where sexual dimorphism is indicated, males and females were considered separately. Selected graphs (fig. 9 and 10) illustrate the major patterns of growth.

The measurements can be divided into two groups: those for which the relationship between the measurement and total length appears linear and those for which it is nonlinear (table 4). For some measurements, the mode of increase is different for males and females. For those measurements in which the relationship between measurement and total length appears linear, that is, for which the value of α in Huxley's (1932) general growth equation, $Y = a + bX^{\alpha}$, is 1, the equation of the least squares regression line is

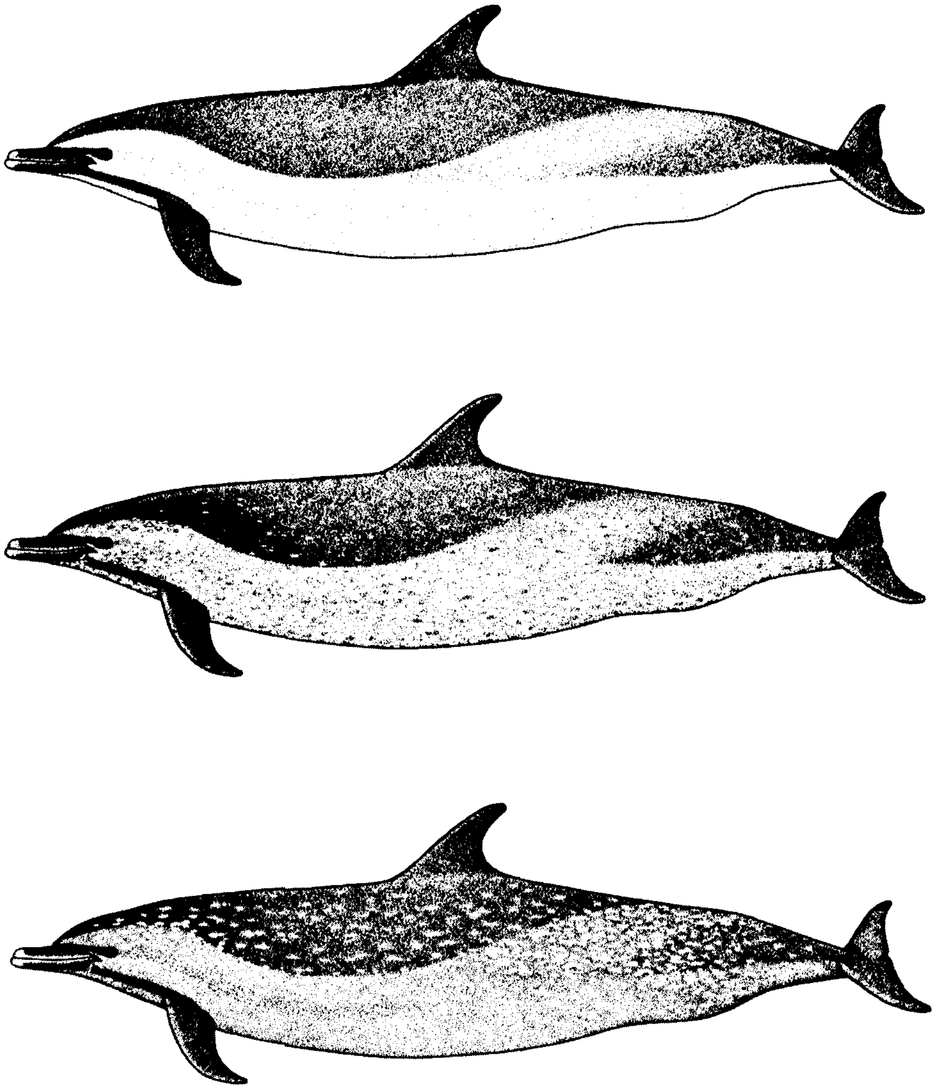


Figure 7. Variation in color pattern of spotted porpoise: (top) Hawaiian, (middle) far-offshore eastern Pacific, (bottom) offshore and coastal eastern Pacific.

included in table 4. For these linear cases, the sign of the Y-intercept of the regression line provides an index to mode of growth. If the intercept is zero, growth has been completely isometric throughout development. If it is positive, growth is negatively allometric; if negative, positively allometric.

Allometric growth entails an exponential relationship between parts. For this reason, the linear model is not appropriate for the data for the complete span of postconceptual development for the measurements where the intercept is not equal to zero. Where data

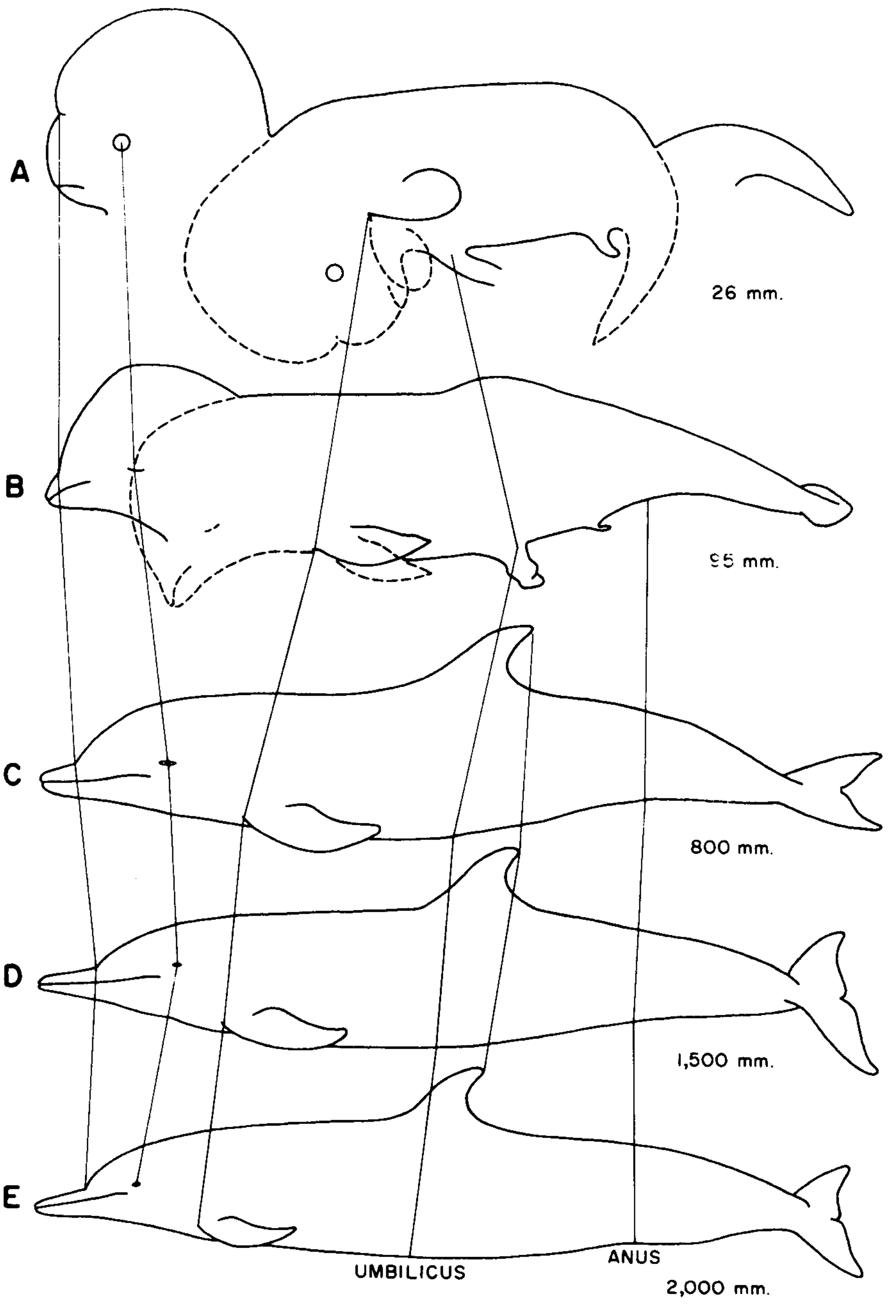


Figure 8. Ontogeny of external proportions of spotted porpoise, drawn from specimens. A. Fetus of *Stenella coeruleoalba* (after Sinclair, 1967). B. Fetus of spinner porpoise. C, D, and E. Postnatal specimens of spotted porpoise. The specimen of *S. coeruleoalba* and the spinner fetus are included in the series because it is felt that interspecific differences are probably insignificant during very early development.

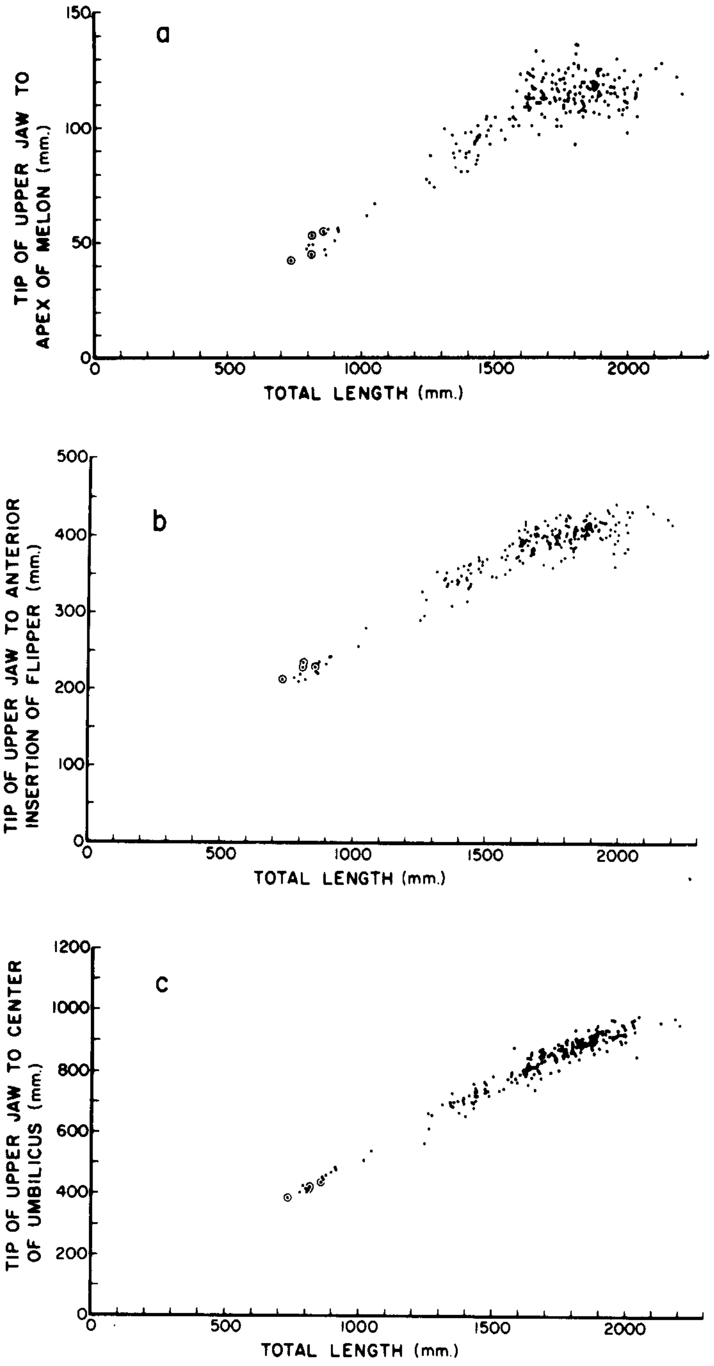


Figure 9. External development of spotted porpoise: scatterplots of external body measurements against total length, demonstrating changing proportions. Circles represent fetal specimens (continued).

are available only for a limited segment of the span of development, however, the linear model provides sufficiently good fits to allow comparison of measurements and of growth patterns.

After the linear instances have been considered, most of the remaining measurements show a similar pattern of increase and variation relative to total body length. They have a linear relationship with total length until approximately 1600 mm, after which they increase much less rapidly, if at all, and exhibit larger variance. These include the long measurements of the anterior portion of the body, the measurements reflecting anterior

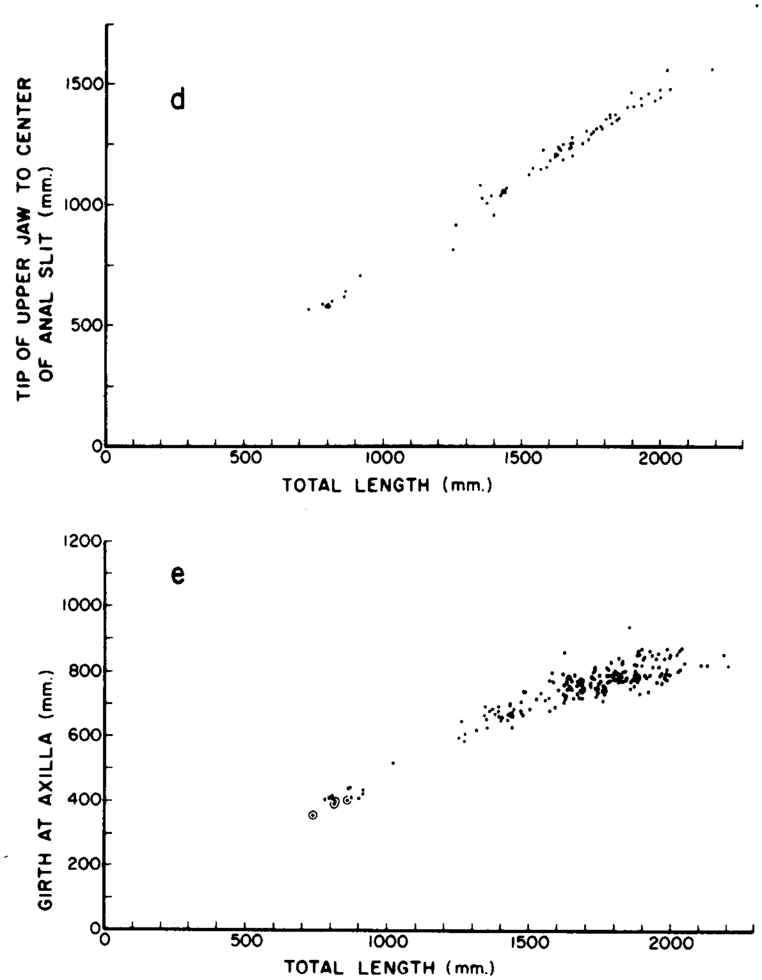


Figure 9 (continued). External development of spotted porpoise: scatterplots of external body measurements against total length, demonstrating changing proportions. Circles represent fetal specimens.

robustness, and those of dimensions of the flippers and the dorsal fin. This trend is perhaps best shown in the measurement of the rostrum (fig. 9a), and is least pronounced in the measurement from tip of upper jaw to tip of dorsal fin. The inflection in the curves at length of about 1600 mm corresponds roughly to the onset of puberty. The inferred pattern of growth is as follows: the length and breadth of the head, anterior girth, and dimensions of the flippers and dorsal fin grow allometrically after birth at a constant rate relative to growth in total body length until the onset of sexual maturity. Afterward they grow more slowly and at a rate that varies greatly between individuals. As noted above (table 4), span of the flukes, as well as distance of the external ear from the center of the eye and, in females, girth at the anus,continue to grow at the same rate relative to growth in total length as in smaller animals. The measurements reflecting relative positions of the genital aperture and anus also increase in this manner. This pattern of growth of the flukes was also found for *Globicephala melaena* by Sergeant (1962).

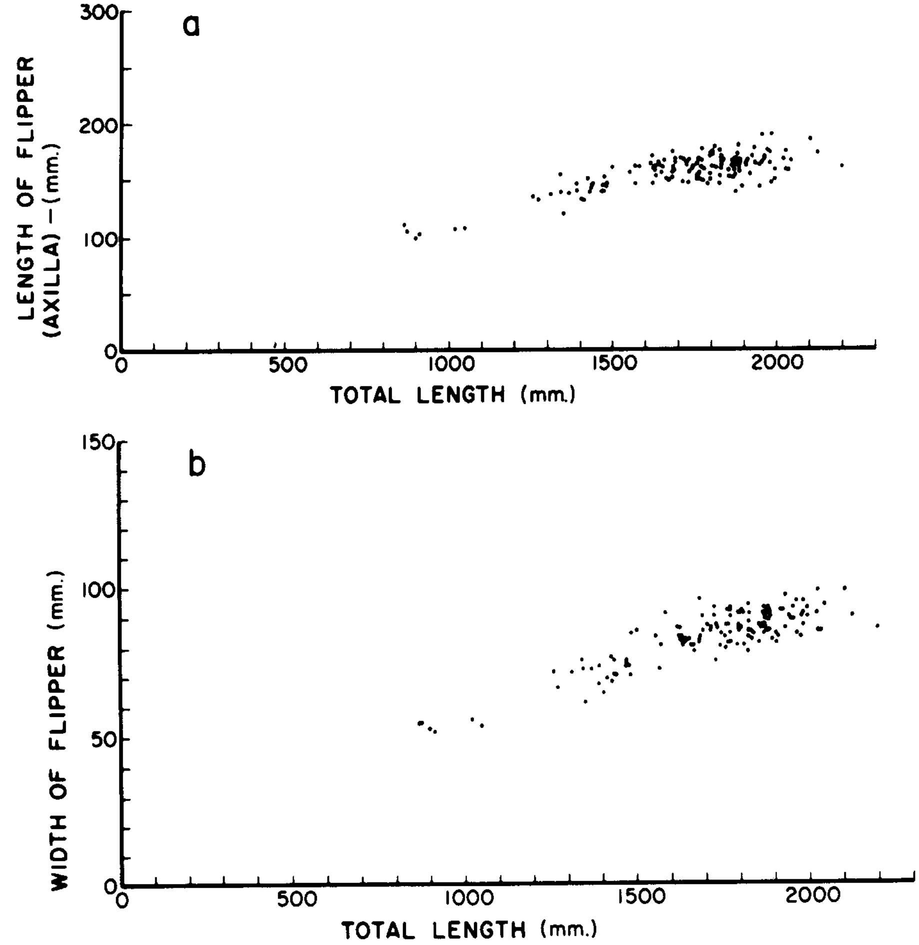


Figure 10. External development of spotted porpoise: scatterplots of appendage measurements against total length, demonstrating changing proportions (continued).

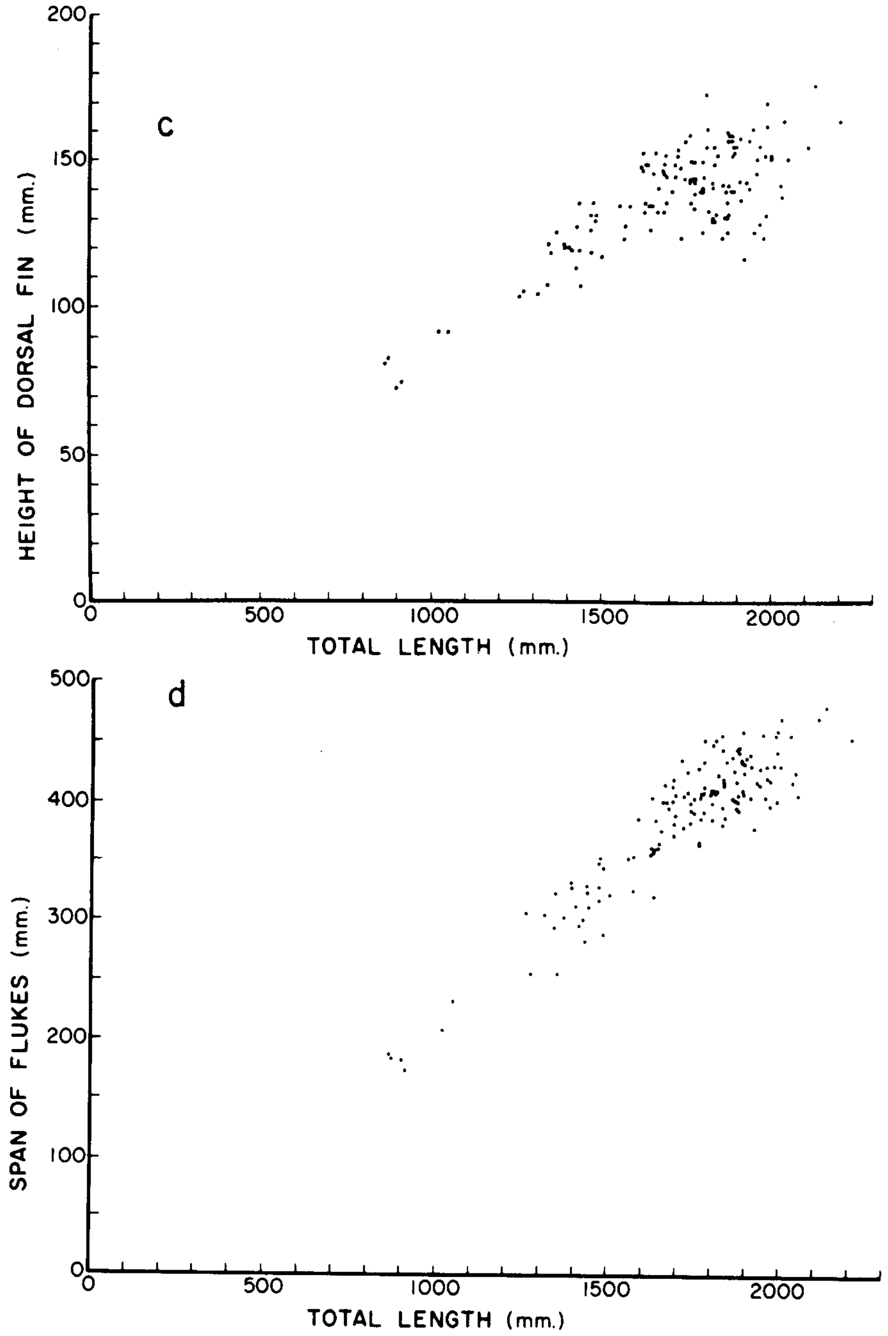


Figure 10 (continued). External development of spotted porpoise: scatterplots of appendage measurements against total length, demonstrating changing proportions.

Girth at the anus in males also shows a change in rate, but of a different sort, and is discussed in the section below on sexual dimorphism.

Progress has been made in developing a method to determine the age of tropical delphinids (see Methods above), and age-correlated data have become available for subsample of the specimens included above. The results obtained in analysis of selected measurements for this subsample do not modify the conclusions reached above. Total length (fig 11a) continued to increase in postpubertal animals ($>$ 160 cm, $\geqslant$ 4 layers), with some dimensions such as snout to anus (fig 11b) keeping pace (the linear instance above), but anterior dimensions, especially length of the snout (fig 11c) level off sharply and show no correlation with age (or total length) in adults (the curvilinear specimen above).

Sexual Dimorphism

The patterns of development of some external dimensions are sexually dimorphic. Although girth at the anus in females increases at the same rate throughout development after birth, in males it increases more rapidly after total length of about 160 cm is reached. Dimorphism is also evident in a plot of girth at anus against number of dentinal layers (fig. 11d). Girth at the anus is on the average greatest in the oldest individuals, and sexual dimorphism is very apparent in large adults ($>$ 10 layers, $\geqslant$ 180 cm total length). In lateral view, an adult male (fig. 5) shows a slight vertical thickening of the caudal stock just behind the anus. This dimorphic feature is more exaggerated in spinner porpoises than in spotted porpoises. I have previously discussed its possible function as a signal for species recognition in mixed schools (Perrin, 1972). Although the genital aperture occupies a progressively more forward position during postnatal growth, it is placed farther forward in the male than in the female; the disparity increases with development.

Dimorphism is present in adults. Adulthood was defined on the basis of examination of gonads. All 9 males over 180 cm total length for which histological examination of the testes were carried out exhibited spermatogenesis. The smallest sexually adult female encountered was 173 cm long (with a single corpus of ovulation). At least one of the ovaries of each of all females over 175 cm (except two, 177 and 183 cm long) contained corpora albicantia or a corpus luteum. These findings were used as a basis for splitting the large sample of specimens for which external measurements (but no histological examinations of gonads) were made into two groups, those males larger than 180 cm and females 175 cm long or longer, supposedly sexually adult, and the smaller animals, supposedly immature. A summary of the results (table 5) indicates that for adult males the total length is greater; the eye and external auditory meatus are farther apart; the distances from snout to dorsal fin, umbilicus, and anus are greater; the girth at the axilla is greater; the girth at the anus is greater (both absolutely and proportionately); and the flipper is wider than in adult females. In adult females, however, the dorsal fin is more posterior, girth at the axilla is proportionately greater, and fluke span is proportionately greater than in adult males. It must be remembered, however, that a large number of

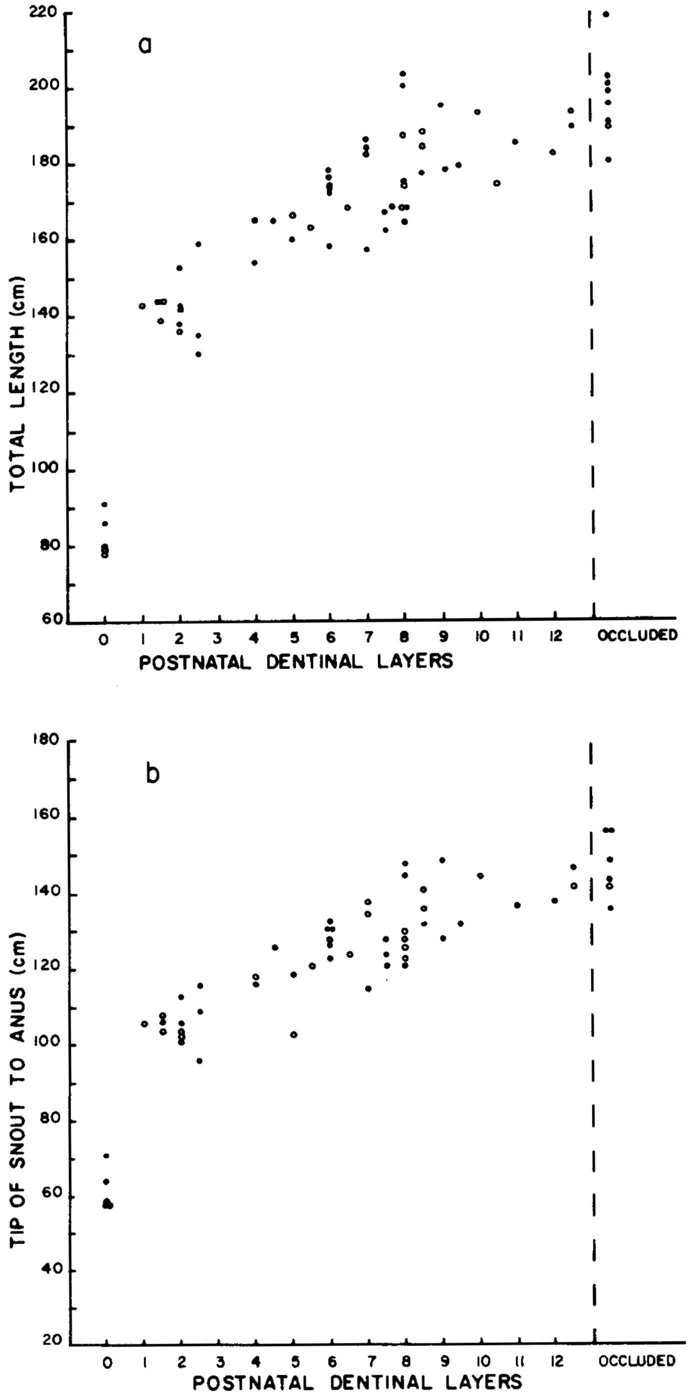


Figure 11. External development of spotted porpoise: scatterplots of external measurements on number of postnatal deninal layers (continued).

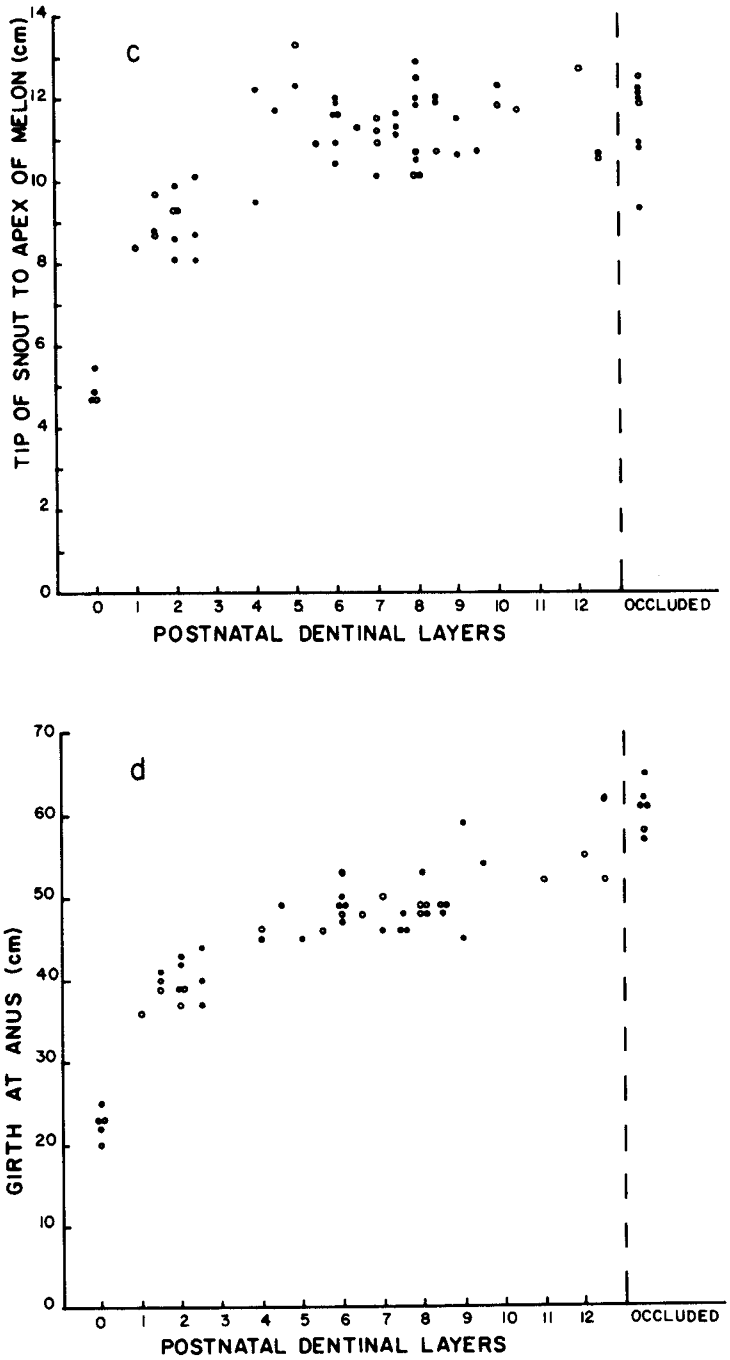


Figure 11 (continued). External development of spotted porpoise: scatterplots of external measurements on number of postnatal layers.

Table 4. Mode of increase of measurements relative to total length of spotted porpoise

Measurement	Mode of increase relative to total length		Equation of least squares regression line, where X = total length, Y = regressed measurement	Correlation coefficient r
	Linear	Nonlinear		
Tip of upper jaw to center of eye		+		
Tip of upper jaw to apex of melon		+		
Length of gape		+		
Tip of upper jaw to external auditory meatus		+		
Center of eye to external auditory meatus	+		Y = 18.5 mm + .017 X	.93
Center of eye to angle of gape		+		
Center of eye to center of blowhole		+		
Tip of upper jaw to blowhole		+		
Tip of upper jaw to anterior insertion of flipper		+		
Tip of upper jaw to tip of dorsal fin		+		
Tip of upper jaw to midpoint of umbilicus		+		
Tip of upper jaw to midpoint of genital aperture: Males	+		Y = 53.3 mm + .627 X	.98
: Females	+		Y = -16.8 mm + .719 X	.99
Tip of upper jaw to center of anus	+		Y = 9.38 mm + .751 X	.99
Girth at axilla		+		
Girth at anus: Males		+		
: Females	+		Y = -15.3 mm + .290 X	.99
Length of flipper, axilla to tip		+		
Width of flipper		+		
Height of dorsal fin		+		
Span of flukes	+		Y = 3.4 mm + .228 X	.92

Table 5. External measurements of adult male and female offshore spotted porpoise

Measurement	Males					Females					Absolute value of significant t, at α = .05	
	Number of specimens	Range (mm)	Mean (mm)	Standard deviation (mm)	CV (100 s/x̄)	Number of specimens	Range (mm)	Mean (mm)	Standard deviation (mm)	CV	Absolute	Percentage of total length
Total length	34[a]	1801-2200	1965	96.2	4.90	59[a]	1750-2128	1860	68.7	3.69	8.36	
Tip of upper jaw to center of eye	34[a]	269-327	297	11.7	3.94	59[a]	273-330	299	10.8	3.61		
Tip of upper jaw to apex of melon	33[a]	93-136	115	8.6	7.48	59[a]	101-136	117	6.8	5.81		
Length of gape	34[a]	238-290	254	12.6	4.96	59[a]	223-283	255	10.7	4.20		
Tip of upper jaw to external auditory meatus	9[c]	317-355	340	12.9	3.79	10[c]	331-349	342	5.5	1.61		
Center of eye to external auditory meatus	9[c]	51-55	53	1.6	3.02	10[c]	46-53	50	2.4	4.80	4.15	
Center of eye to angle of gape	9[c]	43-56	48	4.6	9.58	11[c]	44-52	49	2.6	5.31		
Center of eye to center of blowhole	33[a]	114-136	124	4.5	3.63	59[a]	108-134	122	5.1	4.18		
Tip of upper jaw to blowhole	33[a]	258-325	295	13.2	4.47	59[a]	271-324	297	11.5	3.87		
Tip of jaw to anterior insertion of flipper	34[a]	370-444	413	18.2	4.41	59[a]	363-446	410	15.5	3.78		
Tip of upper jaw to tip of dorsal fin	32[a]	1053-1219	1129	44.5	3.93	58[a]	1020-1229	1105	46.2	4.18	4.04	5.38
Tip of upper jaw to midpoint of umbilicus	33[a]	852-988	927	33.2	3.58	58[a]	809-974	904	31.8	3.52		
Tip of upper jaw to midpoint of genital aperture	9[c]	1208-1378	1301	50.8	3.90	11[c]	1246-1393	1324	41.6	3.14	18.56	
Tip of upper jaw to center of anus	9[c]	1361-1570	1479	63.3	4.28	11[c]	1303-1452	1384	41.0	2.96	4.98	
Girth at axilla	31[a]	768-970	814	35.0	4.30	52[a]	711-934	794	39.6	4.99	4.02	3.40
Girth at anus	8[c]	531-652	600	37.8	6.30	9[a]	488-580	520	30.6	5.88	6.30	2.59
Length of flipper, axilla to tip	25[b]	144-190	166	10.1	6.08	48[b]	139-189	162	10.4	6.42		
Width of flipper	25[b]	84-100	91	4.3	4.73	48[b]	79-98	88	4.6	5.23	3.99	
Height of dorsal fin	24[b]	124-173	146	13.5	9.25	48[b]	117-176	145	12.5	8.62		
Span of flukes	24[b]	397-473	430	24.2	5.63	48[b]	366-491	421	26.1	6.20		2.05

[a] Includes specimens from all collections.

[b] Frozen specimens not included.

[c] Frozen specimens only. These measurements were not made at sea.

simultaneous *t*-tests will produce some erroneously "significant" values owing to chance alone (about 1 in 20 at $\alpha = 0.05$). Therefore, only the higher significant *t*-values, for example, for total lengths and for the girths, can be considered to indicate well-confirmed dimorphism. This same caveat applies to the other uses of long series of *t*-tests in the various tables below.

Individual Variation

Of the long measurements containing the rostrum, length of snout (tip of upper jaw to apex of melon) is most variable. Most of the variation in the other long measurements can be laid to variation in snout length.

The length of the dorsal fin shows great variation among individuals. It is more variable than the length or width of the flipper or the span of flukes, which are about equally variable.

Geographical Variation

Very few external measurement data exist for the spotted porpoise from the eastern Pacific, outside of those collected during this study of animals in the tuna fishery. It is difficult to compare external measurements taken by different observers if the methods of measuring are not precisely specified. Lönnberg (1934) published several measurements taken from the mounted skin of the holotype of *S. graffmani,* which had been preserved in salt (and presumably shrank owing to dehydration) before mounting. Total length of the holotype as thus measured was 224.5 cm, although Lönnberg stated that when freshly caught, the animal was measured by Graffman at 244 cm from snout to a line connecting the tips of the flukes. The specimen was larger than any examined for the present study of the form involved in the tuna fishery. Lönnberg stated that the external measurements made by him were taken in "straight lines" but did not specify whether they were taken point-to-point or parallel to the long axis of the body.

Skulls of spotted porpoise from near the coast are larger than those of animals from the offshore tuna fishery (see section below on variation of the skeleton). Previously unpublished data for 11 coastal specimens in addition to the very large holotype of *S. graffmani* indicate that a similar dichotomy exists in external measurements. Sample sizes of several measurements for this composite series are large enough to allow statistical comparison with the offshore series for those measurements taken on large series at sea (table 6). The measurements are converted from point-to-point to parallel-to-body axis (see Methods, above). Flipper width is not included, because my method of measurement, while aimed at defining functional width of the flipper, renders impossible conversion to the more standard "greatest width" by use of a constant coefficient.

The coastal form is larger in all the torso dimensions than the offshore form. The average length of 5 males (2060-2570 mm) exceeds the upper end of the range for the offshore series. Six females were 1999 to 2140 mm long. The divergence is greatest in tip of snout to flipper insertion, the measurement that most nearly approximates condylobasal length. There is no difference in height of the dorsal fin. There are no differences between the series in proportions, with the exception of flipper length. Flipper length to the axilla is absolutely and proportionately greater in the offshore series. This result is suspect, however, because the flipper is extremely susceptible to shrinkage from drying, and second, because the measurement varies depending on the degree to which the flipper is held away from the body while it is being measured.

External measurements of Hawaiian specimens are available for only a small sample (table 7). Statistical comparisons of means of several of the measurements with those for the offshore series are not warranted because of nonhomogeneity of variance, but it is evident that the series differ modally in several features. The series are comparable in total length; the Hawaiian series for both males (6 specimens, 1816-2021 mm) and females (3 specimens, 1890-2032 mm) lie within the ranges of the offshore series. While the series do not differ in snout length or in the long measurements to dorsal fin and umbilicus, the Hawaiian animals on the average have larger heads, as indicated by greater means for the measurements strongly affected by condylobasal length; namely, snout to eye, length of gape, snout to blowhole, and snout to flipper origin. The snout to blowhole distance also differs when taken as a percentage of total length. Fluke span does not differ between the series, but dorsal fin height is greater in the Hawaiian animals. This may be because this measurement is difficult to make in an objective manner. The point of relative size of flippers and fin will have to be elucidated in the future through comparison of measurements taken by a single investigator.

The finding based on external measurements that the Hawaiian spotted porpoise has a larger head than the spotted porpoise of the eastern Pacific agrees with the results obtained below for the skeleton.

Geographical Variation In Other Odontocetes

Several other small odontocetes have also been found to vary geographically. Variation occurs in size and other external dimensions as it does with the spotted porpoise.

Gihr and Pilleri (1969) compared measurements of 24 specimens of *Delphinus delphis* (17 males and 7 females) from the Mediterranean with those of 26 (11 males and 15 females) from the Atlantic and concluded that "the Mediterranean and Atlantic dolphins are representatives of two different races." The Atlantic form is apparently larger in total length, length of flipper, width of flipper, length of dorsal fin base, and the distance from snout tip to blowhole.

Sergeant and Brodie (1969) found marked geographical variation in the size of white whales, *Delphinapterus leucas,* over distances of only hundreds of kilometers. Extreme differences in body weight of adult males was about threefold. They distinguished three sizes of white whales in the northwest Atlantic: small whales in subarctic estuarine conditions (western part of Hudsons's Bay), medium-sized animals in arctic water having some oceanic influence (all other arctic coasts of Canada and the Saint Lawrence River), and large whales in subarctic conditions under oceanic influence (coast of West Greenland). They were able to correlate positively size with primary production (fixation of carbon) and concluded that the differences bespeak isolation of adjacent populations. The magnitude of this variation is greater than that of the coastal-offshore dichotomy in the spotted porpoise. Both instances, however, involve correlation of geographical variation with precipitously changing environmental features; namely, with productivity related to derivation of surface waters (estuarine vs. oceanic) in *Delphinapterus,* and possibly with distance from shore and/or water depth in *Stenella.*

Table 6. External measurements differing between coastal and offshore series of spotted porpoise

Measurement	Coastal (5 males, 6 females)					Offshore males					Offshore females					Absolute value of significant t, at α = .05; test between coastal mean and closest offshore mean	
	Sample size	Range (mm)	Mean (mm)	Standard deviation (mm)	CV	Sample size	Range	Mean	Standard deviation	CV	Sample size	Range	Mean	Standard deviation	CV	Absolute	Percentage
Tip of snout to center of eye[1]	8	280-330	313	16.4	5.24	34	252-306	278	11.0	3.96	59	256-309	280	10.1	3.61	14.21	
Tip of snout to apex of melon[1]	7	119-131	124	3.9	3.15	32	91-133	112	8.4	7.49	59	98-133	114	6.6	5.82	9.19	
Length of gape[1]	7	240-280	263	14.6	5.55	34	226-276	242	12.0	4.96	59	212-269	243	10.2	4.19	9.25	
Tip of snout to blowhole[1]	7	287-305	297	6.7	2.26	33	240-303	275	12.3	4.47	59	253-302	277	10.7	3.87	13.42	
Tip of snout to anterior insertion of flipper[1]	7	410-436	428	12.6	2.94	34	343-411	382	16.9	4.42	59	336-413	380	14.4	3.78	17.81	
Tip of snout to tip of dorsal fin[1]	2M	1158-1200				32	1000-1158	1073	42.3	3.94	58	969-1168	1050	43.9	4.18		
	4F	1119-1164															
Tip of snout to umbilicus[1]	2M	920-1000				33	839-973	913	32.7	3.58	58	797-959	890	31.3	3.52		
	5F	942-991															
Flipper length to axilla	7	137-180	152	17.9	11.78	25	144-190	166	10.1	6.08	48	139-189	162	10.4	6.42	3.66	3.14

[1] Offshore data converted from point-to-point to parallel-to-long-axis (see text).

Table 7. External measurements differing statistically between series of Hawaiian and offshore (table 6) spotted porpoise

Measurements						Absolute value of significant t, at $\alpha = .05$; test between Hawaiian mean and closest off-shore mean[1]	
	Sample size	Range (mm)	Mean (mm)	Standard deviation (mm)	Coefficient of variability	Absolute	Percentage
Tip of snout to center of eye	10	292-331	309	15.0	4.85	7.79	
Length of gape	9	261-290	268	12.1	4.51	6.69	
Tip of snout to blowhole	10	287-321	301	12.6	4.19	6.39	2.57
Tip of snout to anterior insertion of flipper	8	373-419	406	21.8	5.37	3.42	
Height of dorsal fin	10	133-203	166	21.3	12.83		2.48

[1] Dash indicates no test (because inappropriate, sample too small, or variance nonhomogeneous) or nonsignificant.

Skeleton

Lönnberg (1934) described *S. graffmani* from a specimen consisting of a "skin with the fins in situ, the upper jaw with the tooth row complete on the right side, and the complete lower jaw." The description included measurements of the upper and lower jaws and tooth counts. He later (1938) published a detailed description of the complete skeleton of a second specimen and tooth counts of a third. Hall and Kelson (1959) stated that the rostrum of *S. graffmani* is less than twice the length of the cranial portion of the skull and the tooth count is 43-47 in each row. Van Gelder (1960) published measurements and tooth counts for two skulls that he referred to *S. graffmani.* These four accounts make up the entire osteological literature for spotted porpoise from the eastern tropical Pacific.

The purpose of this section is to describe in qualitative and quantitative terms the development, sexual dimorphism, individual variation, and geographical variation of the skeleton.

Development

If skeletal measurements are to be used as taxonomic characters, we must know how each measurement changes during development. Here I describe patterns of change with development in the skull and postcranial skeleton. The account is based primarily on specimens collected in the tuna fishery aboard the M/V *Carol Virginia* in 1968 and M/V *Pacific Queen* in 1969. Sixty-four of the 69 specimens are divided into the following categories for the purposes of qualitative description:

Class I.	Near-full-term fetuses, with no dentinal layers: 4 (CB length 221 to 237 mm).
Class II.	Newborn individuals, with no dentinal layers: 5 (CB length 221 to 242 mm).
Class III.	Calves in the "two-tone" coloration phase described by Perrin (1970*a*), with 2-4 dentinal layers: 12 (CB length 331 to 236 mm).
Class IV.	Sexually immature subadults; coloration categories mostly "speckled" and "mottled" with some "fused," 4.5-8 dentinal layers: 23 (CB length 356 to 411 mm).
Class V.	Sexually mature but physically immature adults, with vertebral epiphyses not fused along full length of vetebral column and in coloration category "fused"; with 7-9.5 dentinal layers: 5 (CB length 369 to 406 mm).
Class VI.	Physically mature adults with all vetebral epiphyses fused; with 8 or more dentinal layers: 15 (CB length 360 to 404 mm).

The remaining seven specimens consist of: (a) the skulls only of five sexually mature animals, the degree of physical maturity of which is unknown, and (b) of two other specimens (LACM no. 27420, skull only, and LACM no. 27431, complete skeleton), from off Mexico and from an unknown locality in the tuna fishery, respectively, whose skeletal development falls between classes II and III, and are designated below as comprising Class II.5 (with one postnatal dentinal layer).

Cranial Skeleton

The usual practice in analysis of skull growth patterns is to express measurements not only absolutely but also as percentages of a given dimension of the skull. It has been traditional to express measurements as percentages of condylobasal length, but as several functional components of the skull are encompassed in this measurement, its pattern of increase (fig. 12) must of necessity be in itself very complex. Fraser and Noble (1968) initiated the use of parietal width as a comparative base and achieved, to them, more satisfactory results than by use of condylobasal length. In this account of developmental variation, however, the emphasis is on analysis of absolute growth of functional units, rather than on analysis of ratios or relative measurements.

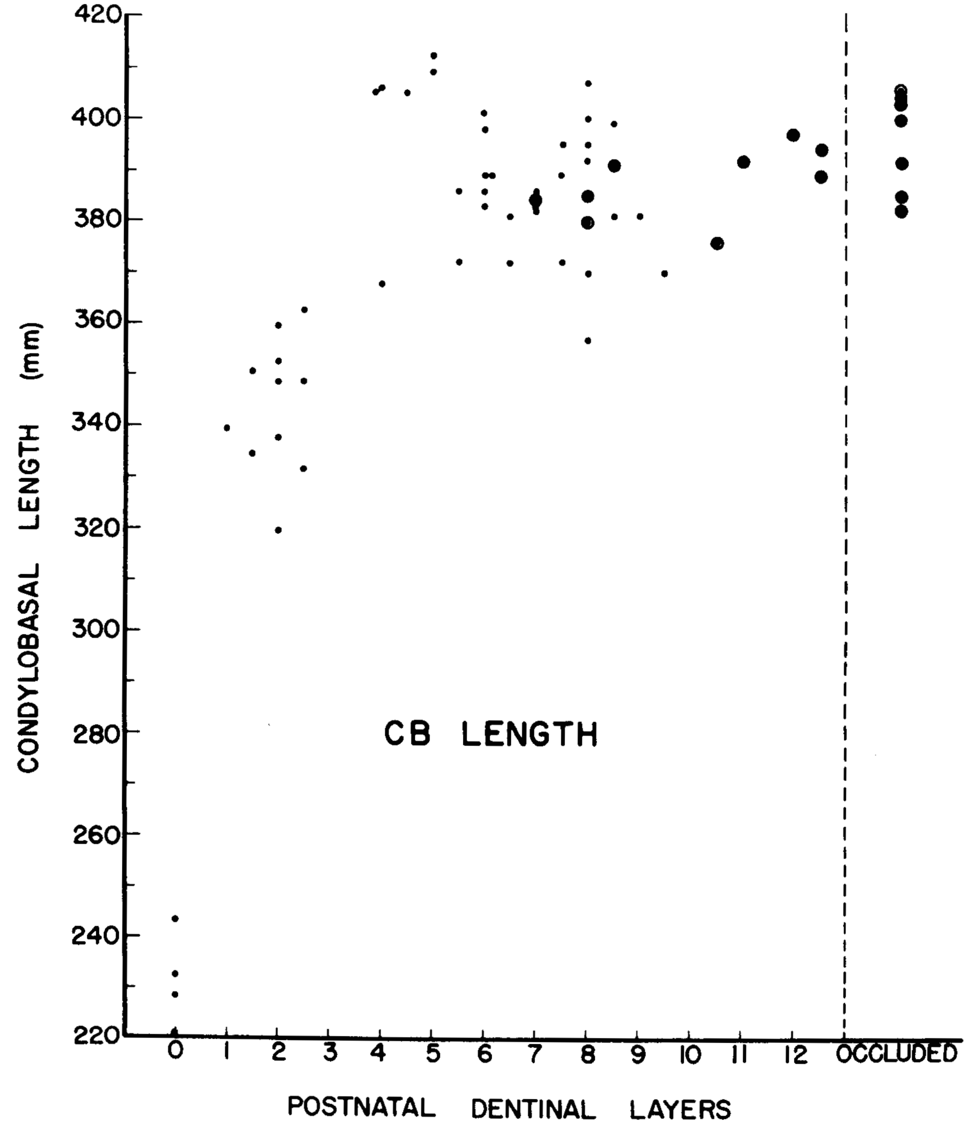


Figure 12. Development of skull of spotted porpoise: scatterplot of condylobasal length on number of postnatal dentinal layers. Large blackened symbols represent fully physically mature specimens, circled symbols represent specimens of unknown degree of physical maturity.

The delphinid skull can be divided into several functional components; namely, the braincase, the feeding apparatus, the vision apparatus, the hearing apparatus, and the breathing and sound-producing apparatus. A priori, it seems obvious that each component would have its own, to a certain extent independent, pattern of development and a typical variance. For example, a young porpoise must breathe immediately upon birth, but need not catch prey until it is weaned, therefore it is to be expected that development of the breathing apparatus will be faster than that of the feeding apparatus. Sound is very important to cetaceans, and sound quality is closely tied to structure. Therefore, it is to be expected that the hearing apparatus will show relatively low plasticity.

The respective developmental patterns should be to a lesser or greater degree correlated, because (1) the direction of development is the same for all, that is, positive, and (2) the systems are physically contiguous and often share ossifications. For example, the posttemporal fossa, as the origin of the temporal muscle, is part of the feeding apparatus, but its dimensions also vary with the braincase, as it is part of the lateral wall of the cranium. Similarly, the mandibular fossa is part of the hearing apparatus, but its length must to some extent be influenced by that of the ramus, which is part of the feeding apparatus. Covariation notwithstanding, however, it makes sense to consider development of the skull in terms of the various functional systems, and that scheme is adhered to in the following account.

Braincase. The degree of ossification of the elements of the braincase (fig. 13) at birth (Classes I and II described above) varies greatly. Posteriorly, ossification may be essentially complete or large fontanelles may persist at the confluence of the parietal, exoccipital and supraoccipital.

By the time one postnatal dentinal layer has been laid down in the teeth (Class II.5) the fontanelles are completely closed. The floor of the braincase is formed medially by the basoccipital, the basisphenoid, and the presphenoid. Ventrolaterally, the alisphenoids extend from the basisphenoid to meet the squamosals, parietals, and frontals, dividing the large ventral hiatus into two parts. The partition of the hiatus by the orbitospenoid may not be complete at birth. During early postnatal development the orbitosphenoid expands anteriorly to close completely the forward portion of the hiatus, and posteriorly to reduce the posterior portion, which persists into adulthood to varying degree as the optic foramen. Dorsolaterally, considerable variation is exhibited at birth in the shapes of the frontal, supraoccipital, and parietal bones. Miller (1923) described the telescoping process that culminates in formation of the supraoccipital crest. During telescoping, the interparietal becomes decreasingly visible in dorsal view of the skull and the suture between the interparietal and supraoccipital rapidly becomes obliterated medially. Lateral traces of the suture persist, however, in specimens of Class III.

The lower part of the parietobasoccipital suture becomes incorporated into the posterior margin of the supratemporal fossa. The progress of closure of the remainder of the parietooccipital sutural system varies greatly. In most adult specimens (Classes V and VI) it is obliterated, but traces remain even in some specimens of Class VI; so degree of closure may not by itself be used as a criterion of age.

The remaining visible sutures of the braincase, the squamosal (within the supratemporal fossa), the alisphenoidal, and the orbitosphenoidal, show signs of fusion only in some of the oldest individuals (Class VI).

Figure 13. Dorsal view of crania in a developmental series of skulls of spotted porpoise: (a) USNM no. 395461, female, no postnatal dentinal layers, Class II; (b) LACM no. 27431, sex unknown, one layer, Class II.5; (c) USNM no. 395610, female, 2 layers, Class III; (d) USNM no. 395397, sexually immature female, 4.5 layers, Class IV; (e) USNM no. 395598, sexually mature but physically immature male, 8 layers, Class V; (f) USNM no. 395597, sexually and physically mature male, 12.5 layers, Class VI.

The foramen magnum is pyriform at birth and becomes oval to varying degree during subsequent development. With some individuals of Class VI the foramen magnum remains pyriform.

Small, apparently nonfunctional foramina may pierce the occipital region posteriorly and ventrally. Although the foramina are large and more numerous among specimens of Classes I, II, and III than in older specimens, they also occur in some physically mature specimens (Class VI).

Scatterplots of the measurements of parietal width and height, and length of the braincase on the number of postnatal layers in the tooth dentine (figs. 14 and 15) show that near-maximum dimensions are attained early in development, long before the onset of sexual maturity (at 4-6 layers) after an initial period of very rapid growth. All dimensions of the braincase appear to continue to increase slowly after the initial rapid growth phase. Regression analysis shows increase in height to be most correlated with age in this phase ($r = .339$, $.02 > P > .01$). An index (fig. 15) compounded of the three measurements [width + height + length ÷ 3] allows easier assessment of this gradual increase by damping the effect of individual variation in proportions and also, being directly proportional to the cube root of cranial volume measured externally, serves as an index of cranial volume. The total increase in the average dimension over the period of gradual growth is approximately 8 mm. To test the possibility that this increase might result from thickening of the cranial wall rather than an actual increase in cranial volume, I drilled a hole in the parietal area of each of four skulls and measured the thickness of the cranial wall. This yielded an expected increase in 1.8 mm in parietal width owing to increasing thickness of the cranial wall. This is much less than the actual average increase of about 8 mm (fig. 15); it must be assumed that the internal cranial dimensions and therefore cranial volume continue to increase after the initial rapid-growth phase. If the cranium be assumed to approximate a sphere, the increase in volume over the period covered by the increase from 2 layers to 13 layers can be roughly estimated as $1/6\ \pi\ [118.2)^3 - (112)^3]$ mm^3 (using the approximate mean values of the volume index in fig. 15 and deducting the growth owing to increased thickness of the cranial wall), or 129 cm^3.

Feeding Apparatus. The parts of the skull concerned primarily with feeding are the rostrum, the posttemporal fossae, the zygomatic and postorbital processes (which bound the posttemporal fossa anteriorly and determine its depth), the mandible, the teeth, and the hyals.

The rostrum is fully ossified at birth, and changes little during subsequent development in the relations and proportions of its various elements, despite the great increase in size (figs. 13-16). In lateral aspect, as the maxillaries grow down to enclose the alveoli, the premaxillaries proportionately become decreasingly elevated above the level of the maxillaries.

The onset of distal fusion of the premaxillaries and maxillaries is variable. Some sexually immature animals (Class IV) exhibit slight fusion and some individuals of Class V exhibit more. Fusion, however, usually occurs at about the onset of sexual maturity (in Class V). The tip of the rostrum begins to thicken laterally and dorsally, until in most old individuals it becomes blunt, quite unlike the rostrum of most younger adults. The mandible follows a similar course of development, with symphyseal fusion commencing in Class V and the tip becoming blunt in older animals.

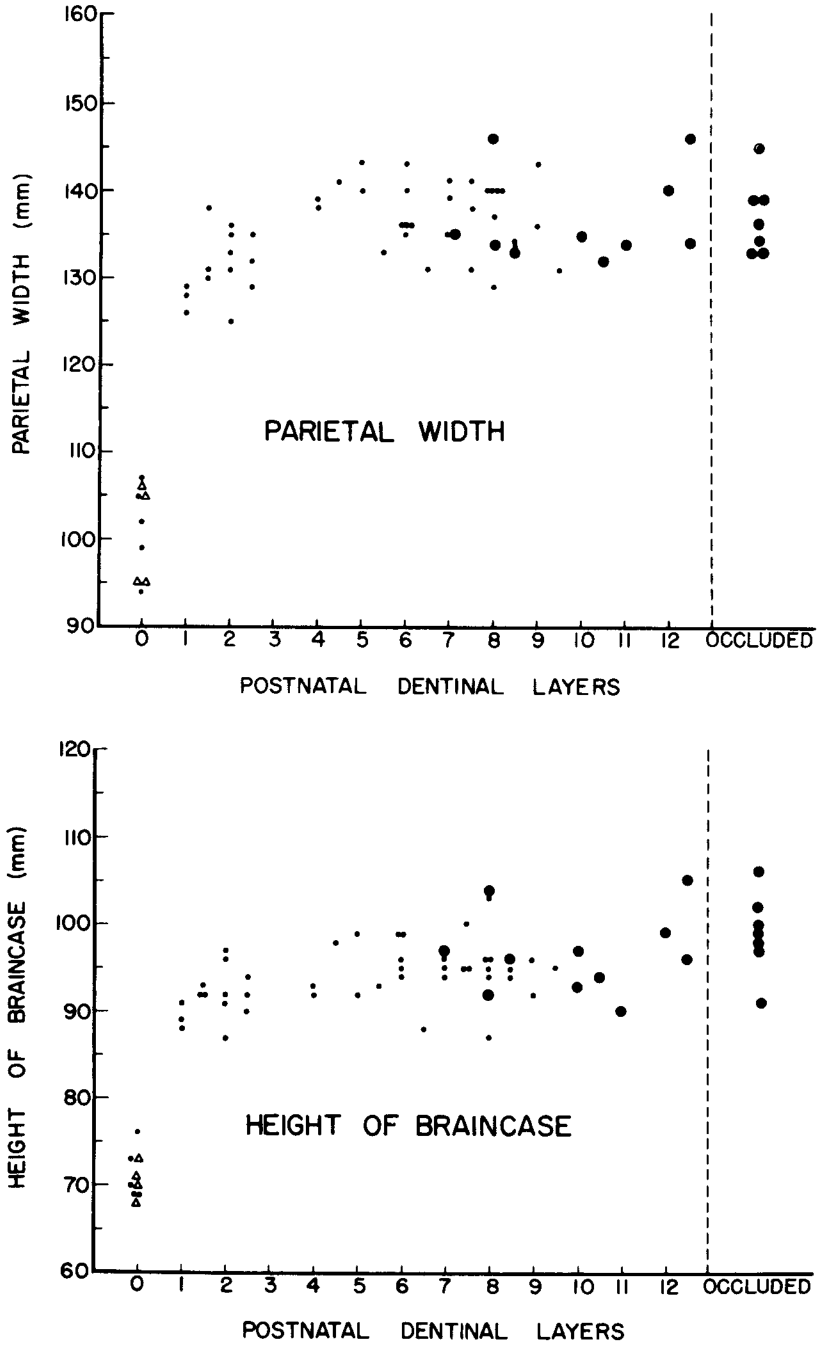


Figure 14. Development of skull of spotted porpoise: scatterplots of parietal width (top) and height of braincase (bottom) on number of postnatal dentinal layers. Triangles are fetuses. Small dots are physically immature specimens. Large dots are physically mature specimens. Circled dots are specimens of unknown degree of maturity.

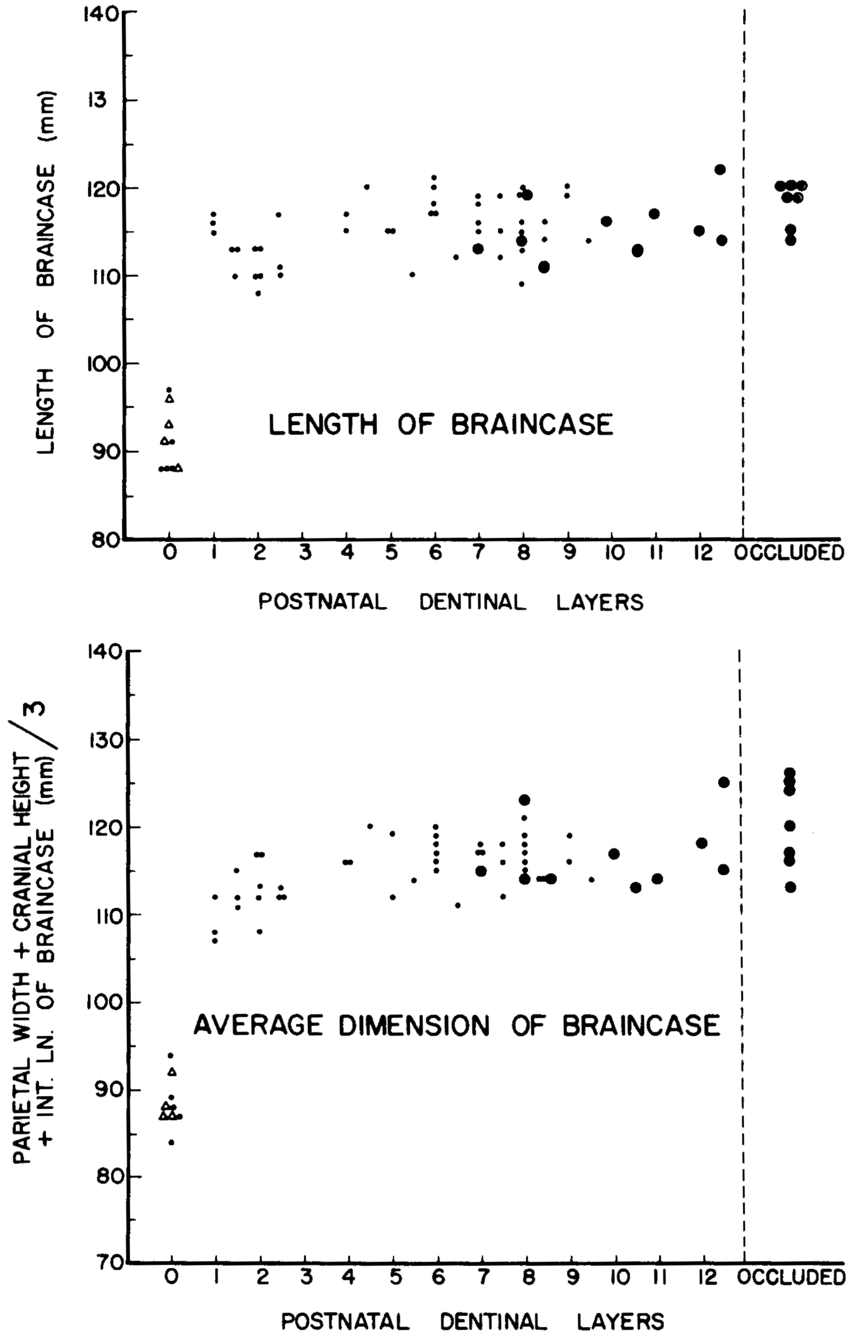


Figure 15. Development of skull of spotted porpoise: scatterplots of length of braincase (top) and average dimension of braincase (bottom) on number of postnatal dentinal layers. Symbols same as figure 14.

The measurements reflecting length of the beak (namely, length of rostrum [fig. 16], length of upper tooth row, length of mandibular ramus, and length of lower tooth row) all increase in a similar manner, with very rapid growth during Classes I to III ($\leqslant 4$ dentinal layers) and attainment of an adult plateau of beak length in Class IV (> 4 layers). Older animals vary less in beak length, but this may be owing to sampling error, as the younger classes are represented by larger samples. The projection of the premaxillaries beyond the maxillaries likewise shows no change after attainment of the adult plateau.

Ratio of rostrum length to basal width, cranial length, and condylobasal length have been used in the taxonomy of *Stenella* (Gray, 1846; Hall and Kelson, 1959; Van Gelder, 1960; Fraser, 1950), and, while the emphasis in this account is on absolute growth of functional units, plots of these ratios on number of dentinal layers (fig. 16) are presented to provide bases of comparison with previous taxonomic work. The respective variances of these measures is discussed below in the section on individual variation. Of the three, the ratio of rostrum length to basal width appears to show least correlation to age.

Although the length of the rostrum reaches a plateau relatively early in development, it continues to grow in width anteriorly (fig. 17) well into adulthood, primarily owing to anterior broadening of the premaxillae.

Comparison of the slopes of linear regressions of log width at base, midlength, and 3/4 length of the rostrum on log of dentine layers (table 8) shows that the growth rate for width is greatest in the distal portion of the rostrum, decreasing proximally.

Table 8. Results of log-log regression analyses of rostral widths on number of postnatal dentinal layers.

Measurement	Sample	Log Equation Intercept a Slope b[1]	Correlation coefficient r
Width of rostrum at base	52	Y = 1.874 mm + .105 X	.963
Width at 1/2 length	60	Y = 1.587 mm + .127 X	.874
Width at 3/4 length	57	Y = 1.414 mm + .143 X	.835

[1] Growth coefficient α in arithmetic growth equation $Y = a + bX^{\alpha}$

The postorbital process, zygomatic process (excluding its mesoventral projection), and (supra- or post-) temporal fossa are components of the feeding apparatus, because they are functionally tied to the temporal muscle. The two processes enclose the temporal fossa, through which the temporal muscle passes. The "posttemporal" fossa is the area occupied by the origin of the muscle, delineated by the posterior perimeter of the temporal fossa proper. In addition, the zygomatic process of the squamosal also functions as the pivot for the lower jaw.

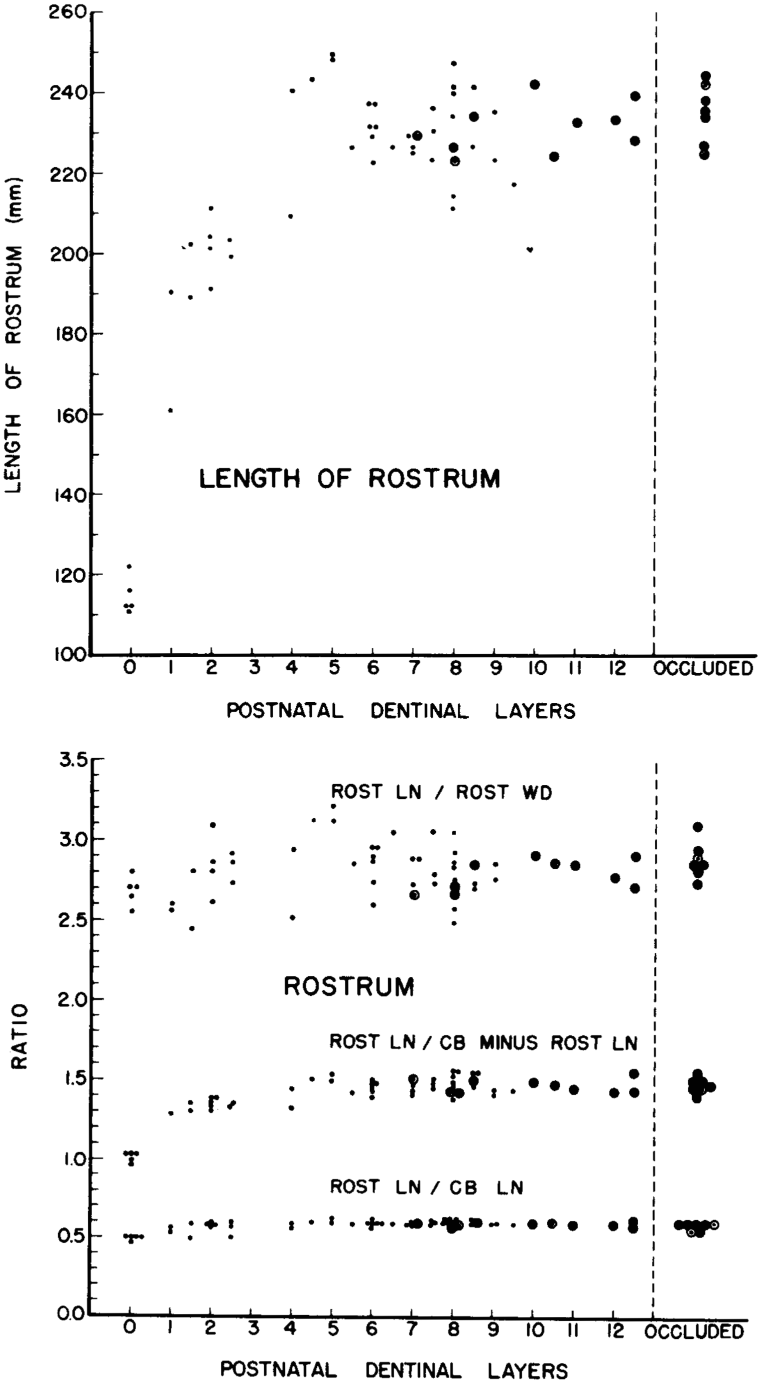


Figure 16. Development of skull of spotted porpoise: scatterplots of length of rostrum (top) and proportional rostral measurements (bottom) on number of postnatal dentinal layers. Symbols same as figure 14.

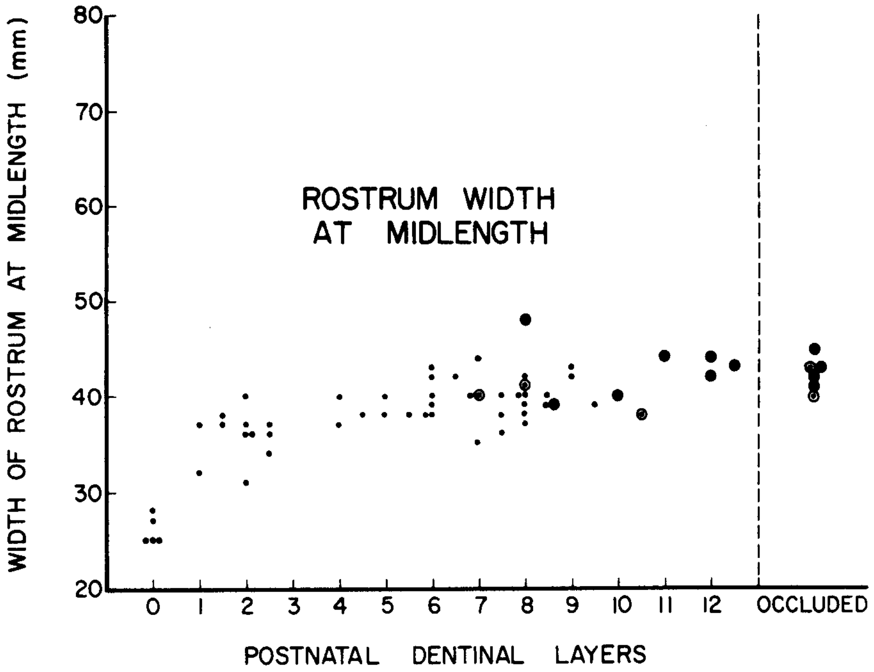


Figure 17. Development of skull of spotted porpoise: scatterplot of rostrum width at midlength on number of postnatal dentinal layers. Symbols same as figure 14.

The postorbital process becomes proportionately more massive with development and projects at an increasingly greater angle from the cranium. At the same time the temporal fossa enlarges and changes in cross section from a flattened oval to a subtriangular or pyriform oval (fig. 18). The zygomatic process shows a similar pattern of development in massiveness and angle of projection.

The posterior limits of the posttemporal fossa are vaguely suggested in Class I and II skulls by bone texture and contour, but it is not until Class III that the fossa is clearly delineated. In older animals, the hindmost rim of the fossa, formed at the parietoexoccipital suture, becomes increasingly thickened and rugose. The squamous portion of the squamosal invades the fossa area, overlaying the parietal, until it reaches its maximum development in Class IV skulls.

The teeth are an important part of the feeding apparatus. At birth they are set in long slots, with very slight ridges delineating the positions of future alveoli. The maxillary furrow for its full length completely penetrates to the underlying premaxillary bone. In the mandible, the furrow penetrates to the mandibular fossa. In Class III skulls the furrows are floored, and in Class IV skulls the alveoli are partitioned off.

The basihyal, thyrohyals, and stylohyals (fig. 19) act as anchors for important muscles involved in lowering the jaw, moving the tongue, and swallowing (Lawrence and Schevill, 1965). Therefore, although these hyoid bones certainly are involved in other functional units, the description of their development is included here in the account of the feeding apparatus. The stylohyals are included below in consideration of the breathing and sound-producing apparatus.

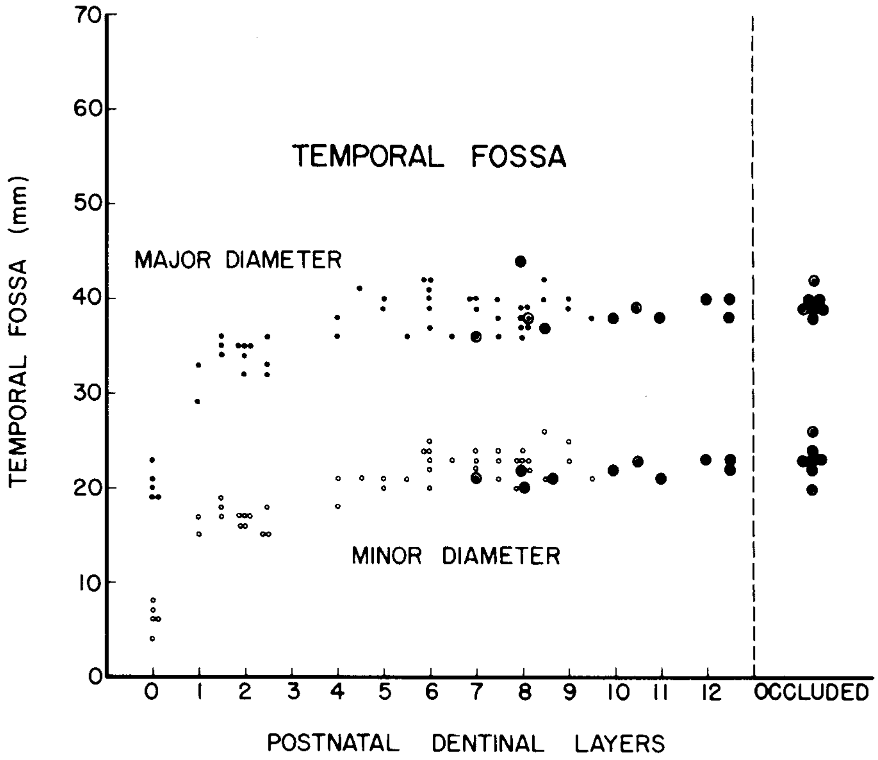


Figure 18. Development of postemporal fossa of spotted porpoise: scatterplot of diameters of postemporal fossa on number of dentinal layers.

At birth, the thyrohyals are not fused to the basihyal, and considerable variation is exhibited in shape of the thyrohyals. Complete fusion of the thyrohyals and basihyal occurs quite late in development (figs. 19 and 20), and does not appear to be correlated with the attainment of physical maturity as adjudged by fusion of the vertebral epiphyses. Some individuals with unfused epiphyses have completely fused hyals, and vice versa.

The basihyal and thyrohyals grow like the other elements of the feeding apparatus, that is, they exhibit a protracted rapid growth phase followed by a flat plateau. An apparent continued growth in length of the osseous thyrohyal in adulthood results from delayed ossification of the proximal cartilaginous portion in fusion of the basihyal and thyrohyals.

Hearing Apparatus. The tympanoperiotic bones are indisputably part of the hearing apparatus. In addition, following Fraser and Purves (1960), I consider the portion of the underside of the skull posterior to the base of the rostrum and lateral to the bony nares and basicranial trough, excluding the zygomatic arch, the glenoid fossa of the squamosal, and the orbital processes, to be functional in hearing. The excavations and sculpturing in this region reflect the positions of air-filled sinuses that presumably insulate the animal's inner ear from phonations produced somewhere in the nasopharyngeal system.

Figure 19. Hyal bones of spotted porpoise: (a-c) neonatals, Class II; (d) Class II.5; (e) Class III; (f) Class IV; (g) Class V; (h) Class VI.

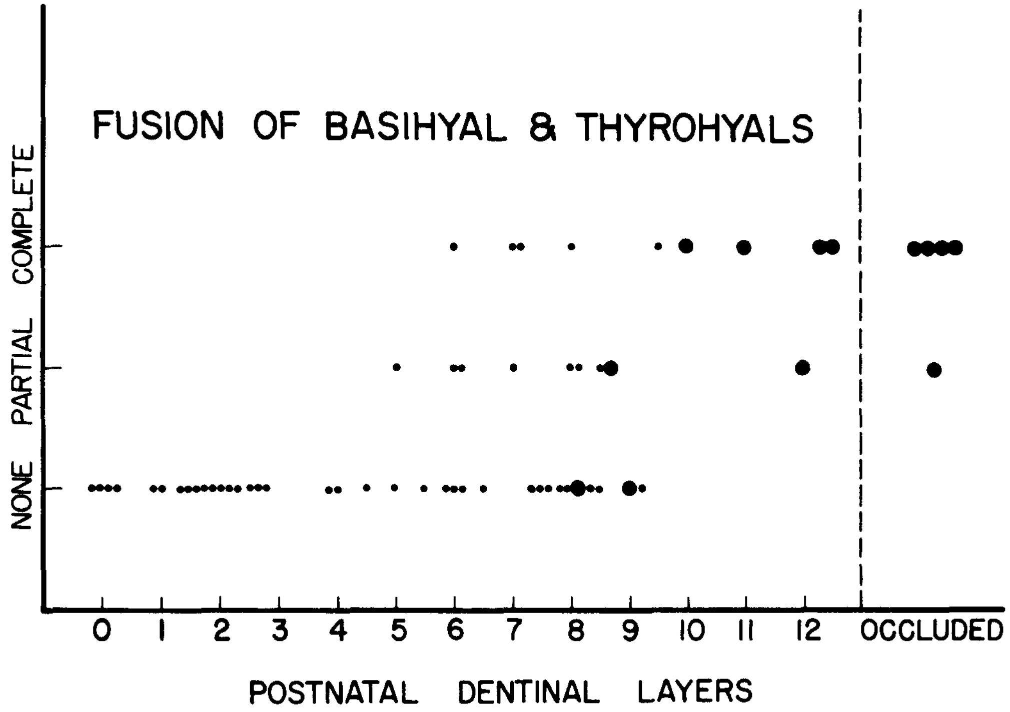


Figure 20. Development of hyoid bones of spotted porpoise: scatterplot of degree of fusion on number of dentinal layers. Symbols same as figure 14.

Following Norris (1963), I provisionally assume that certain elements of the mandible are involved in hearing and therefore also include in the "hearing apparatus" the mandibular fossa and the very thin angular process. The angular process is strongly developed uniquely in Cetacea and apparently does not function as a major muscle anchor. Its presumed function is to bring the end of the mandibular fossa and of its contained fat organ down and back to a position nearly adjacent to the tympanoperiotic, providing a lateral "acoustic window."

In addition to the internally situated incus, malleus, and stapes, the tympanoperiotic has three major components: the periotic, the tympanic bearing the bulla, and the mastoid process. The periotic, including the portion housing the cochlea, is nearly fully developed at birth and shows an average change in length during development of only about 1 mm (fig. 21). The bulla lengthens rapidly after birth about 2 mm to reach the adult plateau of development in Class II.5 animals (1 tooth layer). The mastoid process is similarly fully developed in Class II.5 individuals.

Development of the falciform process of the squamosal parallels closely that of the tympanoperiotic complex, reaching completion in Class II.5 animals.

The air sinus system around the tympanoperiotic, or at least the vestiges of it as seen in the skull, reaches approximately adult configuration in Class II.5 animals, with thickness of isolating spaces greatly increased over that at birth. The supratympanoperiotic hiatus begins to be diminished after birth by osteosclerotic extensions of the squamosal, occipital, and alispenoid, and in most Class III skulls the foramen ovale is partitioned off

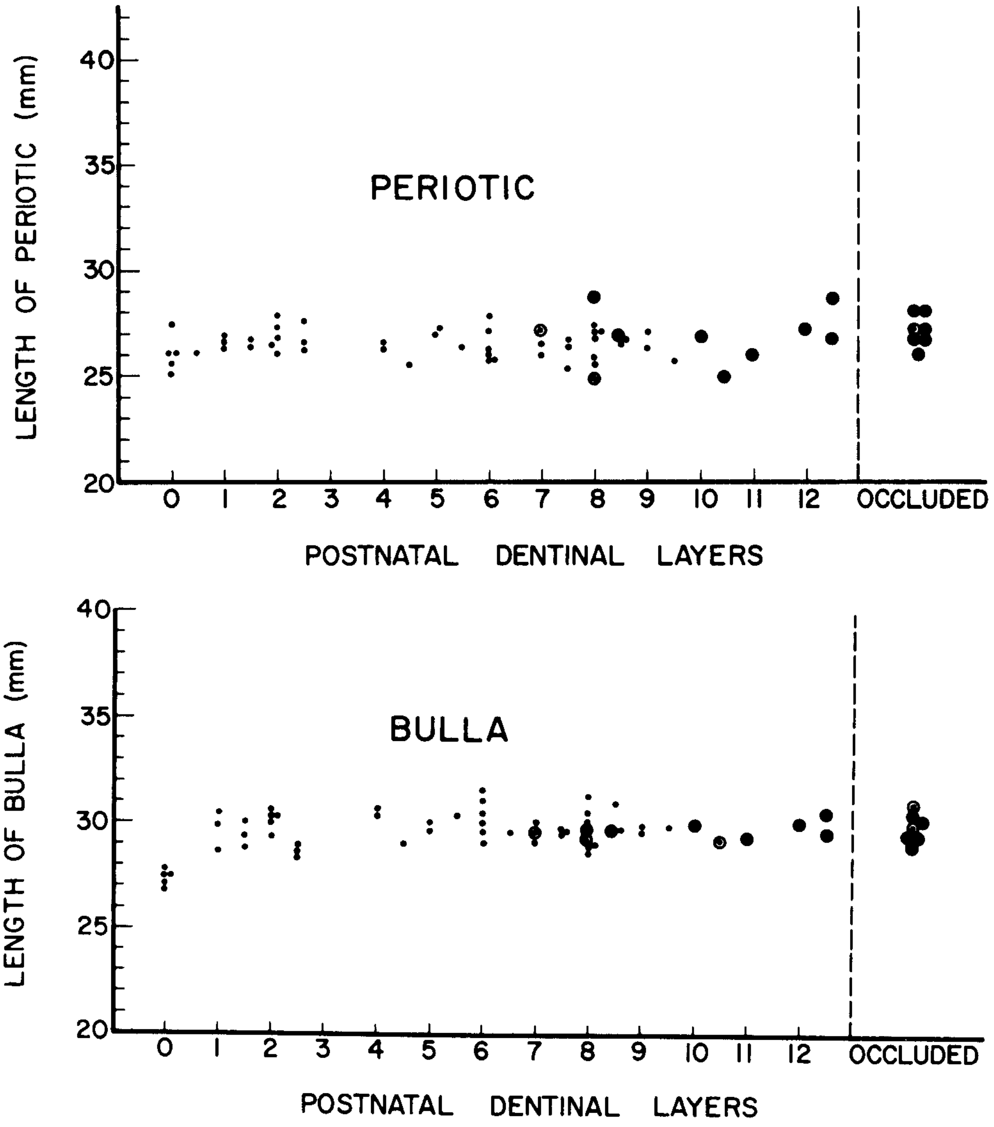


Figure 21. Development of skull of spotted porpoise: scatterplot of length of periotic (top) and bulla (bottom) on number of dentinal layers. Symbols same as figure 14.

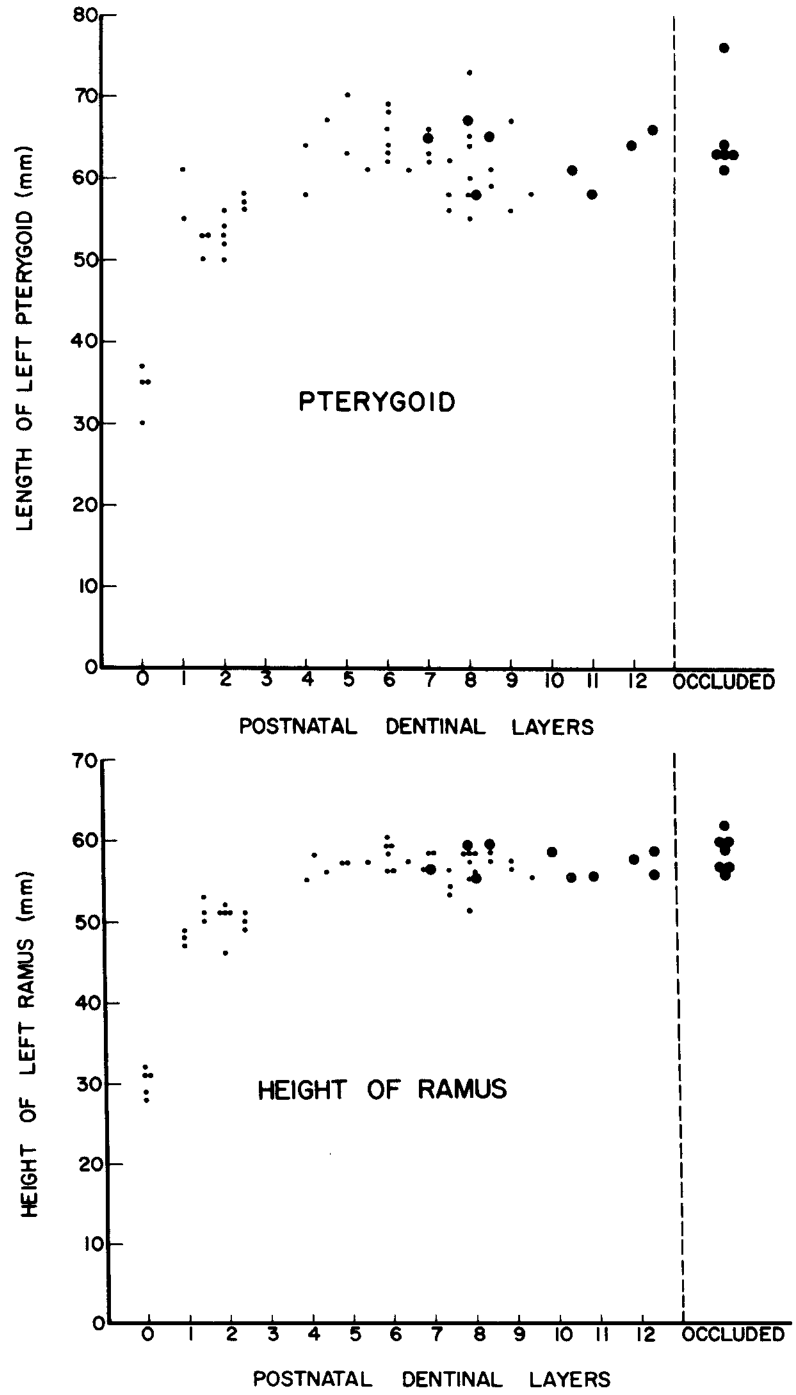


Figure 22. Development of skull of spotted porpoise: scatterplots of length of pterygoid (top) and height of mandibular ramus (bottom) on number of dentinal layers. Symbols same as figure 14.

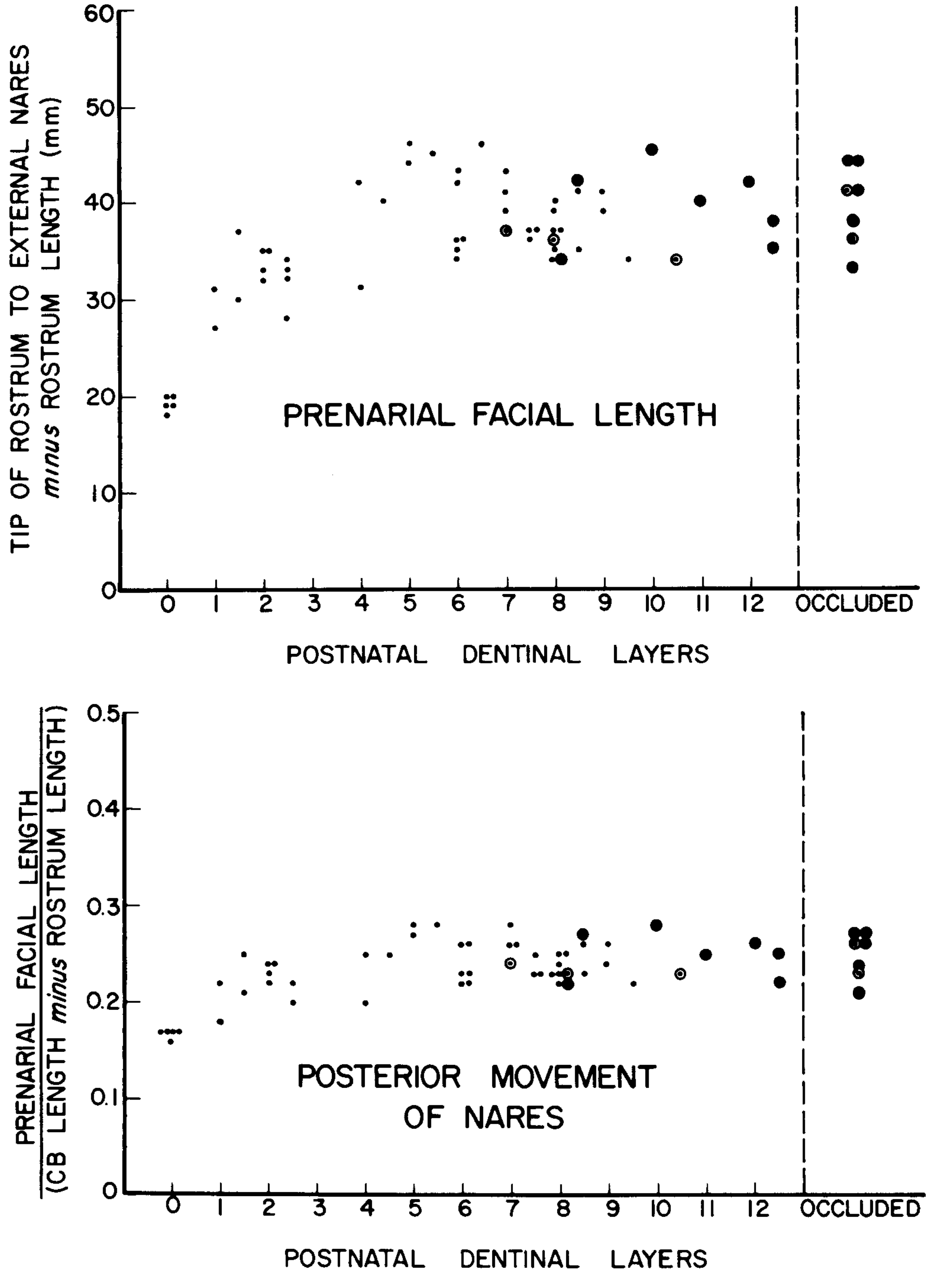


Figure 23. Development of skull of spotted porpoise: scatterplots of prenarial facial length (top) and posterior movement of nares (bottom) on number of dentinal layers. Symbols same as figure 14.

from the hiatus. The subsequent course of reduction of the hiatus, however, varies greatly; some old animals possess quite large openings. The anterior portions of the air sinus system, including the pterygoid fossae, also reach essentially the adult state in Class II.5 skulls. The exception is development of the pterygoid hamuli. Variation in the standard measurement Tip of rostrum to mesial end of posterior edge of left pterygoid, which reflects development of the pterygoid, obviously must be influenced greatly by variation in length of the contained rostrum. A better measure of pterygoid development is Greatest length of the pterygoid (fig. 22). This measurement, exhibiting a protracted initial rapid growth phase, is similar to that of the feeding apparatus. This is interesting in light of Lawrence and Schevill's (1965) suggestion that the pterygoid hamuli may function in feeding to extend the hard palate and direct food away from the end of the larynx.

The measurement of height of the madibular ramus (fig. 22) shows a pattern of increase intermediate between that of the tympanoperiotic and that of dimensions most directly reflecting development of feeding ability, that is, the cross-sectional area of the temporal fossa (fig. 18) with the flat adult plateau attained in young Class IV skulls. This intermediacy is to be expected, because the measurement encompasses the coronoid portion of the ramus, which functions as the area of insertion of the temporal muscle, and the angular process, which probably functions in hearing. The length of the mandibular fossa increases similarly but is influenced by the length of the lower jaw.

Vision apparatus. The antorbital process and supraorbital shelf must certainly function in protecting the eye. The measurements across these structures, however, incorporate the breadth of the facial region. The facial region is primarily functional in breathing and/or sound production (see next section). The length of the orbit stabilizes in Class IV skulls at the adult level.

Breathing and sound-producing apparatus. The most significant feature of the odontocete skull which has to do with breathing is its telescoping (described in detail by Miller, 1923). Telescoping brings the bony nares from the end of the rostrum to a proximal, dorsal position, an adaption to allow the animal to breathe rapidly without lifting his head high out of the water. The expansion of the supraorbital wings of the maxillaries and frontals, also described by Miller, and the occipital crest, provide areas of attachment for muscles functional in breathing (Lawrence and Schevill, 1956). These muscles, and the "basining" (Miller, 1923) of premaxillaries, nasals, and mesethmoid, may also function in sound production and transmission (Norris, et al., 1961; Evans and Prescott, 1962).

Telescoping, or posterior movement of the nares and the adjacent maxillaries, is well along at birth and essentially complete in Class II skulls (fig. 13). The measurement Tip of rostrum to mesial end of anterior transverse margin of right nares reflects position of the nares, but includes the rostrum. A better measure of postnatal development is provided by subtraction of rostral length. This distance reaches adult level in Class IV skulls (fig. 23). The postnatal progress of telescoping, or posterior movement of the nares, can be followed by examining the change in the ratio between this measurement and condylobasal length minus rostrum length (fig. 23).

The pattern of development of this region and of the widths of the external and internal nares is like those of elements of the hearing apparatus, with a short initial rapid growth phase and early attainment of a flat adult plateau in Class IV skulls.

The areas of muscle attachment on the maxillaries, frontals, dorsal and posterior faces of the nasals, and in the prenarial triangle (the origin of the blowhole plug muscle) become increasingly rough and rugose with age. With the exception of the region bordering the antorbital notch, these areas are all smooth at birth. Class IV skulls are extensively roughened, and Class VI skulls are most rugose. The area of insertion of the antero-external layer of the maxillonasolabial muscle (see Lawrence and Schevill, 1956) becomes increasingly thickened and rugose with age, resulting in thickening of the antorbital process.

The extremely variable supraoccipital crest reaches maximum development as measured by occipital overhang in specimens of Class IV and V, and exhibits some erosion in specimens of Class VI (fig. 24). In physically mature individuals (Class VI) the accessory occipital rugosities vary in degree of development.

The measurement of the distance from the anterior end of the junction between the nasals to the hindmost point of the supraoccipital crest is influenced by two forces during development (fig. 24). As telescoping proceeds in early development, with the frontals and associated nasals slipping over the interparietal, the distance decreases sharply. In later development, as the supraoccipital crest thickens, the distance increases to level off to a plateau in physically mature specimens.

The premaxillary shield develops more slowly than the external nares; adult width is attained at Class IV. The postnarial shield, composed of the mesethmoid and anterior surfaces of the nasals, reaches near-adult development much earlier. Anteriorly, a large gap exists at birth between the frontals. A projection of the mesethmoid extends upward into the gap. At or near birth, two accessory centers of ossification appear, and by the time two layers have been laid down in the teeth (Class III), the mesethmoid has reached its adult state of development, overlapping the frontals and nasals to varying degree. The asymmetry of the narial region of the delphinid skull may be linked functionally to sound production. Asymmetry is nearly fully developed at birth and does not decrease during subsequent development as it does in *Psuedorca* (Yamada, 1956).

The pattern of growth of the stylohyal is like that of the prenarial facial length (fig. 23).

Summary. The functional units of the skull have different patterns of postnatal development (fig. 25). At birth, the hearing apparatus and some elements of the breathing and sound-producing apparatus (asymmetry and the postnarial shield) are most precocious, followed by the vission apparatus, the braincase, other elements of breathing and sound-producing apparatus, and the feeding apparatus, in that order. All but the braincase and one component of the breathing and sound-producing system (the internal nares) reach adult size in some Class IV specimens (2-4 dentine layers). The braincase and width of the internal nares continue to grow into physical maturity. The rates of

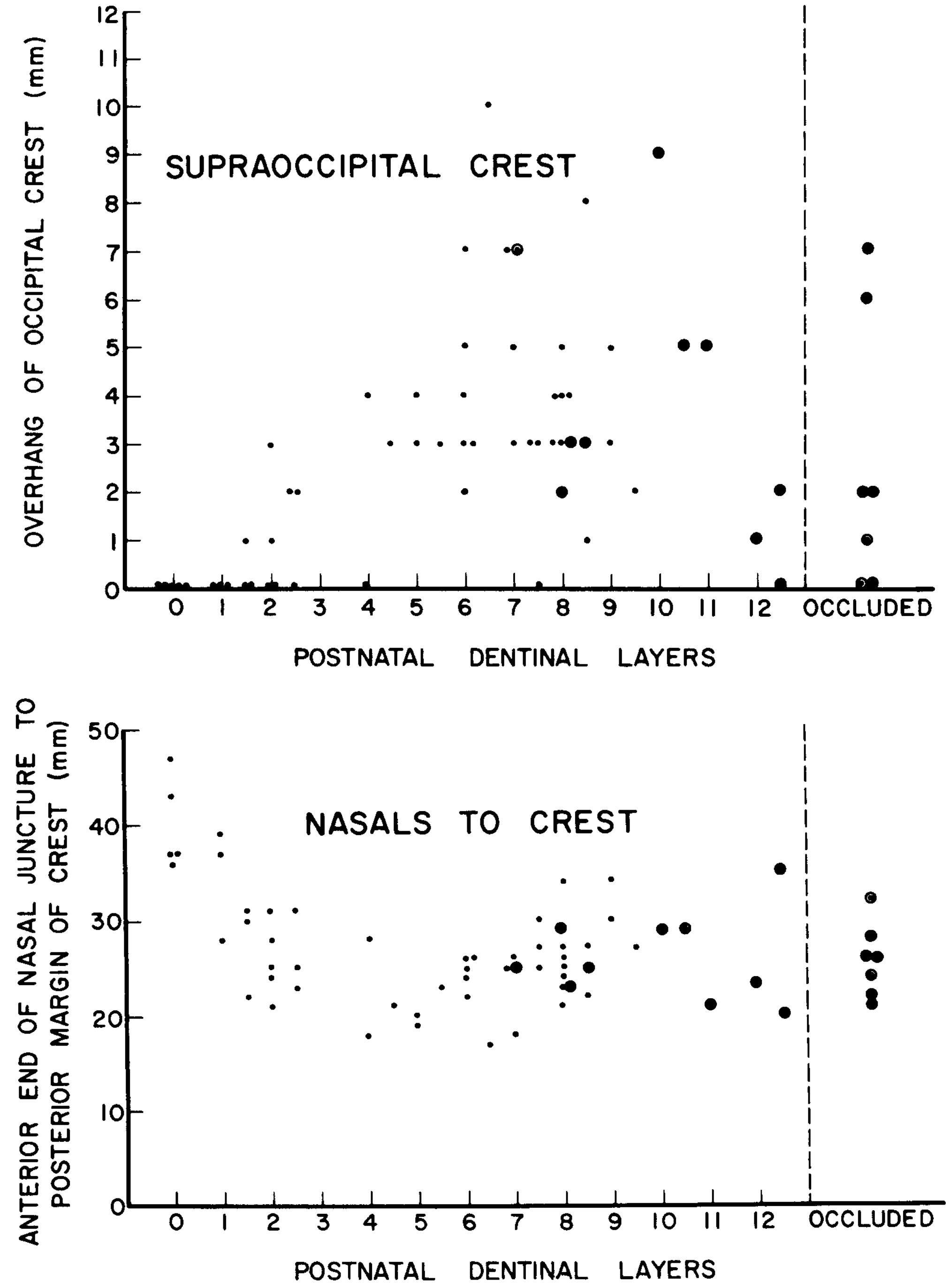


Figure 24. Development of skull of spotted porpoise: scatterplots of overhang of supraoccipital crest (top) and nasals-to-crest distance (bottom) on number of dentinal layers. Symbols same as figure 14.

growth of the other four units are inversely proportional to the respective degrees of precocity at birth, the feeding apparatus growing most rapidly and the nearly fully developed hearing apparatus most slowly. Some standard measurements that pertain to more than one functional unit show intermediate patterns of increase, and others, such as distal width of the rostrum, may be influenced by secondary sexual dimorphism and are therefore more properly considered in that context.

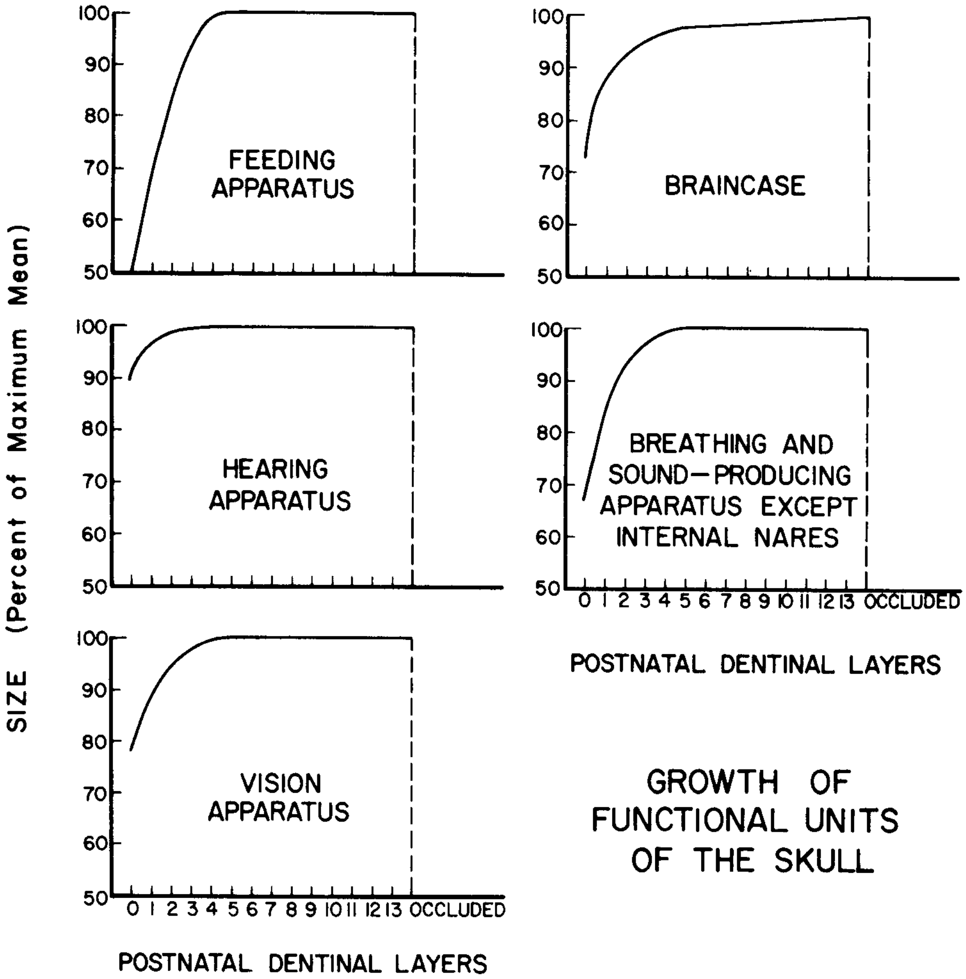


Figure 25. Comparative growth of functional units of the skull of the spotted porpoise, based on average growth rates.

Postcranial skeleton

Variation with growth is analyzed for the axial, anterior appendicular, and posterior appendicular elements of the postcranial skeleton.

Axial postcranial skeleton (fig. 26). At birth, none of the veterbral centra are fused. The neural arches of the atlas and axis are partially fused in some individuals. The neural arches are not yet ankylosed to the centra, and the halves of the neural arches of the first 10-15 vertebrae are not yet ankylosed dorsally. Ossified transverse processes are not yet developed on any vertebrae. In Class II.5 skeletons, the centra and neural arches of the atlas and axis are partially fused, all neural arches are complete and ankylosed to the centra, and ossified transverse processes are present on the atlas, axis, and postcervical vertebrae. The neural arches of 1-3 cervicals may remain permanently incomplete. Fusion of the atlas and axis is not complete until Class IV or V. Class VI specimens may exhibit fusion of the neural arches of the first three cervicals and fusion of the arches and centra of the remaining cervicals in varying combination. The atlas reaches adult dimensions in Class II.5 skulls in width of the articulating surface, in length of transverse process (fig. 27), and in height, which includes height of the articulating surface and height of the neural canal. The neural process (fig. 27) continues to lengthen into adulthood. The transverse processes of the axis develop in the same manner as those of the atlas. The neural spine of the atlas-axis complex may bifurcate with age or remain blunt. Anteriorly, the ridge of the neural spine is well developed in Class III. In Class III and older specimens a small dorsomesially projecting spine may arise at the dorsal end of each half of the articulating surface of the atlas.

The ventrolateral processes on the fifth, sixth, and seventh cervicals are absent at birth but develop to varying degrees to near the adult level in Class III. The tremendously variable first thoracic neural spine develops like the spine of the atlas-axis complex. The remaining neural spines continue to lengthen at least through Class V by distal ossification.

The rate of developmental increase (the value of Huxley's growth coefficient α) during the rapid growth phase of vertebral height decreases from the cephalic end of the vertebral column toward the middle of the column. This is evident in comparison of vertebral heights (centrum plus neural canal) of the atlas-axis complex, first thoracic, and first lumbar. In other words, the age increases at which mature size and proportions are attained. The same pattern is shown by vertebral width (fig. 27), a measurement including the centrum and the transverse processes. Judging from fusion of epiphyses and centra, the vertebrae in the lumbar region also continue to grow in length (fig. 27) until the onset of physical maturity. This protracted growth in the postcranial skeleton agrees with the results for external proportions, indicating cessation of cephalic growth at or before puberty, with continual growth of postcephalic body into adulthood (fig. 27).

The halves of the first 8-10 hemopophyses (chevron bones) are unankylosed at birth. In Class II.5 specimens, all hemopophyses are usually ankylosed, and the first 2-5 arches may be fused to each other in various combinations. In some cases, portions of the first few arches may remain discrete. The hemopophyses continue to lengthen through elongation of the ventral keel at least until physical maturity is reached in Class VI.

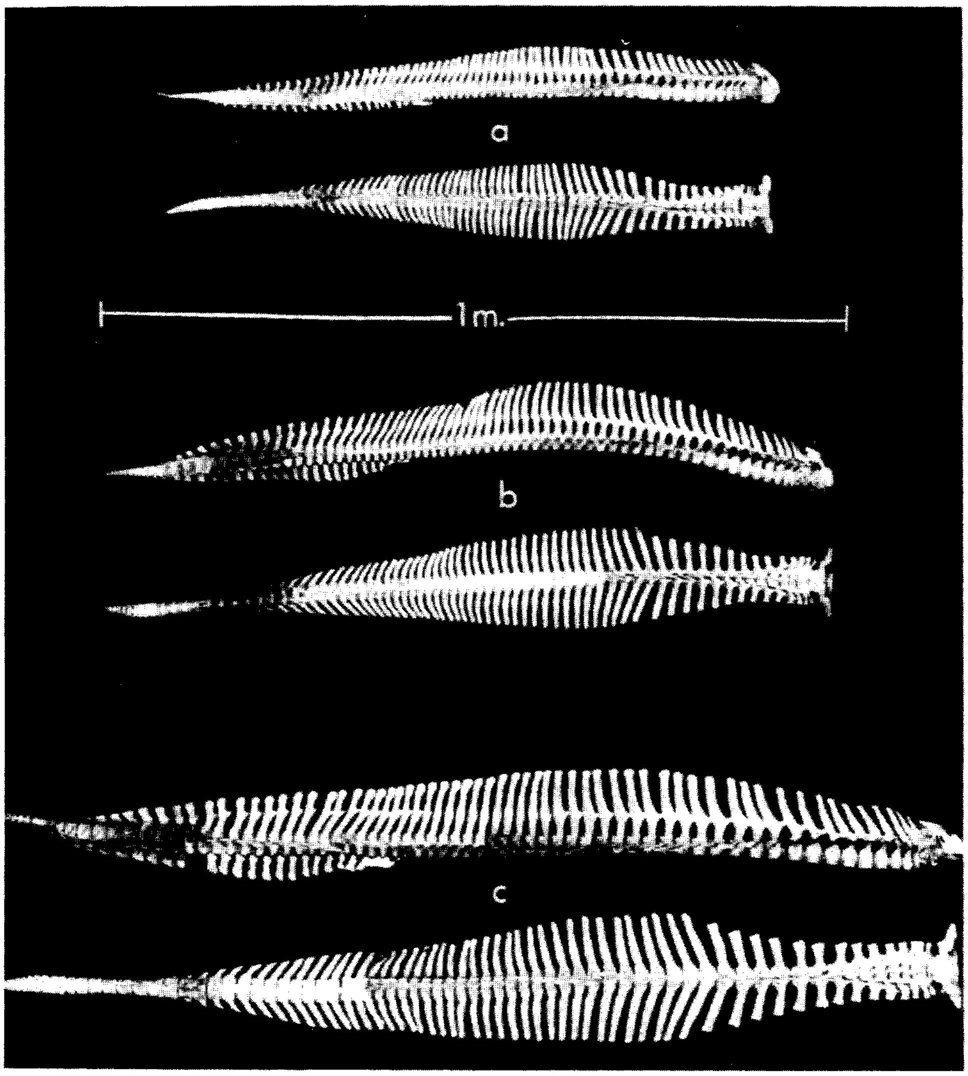


Figure 26. Developmental series of the postcranial axial skeleton of spotted porpoise: (a) LACM no. 27431, sex unknown, one layer, Class II.5; (b) USNM no. 395612, female, 2 layers. Class III; (c) USNM no. 395387, sexually immature male, 6 layers, Class IV (continued).

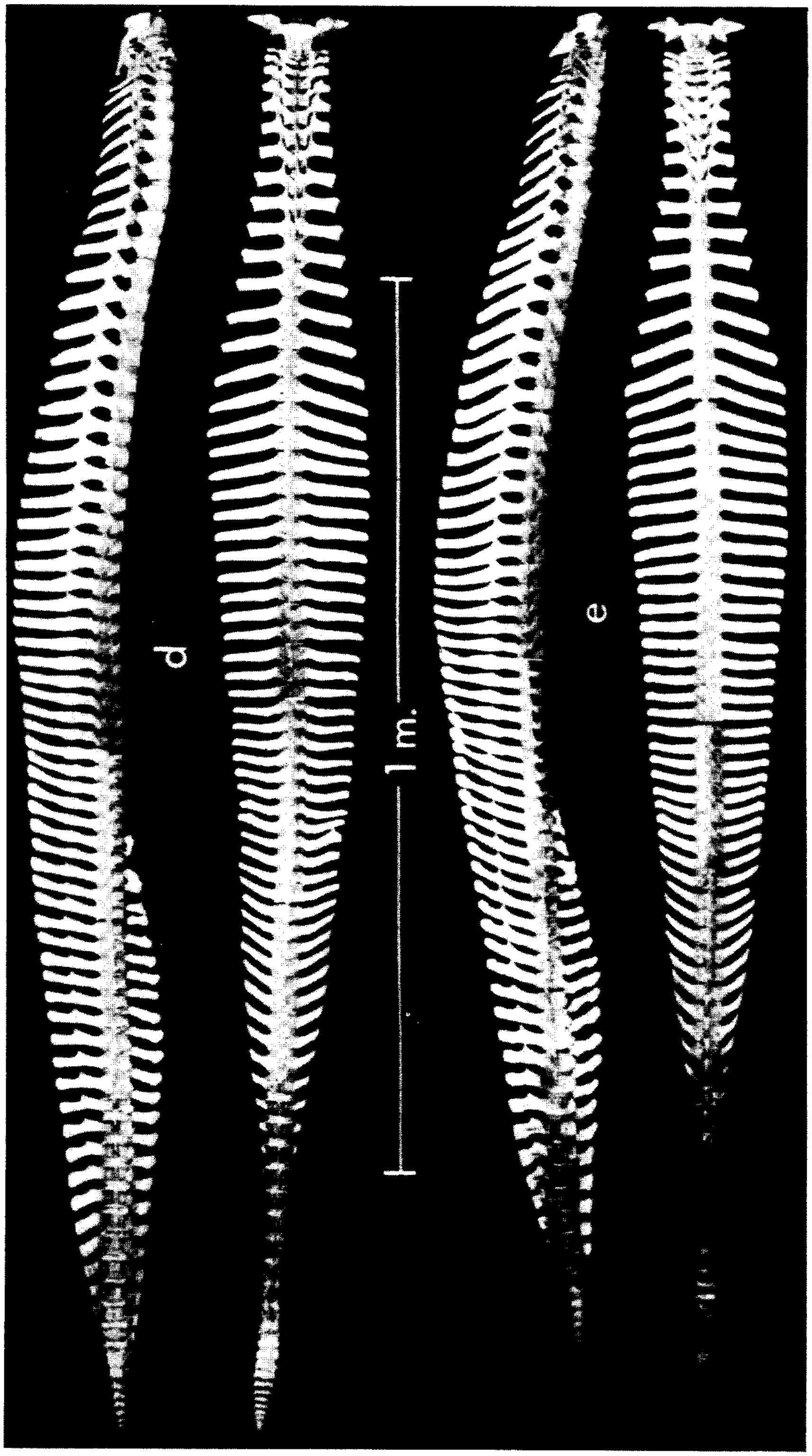


Figure 26. (continued). Developmental series of the postcranial axial skeleton of spotted porpoise: (d) USNM no. 395598, sexually mature but physically immature, 8 layers, Class V; (e) USNM no. 395338, sexually and physically mature female, 11 layers, Class VI.

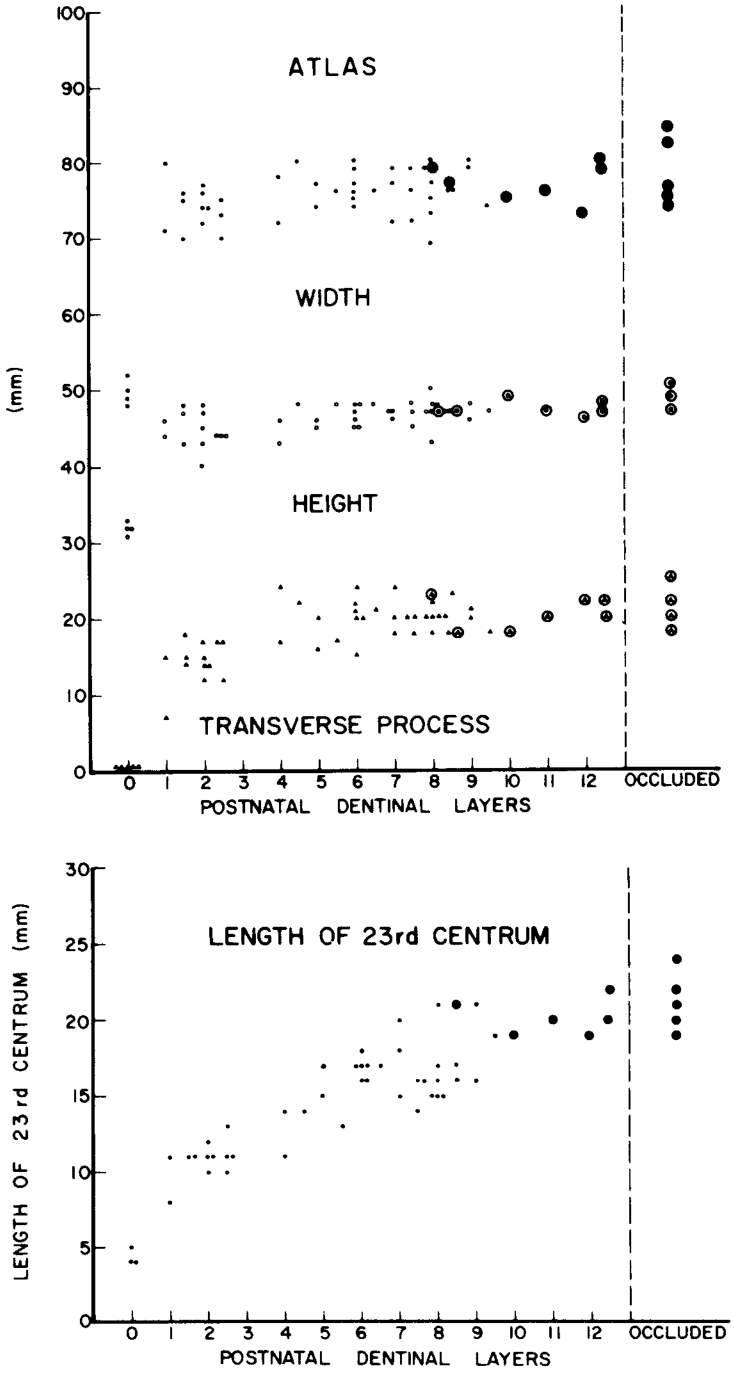


Figure 27. Development of vertebral column of spotted porpoise: scatterplots of measurements and meristics on number of dentinal layers. Small symbols are physically immature specimens; large symbols are mature (continued).

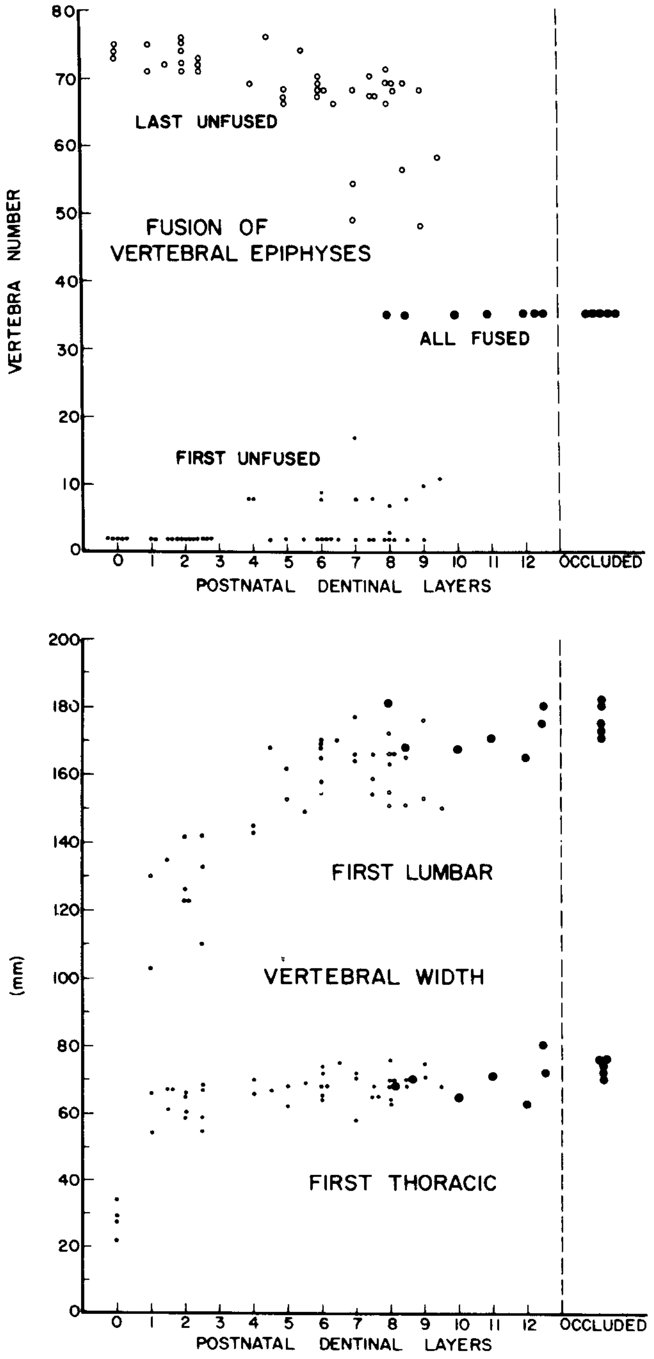


Figure 27 (continued). Development of vertebral column of spotted porpoise: scatterplots of measurements and meristics on number of dentinal layers. Small symbols are physically immature specimens; large symbols are mature (continued).

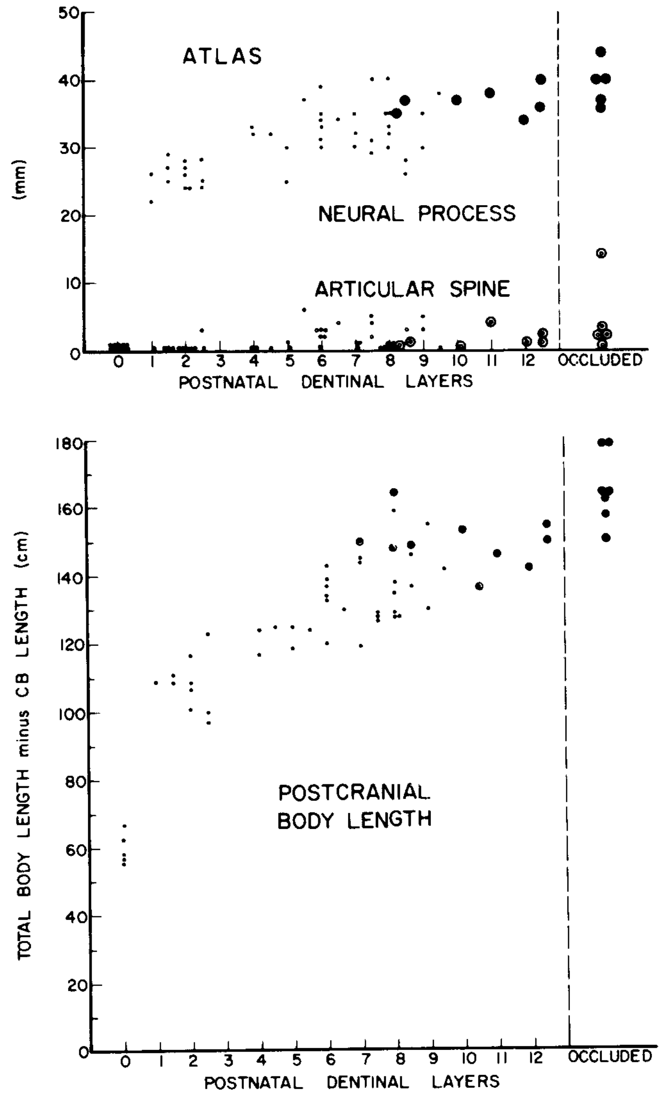


Figure 27 (continued). Development of vertebral column of spotted porpoise: scatterplots of measurements and meristics on number of dentinal layers. Small symbols are physically immature specimens; large symbols are mature.

Vertically perforating foramina occur in the center of the posterior portion of the vertebral column. The series of foramina lengthens during early development as progressive ossification encloses more vessels, moving the average position of the first enclosed opening forward one or two vertebrae. Stability is reached by Class II.5 (one layer in the dentine).

The vertebral ribs (fig. 28) reach adult shape in Class II.5. At birth the capitula of the two-headed ribs (first 4 to 6) are weakly developed, and there is a nearly insensible gradation from the two-headed condition to ribs with a tuberculum only. The hindermost three or four ribs at birth are very slender, and S-shaped to varying degree. The recurvature of the posterior ribs disappears by Class II.5, and they become proportionately more massive proximally. Similar development occurs in the sternal ribs, with adult shape achieved by Class II.5. Both vertebral and sternal ribs, however, continue to increase in absolute length and breadth at least until achievement of physical maturity and possibly beyond (fig. 29).

The shape and degree of ossification at birth of the manubrium of the sternum varies widely. Anterior fusion of the two wings may be complete or incomplete even until Class III is reached. A foramen may be present or absent. Adult shape of the manubrium is not reached until Class IV. Size of the foramen is extremely variable, but the tendency is toward closure with development. The foramen is closed in a significantly higher proportion of physically mature individuals than of immature individuals. After rapid increase in length and breadth up to Class IV, the manubrium continues to grow, albeit more slowly, at least until physical maturity is attained (fig. 29). The depth of the anterior notch also generally continues to increase, although some old individuals have relatively shallow notches.

Two mesosternal elements are ossified at birth. With development, the third mesosternal element, cartilaginous at birth, may or may not ossify. In some older individuals with three mesosternal elements, a small spherical ossification is present in the fourth, cartilaginous element. Thus old adults may possess two, three, or four mesosternal bones, depending on the course of postnatal ossification. The second mesosternal may consist of two side-by-side elements at birth, and traces of the suture of these elements is still visible in some mature specimens.

Fusion of the mesosternals to each other and of the first mesosternal to the manubrium begins in Class IV and proceeds to varying degrees of completeness, from fusion only of the manubrium and first mesosternal, to fusion of all four elements in some individuals. In some individuals, fusion may occur between the manubrium and first mesosternal and between the second and third elements but not between the first and second.

Anterior appendicular skeleton. The blade of the scapula (fig. 30) grows until physical maturity is attained and possibly beyond. The increase in height is more rapid than increase in length, causing the scapula to become progressively longer, proportionately, until the individual reaches physical maturity (fig. 31). The blade in the region of the coracovertebral angle thickens during adulthood and in old individuals the border may become keeled. The entire blade becomes more dished with age, and the accessory spines in the infraspinal fossa become more pronounced. In physically mature animals, the spines on the subscapular surface develop tuberose, posteriorly-directed ridges (fig. 30).

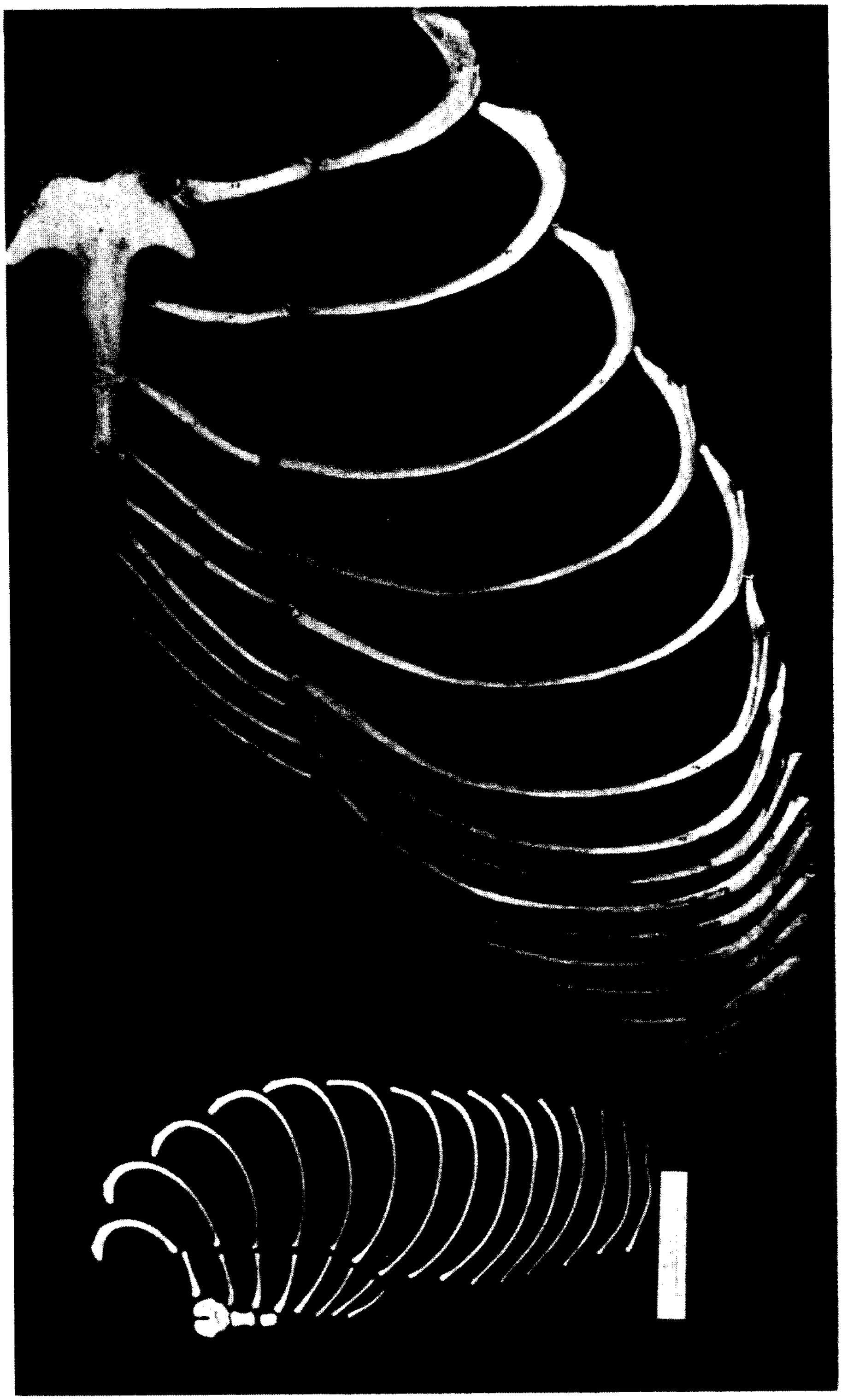


Figure 28. Ribs and sternae of neonatal (left) and physically mature (right) spotted porpoise (specimens *a* and *e* in figure 26).

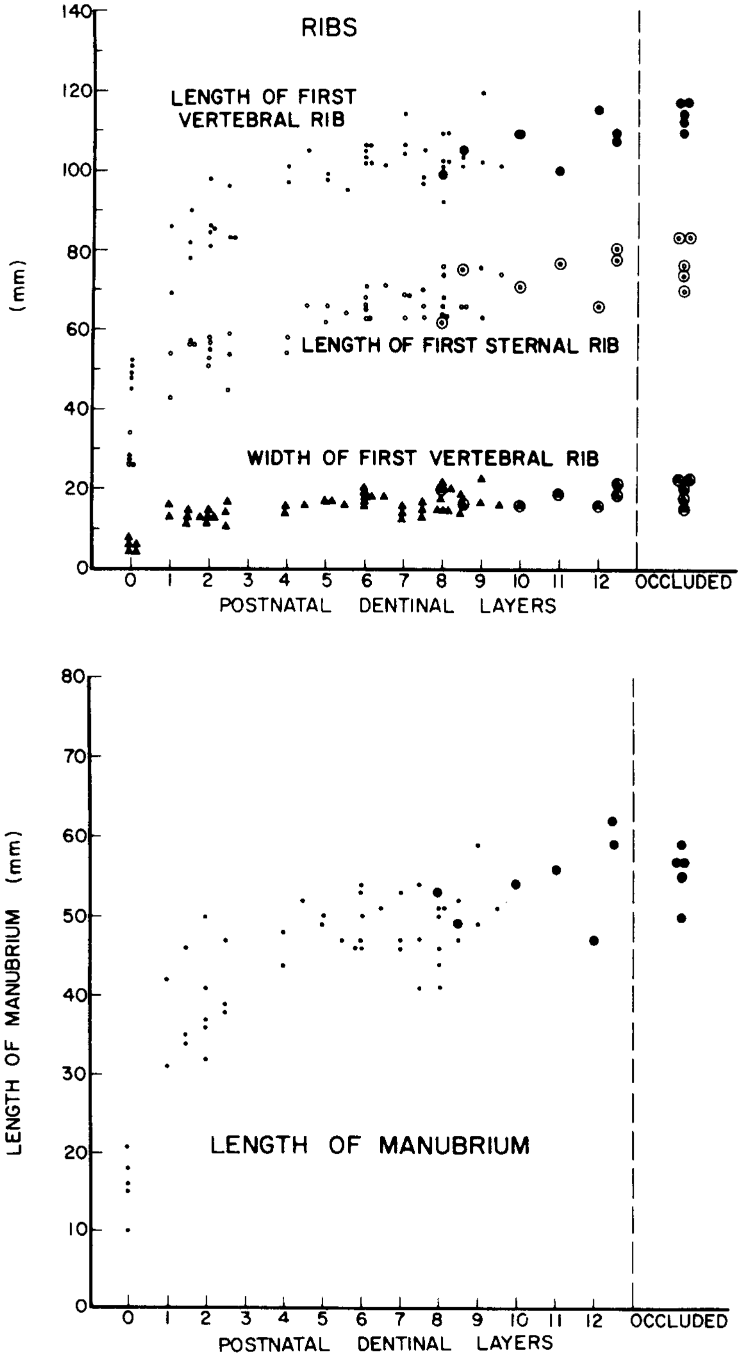


Figure 29. Development of ribs (top) and manubrium (bottom) of spotted porpoise: scatterplots of measurements and meristics on number of dentinal layers (continued).

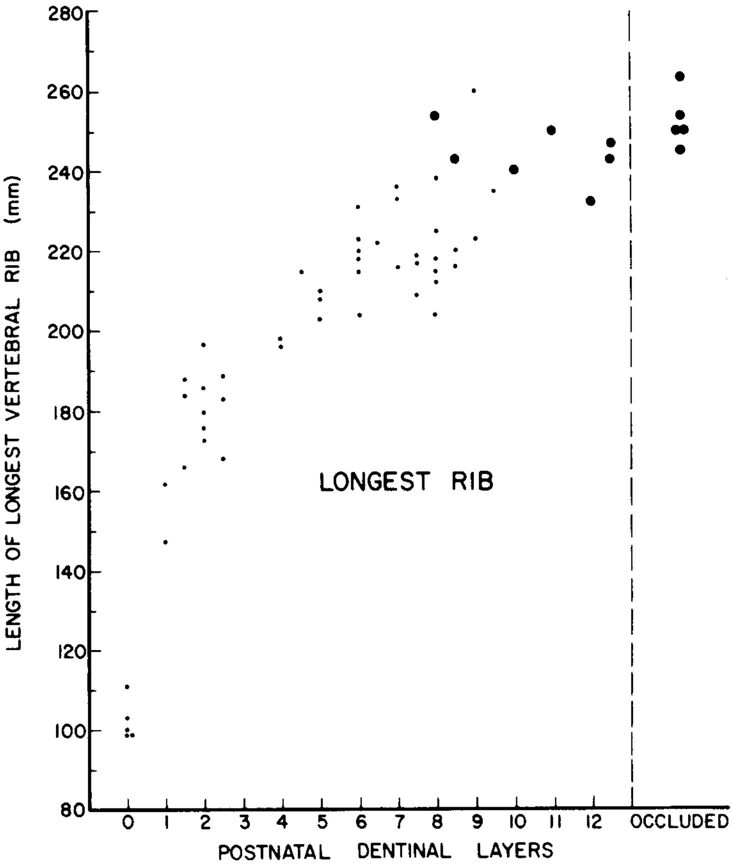


Figure 29 (continued). Development of longest rib of spotted porpoise: scatterplots of measurements and meristics on number of dentinal layers.

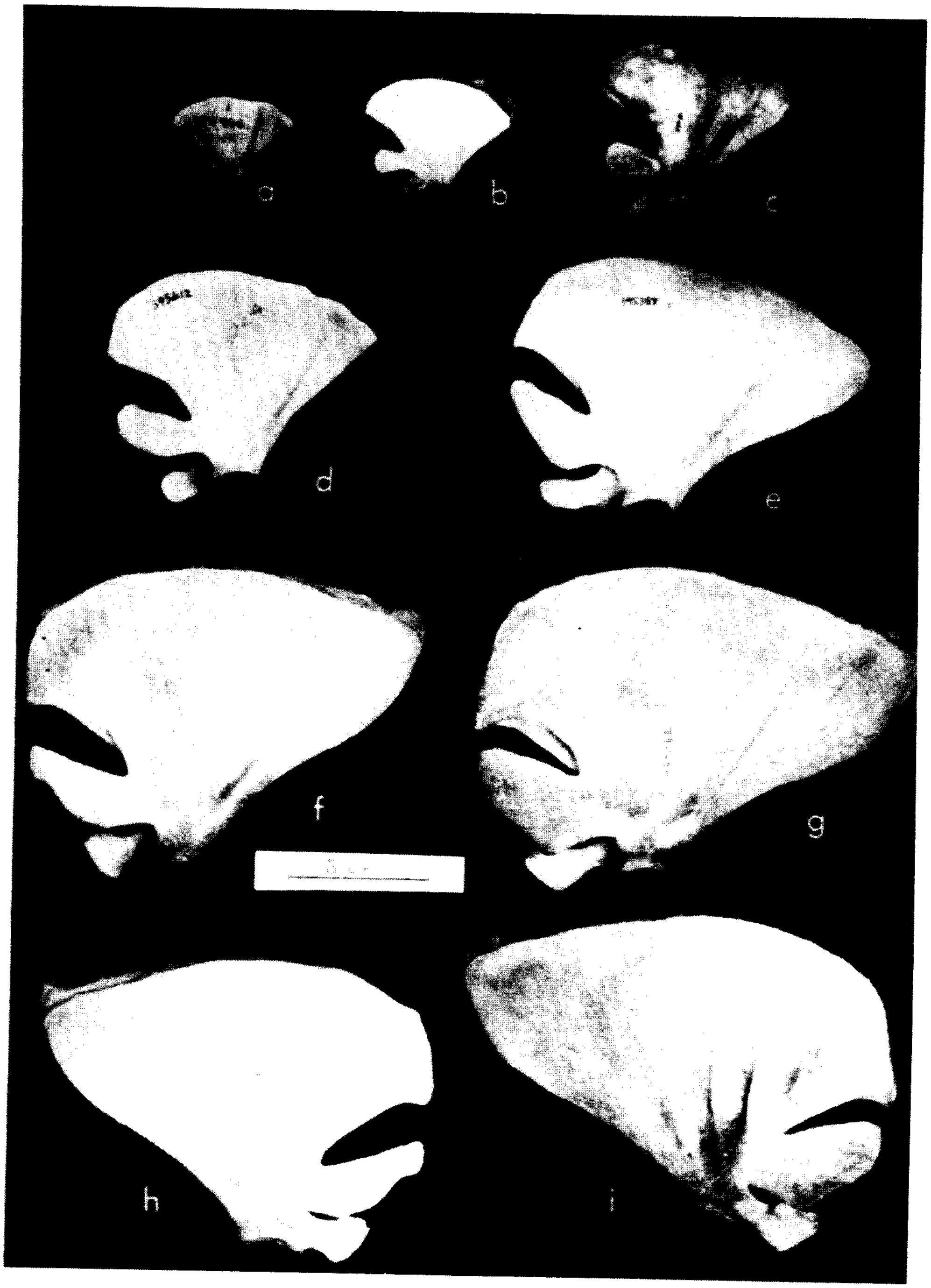


Figure 30. Scapulae of spotted porpoise: (a-g) external views of scapulae of developmental series in figure 35, (h and i) mesial views of scapulae of Class V and VI specimens, illustrating development of tuberose ridges.

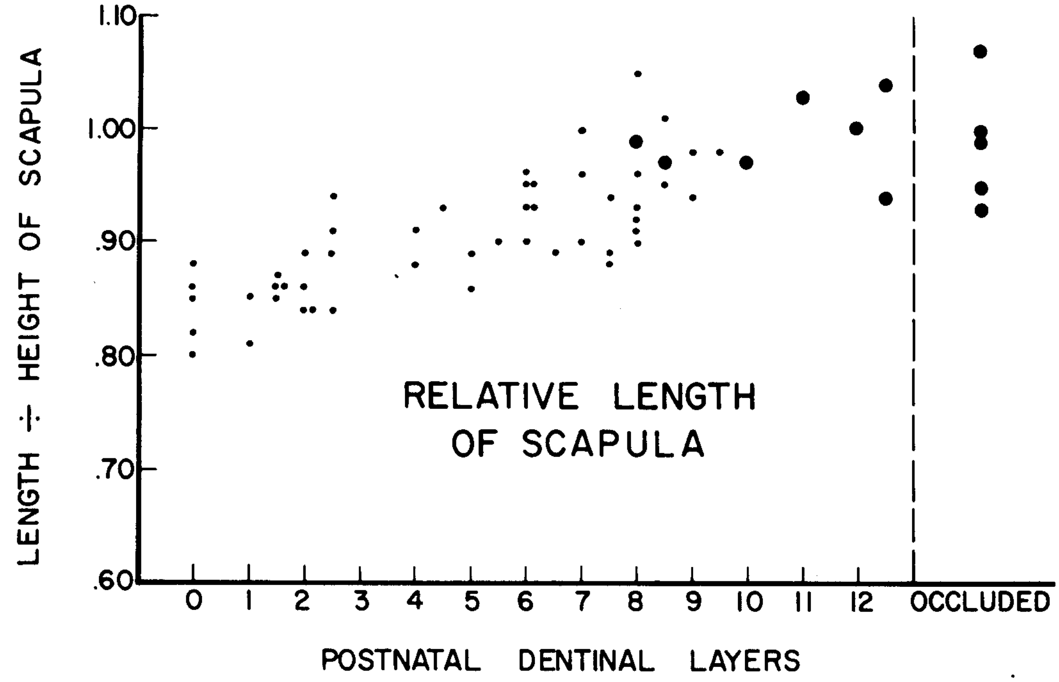


Figure 31. Development of scapula of spotted porpoise: scatterplot of relative length on number of dentinal layers.

The highly variable coracoid and metacromion processes reach adult shape in Class IV animals but continue to grow at a reduced rate into physical maturity.

The forelimb (fig. 32) develops rapidly after birth, and the number of osseous elements increases, to a near-adult shape by Class III. The forelimb then continues to grow slowly until physical maturity is reached. The olecranon process of the ulna, however, does not reach adult shape until Class V.

The usual complement of carpals at birth is five: a proximal row of three and a distal row of two. These correspond to the elements called by Fraser (1950) scaphoid, lunar, and cuneiform; and magnum and unciform, respectively. The element called trapezium by Fraser is unossified at birth. The small element called trapezoid by Fraser is only rarely present in specimens of any age (see section below on individual variation). The carpals increase in breadth at least until physical maturity is attained. The fifth metacarpal is absent at birth. In specimens of Class II.5, the trapezium and fifth metacarpal have become ossified, the latter to varying degree.

The first digit (thumb) has either no ossified phalanges or one at birth and throughout development. The numbers of ossified phalanges in the remaining digits undergo some change during development (fig. 33). Digit II has 6 or, most often, 7 at birth; in animals of Class III and older, the number is 7, 8, or occasionally 9. Digit III has 4 or 5 at birth; the prevailing number after Class II is 5, or occasionally 6. Digit IV has 1, 2, or, rarely, 3 at birth; the number thereafter with rare exception is 2. There are no ossified phalanges on digit V at birth. After ossification of the fifth metacarpal, a single phalanx may

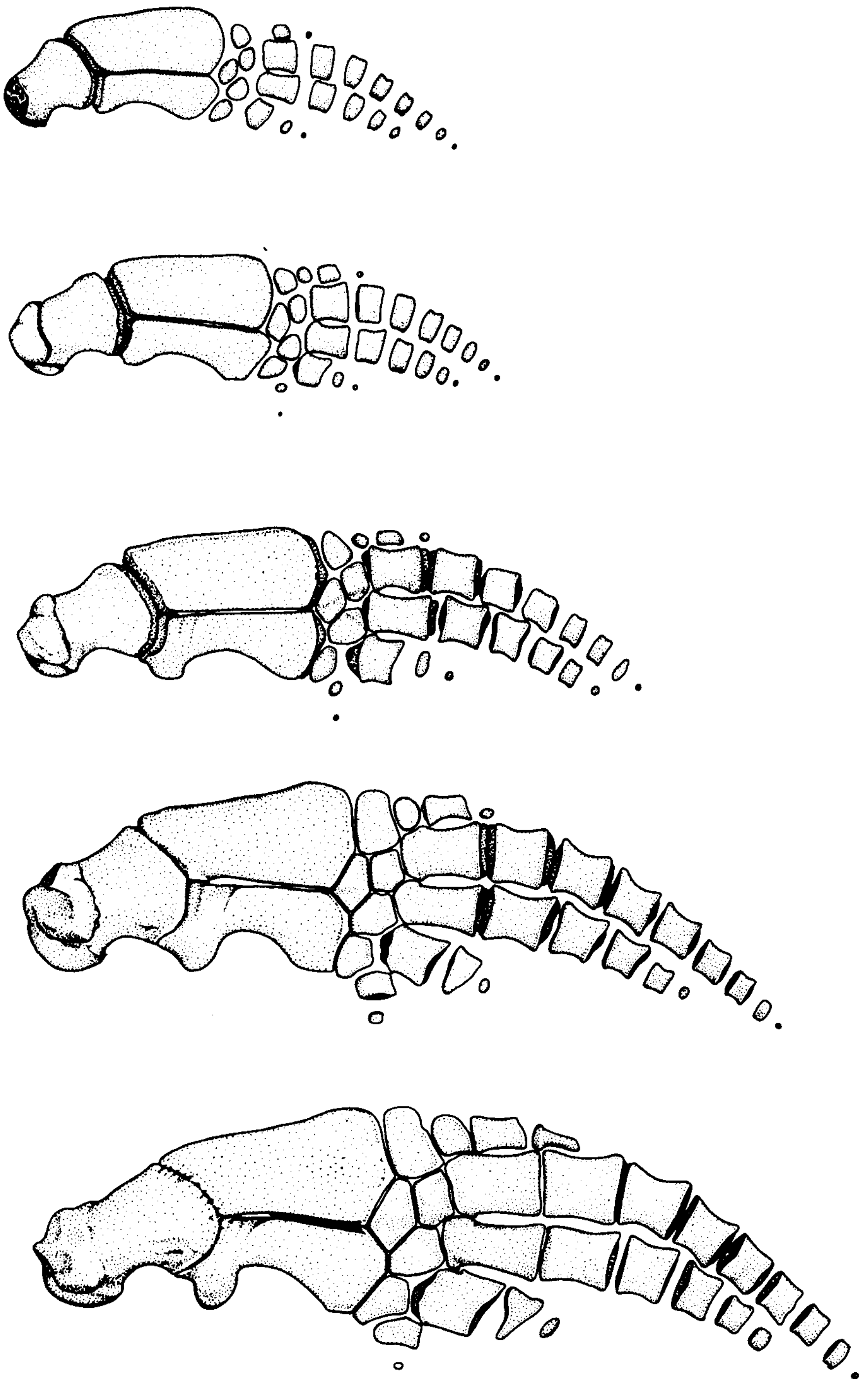
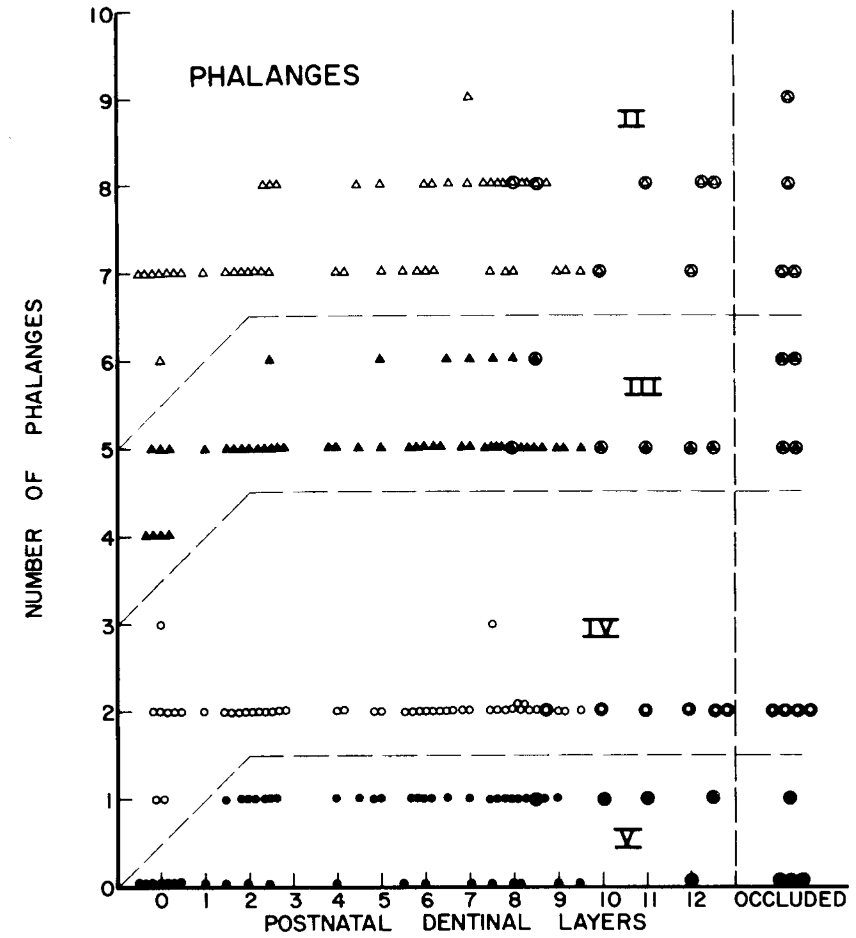


Figure 32. Developmental series of forelimb skeleton of spotted porpoise: (top to bottom) Class II, Class II.5, Class III, Class IV, Class VI.



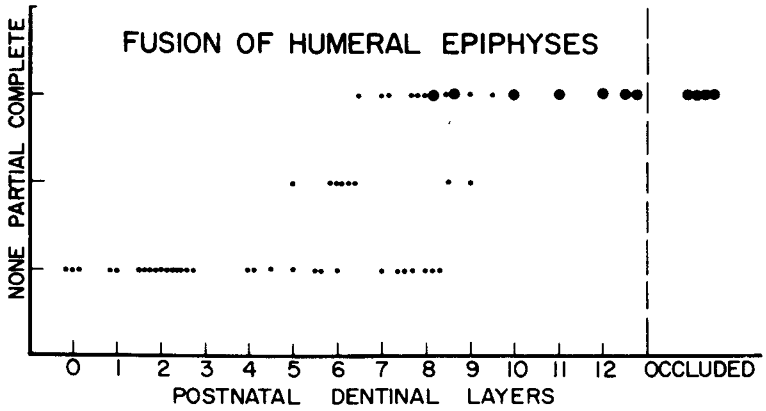


Figure 33. Development of manus of spotted porpoise: scatterplots of number of ossified phalanges on digits II-V (top) and degree of fusion of humeral epiphyses (bottom) on number of dentinal layers.

be added. The usual formulas at birth and in adulthood, then, are respectively: I-0 or 1, II-7, III-4 or 5, IV-1 or 2, V-0; and I-1 or 2, II-7 or 8, III-5 or 6, IV-2, V-1 or 2.

The epiphysis of the humerus is unossified at birth. In Class II.5 specimens it is ossified, and fusion to the humerus begins in Class IV (fig. 33). Fusion is completed on the average sooner than fusion of the vertebral epiphyses, and all "physically mature" animals have completely fused humeral epiphyses. Fusion of other elements of the forelimb (ulna to the radius, carpals to each other and/or to metacarpals, metacarpals to phalanges, phalanges to each other) may occur in physically mature specimens.

Posterior appendicular skeleton. The size and shape of the pelvic rudiments (fig. 34) differ between males and females, and the course of development and adult form and size in both sexes are extremely variable. In some specimens they are not yet ossified at birth. Some adult females have smaller, less complex pelvic bones than do some subadults.

Summary. The postcranial skeleton lags far behind the skull in postnatal development (compare curves in fig. 35 with those in fig. 25), with the exception of its anteriormost elements (atlas, axis, cervicals, first ribs), which reach adult size in subadult animals, albeit continuing to grow at a very slow rate thereafter. Of the remaining elements, the scapula, vertebral centra, and longest ribs show greatest and most protracted postnatal growth, continuing to grow possibly after physical maturity has been attained. The sample of physically mature specimens with determinable number of tooth layers is too small to determine with certainty whether or not growth continues beyond the onset of physical maturity.

Criteria for selection of adult specimens

Much of the taxonomy of Cetacea is of necessity based on skulls only, with little or no correlated data on external characters, reproductive condition, or the postcranial skeleton. When assessing variation in a series of such skulls, a decision must be made as to which specimens to consider effectively adult. The above analyses of developmental variation provide, for the spotted propoise, a basis for such a decision.

Consideration of the growth curves for cranial measurements leads to the conclusion that, except for the braincase and internal nares, the skull reaches adult proportions when about four layers have been laid down in the dentine, as much as two layers before the onset of sexual maturity, and four or more layers before attainment of "physical maturity." Thus, skulls of subadult specimens with 5 layers or more may be safely included in "adult" series, provided that allowance is made for growth of the braincase and nares, which continue at least until attainment of physical maturity. Regression analysis (two-way analysis of variance) of variation in "height of braincase," the cranial measurement most subject to age variation, shows that only about 11% of the variance (r^2) in the present sample of specimens with five or more postnatal dentinal layers is caused by age. This variation is only of consequence when comparing a very young skull with a very old one, where the expected difference owing to age is about 5%. The same applies to developmental variation in width of the internal nares. For purposes of analyses below of sexual, individual, and geographical variation of quantitative cranial characters, all specimens with five or more dentinal layers are included in the series. When teeth

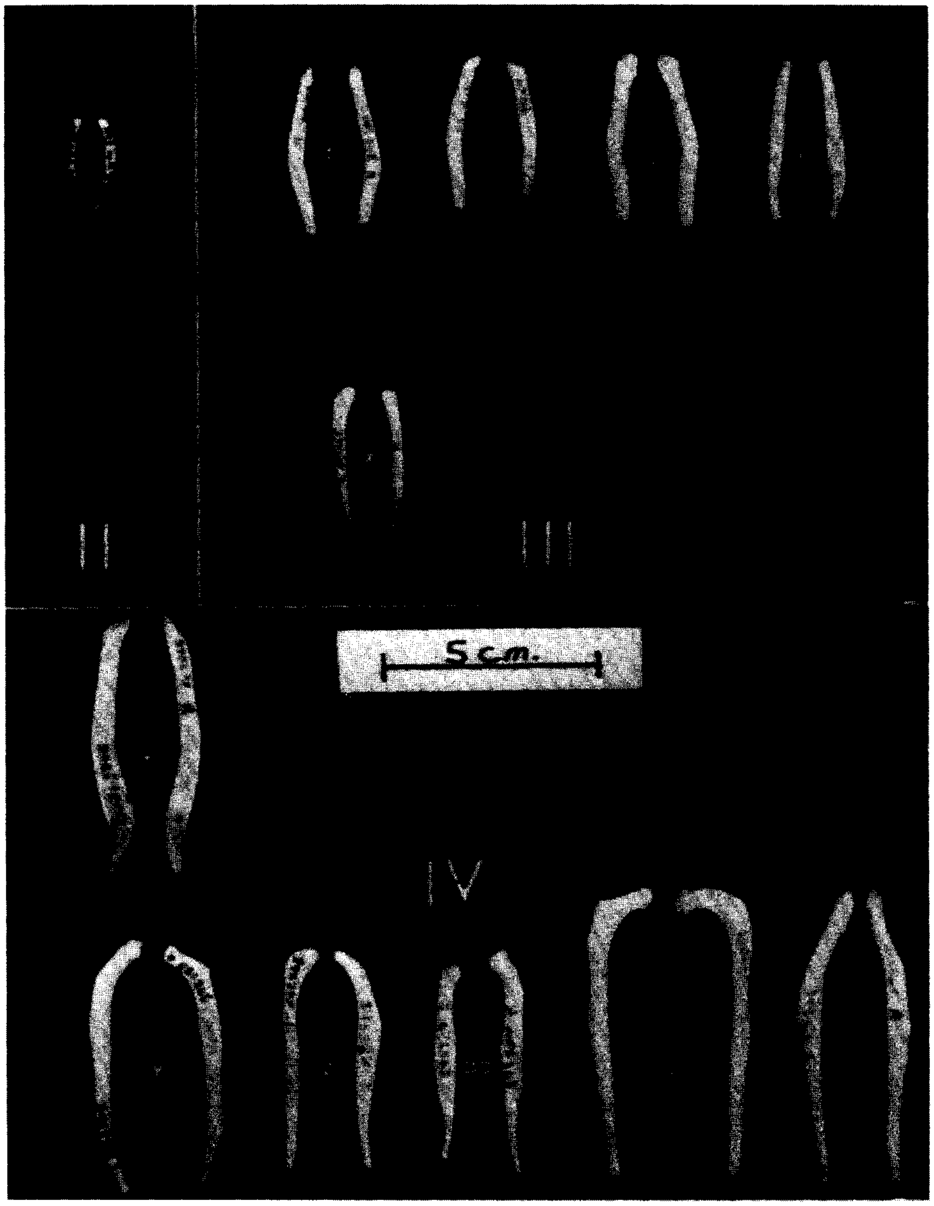


Figure 34. Pelvic rudiments of spotted porpoise, Class II to Class IV. For each class, males are above, females below (continued).

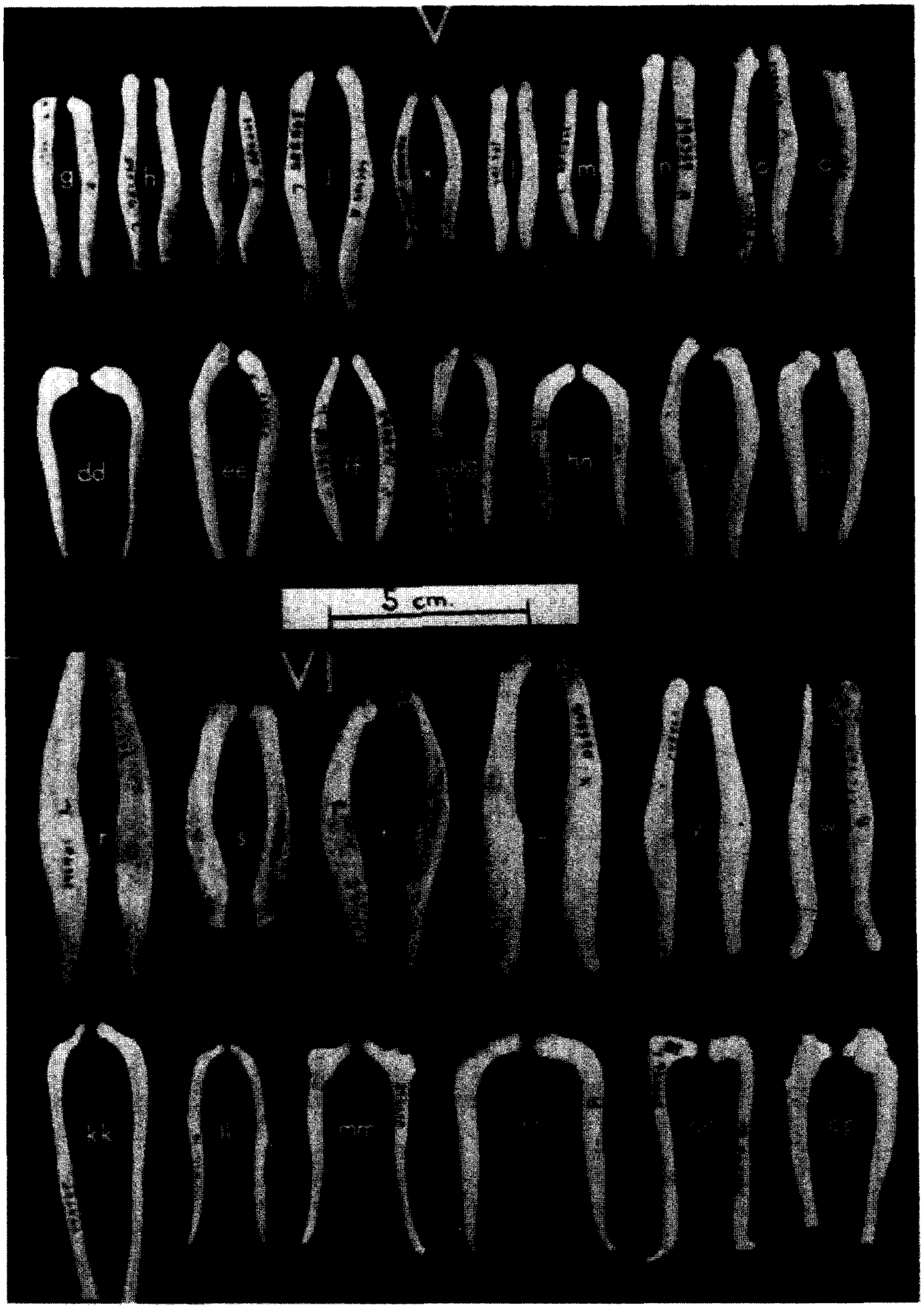


Figure 34 (continued). Pelvic rudiments of spotted porpoise, Classes V and VI. For each class, males are above, females below.

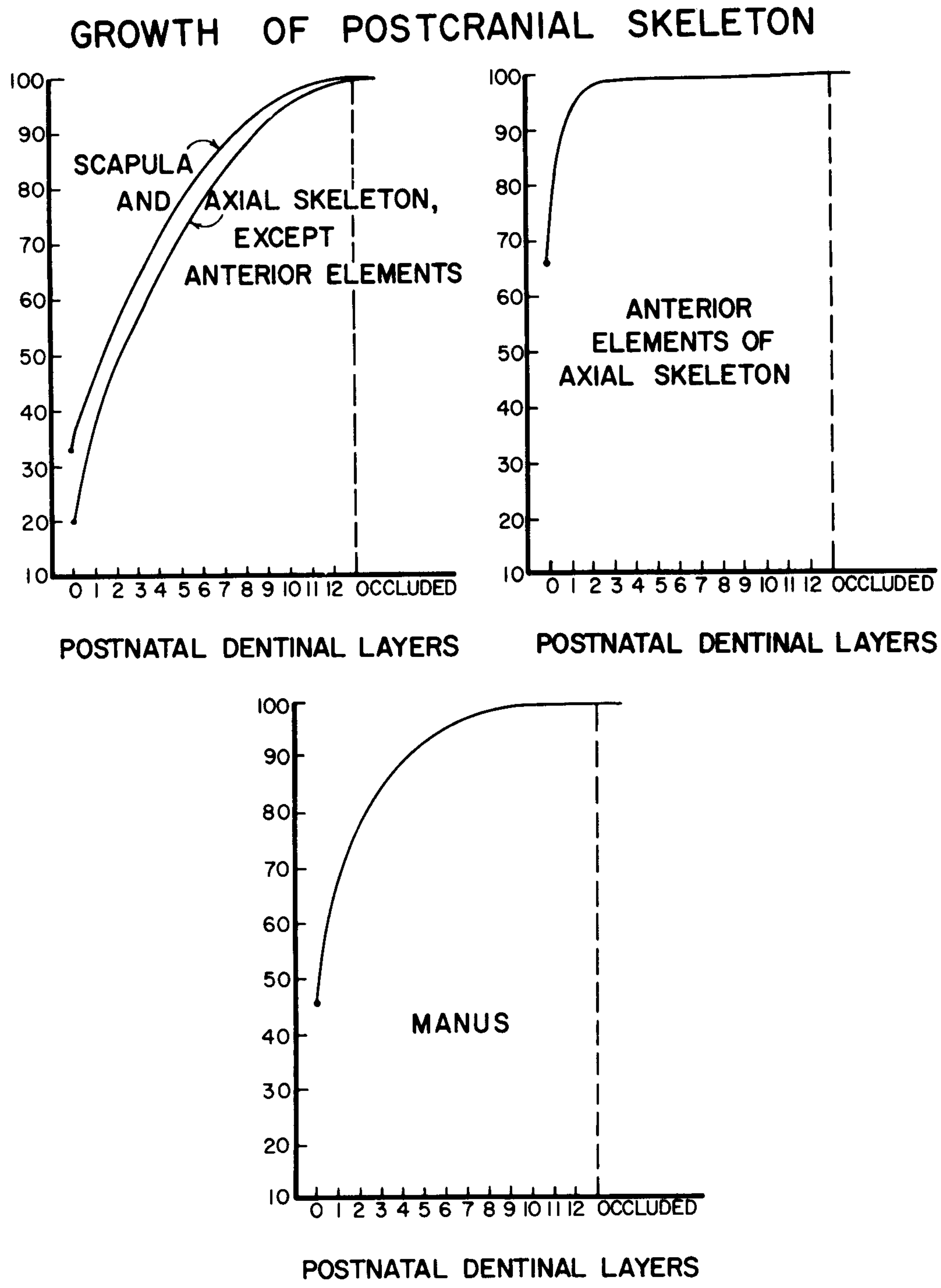


Figure 35. Growth of postcranial skeleton of spotted porpoise based on average growth rates.

were not sectioned, skulls were considered "adult" that exhibited distal fusion of the premaxillaries and maxillareis, a feature closely associated with attainment of sexual maturity (Dailey and Perrin, 1973). As no developmental variation was found for tooth counts, specimens of all ages are included in the series examined for tooth counts.

Which specimens to include in consideration of adult variation in quantitative postcranial skeleton characters is another matter. The protracted growth of the postcranial skeleton makes it advisable to include in an adult series only physically mature specimens (those with fused vertebral epiphyses), as variation owing to growth beyond attainment of physical maturity, if indeed it exists, is probably inconsequential. Even within a mature series, however, variation should be evaluated against the possible developmental component. This has been done here. As for the skull, the inclusiveness of series considered with respect to qualitative characters is determined on the basis of the descriptive accounts of developmental variation.

Sexual Dimorphism

Although sexual differences in the skeleton have been clearly demonstrated for some cetaceans (for example, by Moore, 1968, for certain of the ziphiids), this has not been encountered in any delphinid. Fischer (1881) examined the skulls of two female and two male specimens of *Delphinus delphis* and concluded that males have longer, more regularly tapering rostra less dilated at midlength, more elevated cranial crests, more ovoid posttemporal fossae, and higher crania than females. These conclusions, however, are not to be taken seriously, being based on such a small sample. Similar findings by Fischer for *Tursiops* based on four male and four female specimens were later refuted by True (1889), both on the basis of reexamination of Fischer's data and on the basis of examination of an additional series of 21 skulls; he concluded (p. 37) that variation in cranial proportions is "of little value in determining the sex."

The purpose of this section is to examine sexual variation in a large series of specimens. Dimorphism was detected only in the braincase, feeding apparatus, and postcranial skeleton.

Cranial skeleton

Braincase. The braincase of the male is on the average larger than that of the female. Mean internal length of the cranium (No. 18 in table 9) is greater for males both absolutely and as a percentage of condylobasal length. When expressed as percentage of parietal width, braincase length is not significantly different for males and females, indicating that the difference is one of size, not of proportion. G. Sacher (personal communication) measured the cranial volume of two adults and two near-term fetuses each of males and females from the present series with a direct method and found an average difference in volume of approximately 10%. Externally, the greater length of the male cranium is reflected in greater exposure of the frontals. There is great variation and overlap between the sexes.

Feeding apparatus. The rostra of adult females are on the average longer and more attenuate than those of males, precisely the reverse of Fischer's (1881) findings for *Delphinus* and *Tursiops* based on inadequate series. The dimorphism becomes more pronounced with age. For the full series of 31 females and 32 males (table 9), the average difference is significant at $\alpha = 0.05$ only for Rostrum tip to internal nares (no. 9) and Length of upper tooth row (no. 32) expressed as percentage of condylobasal length; and Rostrum tip to external nares (no. 8), Length of upper tooth row (no. 32), Length of lower tooth row (no. 37), and ramus length (no. 38) expressed as percentage of parietal width. The last four items reflect also the sexual difference in cranial dimensions. A scatterplot of rostral width at 3/4 length (no. 7) on rostral length (no. 2) for 15 physically mature specimens (7 males and 8 females, all physically mature), however, demonstrates clearly the existence of dimorphism in rostral proportions (fig. 36). The means of the ratio between these two measurements are significantly different at $\alpha = .05$; $\bar{x}$ male = 7.37 ± 0.40 (2 x S.E.), $\bar{x}$ female = 8.55 ± 0.36, with no overlap between males and females for the 15 physically mature specimens.

Postcranial skeleton

Width of the first vertebral rib (no. 87) is greater in males. Males more often possess a phalanx in the first digit (no. 114). Dimorphism in the pelvic rudiments was illustrated above (fig. 34) in the section on development. The size and shape of the pelivcs are extremely variable but the male pelvic is more often than not rod-shaped and the female L-shaped to greater or lesser degree. The male pelvic is clearly larger on the average.

Individual Variation

A knowledge of the range and nature of individual osteological variation within what is known or presumed to be an inbreeding unit is of prime importance to the evaluation of differences between samples that must precede taxonomic decision making. With very few exceptions (*Pseudorca crassidens*: Yamada, 1956; *Delphinus delphis*: Kleinenberg, 1956 and Cadenat, 1959) this necessary basic knowledge does not exist for delphinid species.

In this study, I collected two series of complete skeletal specimens of spotted porpoise from single seine net sets, one of 33 animals and the other of 28 (table 10). These samples from presumably inbreeding groups are referred to below as Set 2 and Set 6.

Cranial skeleton

Braincase. In ventral view, the occipital condyles are developed to varying degree. The anterior margins may be sharply delineated and rounded, or pointed in outline, or may grade imperceptibly into the basoccipital plate. The channel between them may be relatively long and narrow with parallel sides, triangular, or even closed. Similarly, the lateral and dorsal margins of the condyles are delineated to varying degree. Sculpturing of the occipital bone above the condyle varies from a faint, shallow indentation to a deep furrow. The medial occipital ridge may be absent or present as a thick prominence. It may extend anteriad to join the frontal crest on the midline of the skull.

Table 9. Skeleton measurements and meristics differing between male and female adult offshore spotted porpoise, with statistical comparisons of means

Variable	Unit	Males					Females					Absolute value of significant t, at $\alpha = .05$		
		Number of specimens	Range	Mean	Standard deviation	Coefficient of variability	Number of specimens	Range	Mean	Standard deviation	Coefficient of variability	Absolute measurements	Expressed as percentage of condylobasal length	Expressed as percentage of parietal width
1. Condylobasal length	mm	32	360-408	387.9	11.21	2.89	31	356-415	390.9	14.52	3.71			
8. Rostrum tip to external nares	mm	32	245-291	267.4	10.27	3.84	31	246-298	274.3	13.93	5.08			3.35
9. Rostrum tip to internal nares	mm	32	249-286	269.8	9.63	3.57	31	243-304	275.7	13.70	4.97		2.99	
17. Braincase height	mm	32	89-106	97.5	4.12	4.23	31	87-102	95.2	3.83	4.03		4.59	
18. Braincase length	mm	32	112-123	117.8	2.98	2.53	31	109-120	114.6	2.84	2.48	4.36		
32. Upper tooth row length	mm	32	180-216	199.1	8.53	4.28	31	186-226	204.8	11.47	5.60		3.39	3.44
33. Upper left teeth	no.	42	37-46	41.3	2.47	5.99	39	37-47	41.4	2.14	5.16			2.88
34. Upper right teeth	no.	42	37-46	41.1	2.20	5.34	40	37-48	41.8	2.32	5.55			2.85
87. First vertebral rib width	mm	6	20-21	20.7	0.52	2.50	6	16-20	17.5	1.76	10.06	4.27		
114. Digit I phalanges	no.	35	0-1	0.9	0.28	31.11	29	0-1	0.6	0.49	81.67	3.07		
120. Pelvic length (left)	mm	5	58-86	75.0	11.14	14.85	5	52-70	58.0	7.04	12.13	2.88		

Table 10. Skeleton measurements and meristics for two single-school series of spotted porpoise (continued)

Variable	Unit	Set 2					Set 6				
		Number of specimens	Range	Mean	Standard deviation	Coefficient of variability	Number of specimens	Range	Mean	Standard deviation	Coefficient of variability
1. Condylobasal length	mm	22	356-411	388.4	14.90	3.84	19	369-406	390.2	8.35	2.14
2. Rostrum length	mm	22	210-248	230.9	10.61	4.59	19	214-247	232.2	7.76	3.34
3. Rostrum width at base	mm	22	77-91	82.4	3.71	4.50	19	77-86	81.0	2.36	2.91
4. Rostrum width at 60 mm	mm	22	49-61	54.6	3.09	5.66	19	52-61	55.6	2.71	4.88
5. Rostrum width at midlength	mm	22	35-44	40.1	2.29	5.70	19	36-48	40.8	3.10	7.60
6. Premaxillary width at rostral midlength	mm	22	19-27	21.7	1.91	8.78	19	18-27	22.0	2.47	11.24

7. Rostrum width at 3/4 length	mm	22	24-31	27.5	2.11	7.66	19	24-36	28.6	2.91	10.19
8. Rostrum tip to external nares	mm	22	245-294	270.5	13.39	4.95	19	248-283	269.8	9.06	3.36
9. Rostrum tip to internal nares	mm	22	243-293	272.0	13.24	4.87	19	250-285	272.5	9.33	3.42
10. Preorbital width	mm	21	134-154	145.0	4.28	2.96	19	137-154	145.0	3.45	2.38
11. Postorbital width	mm	21	152-173	163.1	4.47	2.74	19	159-173	163.4	3.25	1.99
12. Least supraorbital width	mm	22	133-154	144.1	4.70	3.26	19	138-151	143.5	3.32	2.32
13. External nares width	mm	22	37-44	40.7	1.61	3.95	19	37-46	41.8	2.02	4.82
14. Zygomatic width	mm	22	153-174	161.6	4.33	2.68	19	158-174	163.2	3.60	2.21
15. Greatest width of premaxillaries	mm	22	61-68	64.9	2.11	3.26	19	60-69	64.5	2.70	4.18
16. Parietal width	mm	22	129-146	137.4	4.76	3.46	19	129-146	137.3	3.89	2.83
17. Braincase height	mm	22	87-105	95.1	3.90	4.09	19	94-104	97.3	2.71	2.78
18. Braincase length (M)	mm	11	112-122	117.2	3.43	2.93	12	115-121	118.4	1.83	1.55
(F)		11	109-120	115.6	2.69	2.33	7	111-117	114.4	1.99	1.74
19. Posttemporal fossa length	mm	22	60-75	67.4	3.79	5.62	19	64-77	69.1	3.42	4.96
20. Posttemporal fossa width	mm	22	47-58	51.8	2.99	5.76	19	48-63	53.9	3.16	5.86
21. Temporal fossa major diameter	mm	22	36-42	39.0	1.70	4.37	19	37-44	39.4	1.89	4.81
22. Temporal fossa minor diameter	mm	22	18-26	22.2	1.89	8.54	19	20-25	22.6	1.12	4.93
23. Projection of premaxillaries	mm	19	14-25	17.8	2.94	16.50	16	12-21	17.3	2.36	13.62
24. Nasals to crest (M)	mm	11	20-35	27.0	5.20	19.25	12	22-34	26.4	2.94	11.12
(F)		11	18-29	23.5	3.33	14.13	7	20-27	24.1	2.27	9.39
25. Orbit length	mm	22	44-51	47.1	1.73	3.66	19	44-50	46.7	1.83	3.91
26. Antorbital process length	mm	22	30-38	34.8	2.43	6.98	19	30-38	34.9	1.94	5.56
27; Internal nares width	mm	22	42-50	45.6	2.17	4.76	19	44-53	47.1	2.26	4.79
28. Pterygoid length	mm	22	55-70	61.8	4.83	7.82	19	58-76	64.7	4.71	7.29
29. Occipital overhang	mm	22	0-9	3.7	2.68	71.79	19	2-6	3.5	1.31	37.06
30. Bulla length	mm	22	29-31	29.8	.45	1.52	19	29-33	30.1	.96	2.97
31. Periotic length	mm	22	26-28	26.6	.48	1.80	19	25-29	26.9	1.04	3.87
32. Upper tooth row length	mm	22	180-220	200.7	10.25	5.11	19	187-219	202.3	8.44	4.17
33. Upper left teeth	no.	32	37-45	41.4	2.25	5.45	27	37-48	41.3	2.66	6.44
34. Upper right teeth	no.	32	38-45	41.3	2.23	5.41	27	37-47	41.4	2.71	6.54
35. Lower left teeth	no.	33	36-45	40.5	2.06	5.09	28	34-46	40.1	2.72	6.77
36. Lower right teeth	no.	33	37-45	40.7	2.02	4.96	28	34-45	40.2	2.47	6.14
37. Lower tooth row length	mm	21	177-220	196.5	9.86	5.02	19	180-210	194.3	8.37	4.31
38. Ramus length	mm	21	296-347	327.4	14.52	4.43	19	306-343	328.3	8.56	2.61
39. Ramus height	mm	22	51-59	56.3	1.73	3.07	19	53-60	57.3	1.89	3.29
40. Mandibular fossa length	mm	22	90-116	103.8	5.61	5.41	19	98-114	104.4	4.36	4.18
41. Deviation from symmetry	degrees	22	3-10	8.1	1.72	21.21	18	5-9	7.7	1.14	14.84
42. Basihyal length	mm	20	25-33	29.4	2.14	7.27	18	27-32	29.1	1.41	4.84
43. Basihyal width	mm	19	29-42	34.5	2.65	7.70	18	29-39	33.9	2.84	8.36
44. Thyrohyal width	mm	19	15-19	17.5	1.17	6.71	18	14-20	17.5	1.47	8.37
45. Thyrohyal length	mm	19	46-60	53.5	2.95	5.51	18	43-62	53.4	4.88	9.13
46. Stylohyal width	mm	19	11-13	11.9	.85	7.10	18	11-13	12.0	.77	6.39

Table 10 (continued). Skeleton measurements and meristics for two-school series of spotted porpoise

Variable	Unit	Set 2					Set 6				
		Number of specimens	Range	Mean	Standard deviation	Coefficient of variability	Number of specimens	Range	Mean	Standard deviation	Coefficient of variability
47. Stylohyal length	mm	19	63-74	69.1	2.93	4.25	18	61-73	68.6	3.45	5.03
48. Thoracic vertebrae	no.	30	15-17	16.0	.61		25	15-17	16.1	.64	
49. Lumbar vertebrae	no.	28	17-23	20.0	1.53		19	18-22	19.7	1.15	
50. Caudal vertebrae	no.	27	36-42	38.1	1.54		18	36-41	38.8	1.22	
51. Total vertebrae	no.	23	79-83	81.0	1.15		21	79-83	81.2	1.00	
52. Fused cervical vertebrae	no.	6	2-3	2.2	.37		6	2-7	2.8	1.86	
53. Atlas width	mm	6	73-80	76.2	2.79	3.66	6	77-84	79.7	2.80	3.54
54. Atlas height	mm	6	46-49	47.3	1.03	2.18	6	47-50	48.0	1.26	2.64
55. Atlas lateral process length	mm	6	18-25	21.0	2.37	11.27	6	18-24	20.8	2.56	12.30
56. Atlas neural spine length	mm	6	30-40	35.8	3.49	9.73	6	35-44	38.7	3.33	8.60
57. Atlas dorsal ridge height	mm	6	1-4	2.5	1.05	41.96	6	1-4	2.3	1.03	44.26
58. Atlas dorsolateral spine length	mm	6	0-4	1.7	1.63	97.98	6	0-14	3.5	5.24	149.83
59. Axis lateral process length	mm	6	16-25	19.3	3.08	15.91	6	16-22	19.5	2.07	10.63
60. Cervical vertebrae incomplete	no.	6	0-1	.3	.47		6	0-1	.3	.47	
61. Greatest ventrolateral cervical process on	no.	6	6-6	.6	0		6	6-6	6.0	0	
62. First vertical foramen on	no.	33	55-61	57.5	1.64		28	55-59	57.5	1.20	
63. First vertebra with reduced metapophyses	no.	30	28-35	31.5	1.91		26	24-34	31.8	2.29	
64. Last transverse process on	no.	30	61-66	63.0	1.30		27	62-65	63.3	.72	
65. Last neural spine on	no.	30	67-71	68.3	1.09		27	67-70	68.5	.98	
68. First caudal with vertical spine	no.	30	56-63	60.6	1.57		27	59-64	61.2	1.19	
69. First thoracic neural spine length	mm	6	19-37	29.0	6.10	21.03	6	9-32	23.8	9.35	39.22
70. Second thoracic neural spine length	mm	6	32-43	39.2	4.36	11.12	6	34-44	39.0	3.85	9.86
71. Tenth thoracic neural spine length	mm	6	55-70	62.7	6.22	9.92	6	55-67	61.2	4.58	7.49
72. Last thoracic neural spine length	mm	6	67-78	72.2	4.02	5.57	6	63-76	69.3	5.54	7.99
73. First thoracic vertebra height (M)	mm	2	44-48	-	-	-	4	45-46	-	-	-
(F)		4	44-47	-	-	-	2	46-51	-	-	-
74. First thoracic vertebra width	mm	6	63-80	70.3	5.99	8.52	6	68-76	72.5	3.21	4.43
75. First lumbar vertebra height	mm	6	46-52	49.3	1.97	3.99	6	48-52	49.2	1.47	2.99
76. First lumbar vertebra width	mm	6	165-180	171.8	5.64	3.28	6	168-182	176.7	5.16	2.92
77. 23rd centrum length	mm	6	19-21	19.8	.68	3.46	5	21-24	21.8	1.17	5.35

78. Left vertebral ribs	no.	28	15-17	15.9	.63		21	15-17	16.0	.59	
79. Right vertebral ribs	no.	26	15-17	15.8	.61		20	15-17	16.1	.60	
80. Left 2-headed ribs	no.	33	4-7	5.5	.71		28	4-7	5.5	.74	
81. Right 2-headed ribs	no.	33	4-7	5.6	.66		28	4-7	5.4	.74	
82. Left floating ribs	no.	26	0-2	1.3	.53		20	0-2	1.0	.46	
83. Right floating ribs	no.	24	0-2	1.2	.48		20	0-2	1.1	.51	
84. Left sternal ribs	no.	24	9-11	9.4	.65		18	9-11	9.5	.62	
85. Right sternal ribs	no.	23	9-11	9.3	.65		19	9-11	9.5	.61	
86. First vertebral rib length	mm	6	100-119	111.3	7.06	6.34	6	105-113	109.5	2.81	2.57
87. First vertebral rib width (M)	mm	2	21-23	-	-	-	4	19-21	-	-	-
(F)		4	16-19	-	-	-	2	16-20	-	-	-
88. Longest vertebral rib length	mm	6	232-261	246.7	9.87	4.00	6	243-254	248.0	4.98	2.01
89. First sternal rib length	mm	6	66-79	73.8	4.71	6.38	6	70-83	76.3	4.59	6.01
90. Manubrium width	mm	6	79-97	87.5	7.87	8.99	6	73-92	83.8	6.18	7.37
91. Manubrium length	mm	6	47-62	55.8	5.12	9.16	6	49-59	55.3	3.88	7.01
92. Manubrium notch depth	mm	6	5-19	10.5	4.93	46.95	6	5-11	8.5	2.07	24.40
93. Manubrium foramen length	mm	6	0-4	1.7	1.97	117.98	6	0-11	6.2	4.07	66.00
94. Mesosternal elements	no.	6	2-3	2.8	.20		6	2-3	2.8	.37	
95. Mesosternals fused	no.	6	1-2	1.5	.50		6	1-3	1.5	.76	
96. Chevron bones	no.	23	26-33	29.7	1.79		16	28-32	30.5	1.03	
97. Chevron bones fused in first series	no.	6	2-3	2.5	.50		6	0-2	1.7	.75	
98. First chevron on	no.	29	41-47	43.7	1.49		21	41-46	43.6	1.16	
99. Last chevron on	no.	24	70-77	72.5	1.69		18	70-75	72.8	1.34	
100. First chevron length	mm	6	3-23	11.2	6.79	60.85	5	3-11	6.6	3.21	48.63
101. Longest chevron length	mm	6	40-48	43.2	2.86	6.62	6	41-48	45.8	2.64	5.76
102. Last chevron length	mm	5	2-4	2.8	.84	29.88	4	3-4	3.3	.50	15.38
103. Scapula height	mm	6	101-114	106.8	4.45	4.16	6	101-111	106.2	4.36	4.10
104. Scapula length	mm	6	99-118	108.3	6.25	5.77	6	100-110	103.2	3.60	3.50
105. Coracoid length	mm	6	28-33	29.8	1.72	5.77	6	26-38	31.0	4.00	12.90
106. Coracoid width	mm	6	10-30	19.0	6.99	36.77	6	15-24	18.5	3.39	18.33
107. Metacromion width	mm	6	24-46	38.8	7.99	20.56	6	29-47	40.7	7.17	17.64
108. Humerus length	mm	6	47-51	48.7	1.37	2.81	6	43-49	46.7	2.58	5.53
109. Humerus width	mm	6	33-36	33.8	1.17	3.46	6	33-35	34.2	.75	2.20
110. Radius length	mm	6	59-67	62.5	3.02	4.83	6	58-63	61.3	1.86	3.04
111. Radius width	mm	6	30-33	31.2	.98	3.15	6	29-33	30.7	1.63	5.32
112. Ulna length	mm	6	53-57	55.5	1.64	2.96	6	52-56	53.3	1.75	3.28
113. Carpal row width	mm	6	51-61	55.8	4.17	7.46	5	53-60	54.8	2.95	5.38
114. Digit I phalanges (M)	no.	2	1-1	-	-		4	0-0	-	-	
(F)	no.	4	0-1	-	-		2	0-0	-	-	
115. Digit II phalanges	no.	31	7-9	7.4	.62		23	7-8	8.4	.50	
116. Digit III phalanges	no.	31	4-6	5.1	.40		25	5-6	5.1	.28	
117. Digit IV phalanges	no.	30	2-2	2.0	0		22	2-3	2.1	.35	
118. Digit V phalanges	no.	30	0-1	.6	.50		24	0-1	.6	.50	

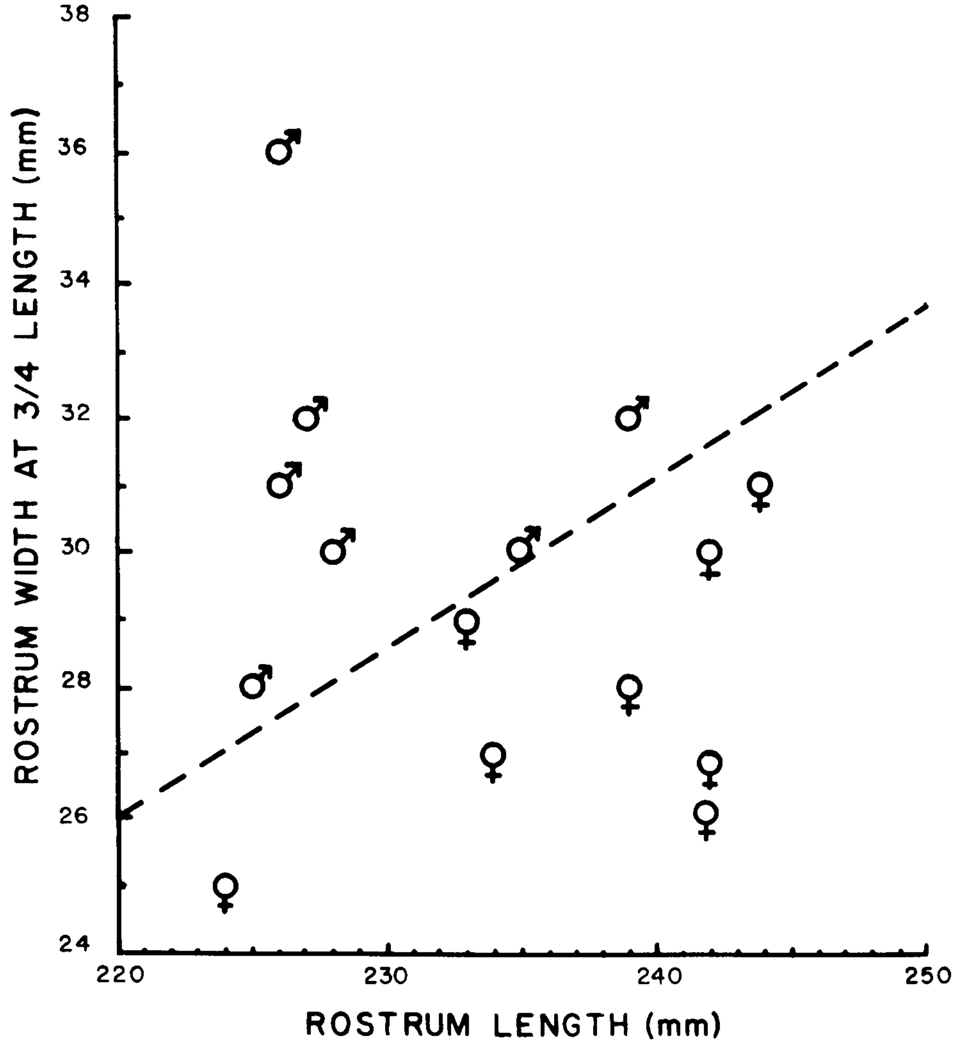


Figure 36. Sexual dimorphism of physically mature spotted porpoise in proportional width of rostrum at 3/4 length against rostrum length.

Although a significant component of variation in length of the occipitofrontal portion of the vertex confluence is ascribable to sexual dimorphism (see previous section), individual variation in length, as well as width, of this feature is considerable. Correlated with this feature is degree of exposure of the frontals and rudimentary interparietal. Development of the occipital overhang is not strongly correlated with development of musculature (James G. Mead, personal communication; based on detailed dissections) and shows great individual variation in addition to that owing to age. Width and height of the braincase show comparable variation. Length is least variable of the braincase measurements in absolute terms.

Feeding apparatus. The feeding apparatus is more variable than the braincase. The rostrum is more variable than the cranium in length, but not in width (by criterion of Lewontin's [1966] test, at $\alpha = 0.05$). Relation of rostral dimensions to parietal width did not in any case significantly decrease variation and some cases increased it, indicating that the rostrum and braincase vary to some degree independently.

Although a significant proportion of variation in rostrum size and shape results from sexual dimorphism and age (see previous section), individual variation among adults of the same sex and similar age is striking and can probably best be expressed by the coefficients of variation (5.91 for Set 2 and 4.71 for Set 6) of the ratio of rostrum length to basal width. The ratio ranges from 2.58 to 3.21 in Set 2 ($N = 22, \bar{x} = 2.81, s = 1.66$) and from 2.49 to 3.06 in Set 6 ($N = 19, \bar{x} = 2.87, s = 0.135$). The mandible varies in the same way.

The premaxillaries are subject to considerable variation in the amount of dorsal contact; in some individuals these bones are completely separated for the full length of the rostrum. A similar situation obtains ventrally with respect to the contact of the maxillaries, although in all specimens examined the maxillaries are in contact at least at the level of the end of the tooth row. The exposure of the vomer varies similarly (fig. 37).

The premaxillaries are usually roughened dorsally where they meet the rough, less dense maxillaries. The extent of this encroachment varies considerably; in some specimens the premaxillaries are roughened laterally only in the distal third of the rostrum.

The range in tooth counts is 9 (37-45) and 10 (36-45) for upper and lower jaws respectively, in Set 6. On the average there is one more tooth in the upper than in the lower row. The foremost pair of mandibular teeth is often completely buried and can be detected only by probing or by grinding the bone. In specimens with high tooth counts and/or relatively short snouts, the hindmost teeth in both the mandibular and maxillary rows may become atypically crowded and/or reduced in size (fig. 37).

The size of the posttemporal fossa (measurement nos. 19, 20, 21, and 22) varies considerably among animals of the same sex and similar age; least variable among the absolute measures in both single-school samples is the major diameter of the opening through which the temporal muscle passes (no. 21). Degree of definition of the posttemporal fossa also varies markedly, from specimens in which the boundary is scarcely discernible or intermittent to those in which it is a complete strongly developed flange. Degree of development of this feature is correlated with degree of development of the highly variable occipital overhang (fig. 24).

The hyals are extremely variable in both size and shape. The body of the basihyal may be nearly rectangular or trapezoidal. Its posterior process varies markedly in width and may be entire or bifurcate. The thyrohyals vary widely in shape and in the angle of attachment to the basihyal. Degree of fusion of the hyals, although determined in part by age (see section on development), varies within series of specimens of similar age, including physically mature animals. The length of the thyrohyal, although also in part age-determined, varies within series of specimens of similar age, including physically mature animals. The stylohyals also vary widely, in length and robustness.

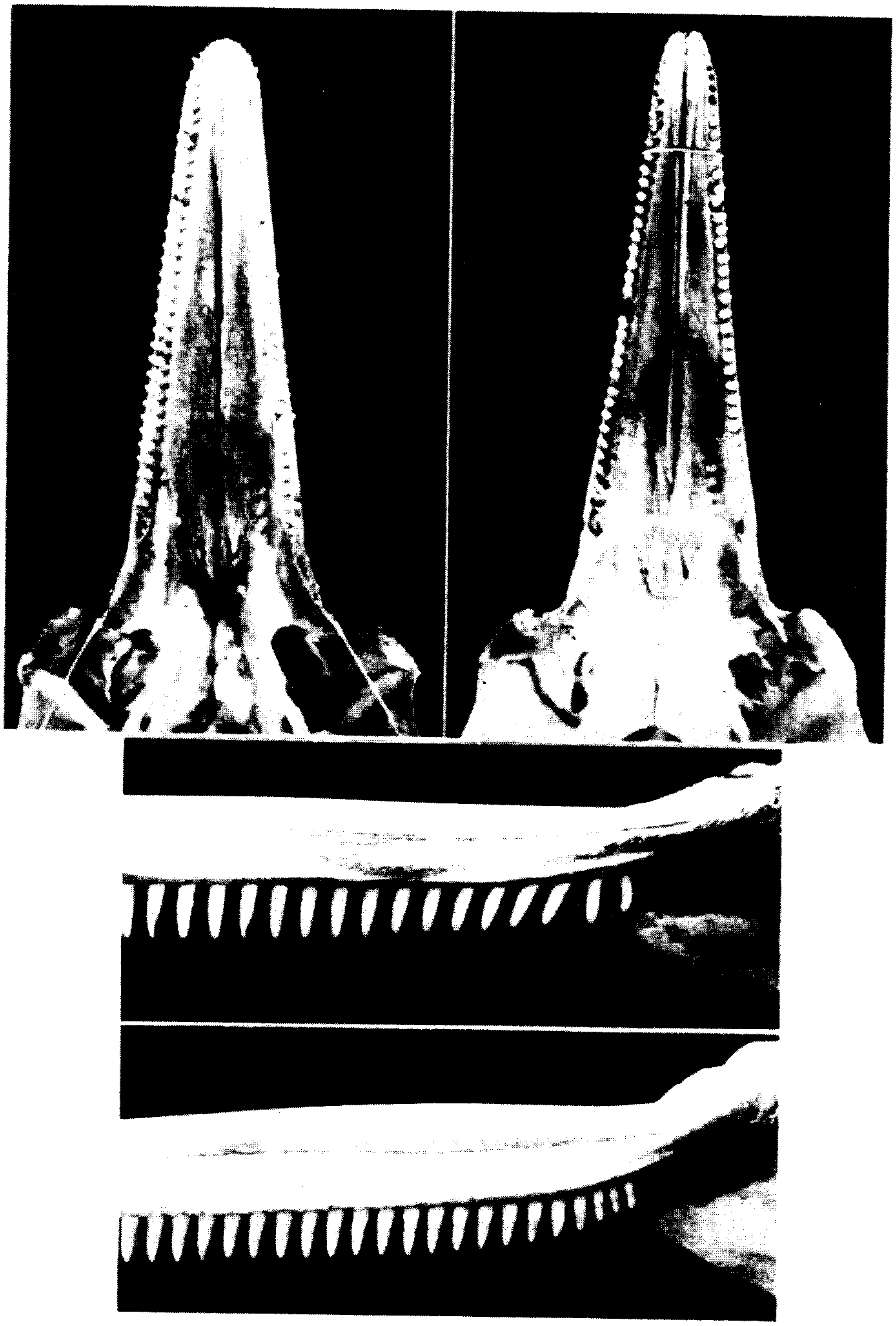


Figure 37. Individual variation in elements of the feeding apparatus of the skull of adult spotted porpoise: ventral view of rostra with no exposure of vomer (top left) and (top right) vomer exposed, (bottom) variation in spacing and size of posterior teeth in upper tooth row.

Figure 38. Individual variation of skull of adult spotted porpoise in ventral aspect: (top) variation in shape of falciform process; (bottom right) presence and absence of segmented squamosal-alisphenoid bar above falciform process; (bottom left) variation in shape and mesial separation of pterygoids.

Vision apparatus. In most individuals the orbit is rounded in outline, but in some, dorsal flattening creates a slight rectangularity. Also, in some specimens, the outline of the orbit is distorted by greater than usual posterior extension of the lacrimal.

Hearing apparatus. The lengths of the tympanoperiotics (nos. 30 and 31 in table 10) have relatively low coefficients of variation, especially in the sample for Set 2. Most variation in length of the bulla is owing to varying extension of the thin anteroventral lip of the tympanic tube. In some individuals, however, the bones are noticeably smaller or larger than usual. There is also considerable variation in the shape of the other end of the bulla, and the margin of the "mastoid process" (actually composed of extensions of the mastoid and squamosal) is quite variable in size, outline, and degree of compactness. Features more intimately involved in the physical processes of hearing, however, such as the promontorium, the sigmoid processes, and the posterior conical process, are more constant in size and shape, even among tympanoperiotics of disparate overall size.

In ventral view of the skull, the falciform process of the squamosal varies greatly in length, robustness, and distal elaboration (fig. 38, top). In some individuals, the elaboration extends anterodorsad to form a three-dimensional basketwork of delicate bones in contact with the alisphenoid. Mesial definition of the tympanosquamosal recess varies from complete absence to a depression bounded by an excavated flange 2 or 3 mm high. The foramen ovale may be essentially flush or may be surrounded by an elevated infundibulum of varying height. In some individuals the foramen is partly closed by osteosclerotic invasion. Three of 40 specimens examined exhibit a discrete mandibular foramen, adjacent and anteromesial to the formen ovale. In some individuals the foramen ovale is lost in a larger hiatus in the alisphenoid. The lateral bar of bone, just dorsal to the falciform process, formed by mesial extension of the squamosal and ventral development of the alisphenoid and perhaps serving a structural reinforcing function, varies remarkably in its degree of development: in some specimens it is so weakly expressed as to be essentially absent; and in others, it is a massive structure bearing an obvious transverse suture (fig. 38, middle). Weak development of this structure appears to be compensated for by increased anterior thickening of the alisphenoid.

Aspects of the base of the skull that delimit the peribullary space, namely, form and size of the basoccipital crests and excavation of the paroccipital processes, are rather more constant in their expression than are the features discussed above, although in some specimens the ventral margins of the crests are less entire than in most.

The tips of the pterygoid hamuli may diverge at an acute angle or form only a gentle curve posteriorly (fig. 38, bottom). The pterygoids may be in contact mesially or may be separated by as much as 8 mm. Fenestration is variable, being completely absent in some specimens and extensive in others.

The lateral wing of the palatine is extremely variable in expression. In lateral view, it may stop short of the dorsally-directed notch in the mesial lamina or extend posteriad to nearly touch the sphenoid wing. In some it is nearly absent, and in others extends posterolaterely around the posterior margin of the palatine, to form a horizontal shelf or bridge below the antorbital fossa. Such extension is correlated with the elaboration of the falciform process described above. The deep fossa formed at the juncture of the mesial lamina and the sphenoid wing varies considerably in depth and definition.

The configuration of the antorbital fossa varies markedly, from a small rather well-defined ovate or pyriform aperture, to a large open area (fig. 39).

Breathing and sound-producing apparatus. The prenarial triangle in most individuals is concave but in some is flat and nearly level with the denser lateral portions of the premaxillae. The triangle may be essentially featureless or may be very rugose and scored with transverse furrows. There is little variation in the overall conformation of the prenarial shield, although in some individuals the usual pronounced hump on the lateral margin of the right premaxillary is all but absent. In some specimens the posterior extremity of the right premaxillary stops short of the nasal, in others it extends beyond it for as much as a centimeter.

The ossified portion of the mesethmoidal shield varies dorsally from being truncated short of the nasals to being a broad triangle nearly covering the anterior aspect of the nasals. The nasals, and the vertex of which they are the major component, vary greatly in height and width. The right nasal may be incompletely bipartite.

The degree to which the maxillaries overlay the frontals varies from nearly complete coverage, leaving only a small (~ 2 cm square) area of the frontal exposed behind the nasal, to a state in which the frontals are exposed for their full width.

The antorbital notch varies in depth from 0 mm to approximately 6 mm and also shows considerably variation in form (fig. 39).

Summary. Some feeling for the relative variability of the functional units of the cranium can be had by examination of figure 40, in which coefficients of variation for cranial measurements are presented in an analog fashion and separated into groups according to which functional unit supposedly has greatest influence on absolute size of the measurements. Excluded are measurements that are extremely variable, including projection of premaxillaries (no. 23), nasals to crest (no. 24), and occipital overhang (no. 29); those for which it would appear that size is not most influenced by the functional unit to which they belong primarily; and those for which the functional relationship is unclear, including zygomatic width (no. 14), pterygoid length (no. 28), and length of mandibular fossa (no. 40). It appears that the feeding apparatus is the most variable, closely followed by the breathing and sound-producing apparatus, and that the braincase, hearing, and vision apparatuses are significantly less variable.

The series of "adult" skulls impressed me with the correlation of functionally seemingly unrelated structures in contribution to overall shape. Some skulls seem very long, in every respect; others seem very short, again with many features contributing to the impression. The aspect of individual variation can be examined from the synthetic standpoint of determining general factors, as opposed to the reductionist standpoint of considering more-or-less independent variances associated with functional systems. General factors can be examined with principal components analysis, which is a method for summarizing simultaneous variation of a large number of variables in terms of a few major "factors" (see Methods above). This analysis was performed on 25 cranial measurements of 37 of the specimens from Sets 2 and 6.

Figure 39. Individual variation in skull of adult spotted porpoise in (top) size of antorbital fossa, and (bottom) development of antorbital notch.

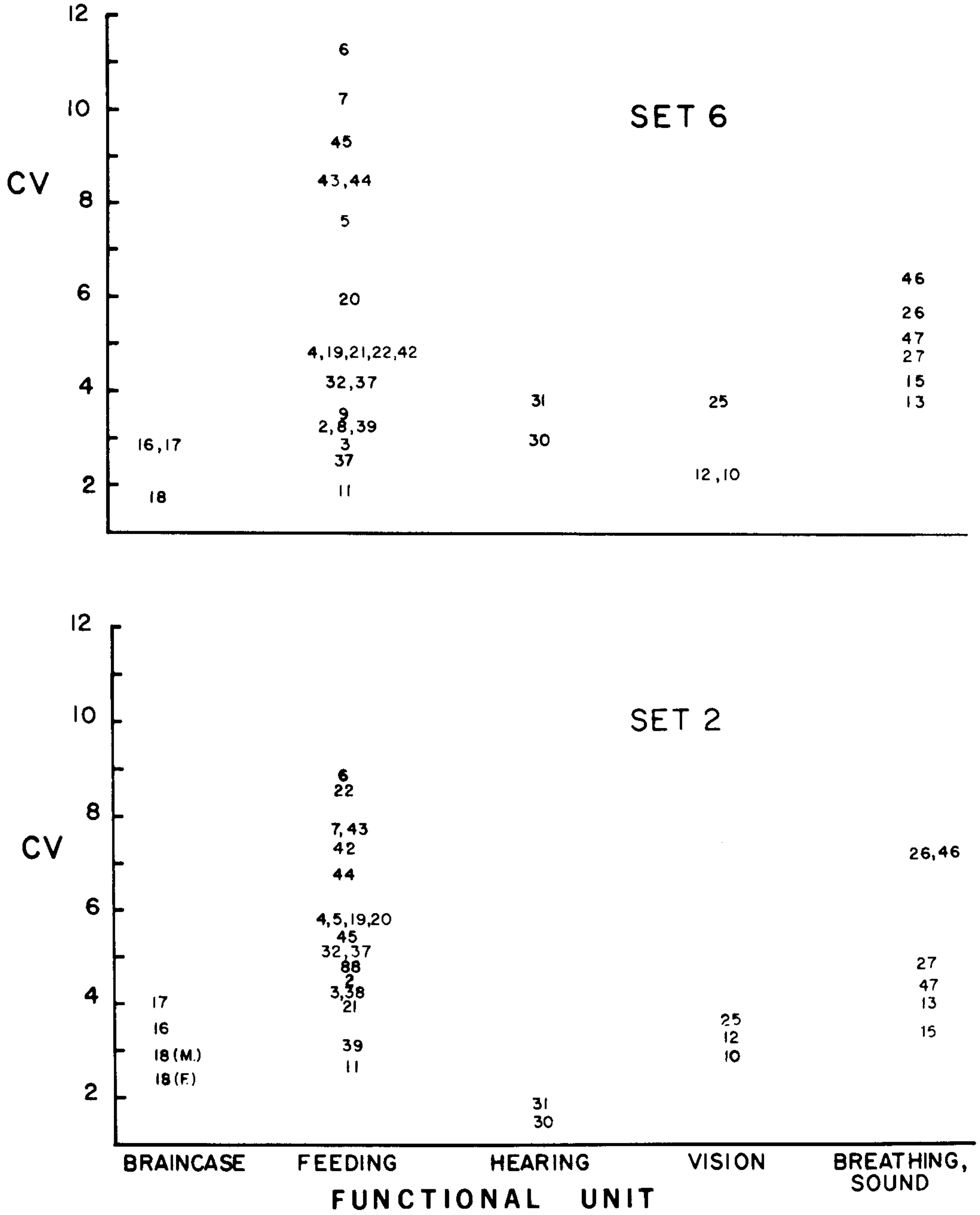


Figure 40. Comparative individual variation of functional units of skull of adult spotted porpoise in two single-school samples. Numbers refer to measurements listed in table 12 and illustrated in figure 2. Coefficients of variability on vertical axis.

Table 11. First principal component in principal components analysis of skull measurements of spotted porpoise.

Specimen field number	Score	Sex	Maturity ++physical +sexual	Dentinal layers	Condylobasal length (mm)	
CV 287	0.709	M		6.0	400	
CV261	0.694	F		5.0	411	
CV293	0.595	M	+	8.0	406	
CV313	0.550	M		5.0	408	58% males
CV265	0.534	M	++	9.0	399	Average 8.2 layers
CV268	0.507	F	++	(-)	404	Average condylobasal
CV 279	0.491	M	++	(-)	401	length = 400 mm
CV 289	0.405	M		8.5	398	
CV 270	0.354	F	++	12.0	396	
CV 319	0.344	F		8.0	394	
CV 280	0.311	M	++	8.0	384	
CV 291	0.263	F	++	12.5	393	
CV 281	0.237	F		6.0	397	
CV 282	0.152	F		8.0	391	
CV 309	0.133	F	++	8.5	390	
CV 273	0.124	F		(-)	391	42% males
CV 277	0.115	F	+	(-)	397	Average 8.1 layers
CV 292	0.075	M	++	12.5	388	Average condylobasal
CV 274	0.020	M		6.0	388	length = 391 mm
CV 259	-0.005	M		7.5	394	
CV 278	-0.015	M		(-)	398	
CV 271	-0.040	F	+	7.0	381	
CV 263	-0.067	M		6.0	388	
CV 272	-0.103	F	++	11.0	391	
CV 316	-0.156	M		9.0	380	
CV 269	-0.175	F	+	7.0	385	
CV 264	-0.186	M		6.0	385	
CV 320	-0.205	M		7.5	388	69% males
CV 275	-0.224	M		7.0	382	Average 7.7 layers
CV 290	-0.242	F		5.5	385	Average condylobasal
CV 276	-0.271	M		6.0	382	length = 377 mm
CV 311	-0.345	M	++	11.0	384	
CV 315	-0.480	M		7.5	371	
CV 260	-0.748	F	+	8.0	369	
CV 267	-0.835	M	+	9.5	369	
CV 310	-1.038	M	+	(-)	360	
CV 312	-1.481	F		8.0	356	

Table 12. Second principal component in principal components analysis of skull measurements of spotted porpoise.

Specimen field number	Score	Sex	Maturity ++physical +sexual	Dentinal layers	Zygomatic width (mm)	
CV 280	1.337	M	++	8.0	174	
CV 292	0.647	M	++	12.5	167	
CV 287	0.507	M		10.0	174	
CV 260	0.439	F	+	8.0	164	83% males
CV 265	0.411	M	++	9.0	168	Average 9.1 layers
CV 275	0.381	M		7.0	161	Average zygomatic
CV 267	0.262	M	+	9.5	159	width = 165 mm
CV 279	0.254	M	++	(-)	167	
CV 270	0.228	F	++	12.0	165	
CV 316	0.206	M		9.0	162	
CV 310	0.154	M	+	(-)	161	
CV 276	0.124	M		6.0	158	
CV 271	0.117	F	+	7.0	162	
CV 272	0.107	F	++	11.0	161	
CV 311	0.099	M	++	10.0	163	
CV 293	0.074	M	+	8.0	165	67% males
CV 309	0.001	F	++	8.5	166	Average 7.8 layers
CV 289	-0.018	M		8.5	164	Average zygomatic
CV 273	-0.019	F		(-)	164	width = 163 mm
CV 315	-0.025	M		7.5	158	
CV 319	-0.047	F		8.0	164	
CV 274	-0.067	M		6.0	163	
CV 290	-0.134	F		5.5	160	
CV 264	-0.157	M		6.0	163	
CV 320	-0.173	M		7.5	159	
CV 263	-0.173	M		6.0	161	
CV 291	-0.180	F	++	12.5	160	
CV 281	-0.288	F		6.0	164	38% males
CV 282	-0.298	F		8.0	162	Average 7.3 layers
CV 278	-0.320	M		(-)	158	Average zygomatic
CV 268	-0.345	F	++	(-)	162	width = 160 mm
CV 269	-0.365	F	+	7.0	160	
CV 259	-0.381	M		7.5	163	
CV 312	-0.414	F		8.0	153	
CV 261	-0.522	F		5.0	162	
CV 313	-0.693	M		5.0	157	
CV 277	-0.712	F	+	(-)	160	

In evaluation of the results of principal components analysis, the first component is generally taken to represent size and the second, shape (Jolicoeur and Mosimann, 1960; Cooley and Lohnes, 1962; Seal, 1964). Interpretation of components beyond the second is usually not attempted, because of uncertainty as to exactly what they represent in geometrically meaningful terms and because of the small size of each in terms of percentage of total variance.

The 37 specimens can be ranked by score for each of the first two principal axes (tables 11 and 12), which account for 33% and 22% of the variance. Included for each specimen are sex, degree of maturity, number of postnatal dentinal layers, and value for the measurement that contributes most to the component in question. The absolute values of the products of loading coefficients (eigenvectors) and means of the measurement (grand mean of specimens in tables 11 and 12) are used as an index of relative determining power of the measurements. For each component, these data are summarized over each of three arbitrary subsample increments to facilitate examination of trends within the ranked order.

The largest component of the variance (33%) of the series, to which condylobasal length is the best index, is associated with individual variation in size and is not significantly associated with developmental or sexually derived variation. Comparison of two skulls (fig. 41, left) from opposite parts of the ranked order for the first axis (but with comparable positions along the second axis) demonstrates association of the variance with scale rather than proportion.

The second component (22%) is apparently another matter entirely. It is primarily associated with a proportional width factor (zygomatic width is the greatest contributor), and score is strongly influenced by sex and age in combination. Older and/or male skulls tend to be proportionately broader than younger and/or female skulls. Condylobasal length is a negative contributor to the score, reflecting the above-discussed longer snout length of old females. Again, comparison of skulls from opposite ends of the ranked order (fig. 41, right) demonstrates the nature of the variation encompassed by this particular component of the total variance.

Postcranial skeleton

Axial postcranial skeleton. It is most appropriate to consider meristic variation in the vertebral column in terms of absolute variation, as indicated by range and standard deviation. From this standpoint, the thoracic series (no. 48), together with the vertebral ribs (nos. 78 and 79), two-headed ribs (nos 80 and 81), sternal ribs (nos. 84 and 85), and floating ribs (nos. 82 and 83), is least variable, with range 2-4 and standard deviation less than 0.8. The lumbar and caudal series, with associated meristic characters, are about equally variable, with range 5-8 and standard deviation 1-2. Total vertebral count has a range of only 5 (nos. 79-83) in both samples, indicating some degree of compensation between the series. Similarly, absolute variation in total number of hemopophyses is about equal to variation in location of first and last hemopophyses.

The atlas varies sharply in ventral outline of the cranial articulating surface, size and angle of projection of the transverse processes, length and robustness of the neural spine, and degree of development of the accessory spine on each side of the dorsal edge of the

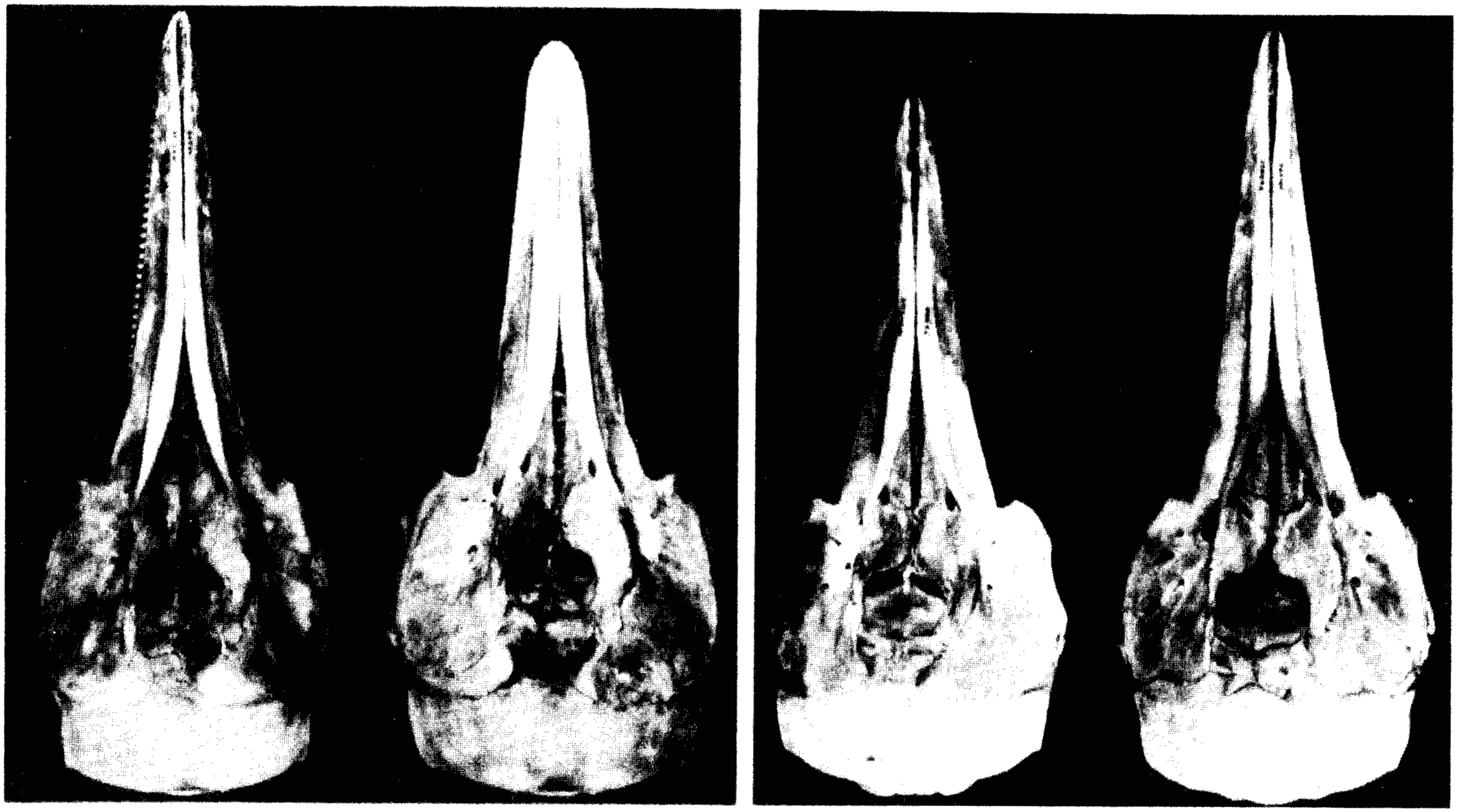


Figure 41. Individual variation of crania of adult spotted porpoise, along principal component axes representing general size and width factors: (right to left) CV 291 (USNM no. 395596), adult female, 12.5 layers and CV 312 (USNM no. 395466), adult female, 8 layers, divergent on axis 1 (size), but nearly coequal on axis 2 (width); CV 280 (USNM no. 395391), male, 8 layers, and CV 277 (USNM no. 395388), adult female, at extremes on axis 2 but co-equal on axis 1.

cranial articulating surface. The accessory spine may form something resembling a neural arch. The coefficients of variation indicate that the variability of the atlas in its height (no. 54) and in the width of its cranial articulating surface (no. 53) is significantly lower than for the apophyses (nos. 55 and 56).

Development of the ventral keel and accessory spine of the axis is correlated with development of the neural spine of the atlas, in some specimens both being very weakly developed. In some specimens they extend posteriad to articulate with a facet on the third vertebra. Development of the lateral processes of the axis does not appear to be correlated with that of the lateral processes of the atlas. The axis is firmly fused to the atlas except for a portion of the neural arch on each side. In some individuals the third cervical is similarly fused to the axis, and fusion may occur between other elements of the series in varying combination. The number of cervicals bearing incomplete arches is variable. One of the six physically mature specimens from Set 2 and two from Set 6 each have one cervical with an incomplete arch. In some individuals one side of the incomplete arch may even develop a long neural spine. Development of the ventrolateral processes on the fith and sixth cervicals also exhibits great individual variation. In some specimens, greatest development is on the seventh vertebra.

Development of the neural spine of the first thoracic vertebra varies widely among individuals, as does thickness of the centrum. In one subadult the arches of the last cervical and the first thoracic are incomplete, and the left side of the arch of the thoracic is fused to the right side of the arch of the cervical. The second thoracic is the first bearing a neural spine. The vertebral count (83) for this specimen is at the extreme upper end of the range for all specimens examined. Variability of the length of the neural spines decreases posteriad along the thoracic series (nos. 69, 70, 71, and 72). A similar posteriorly increasing stability is apparent in the transverse processes (nos. 74 and 76).

In the caudal series, variation is most obvious in the size, shape, and fusion of the hemopophyses, or chevron bones. The first five chevron bones, comprising of ten elements, may be fused in almost any combination, with differences between right and left sides. The first arch is most variable in size (no. 100), the last (no. 102) is next most variable. The length of the longest arch (no. 101), usually tenth or eleventh in the series, is most stable. Considerable variation is present in the terminus of the vertebral column, in the taper and in the size of the last vertebra. In some specimens the last two vertebrae are fused.

The vertebral ribs vary in length, robustness, and curvature. In some specimens, the capitulum is extremely short and slender. Pronounced uncinate processes exist on the first vertebral ribs of some specimens.

The number of two-headed ribs may vary between sides of a single specimen. Often, one member of the last pair in a series of elements is more developed than the other. When this is true for one series, it usually holds for other series in the same skeleton. For example, if the last left vertebral rib is longer than the right, then the last left sternal rib is longer, the last left two-headed rib shows greater development of the capitulum, and so on. The floating ribs may be absent.

The sternal ribs vary in length, robustness, and curvature along with the vertebral ribs. In some specimens the first sternal rib on one side bifurcates distally and articulates with the manubrium in two places. The anterior prong of the bifurcation may be a separate bone. The sternum is extremely variable in every respect (fig. 42). The manubrium may

Figure 42. Individual variation in sternum of physically mature spotted porpoise. Top and bottom rows are each from a single school.

be perforate or nonperforate; it may have one lateral process on each side, or two; it may be asymmetrical; and it varies greatly in massiveness and overall contour. There may be two or three mesosternal elements. Each may be comparatively short and robust or long and slender. The last mesosternal may be a well-developed element or a very small ossification, and may be entire, bipartite, or perforate. The pattern of fusion varies among physically mature specimens.

Anterior appendicular skeleton. Among the measurements of the scapula (nos. 103-107), widths of the coracoid and metacromion processes show greatest variability. Also quite variable are the shape of the metacromion process, the outline of the coracovertebral border, and the topography of the infraspinal fossa. In some specimens the supraspinal fossa opens anteriorly, in others laterally.

The proximal forelimb (nos. 108-112) is about as variable as the scapula and the posteriormost elements of the axial skeleton, much less so than the middle and posterior vertebral column, the ribs, and the sternum, although the radius and ulna of some specimens are noticeably longer and slenderer than those of others. The carpal series varies in number and precise relationships of elements. The trapezium may be absent. The lunar and unciform may be fused. The trapezoid is rarely present. One metacarpal is consistently present on each digit. Variation in phalangical counts is described in the section on development.

Posterior appendicular skeleton. The extreme variation in size and form of the pelvic rudiment is illustrated above in the section on development. Nothing approaching the complex appendicular structure, reported by Lönnberg (1938) for a large male from the type locality of *S. graffmani,* consisting of pelvic and femoral rudiments on one side and separate rudiments of ischium, ileum, and femur on the other, was encountered in any of the skeletons examined. All rudiments examined consist of a single rodlike bone with variable distal development.

Comparison with variation in other species

The nature and range of variation discussed above for samples that are probably from single populations are not surprising in veiw of the patterns of variation in other, terrestrial mammals. Allen in 1894 documented similar variation in a population of *Neotoma.* This paper contains a statement hauntingly reminiscent of True's (1889) above-quoted complaint of puzzlement over cranial variation in *Stenella.* Allen said, "Thus in a series of fifty skulls of *Neotoma micropus* it would be easy to select extremes, of even individual variation, that depart so widely from the average, in one or more characters, as to deceive even an expert, on considering these alone, into the belief that they must represent very distinct species; yet in the present instance the proof that such is not the case is overwhelming."

The results also closely parallel those obtained in the very few previously accomplished studies of individual variation in the Delphinidae (sensu lato). Yamada (1956) examined skeletal material of 124 of approximately 150 false killer whales, *Pseudorca crassidens* (Owen), that stranded over a 30-mile stretch of coast in the Dornoch Firth, Scotland, in October 1927. He did not include sample sizes, data, or statistics in his paper, but stated with respect to the skull that "the breadth of braincase varies little, except that broader dimensions occur in greater skulls." He found, however, that the tip of the rostrum varies considerably in form, "from pointed and tapering ends through round ones to stumps." These findings concerning relative variability of the braincase and elements of the feeding apparatus coincide well with the pattern in the spotted porpoise. Yamada also stated that "some [of the skulls] are very slender, some are stout and very broad, but the indices between either transverse or longitudinal dimensions usually show very high linear correlation, whereas others are less correlated," a result indicating a situation parallel to that in the spotted porpoise where general length and width factors (principal axes of variation) can be defined. Yamada's findings with respect to meristic epigenetic variation in the postcranial skeleton also closely followed the patterns defined here for the spotted porpoise.

Cadenat (1959) published data for several series of *Delphinus delphis* L. captured at various localities on the west coast of Africa. In 57 specimens, he found tooth counts to range from 41 to 55. The greatest range in a single sample was 41-48 in 14 specimens captured together on the coast of Senegal. These ranges are similar to those encountered in the spotted porpoise.

Kleinenberg (1956) published extensive data including osteological measurements, on *Tursiops, Delphinus,* and *Phocoena* in the Black Sea, but unfortunately no indication of degree of maturity of the individual specimens is included, making difficult the isolation of individual variation.

Fraser (1966) examined a large series, from Saint Helena Island in the South Atlantic, of *Stenella* cf. *capensis,* a form closely related to if not conspecific with the spotted porpoise of the eastern Pacific. On the basis of the uniformity of the sample, he inferred that the Saint Helena population is an isolated interbreeding unit. He published averages, ranges, standard deviations, and coefficients of variability for condylobasal length and 13 other measurements expressed as percentage of condylobasal length for 39 adult skulls. Data on sex of the specimens were not available. Comparison of the coefficients of variability with the coefficients for the characters found to be nondimorphic in the spotted porpoise (table 5) show constancy of proportion similar to that in the two single-set series of spotted porpoise. Three of the coefficients for 11 comparable measurements in the Saint Helena series were greater than for both eastern Pacific series, five were lesser than for both, and three were intermediate between the two series.

The several forms thus far studied agree closely in the nature and extent of individual variation. This indicates that the results reported here for large series of spotted porpoise probably apply generally to the Delphinidae and can be used as a basis for evaluation of the siginificance of variation encountered within or between smaller samples of species of *Stenella,* or species of other delphinid genera.

Geographical Variation

I found pronounced geographical variation in the spotted porpoise in skeletal characters. Geographical variation has not previously been analyzed adequately for any form of *Stenella,* primarily because of the paucity of available material from known localities. Fraser (1950) examined skull variation in the spotted porpoise in great detail, but 15 of the 31 specimens available to him were from unknown localities (discussed above in Historical Review).

This analysis of geographical variation is based on 132 specimens from known localities in the eastern tropical Pacific and 15 from Hawaii. The area covered in the eastern Pacific (fig. 43) extends from Guaymas, Sonora, Mexico (27°56′N, 111°08′W) in the north to Gorgona Island, Colombia (~ 3°N, 78°20′W) in the south, and seaward to 135° W (approximately midway bewteen Clipperton Island and Hawaii). The only measurements not made by me are those published by Lönnberg (1934, 1938).

Skeletal specimens included in analysis of geographical variation

Coastal–1 from 13°15′N, 79°25′W (USNM 254671), 8 from ~7-9°N, 78°30′W (USNM 261427-34), 1 from ~3°N, 78°20′W (USNM 258641), 1 from ~27°56′N, 111° 08′W (CAS 12763), 1 from 21°52′N, 105°54′W (CAS 5581), 2 from 21°10′N, 106° 10′W (AMNH 80559 and CAS 5582), 1 from ~16°14′N, 98°29′W (AMNH 130216),

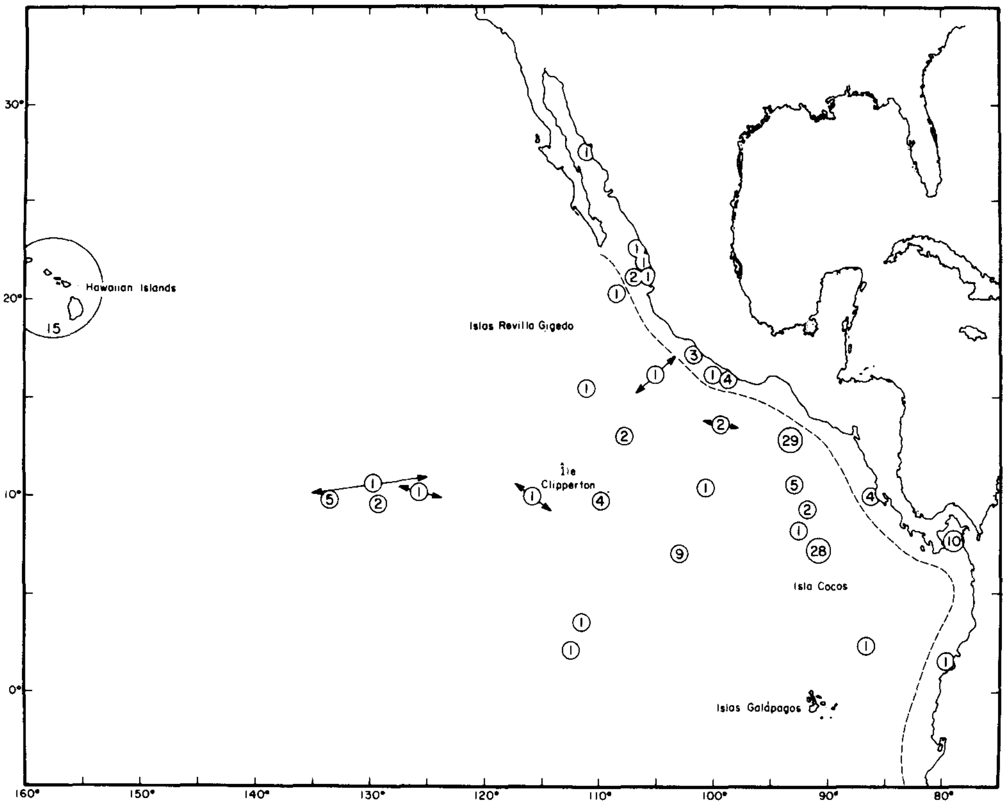


Figure 43. Provenance of specimens used in analysis of geographical variation of skeleton of spotted porpoise. Dashed line separates coastal and offshore forms.

3 from 17°32'N, 101°44'W (USNM 395926-8), 2 from 9°57'N, 85° 56'W (USNM 395935-6), 1 from 9°50'N, 85°48'W (USNM 395937), 1 from 21°21'N, 105°31'W (MMBL 65-1), 1 from 22°58'N, 106°21'W (MMBL 66-3), 1 from 16°15'N, 98°55'W (USNM 395929), 1 from 9°53'N, 85°54'W (USNM 395938), 1 from 7°58'N, 82°02'W (USNM 259311), holotype of *Prodelphinus graffmani* Lönnberg, 1934, and 1 additional skeleton measured by Lönnberg from 16°58'N, 109° 55'W.

Offshore–33 from 12°51'N, 93°18'W (USNM 395276-7, 395330-4, 395336-9, 395395, 395397, 395417, 395458-9, 395461-2, 395464, 395467-8, 395528, 395530, 395594-5, 395597, 395603-6, 395608-9, 395611), 28 from 7°11'N, 90°32'W (USNM 395276-7, 395327-9, 395380, 395385, 395387-94, 395396, 395398, 395460, 395463, 395465-6, 395529, 395532, 395535, 395607, 395612-3, 395616), 5 from 10°31'N, 92°52'W (USNM 395207, 395264-6, 395268), 1 from 7°50'N, 90°32'W (SWFC - CV 160), 2 from 9°N, 92°W (SWFC - WP SG02), 1 from 9°50'-10°36'N, 89°47'-102°02'W (CAS 15663), 2 from 13°30'-14°06'N, 88°-100°56'W (MVZ 140640, CAS 15662), 1 from 14°20'N, 107°20'W (LACM - RLB 404), 2 from 12°08'N, 105°46'W (LACM - WAW 42 and 51), 1 from ~17°N, 100°45'W (LACM - WAW 55), 1 from 2°30'N, 86°W (USNM 396034), 2 from 9°28'N, 129°18'W (USNM 396027, 396175), 1 from 9°20'N, 110°44'W (USNM 396028), 1 from 11°N, 125°W or 10°-12°N, 135°-136°W (USNM 396029), 5 from 9°47'N, 133°25'W (USNM 396018-9, 396022, 396024-5), 2 from 8°10'N, 106°53'W (USNM 395407, SWFC - LGB 199), 1 from 7°47'N, 100°50'W (USNM 395410), 9 from 7°N, 103°W (SWFC - JSL 88-96), 1 from 14°55'N, 105°20'W-16°45'N, 103°04'W (LACM - GDF 48), 1 from 18°N, 107°W (SDMNH 21199), 1 from 9°-10°N, 114°-118°W (USNM 396038), 1 from 10°-11°N, 124°-128°W (USNM 396171), 1 from 8°N, 107°W (USNM 395408).

Hawaiian–8 from Hawaiian Islands (SWFC - WFP 92, USNM 112832-3, LACM 27069, LACM - NUHA, LACM - KAHILI, USNM 23290, MCZ 51701), 1 from Oahu (UBC 8511), and 6 from Penguin Banks, Molokai (USNM 395857-80).

AMNH = American Museum of Natural History, New York, N.Y., CAS = California Academy of Science, San Francisco, Calif., LACM = Los Angeles (Calif.) County Museum, MCZ = Museum of Comparative Zoology, Harvard University, Cambridge, Mass., MMBL = Marine Mammal Biological Laboratory, Sand Point NAS, Seattle, Wash., MVZ = Museum of Vertebrate Zoology, University of California, Berkely, SDMNH = San Diego (Calif.) Museum of Natural History, SWFC = Southwest Fisheries Center, La Jolla, Calif., UBC = University of British Columbia, Vancouver, USNM = U.S. National Museum, Washington, D.C.

The eastern Pacific skeletons fall into two groups, referred to below as the "coastal form" and the "offshore form." The 28 in the "coastal" group are from the Gulf of California, the coast of southern Mexico, the coast of Costa Rica, the Bay of Panama, and Gorgona Island, Colombia, and were all collected by harpooning or as beach pickups. The 19 "adult" skulls in this group range from 419 to 460 mm in condylobasal length, and the group includes the type specimen of *S. graffmani* (Lönnberg, 1934), for which the length of the mandible is known but not condylobasal length. The 104 "offshore" specimens were all collected in the tuna seine fishery in open, offshore waters; "adult" skulls (68) in this group range from 356 to 411 mm in condylobasal length. The most onshore specimen was captured "50 miles (80 km) west of Acapulco, Mexico," but tuna boat logbooks show that net sets are often made within 20-25 km off the coast on large schools of "spotters."

The smallest male skull, largest male skull, and a modal female skull (in CB length) are illustrated for the coastal and offshore groups (figs. 44-47). True (1906) published photos of two Hawaiian skulls; this form is not illustrated here.

Specimens in the two eastern Pacific groups are easily discriminated by eye on the basis of size; the coastal skulls are larger. The difference in size is not because of differential age makeup in the two samples; 6 of the 9 "juvenile" coastal skulls are longer than the longest "adult" offshore skull. The number of dentinal layers has not yet been examined for the coastal specimens, but the age structures of the two samples are similar, by the criterion of fusion of the premaxillary and maxillary bones. The differences between the two groups are most pronounced at the northern and southern ends of the range; the two largest coastal skulls are from Guaymas in the Gulf of California and from the Bay of Panama. The smallest is from the coast of Mexico between Manzanillo and Acapulco.

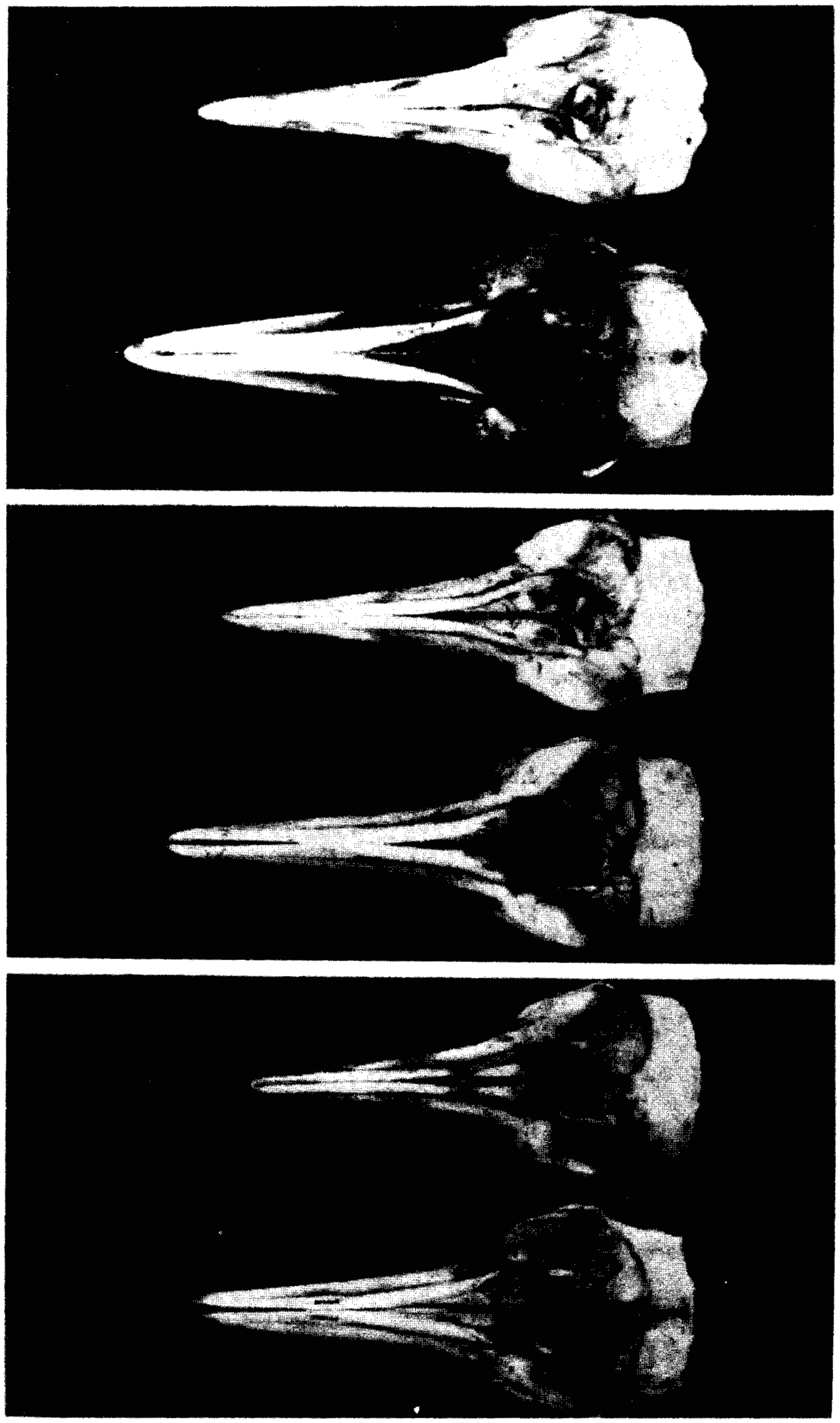


Figure 44. Geographical variation in skull of spotted porpoise: dorsal view of crania of shortest, modal and longest in coastal (left in each pair) and offshore (right) series. Coastal specimens are USNM No. 395928, MMBL No. 65-1 and USNM No. 261432 (skull is mislabeled in photo). Offshore specimens are USNM No. 395464, 395463 and 395467. Data are in table 13 (continued).

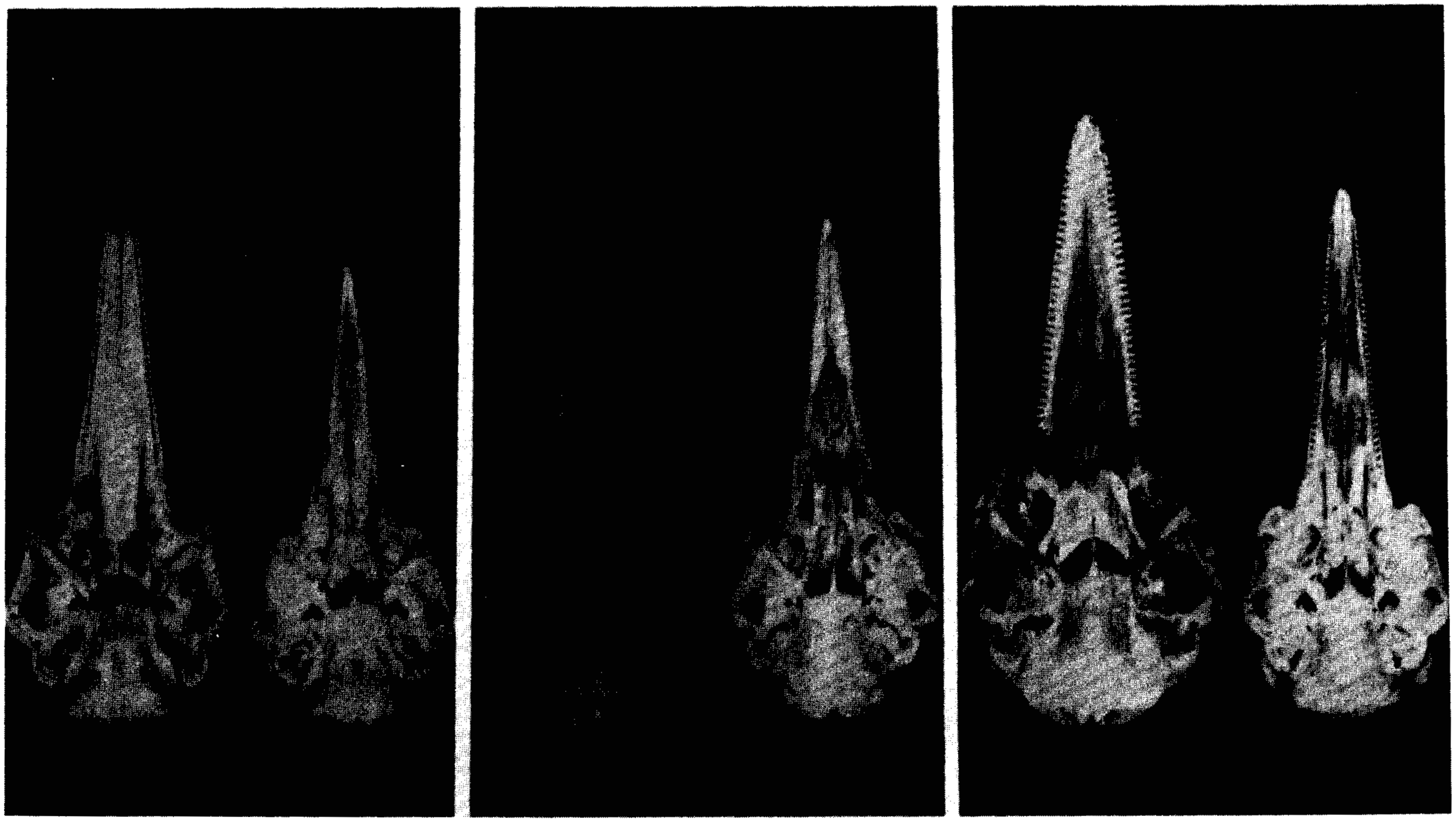


Figure 44 (continued). Geographical variation in skull of spotted porpoise: ventral view of crania of shortest, modal and longest in coastal (left in each pair) and offshore (right) series. Coastal specimens are USNM No. 395928, MMBL No. 65-1 and USNM No. 261432 (skull is mislabeled in photo). Offshore specimens are USNM No. 395464, 395463 and 395467.

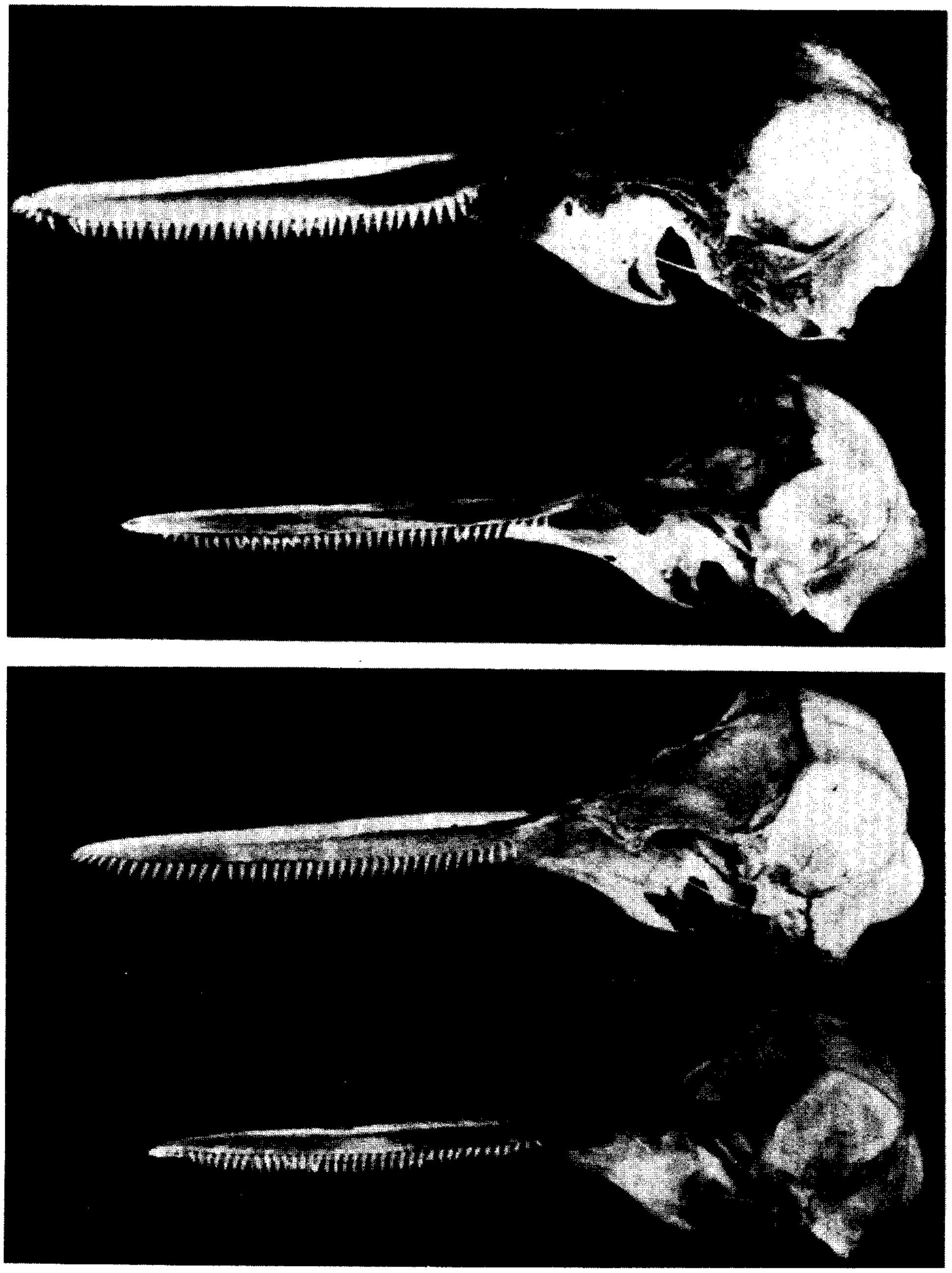


Figure 45. Lateral view of skulls in figure 44 (longest at top, modal at bottom). Coastal specimen at top in each pair (continued).

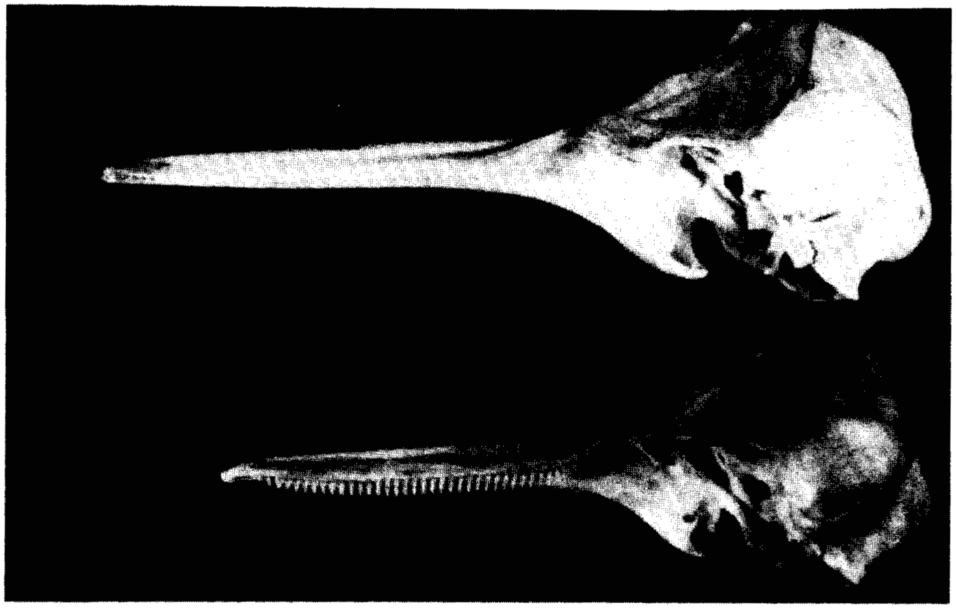


Figure 45 (continued). Lateral view of shortest skull in figure 44. Coastal specimen at top.

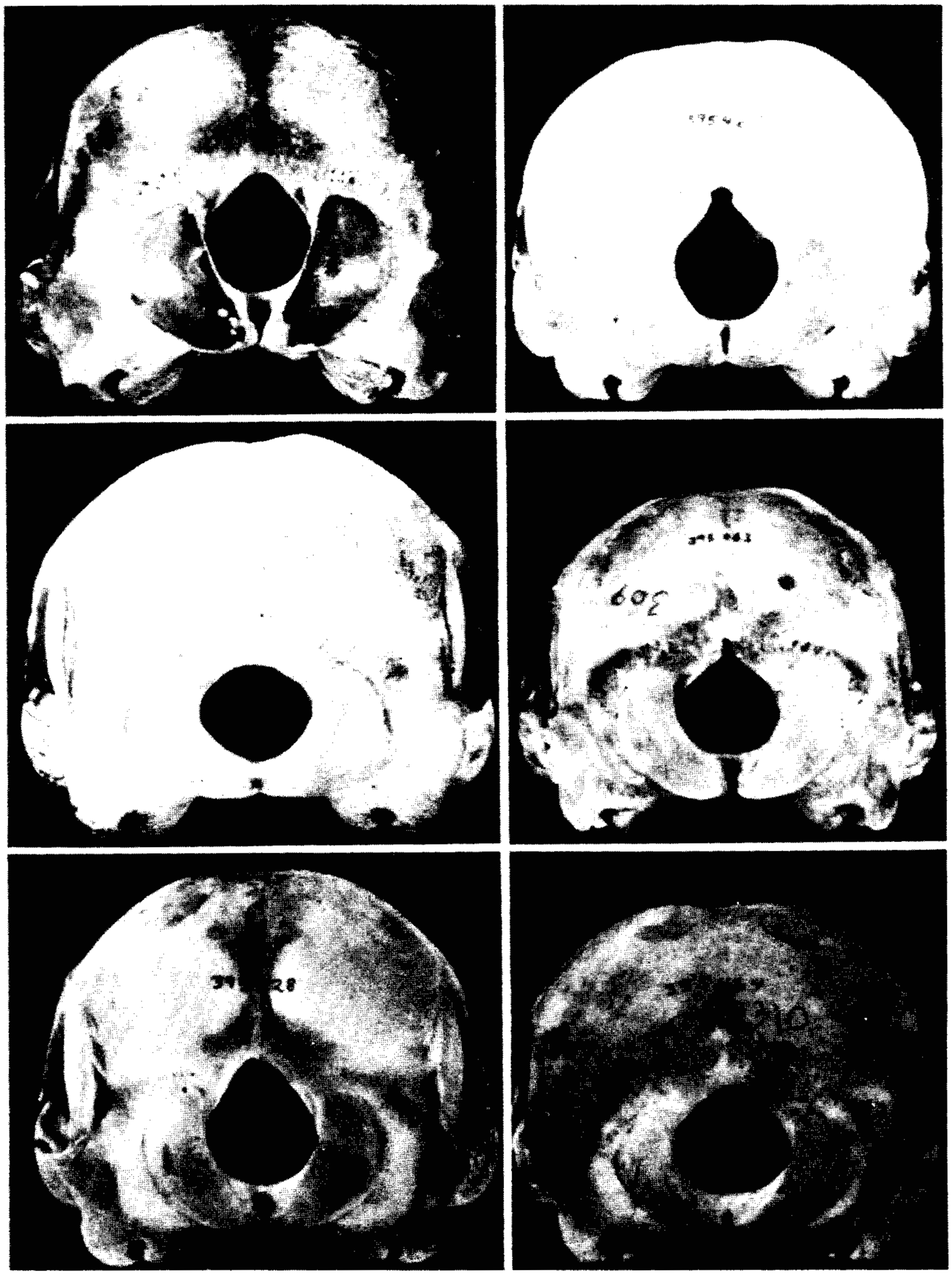


Figure 46. Occipital view of skulls in figure 44 (longest at top, modal in center, shortest at bottom). Coastal specimen at left in each pair.

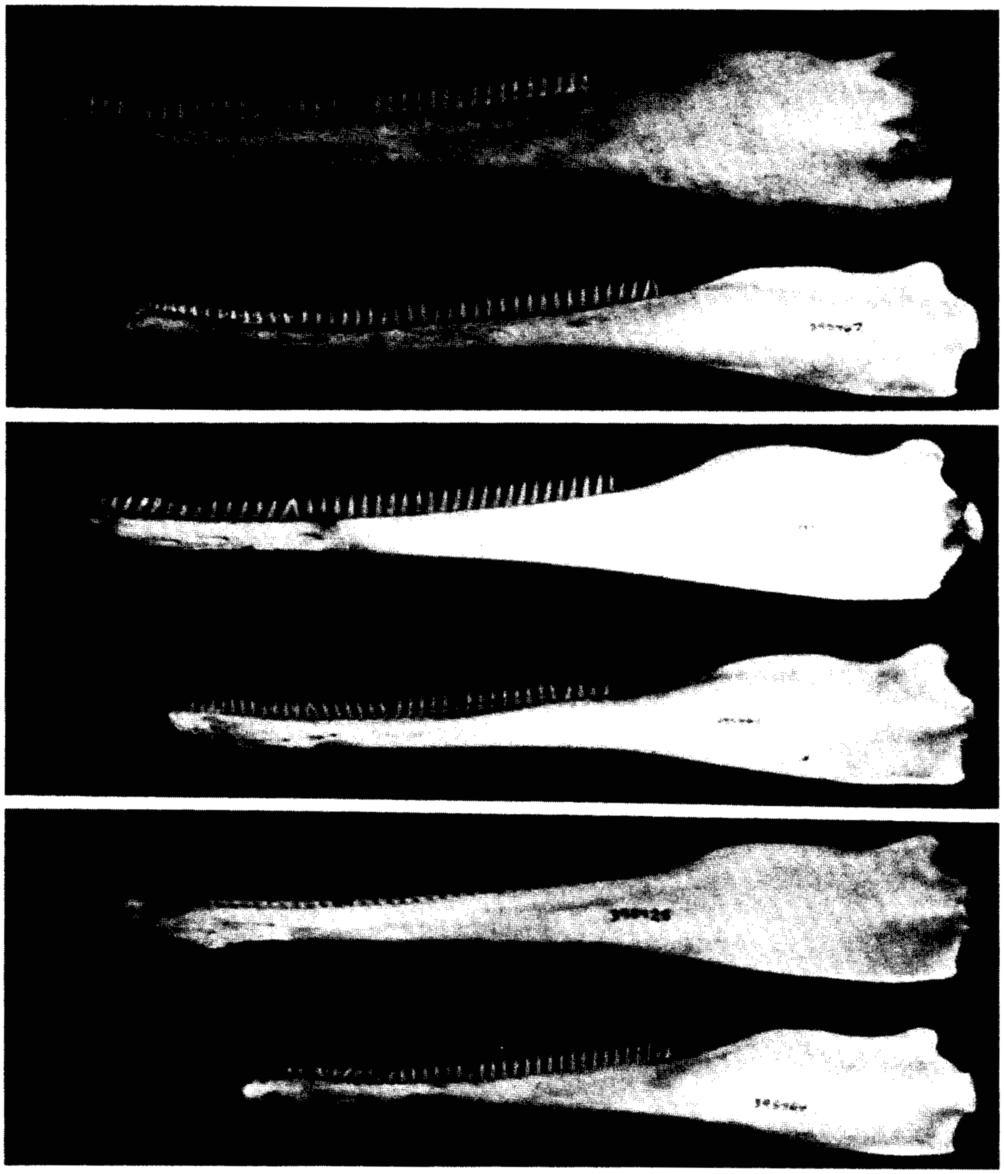


Figure 47. Lateral view of mandible of skulls in figure 44 (longest at top, modal in center, shortest at bottom). Coastal specimen at top in each pair.

Table 13a. Skeleton measurements and meristics of coastal and offshore adult spotted porpoise, with statistical comparisons of means (continued)

Variable	Unit	COASTAL				OFFSHORE				Absolute value of significant t, at $\alpha = .05$
		Number of specimens	Range	Mean	Standard deviation	Number of specimens	Range	Mean	Standard deviation	
1. Condylobasal length	mm	18	419-460	436.9	10.81	68	356-411	389.9	12.25	14.81
2. Rostrum length	mm	17	249-275	261.1	6.32	68	210-249	232.2	9.69	11.66
3. Rostrum width at base	mm	18	82-100	90.3	4.85	70	74-91	82.1	3.56	8.06
4. Rostrum width at 60 mm	mm	17	56-77	64.8	5.84	70	46-63	55.4	3.33	8.85*
5. Rostrum width at midlength	mm	18	43-60	48.7	5.04	67	35-48	40.8	2.84	8.73*
6. Premaxillary width at rostral midlength	mm	18	20-32	26.4	2.96	67	17-28	22.2	2.25	6.56
7. Rostrum width at 3/4 length	mm	17	29-43	34.3	4.23	65	23-36	28.4	2.65	7.14*
8. Rostrum tip to external nares	mm	18	289-316	303.3	7.37	68	245-294	271.3	11.91	10.83*
9. Rostrum tip to internal nares	mm	17	293-320	306.3	7.47	66	243-293	272.9	11.57	11.28
10. Preorbital width	mm	17	153-178	161.2	7.97	69	134-163	146.0	5.20	9.63*
11. Postorbital width	mm	17	172-196	180.0	7.32	69	151-178	164.2	4.96	10.63*
12. Least supraorbital width	mm	18	150-177	159.1	8.41	70	131-160	144.5	5.18	9.27*
13. External nares width	mm	17	43-52	46.6	2.45	70	37-47	41.5	2.06	8.82*
14. Zygomatic width	mm	15	173-198	181.6	8.31	70	148-177	163.0	5.19	11.20*
15. Greatest width of premaxillaries	mm	18	66-76	71.7	2.63	70	57-71	64.9	2.84	9.11
16. Parietal width	mm	17	135-153	145.8	5.27	70	129-150	137.6	4.68	6.32
17. Braincase height	mm	17	97-113	105.8	4.02	70	87-107	96.3	4.21	8.42
18. Braincase length (M)	mm	8	123-136	130.0	5.10	37	110-123	117.4	3.33	8.79
(F)	mm	4	121-131	126.0	5.77	32	109-122	115.3	2.91	6.18
19. Posttemporal fossa length	mm	17	73-97	83.2	6.25	70	56-77	67.6	4.24	12.32*
20. Posttemporal fossa width	mm	17	55-79	65.4	5.82	70	46-63	52.8	3.33	11.88*
21. Temporal fossa major diameter	mm	14	40-51	46.0	2.93	70	35-44	38.8	1.81	
22. Temporal fossa minor diameter	mm	14	24-37	28.1	3.81	70	18-27	22.6	1.98	7.94*
23. Projection of premaxillaries	mm	13	13-24	17.6	2.84	50	12-25	17.8	2.82	
24. Nasals to crest (M)	mm	8	26-51	35.9	7.57	37	19-38	26.8	4.85	4.33
(F)	mm	4	24-36	31.5	5.45	33	17-31	23.3	3.57	4.11
25. Orbit length	mm	17	49-54	51.1	1.54	70	44-53	47.0	2.00	7.89
26. Antorbital process length	mm	17	34-51	41.4	4.43	70	30-42	35.6	2.38	
27. Internal nares width	mm	17	48-60	52.8	3.17	70	40-54	36.4	2.62	8.66

28. Pterygoid length	mm	13	61-75	68.4	4.22	65	55-76	62.8	4.53	4.11
29. Occipital overhang	mm	15	0-11	2.5	3.09	70	0-10	3.7	2.44	
30. Bulla length	mm	3	30-32	31.0	—	66	29-33	29.9	0.75	
31. Periotic length	mm	2	27-28	27.5	—	66	25-30	26.9	0.95	
32. Upper tooth row length	mm	18	215-240	228.9	7.05	67	180-220	201.8	9.22	11.57
TEETH:										
33. Upper left	no.	24	37-46	40.9	2.29	93	37-48	41.5	2.20	
34. Upper right	no.	24	37-46	40.8	2.37	93	37-47	41.4	2.19	
35. Lower left	no.	25	36-44	39.9	2.04	91	34-45	40.4	2.19	
36. Lower right teeth	no.	26	36-43	40.0	1.74	93	34-46	40.6	2.05	
37. Lower tooth row length	mm	18	202-242	225.2	9.01	65	177-220	195.8	9.08	12.18
38. Ramus length	mm	18	352-393	372.4	10.20	66	296-347	328.5	12.17	14.00
39. Ramus height	mm	19	73-97	65.9	3.84	69	50-62	56.8	2.30	13.03*
40. Mandibular fossa length	mm	14	108-120	114.7	3.62	70	90-124	104.0	5.58	6.87
41. Deviation from symmetry	degrees	16	4-11	7.3	2.21	69	0-10	6.5	3.11	
42. Basihyal length	mm	8	30-41	34.5	3.66	62	24-36	29.5	2.28	5.41*
43. Basihyl *width*	*mm*	8	34-47	38.3	4.77	61	26-42	34.1	2.91	3.54*
44. Thyrohyal width	mm	8	17-22	19.4	1.60	61	14-29	17.7	2.10	2.20
45. Thyrohyal length	mm	8	56-68	60.3	4.33	61	40-62	53.3	4.17	4.45
46. Stylohyal width	mm	8	11-13	12.1	0.83	61	9-15	11.9	0.95	
47. Stylohyal length	mm	8	65-78	74.1	4.39	61	57-78	69.4	4.01	3.09
48. Thoracic vertebrae	no.	8	15-17	15.5	0.76	77	15-17	16.0	0.60	
49. Lumbar vertebrae	no.	6	17-22	19.3	1.75	62	17-23	19.8	1.37	
50. Caudal vertebrae	no.	6	34-37	35.8	1.17	59	34-42	38.1	1.57	3.48
51. Total vertebrae	no.	9	77-79	77.7	0.87	61	77-83	80.8	1.32	6.81
52. Fused cervical vertebrae	no.	3	2-2	—	—	15	2-3	2.1	0.35	—
53. Atlas width	mm	3	88-90	—	—	16	73-84	77.8	2.96	—
54. Atlas height	mm	3	54-61	—	—	16	46-50	47.4	1.09	—
55. Atlas lateral process length	mm	2	26-28	—	—	16	18-25	21.3	2.27	—
56. Atlas neural spine length	mm	3	42-48	—	—	16	30-44	36.8	3.47	—
57. Atlas dorsal ridge height	mm	3	4-6	—	—	16	1-4	2.4	0.96	—
58. Atlas dorsolateral spine length	mm	3	0-3	—	—	16	0-14	3.2	4.10	—
59. Axis lateral process length	mm	3	23-25	—	—	16	16-25	19.5	2.22	
60. Cervical vertebrae incomplete	no.	3	0-1	—	—	14	0-3	0.5	0.85	—

*Variance homogeneous at $\alpha = 0.1$ but not at .05. Blank indicates variance nonhomogeneous; dash indicates t insignificant.

Table 13a (continued). Skeleton measurements and meristics of coastal and offshore adult spotted porpoise, with statistical comparisons of means

Variable	Unit	COASTAL				OFFSHORE				Absolute value of significant t, at α = .05
		Number of specimens	Range	Mean	Standard deviation	Number of specimens	Range	Mean	Standard deviation	
61. Greatest ventrolateral cervical process on	no.	3	6-6	—	—	15	5-6	5.9	0.21	—
62. First vertical foramen on	no.	9	53-57	54.3	1.22	81	52-61	57.2	1.62	5.20
63. First vertebra with reduced metapophyses	no.	8	30-33	31.4	1.06	76	24-35	31.3	2.39	—
64. Last transverse process on	no.	10	60-62	60.7	0.82	78	59-66	62.9	1.30	5.21
65. Last neural spine on	no.	10	65-67	65.8	0.79	77	64-71	68.1	1.26	5.61
68. First caudal with vertical spine	no.	10	56-62	59.1	1.60	77	56-64	60.8	1.50	3.35
69. First thoracic neural spine length	mm	3	28-42	—	—	16	9-37	24.9	8.50	—
70. Second thoracic neural spine length	mm	3	45-53	—	—	16	32-44	39.3	3.79	—
71. Tenth thoracic neural spine length	mm	2	60-78	—	—	16	55-70	62.3	5.02	—
72. Last thoracic neural spine length	mm	3	78-91	—	—	15	63-81	72.1	5.28	—
73. First thoracic vertebra height	mm	2	51-60	—	—	16	44-51	46.9	1.88	—
74. First thoracic vertebra width (M)	mm	2	79-82	—	—	8	68-80	73.6	4.28	—
(F)		0	—	—	—	8	63-76	70.0	4.14	—
75. First lumbar vertebra height	mm	2	57-67	—	—	15	46-52	48.9	1.71	—
76. First lumbar vertebra width	mm	2	189-207	—	—	15	165-188	174.8	6.34	—
77. 23rd centrum length	mm	2	24-27	—	—	14	19-25	21.1	1.75	2.64
78. Left vertebral ribs	no.	7	15-16	15.3	0.49	68	15-17	15.9	0.58	2.64
79. Right vertebral ribs	no.	8	15-17	15.5	0.76	66	15-17	15.9	0.59	—
80. Left 2-headed ribs	no.	11	4-6	5.4	0.67	84	4-7	5.5	0.75	—
81. Right 2-headed ribs	no.	11	4-6	5.3	0.79	83	4-7	5.6	0.72	—
82. Left floating ribs	no.	8	1-1	1.0	0	65	0-2	1.1	0.54	—
83. Right floating ribs	no.	8	1-1	1.0	0	64	0-2	1.1	0.53	—
84. Left sternal ribs	no.	7	8-10	9.1	0.69	62	8-11	9.4	0.62	—
85. Right sternal ribs	no.	7	9-10	9.1	0.38	60	8-11	9.4	0.63	
86. First vertebral rib length	mm	3	126-143	—	—	16	100-119	110.6	5.69	—
87. First vertebral rib width (M)	mm	2	19-27	—	—	7	20-24	31.6	1.40	—
(F)		0	—	—	—	8	16-22	18.4	2.26	—
88. Longest vertebral rib length	mm	3	281-313	—	—	16	232-263	248.9	9.04	—
89. First sternal rib length	mm	3	80-85	—	—	16	66-85	76.3	5.03	—

90. Manubrium width	mm	3	104-106	—	—	16	63-97	84.0	8.25	—
91. Manubrium length	mm	3	62-72	—	—	16	46-95	57.3	11.09	—
92. Manubrium notch depth	mm	3	6-10	—	—	16	5-19	9.6	3.24	—
93. Manubrium foramen length	mm	3	2-8	—	—	16	0-11	3.6	3.67	—
94. Mesosternal elements	no.	2	3-4	—	—	13	2-3	2.7	0.48	—
95. Mesosternals fused	no.	2	1-2	—	—	15	1-3	1.7	0.62	—
96. Chevron bones	no.	0	—	—	—	53	26-33	30.0	1.50	—
97. Chevron bones fused in first series	no.	2	2-2	—	—	15	0-4	2.2	1.08	—
98. First chevron on	no.	6	41-44	42.5	1.38	66	41-47	43.7	1.26	2.22
99. Last chevron on	no.	0	—	—	—	59	70-77	72.6	1.45	—
100. First chevron length	mm	2	10-14	—	—	14	3-23	9.3	5.22	—
101. Longest chevron length	mm	2	56-56	—	—	16	40-49	44.7	2.87	—
102. Last chevron length	mm	0	—	—	—	11	2-4	3.0	0.63	—
103. Scapula height	mm	3	130-135	—	—	16	101-123	108.2	5.82	—
104. Scapula length	mm	3	121-128	—	—	16	99-124	107.5	6.73	—
105. Coracoid length	mm	3	37-39	—	—	16	26-38	30.6	2.80	—
106. Coracoid width	mm	3	22-27	—	—	16	10-30	18.7	4.87	—
107. Metacromion width	mm	3	42-57	—	—	16	24-51	40.9	7.41	—
108. Humerus length	mm	3	54-62	—	—	16	43-53	48.1	2.41	—
109. Humerus width	mm	3	41-44	—	—	16	32-36	34.0	1.15	—
110. Radius length	mm	3	74-77	—	—	16	56-67	61.9	2.86	—
111. Radius width	mm	3	36-40	—	—	16	27-34	30.8	1.77	—
112. Ulna length	mm	3	63-65	—	—	15	48-61	54.4	3.02	—
113. Carpal row width	mm	3	67-73	—	—	14	49-62	55.8	4.28	—
PHALANGES:										
114. Digit I (M)	no.	2	2-2	—	—	7	2-2	2.0	0	—
(F)		0	—	—	—	6	1-2	1.8	0.54	—
115. Digit II	no.	8	6-7	6.5	0.53	73	7-9	7.5	0.58	4.66
116. Digit III	no.	7	4-5	4.6	0.53	71	4-6	5.1	0.42	2.94
117. Digit IV	no.	6	1-2	1.5	0.56	72	2-3	2.1	0.26	4.88
118. Digit V	no.	6	0-1	0	0.89	70	0-1	0.6	0.48	2.72
119. Pelvic length (left) (M)	mm	1	80	—	—	6	58-81	75.0	12.95	—
(F)		0	—	—	—	7	51-81	62.3	10.86	—
120. Pelvic length (right) (M)	mm	0	—	—	—	6	58-81	73.7	8.64	—
(F)		0	—	—	—	7	52-86	62.0	12.04	—

Table 13b. Skeleton measurements and meristics of Hawaiian spotted porpoise, with statistical comparison with offshore series

Variable	Unit	Number of specimens	Range	Mean	Standard deviation	Absolute value of significant t, at $\alpha = .05$
1. Condylobasal length	mm	12	395-440	413.6	12.36	6.17
2. Rostrum length	mm	12	240-269	250.8	9.08	6.18
3. Rostrum width at base	mm	13	86-94	89.2	2.27	6.91
4. Rostrum width at 60 mm	mm	13	58-66	62.5	2.54	7.29
5. Rostrum width at midlength	mm	12	43-49	45.9	1.93	5.96
6. Premaxillary width at rostral midlength	mm	12	21-27	24.4	1.98	3.17
7. Rostrum width at 3.4 length	mm	12	28-35	31.8	2.08	4.20
8. Rostrum tip to external nares	mm	12	274-321	293.4	12.31	5.90
9. Rostrum tip to internal nares	mm	12	273-318	294.1	11.40	5.85
10. Preorbital width	mm	13	149-164	158.0	5.31	7.61
11. Postorbital width	mm	13	163-182	173.6	5.80	6.10
12. Least supraorbital width	mm	13	145-162	155.6	5.58	7.01
13. External nares width	mm	13	38-46	42.3	2.10	—
14. Zygomatic width	mm	13	164-181	172.2	5.75	5.77
15. Greatest width of premaxillaries	mm	13	65-71	68.9	1.93	4.86
16. Parietal width	mm	13	135-150	141.0	4.83	2.39
17. Braincase height	mm	13	91-109	98.0	5.26	—
18. Braincase length (M)	mm	7	112-121	117.0	3.06	—
(F)	mm	2	118-119	—	—	—
19. Posttemporal fossa length	mm	13	57-70	62.0	4.24	4.37
20. Posttemporal fossa width	mm	13	42-56	50.2	3.80	2.53
21. Temporal fossa major diameter	mm	11	35-41	38.8	1.78	0
22. Temporal fossa minor diameter	mm	11	22-27	24.0	2.00	2.18

23. Projection of premaxillaries		mm	9	16-24	20.7	2.45	2.89
24. Nasals to crest	(M)	mm	7	16-32	24.3	4.99	—
	(F)	mm	2	19-29	—	—	—
25. Orbit length		mm	13	46-56	50.1	2.75	4.82
26. Antorbital process length		mm	13	35-42	38.2	2.20	3.66
27. Internal nares width		mm	13	44-55	48.7	2.95	2.85
28. Pterygoid length		mm	12	60-79	67.5	5.68	3.17
29. Occipital overhang		mm	13	1-14	5.8	3.36	2.68
30. Bulla length		mm	12	30-33	31.2	1.15	5.05
31. Periotic length		mm	11	25-29	27.8	1.36	2.72
32. Upper tooth row length		mm	12	200-232	215.9	8.43	4.94
TEETH:							
33. Upper left		no.	11	38-44	41.5	1.92	—
34. Upper right		no.	12	38-44	42.3	1.60	—
35. Lower left		no.	13	36-42	39.9	2.06	—
36. Lower right		no.	13	36-42	39.9	1.71	—
37. Lower tooth row length		mm	12	200-236	210.9	9.75	5.23
38. Ramus length		mm	12	339-379	351.4	11.63	6.03
39. Ramus height		mm	13	53-61	57.5	2.26	—
40. Mandibular fossa length		mm	11	102-114	106.6	3.23	—
41. Deviation from symmetry		degrees	13	5-10	7.1	1.62	—
42. Basihyal length		mm	7	27-37	32.4	2.99	3.09
43. Basihyal width		mm	7	34-42	38.0	2.77	3.37
44. Thyrohyal width		mm	7	16-23	19.1	2.54	—
45. Thyrohyal length		mm	7	49-64	56.3	5.22	—
46. Stylohyal width		mm	8	11-15	13.0	1.51	2.85
47. Stylohyal length		mm	8	68-77	71.9	3.64	—

The coastal series is more variable than the offshore series in most measurements, and the Hawaiian series is very small, making statistical comparison difficult. In many measurements, however, there is complete separation, and differences between the series (table 13a and b) are obvious and certainly significant.

Cranial skeleton

The sample for cranial measurements is limited to specimens regarded as adults, by the criterion of having 5 or more layers in the postnatal dentine or, for skulls for which teeth have not been sectioned, by the criterion of distal fusion of the premaxillaries and maxillaries.

Braincase. The coastal and offshore series are not as divergent in dimensions of the braincase as they are in condylobasal length. In parietal width (no. 16 in table 13) the overlap is nearly complete (fig. 48). Disparity is greatest in braincase length for males (no. 18) and intermediate in braincase height (no.17).

The Hawaiian series (table 13b) overlaps the offshore series in all measurements and counts. The braincase of the Hawaiian form is on the average larger only in parietal width, and that but slightly.

Feeding apparatus. It is in the feeding apparatus that the two eastern Pacific groups are most divergent. This is best exemplified in length of the ramus (fig. 48), where there is no overlap. The porpoise groups are modally different in absolute length and widths of the rostrum (nos. 2-7). The disparity in width of the rostrum increases distally. The rostrum of the offshore form is thus on the average more attenuate. Average ratio of rostrum length to width at the base is nearly the same in the coastal and the offshore series (2.91 opposed to 2.84). The ratio of length to 3/4 width, however, is 5.41 (4.45-6.00) in the coastal and 5.74 (4.80-6.56) in the offshore series. The two series are similar in tooth counts, but the tooth rows are longer in the coastal series. The teeth in the coastal skulls are on the average larger than in the offshore skulls, both in length and diameter. Length is difficult to measure in a consistent fashion because of differential wear at the tip of the tooth, but diameter can easily be measured uniformly in a transverse direction at the alveolus. This measurement, taken at midlength of a maxillary tooth row, shows overlap for the two groups but pronounced modal difference (fig. 48).

The temporal fossa (nos. 19-22) is much larger in the coastal form, but with overlap in the ranges of all four dimensions. The mean area of muscle attachment calculated as $\pi[(\text{ave. length} + \text{average width of fossa})/4]^2$ is 43.4 cm^2 in the coastal specimens, as opposed to 28.5 cm^2 in the offshore form, an increase of 50%. The cross-sectional area of the fossa proper through which the temporal muscle passes, calculated similarly using measurements 21 and 22, is 10.8 cm^2 in the coastal specimens as opposed to 7.4 cm^2 in the offshore specimens, an increase of 46%. This considerable disparity in size of the temporal fossa, and presumably in strength of jaw closure, influences the breadth of the skull across the processes enclosing the fossa, namely, the postorbital process and the zygomatic process. Consequently, the differences between the two groups in these widths (nos. 11 and 14) are relatively greater than in parietal width (no. 16), with less overlap.

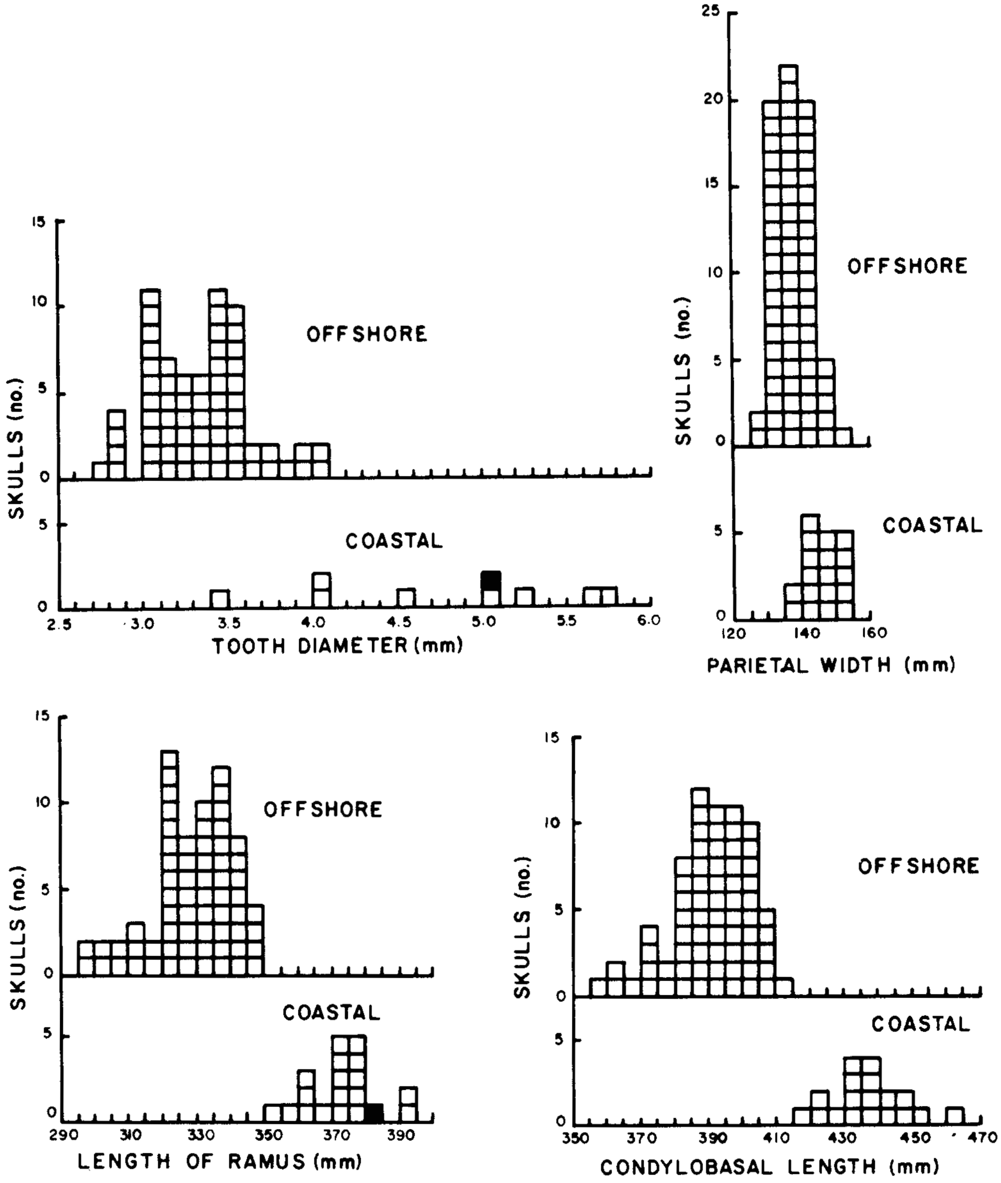


Figure 48. Comparisons of skull measurements of coastal and offshore series of spotted porpoise: (upper left) tooth diameter, (upper right) parietal width, (lower left) length of ramus, (lower right) condylobasal length. Blackened square represents type specimen of *Stenella graffmani* (Lönnberg).

The basihyal and thyrohyals (nos. 42-43) are less disparate between the groups than are the other elements of the feeding complex. This probably reflects their functions in breathing and/or sound producing as well as feeding. The stylohyals, known to function in the breathing and sound-producing apparatus as the origin of the stylopharyngeal muscle, are very similar in the two series. Width of the stylohyal (no. 46) is one of the four adequately sampled skull measurements (the others are projection of premaxillaries—no. 23, occipital overhang—no. 29, and deviation from symmetry—no. 41) for which the means for the two series are not significantly different at $\alpha = .05$.

The Hawaiian series differs most from the offshore series in the feeding apparatus. The Hawaiian animal has a longer, broader rostrum, both absolutely and proportionately, but tooth count and diameter are the same and the posttemporal fossa is on the average smaller, indicating a lesser development of the temporal muscle. Tooth diameter in 10 adult skulls ranges from 3.1 to 3.9 mm (average 3.35). This is entirely contained in the range of the offshore series and overlaps the coastal series by only one specimen.

Vision apparatus. The orbit (no. 25) is longer in the coastal form, but the differential is not as great as in condylobasal length and dimensions of elements of the feeding apparatus. The orbit is also longer in the Hawaiian form but not when taken as percentage of condylobasal length.

Hearing apparatus. The three ear bones available for the coastal series in both measurements (nos. 30 and 31) fall within the ranges for the offshore series. The ear bones of the Hawaiian series are larger absolutely but not larger relative to condylobasal length.

Breathing and sound-producing apparatus. Divergence in width of the premaxillary shield (no. 15) and width of the external and internal nares (nos. 13 and 27) is not as great as for most elements of the feeding apparatus. Most divergent is length of the preorbital process (no. 26), and least divergent are length and width of the stylohyals (nos. 46 and 47). There is overalp between the series in all aspects of this system, and complete correspondence in at least one measurement, width of the stylohyal.

Summary. The differences in skull measurements between the coastal and offshore series are greatest in the feeding apparatus (fig. 49) and can be summarized in an analog fashion in terms of the functional systems, using values of Student's *t* (fig. 50). Excluded are measurements that are extremely variable, including projection of premaxillaries (no. 23) and occipital overhang (no. 29); and those for which it would appear that size is not most influenced by the functional unit to which they belong or for which the functional relationship is unclear, including length of the mandibular fossa (no. 40) and pterygoid length (no. 28). This demonstrates that the difference between the coastal and offshore forms is not one of size alone but of proportion as well. The feeding apparatus is proportionately more disparate in the two groups than are the other functional systems. My interpretive hypothesis follows. The major selection pressure impinging on skull size and proportion has to do with feeding. A more robust feeding apparatus

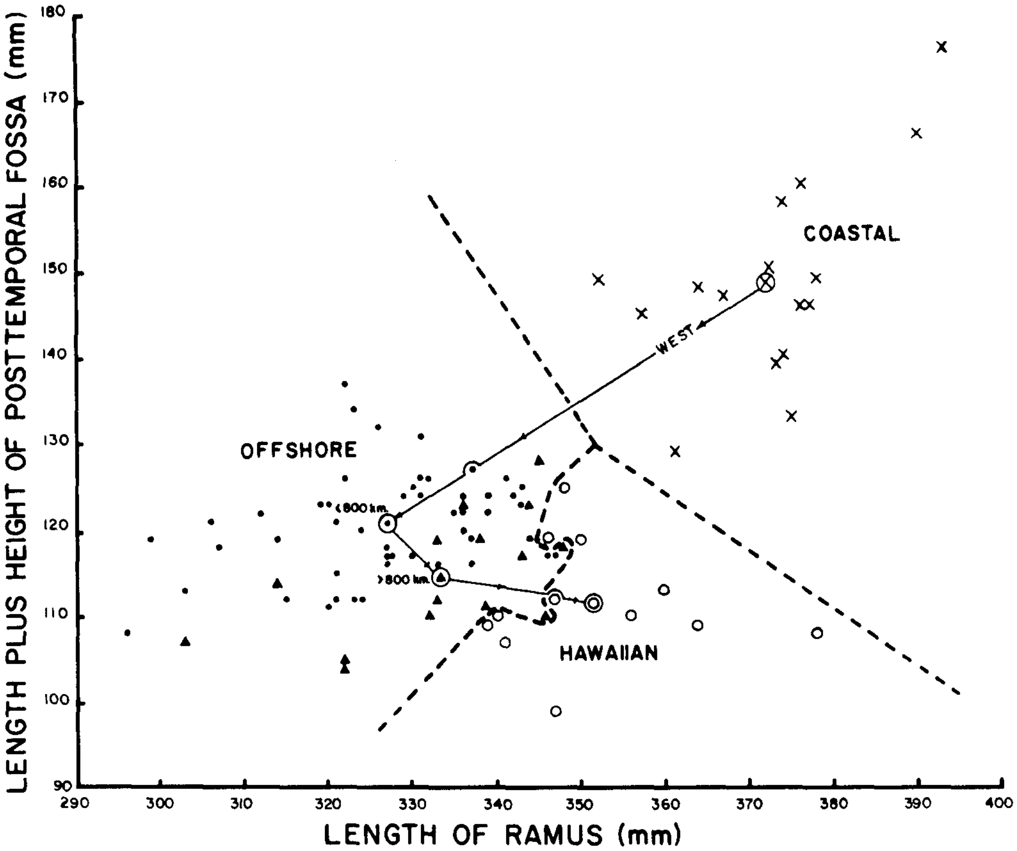


Figure 49. Geographical variation in the skull of the spotted porpoise in eastern Pacific and Hawaiian waters. Circled symbols are series means.

is advantageous along the coast where available prey, including demersal fishes, may be larger and more irregularly and heavily constructed than offshore. A smaller, more finely constructed feeding apparatus and greater maneuverability are favored in the pelagic habitat where the major diet items are small squid and small, streamlined, relatively defenseless but fast-moving fishes (exocoetids, myctophids, small scombrids, and others). The easiest route to a more robust or more lightly constructed feeding apparatus is along the independent general length and width axes that I defined and discussed above in the section on individual variation, with the emphasis on length. These axes also, to a lesser extent, influence the other systems, carrying them along behind the feeding apparatus. Homeostasis of nonfeeding elements of the skull probably operates through other selection vectors impinging on independent components of the variance associated with each system.

There is also geographical variation within the total offshore series, with the axis of variation oriented east and west. If the series be divided into those from within 800 km

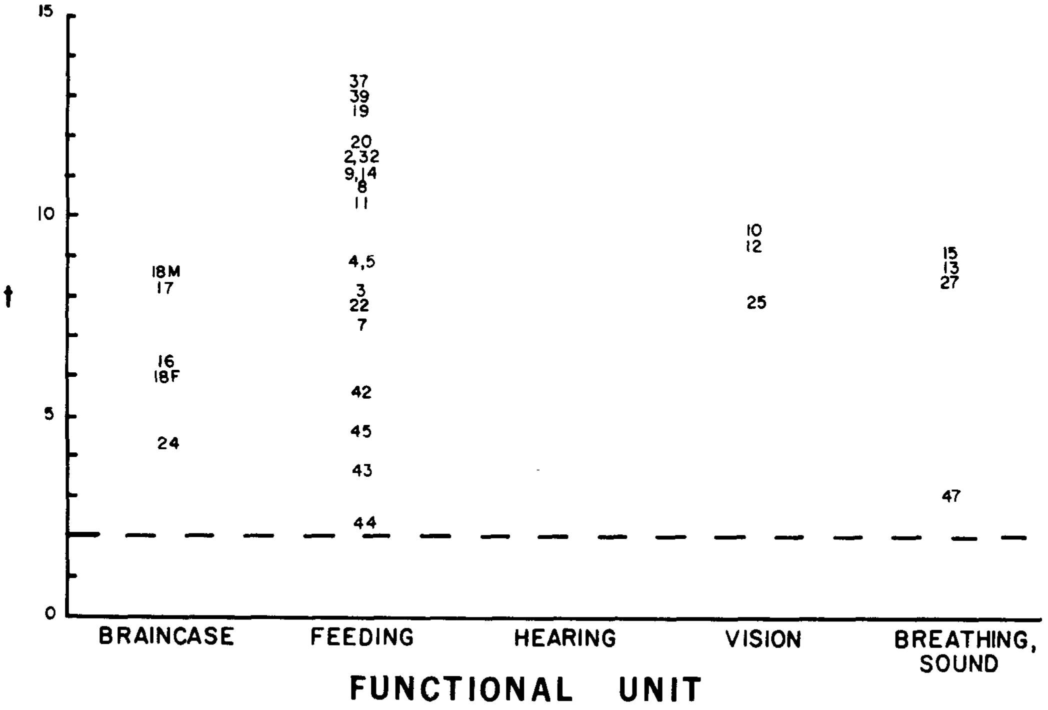


Figure 50. Comparative geographical variation of functional units of skull, in terms of Student's *t*, for coastal and offshore series of spotted porpoise. Measurements listed in table 2 and illustrated in figure 2. Compare with figure 40.

of the mainland (80 specimens) and those from more than 800 km from the mainland (25 specimens), the geographical trend becomes apparent. The 800 km limit falls roughly on a line extending from outside the Revilla Gigedo Islands to just inside Clipperton Island, and thence to Cocos Island. This also corresponds very roughly to the shoreward limit of distribution of the "whitebelly spinner" (see section below on *S. longirostris*). A similar division was used above in discussing trends in coloration and external morphometrics. For all the included skull measurements except length of the temporal fossa, the mean for the far offshore series is greater. The two series overlap in all measurements. The feeding, hearing, vision, and breathing and sound-producing apparatuses are all about equally divergent, but dimensions of the braincase are not affected, indicating a slight mean difference in skull proportions as well as size. An idea of the scope of the geographical variation within the offshore area relative to that between the coastal and offshore forms can be had by comparison of figure 51 with figure 50. The most divergent measurements among offshore specimens are widths, not lengths as in the coastal-offshore dichotomy.

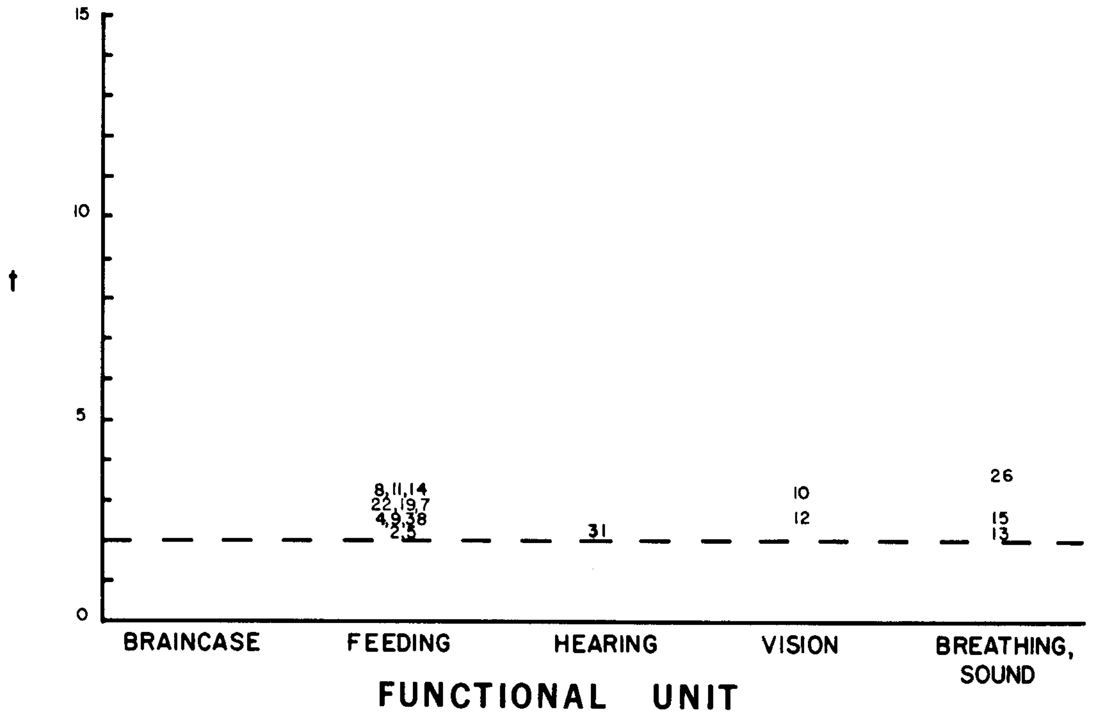


Figure 51. Comparative variation of functional units, of skull, in terms of Student's *t* between "offshore" and "far offshore" series of spotted porpoise.

The Hawaiian series continues the east-west trend within the offshore series and converges with the coastal series in condylobasal length and other measurements (fig. 49) reflecting length of the feeding apparatus. The offshore specimens from the westerly part of the range of the series are most Hawaiian like. Those to the east are both less Hawaiian like and sharply differentiated from the immediately adjacent coastal series. The dip in the curve yielded by connecting the four means left to right in figure 49 indicates that not only allometric growth is at work. The feeding apparatus does not simply become more robust proportionately as the skull becomes larger. Selection apparently impinges on a component of the variance in the feeding apparatus which is to some degree independent of a general size factor.

Postcranial skeleton

The series also differ in postcranial measurements. The sample is limited to physically mature specimens. The coastal series of mature skeletons is unfortunately very small, consisting of two from the Bay of Panama and the single specimen from Guaymas in the Gulf of California. As stated above, the difference in size between the coastal and offshore animals is most extreme at the northern and southern ends of the range, and these three skeletons in half the postcranial measurements are all larger than any of the 16 mature offshore skeletons measured (table 13).

The samples are somewhat larger for the meristic characters, including specimens of all ages, and here some disparity is also evident. Total number of vertebrae in the coastal series ranges from 77 to 79 (average 77.7) and in the offshore series from 77 to 83 (average 80.8). The two samples probably belong to different distributions (fig. 52). The offshore form has on the average a longer caudal series (no. 50). This is reflected also in the positions of the first vertical foramen (no. 62) and last transverse and neural processes (nos. 63 and 64). The three coastal specimens have forelimbs larger than those of the offshore specimens, but in the mesial three digits (nos. 115-117), hyperphalangy is greater in the offshore animals, a result that agrees well with the findings above for external length of the flipper.

The sample of mature skeletons from the far offshore region is too small to allow similar analysis of postcranial measurements, but variation is evident in the postcranial meristics. The specimens in the series from more than 800 km offshore tend to have fewer vertebrae (fig. 52) and different means for the positions of the first vertical foramen, last transverse process, last neural spine, and the first caudal vertebra bearing a vertical neural spine, which are all shifted posteriorly. When the far offshore specimens are subtracted from the distribution of vertebral number (fig. 49), the difference between the coastal form and the adjacent offshore form (including now only those within 800 km of the coast) becomes even more pronounced, with very little overlap. The animals from very far offshore, then, are more similar to the coastal form in skull size (except the temporal fossa) and vertebral meristics than are those from within 800 km. A reversal of this trend is indicated in the manus, in that hyperphalangy is the more developed in the far-offshore specimens in the offshore series (no. 115).

The sample sizes for postcranial measurements of the Hawaiian series are very small (only two physically mature specimens are available). Both specimens lie outside the range of the offshore series in width of the first thoracic vertebra, length of the longest rib, length of the first sternal rib, and length of the longest chevron. The larger of the two lies inside the range of the offshore series only in atlas width, length of the first thoracic neural spine, width of the first lumbar, width of the first vertebral rib, height of the scapula, widths of the humerus and radius, width of the first row of carpals, and lengths of the pelvics. These results indicate that the Hawaiian animal has a more massive skeleton with larger rib cage and broader flippers than does the offshore form, but examination of larger series is needed for confirmation. In meristics the Hawaiian ranges are all contained in the offshore ranges.

CLASSIFICATION AND DIAGNOSES

I conclude on the basis of the evidence presented above that the spotted porpoises in the eastern Pacific and in Hawaiian waters belong to a single species, with a possible gap in the distribution between the westernmost limits of the eastern Pacific populations and the Hawaiian population.

The relationships of the Hawaiian population with those in the southern and western Pacific and Indian Oceans badly need to be examined. True's (1889 and 1906) work remains the best on the group, and I therefore provisionally apply the name *Stenella attenuata* to the eastern Pacific and Hawaiian spotted porpoise, implying that a single species extends from the west coast of the Americas to at least the southern Atlantic and

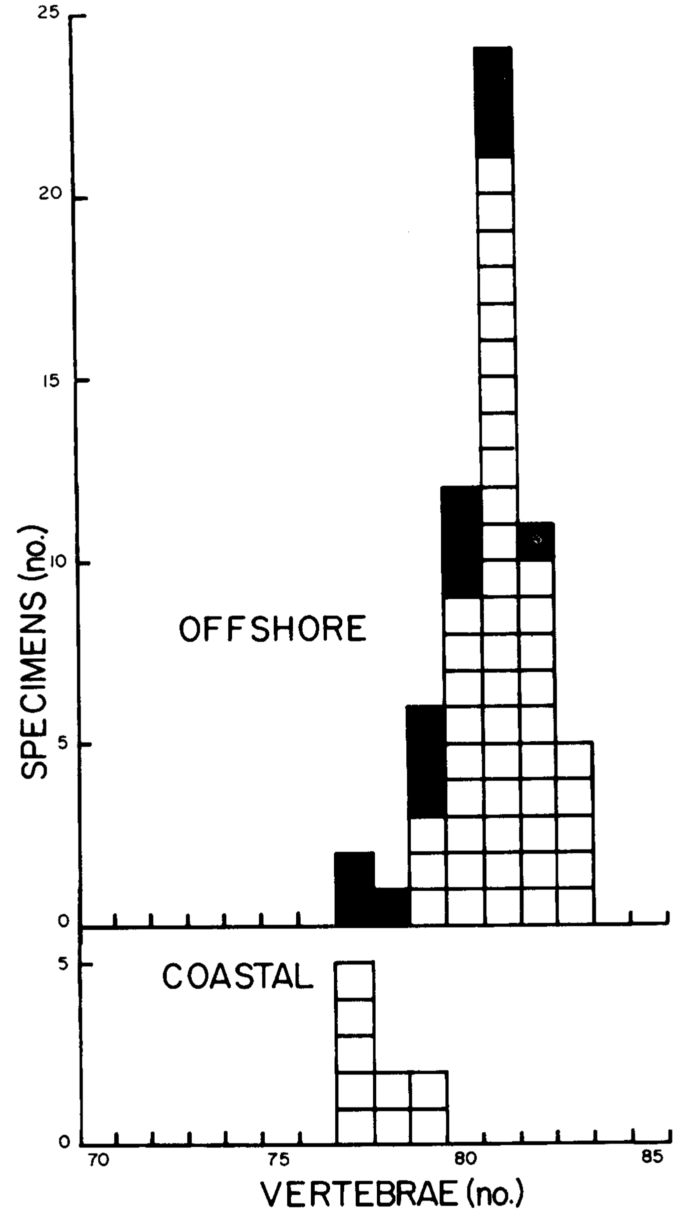


Figure 52. Comparison of vertebral counts of coastal and offshore porpoise. Shaded squares represent "far offshore" specimens.

that True was correct in referring Gray's (1846) type specimen to such a species. If and when series from the western and south Pacific, Indian, and southern Atlantic Oceans are compared to series of animals from the North Atlantic that have flipper-to-gape stripes, and as seems likely, found not to differ from them, then the name *S. frontalis* (G. Cuvier) shall apply. As discussed above, other earlier names are *dubia* G. Cuvier (revived by Rice and Scheffer, 1968), *pernettensis* Blainville (suppressed by van Bree, 1971*a*), *malayana* Lesson, and *velox* G. Cuvier, but these all seem destined for suppression because of inadequate descriptions and/or long-standing nonusage.

The series of coastal specimens examined here is discretely separable from the series of the offshore specimens in skeletal characters, but I provisionally relegate the coastal form to only subspecific status as *S. attenuata graffmani* for the following reasons: (1) The forms are allopatric and in contact, and the boundary between them has been determined in a rather arbitrary manner. In short, a cline may exist. (2) The series of coastal specimens is rather small (19 for cranial characters). It seems likely that examination of a larger series of coastal animals will reveal overlap in perhaps all of the characters in which there presently is separation. (3) Differences between the coastal and offshore series are most pronounced at the northern and southern extremes of the range, where there is apparent spatial separation of the forms (by Baja California in the north and a distributional hiatus in the south), suggesting that in the central reaches of the "boundary" there may be an inshore-offshore gene flow.

Whatever the future course of the taxonomy of the spotted porpoises may be, it seems likely that the coastal population will retain at least subspecific status, and that the name *graffmani* will apply to it. All of the holotypes of the other described species, except that of *S. plagiodon*, are outside the range (smaller) of the coastal form in several characters. As discussed above, the type of *S. plagiodon* almost certainly belongs to a different species, with a different basic color pattern.

The eastern Pacific offshore form deserves subspecific recognition relative to the populations to its east and west but cannot as yet be named. The type of *S. attenuata* falls well within the range of the offshore series in all skull measurements and proportions (measurements in True, 1889 and Fraser, 1950), but is from an unknown locality and of unknown external appearance. The same applies to the Hawaiian form (distributed within an unknown range to the west and south of Hawaii). I therefore provisionally refer to the two populations as *S. attenuata* subspecies A and B, respectively, either of which may or may not eventually prove to be *S. a. attenuata.*

A commonly used criterion of subspecific level difference between populations is whether or not 90% of the specimens can be unequivocally assigned to the proper group on morphological grounds (Mayr,1970). While such is obviously the case for the coastal versus the offshore and Hawaiian series of skeletal specimens (fig. 49), the situation is less clear cut for the offshore versus the Hawaiian series. Much better definition can be attained through the use of discriminant analysis. Using a stepwise discriminant analysis program (see Methods), discriminant functions were calculated by analysis of 25 measurements for 76 adult skulls (11 coastal, 53 offshore, and 12 Hawaiian). The computer program used does not provide for missing observations. Therefore, both to maximize the small coastal and Hawaiian samples and to maximize the number of measurements included, some measurements were deleted from the original list, and some damaged offshore skulls were not included in the analysis. Using the loading coefficients for the two discriminant functions (table 14), the 76 specimens and the group means were plotted on the discriminant axes (fig. 53). With this procedure, and using the criterion of nearest group mean, all 76 specimens can be correctly classified.

The possibility exists, of course, that the observed differences between the geographical series are manifestations of phenotypic responses to local environmental factors. It seems more likely, however, that the differences are genetic, and I chose this alternative as the basis for the following diagnoses.

Diagnoses of Subspecies of Spotted Porpoise, *Stenella attenuata* (Gray, 1846), of the Eastern Pacific and Hawaii

A. Eastern Pacific Coastal Spotted Porpoise, *Stenella attenuata graffmani* (Lönnberg, 1934).

Coloration. As described by Perrin (1970*b*), with dorsal spotting sparse to heavy (criteria defined in table 3), but medium to heavy in most specimens.

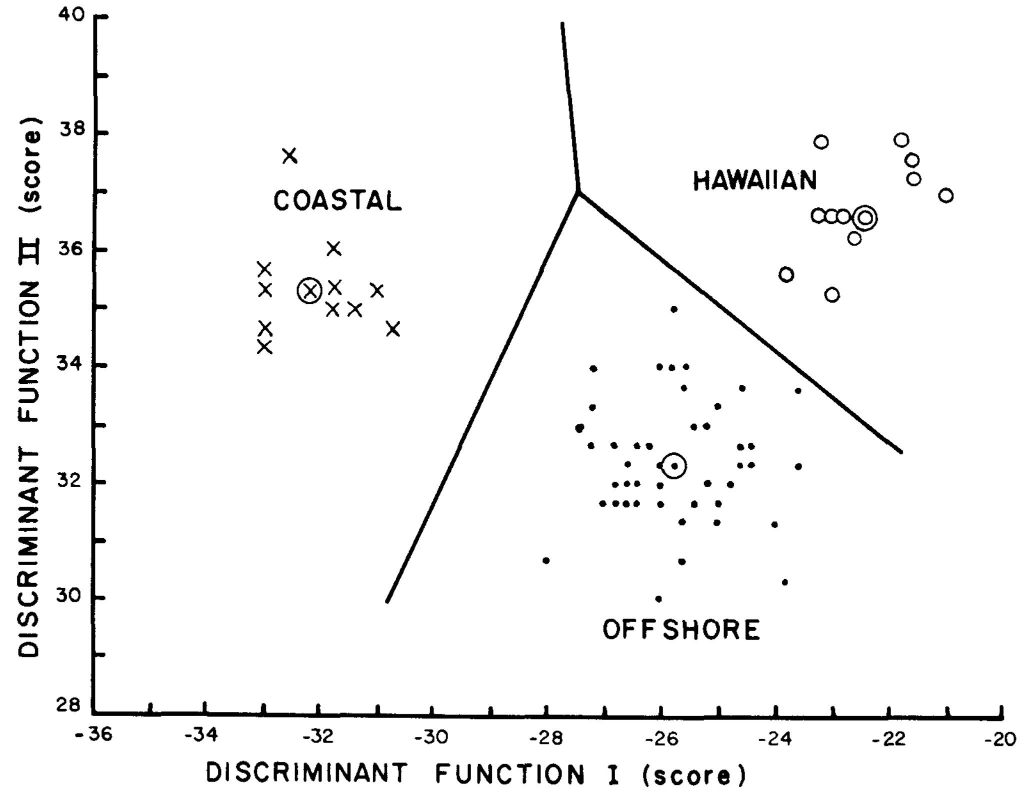


Figure 53. Geographical series of skeletal specimens of spotted porpoise plotted on discriminant functions based on 25 measurements. Circled symbols are series means.

Table 14. Loading coefficients for discriminant functions separating Coastal, Offshore, and Hawaiian series of crania of spotted porpoise. Measurement numbers refer to figure 2

Number	Measurement	Discriminant function I	Discriminant function II
1	Condylobasal length	-.04744	.00935
2	Length of rostrum	.18259	.14149
3	Width of rostrum at base	-.05059	.04348
4	Width of rostrum at 60 mm	.04468	.16630
5	Width of rostrum at midlength	-.27824	.13520
6	Width of premaxillaries at midlength of rostrum	.19415	-.01358
7	Width of rostrum at 3/4 length	.39112	-.19823
8	Tip of rostrum to external nares	-.12195	-.09233
9	Tip of rostrum to internal nares	.04816	-.01027
10	Preorbital width	.16880	.14772
11	Postorbital width	-.07486	-.07671
12	Least supraorbital width	-.06304	-.03383
13	Width of external nares	-.29585	-.07682
14	Zygomatic width	.02190	-.00923
15	Greatest width of premaxillaries	.06746	.16174
16	Parietal width	.16437	.03966
17	Height of braincase	-.13052	-.02017
18	Length of braincase	-.13047	-.02573
19	Length of posttemporal fossa	-.11854	-.03263
20	Width of posttemporal fossa	-.25754	-.03507
25	Length of orbit	.06786	.10140
27	Width of internal nares	.03393	-.05702
32	Length of upper toothrow	-.07245	-.02817
38	Length of ramus	-.03438	.03825
39	Height of ramus	-.10580	-.06551

External size and shape. Adults 2.0-2.6 m long; distance from tip of upper jaw to anterior end of flipper insertion (taken parallel to body axis) 41-44 cm (20-22% of body length), to center of eye 28-33 cm (13-17%).

Skeleton. Condylobasal length 419-460 mm; rostrum length 249-275 mm (168-196% parietal width); rostrum width at 60 mm, 56-77 mm (38-53% parietal width); ramus length 352-393 mm (242-270% parietal width); posttemporal fossa length 73-97 mm (51-65% parietal width); posttemporal fossa width 55-79 mm (37-53% parietal width); preorbital width 153-178 mm (105-124% parietal width); tooth diameter (transverse diameter at alveolus of tooth at midlength of maxillary row) 3.5-6.0 mm; total number of vertebrae 77-79; first perforating vertical foramen on vertebra no. 53-57; phalangeal formula for digits II-V: 6-7, 4-5, 1-2.

Range. Occurs within about 20-25 km of the shore on the open coast, and in gulfs and embayments, from Guaymas, Sonora, Mexico (Gulf of California) to Gorgona Island, Colombia, usually in small groups or schools or fewer than 100 individuals.

The type specimen of *S. graffmani* (Lönnberg, 1934) and the second specimen described by Lönnberg (1938) from the type locality, Acapulco, are of this subspecies; as are also the specimens reported on by Van Gelder (1960), Bowman (1958), Hall and Kelson (1959), Hershkovitz (1966), Neiland, Rice, and Holden (1970), and Miller and Kellog (1955). None examined from the tuna fishery are of this subspecies, although logbook records of net sets close to shore may indicate minor involvement. This form is called by tuna fishermen "humpback spotter" or "bull spotter" and is reputed not often to be associated with schools of tuna.

B. Eastern Pacific Offshore Spotted Porpoise, *Stenella attenuata* subspecies A (unnamed?).

Coloration. As described by Perrin (1970*a*), with dorsal spotting sparse to heavy (most specimens from more than 800 km offshore are sparsely spotted).

External size and shape. Adults 1.7-2.3 m long, tip of upper jaw to flipper insertion 38-42 cm (17-23% of body length), to center of eye 25-31 cm (13-17%).

Skeleton. Condylobasal length 356-411 mm; rostrum length 210-249 mm (149-186% parietal width); rostrum width at 60 mm, 46-63 mm (34-46% parietal width); ramus length 296-347 mm (213-261% parietal width); posttemporal fossa length 56-77 mm (41-55% parietal width); posttemporal fossa width 46-63 mm (33-44% parietal width); preorbital width 134-163 mm (98-118% parietal width); tooth diameter 2.7-4.1 mm; total number of vertebrae 77-83 (only the specimens from more than 800 km offshore have been found to have 77-78 vertebrae); first vertical foramen on vertebra no. 52-61; phalangeal formula for digits II-IV: 7-9, 4-6, 2-3.

Range. Occurs from about 25 km offshore on the open coast from Cabo San Lucas, Baja California del Sur, Mexico, to Colombia, west to at least 145°W longitude in tropical waters. May occur seasonally as far north as Bahia Sebastian Vizcaino. Occurs in schools of from a few individuals to several thousand.

This form is heavily involved in the tropical tuna seine fishery (Perrin, 1970a). Specimens belonging to this subspecies include those referred to *Stenella fraffmani* in Boice, Swift, and Roberts (1964), Dailey and Brownell (1972), Dailey and Perrin (1973), Daugherty (1966), Evans and Prescott (1962), Fitch and Brownell (1968), Green, Perrin and Petrich (1971), Harrison (1969a and b), Harrison, Boice, and Brownell (1969a and b), Harrison, Johnson and Tedder (1967), Mitchell (1970), Nishiwaki (1966, 1967), Perrin (1968, 1969, 1970a, 1970b), Perrin and Hunter (1972), Perrin and Orange (1971), Perrin and Roberts (1972), and Pilson and Waller (1970).

Of the three subspecies defined here, only this one brackets the holotype of *S. attenuata* (Gray 1846)–from unknown locality–in all skull measurements and proportions. The holotype in condylobasal length falls within the range of only this subspecies (when larger series of the coastal and Hawaiian forms become available, this situation may no longer obtain).

C. Hawaiian Spotted Porpoise, *Stenella attenuata* subspecies B (unnamed?).

Coloration. Ground pattern (everything except spots) as described by Perrin (1970*a*). In contrast with the eastern Pacific subspecies (described above), the cape is darker and lateral field lighter, yielding a more pronounced contrast. Only subadults are noticeably spotted (ventrally); dorsal spots are absent or sparse, and in the adult the ventral mottling present in eastern Pacific subspecies is so faint as to be hardly noticeable.

External size and shape. Adults 1.8-2.1 m, tip of upper jaw to flipper insertion 37-42 cm (19-24% body length), to center of eye 29-33 cm (14-18% body length).

Skeleton. Condylobasal length 395-440 mm; rostrum length 240-269 mm (163-194% parietal width); rostrum width at 60 mm, 58-66 mm (40-48% parietal width); ramus length 339-379 mm (233-257% parietal width); posttemporal fossa length 57-70 mm (41-48% parietal width); posttemporal fossa width 42-56 mm (30-38% parietal width); preorbital width 149-164 mm (104-118% parietal width); tooth diameter 3.1-3.9 mm; total number of vertebrae 79 (two specimens examined); first vertical foramen on vertebra no. 54-56 (four specimens); digits II-IV: 8, 6, 3 (two specimens).

Range. Occurs in Hawaiian waters to an unknown distance offshore. Has been observed between the islands and at Penquin Bank off Molokai (personal communication, K.S. Norris).

Relationships between this form and the dorsally more spotted form(s) in the southern and western Pacific have not been investigated. Porpoise from Hawaiin waters referred in the literature to *S. attenuata* are of this subspecies.

Specimens from unknown localities in the eastern Pacific may also be classified by application of the discriminant functions in table 14 and comparison of the scores with the scatterplot in figure 53.

Summary of Differences between the Subspecies

Differences between the subspecies can be summarized in qualitative terms. The coastal form is on the average larger and more spotted than the offshore and Hawaiian forms. The Hawaiin form is less spotted and has a proportionately larger head than the offshore form. The coastal form has the fewest vertebrae, the offshore form has the most. The skull of the coastal form is large and massive, that of the offshore form is small and more lightly built, and that of the Hawaiin form is large and lightly built. The coastal form is largely neritic, the offshore form inhabits the high seas, and the Hawaiian form frequents the oceanic Hawaiian Islands.

SPINNER PORPOISE

The spinner porpoise is the second most important delphinid involved in the tuna fishery, after the spotted porpoise. Knowledge about the spinner porpoise in the eastern tropical Pacific was also very scanty before the United States government began to investigate their biology because of their involvement in the tuna fishery. Only three records of spinner porpoise in the eastern Pacific were published before these studies began in 1967. Nelson (1889) reported sighting schools of long-snouted animals near the Tres Marias Islands and referred them to *Prodelphinus* [= *Stenella*] *longirostris* (Gray 1828). He collected a specimen that was later referred to *S. microps* (Gray 1846) by Miller and Kellogg (1955). True (1889) reported on a specimen collected from the research vessel *Albatross*, "in the Pacific Ocean, between the Galápagos Islands and Panamá." Beddard (1900) included the Gálapagos Islands in the range of *Prodelphinus longirostris* but did not specify the basis for so doing. It seems likely that the Galápagos were included on the basis of True's record from "between Panamá and the Galápagos" [not "halfway between the Isthmus of Panamá and the Galápagos" (translation: Cabrera and Yepes, 1940) or "near the Galápagos Islands" (Roberts, 1951)]. There is, then, no evidence that spinners occur near the Galápagos. True's record probably also forms the basis for inclusion of *S. longirostris* in other faunal lists for the west coast of South America, such as Mann's (1957). Hershkovitz listed *S. longirostris* from Chile (Cape Horn) according to Beddard (1900), but Beddard did not include Chile in the range. The southernmost published record, therefore, is some point "between Panamá and the Galápagos Islands," and there is certainly no basis whatsoever for Marcuzzi and Pilleri's (1971) mapping of the range of *S. longirostris* as extending from Cabo San Lucas to Cape Horn.

The third early published record for the eastern tropical Pacific of spinners was by Hester, Hunter, and Whitney (1963), who referred them to *S. microps* (Gray 1846). The identification was made by C.O. Handley, Jr., and was based on specimens from off Guatemala.

The area of the yellowfin tuna fishing grounds involving spinners (fig. 54) corresponds very closely to that for the spotted porpoise (fig. 3), with a slightly lesser extension to north and south. The majority of net sets in the IATTC data were made on mixed "schools" of spotted and spinner porpoise.

The distribution of more reliable records (fig. 55) also conforms closely to that for the spotted porpoise (fig. 4). Again there is the apparent gap between the westernmost limits of the range of the eastern Pacific forms and Hawaiian waters where spinners, referred variously to *Stenella longirostris* (Gray) and to *S. roseiventris* (Wagner), occur (Perrin, 1972).

HISTORICAL REVIEW

Atlantic Ocean

Pernetty (1769) was the first to record observations of a spinner porpoise, as well as of a spotted porpoise. The animals, seen six days after passing Boa Vista in the Cape Verde Islands (6°43 N, 25°17 W, fide Fraser, 1950) "leaped at least three or four feet

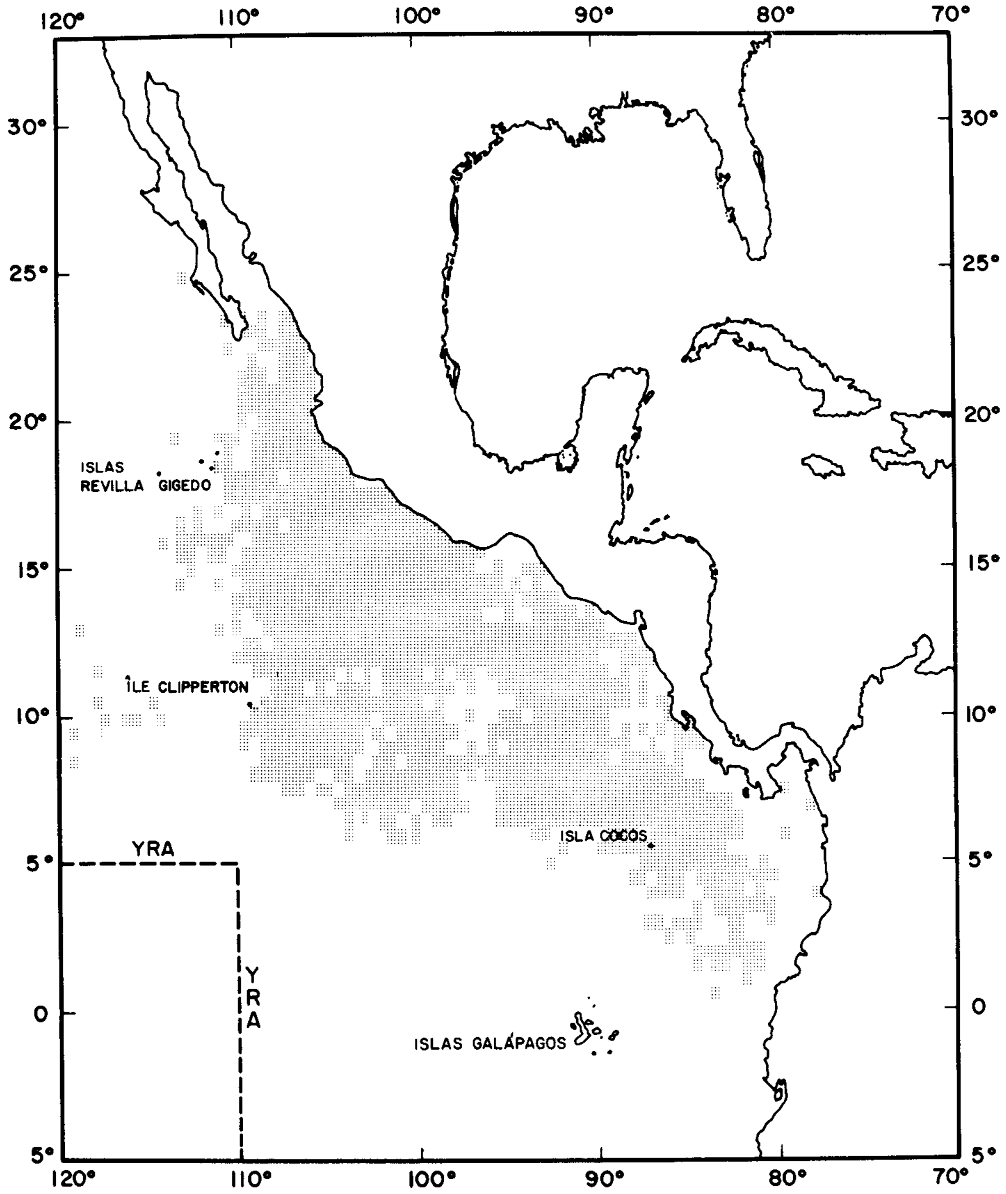


Figure 54. Distribution of purse seine net sets on spinner porpoise in the Commission Yellowfin (tuna) Regulatory Area, 1963-1970, by 1/2-degree squares. From tuna boat logbook data provided by the Inter-American Tropical Tuna Commission.

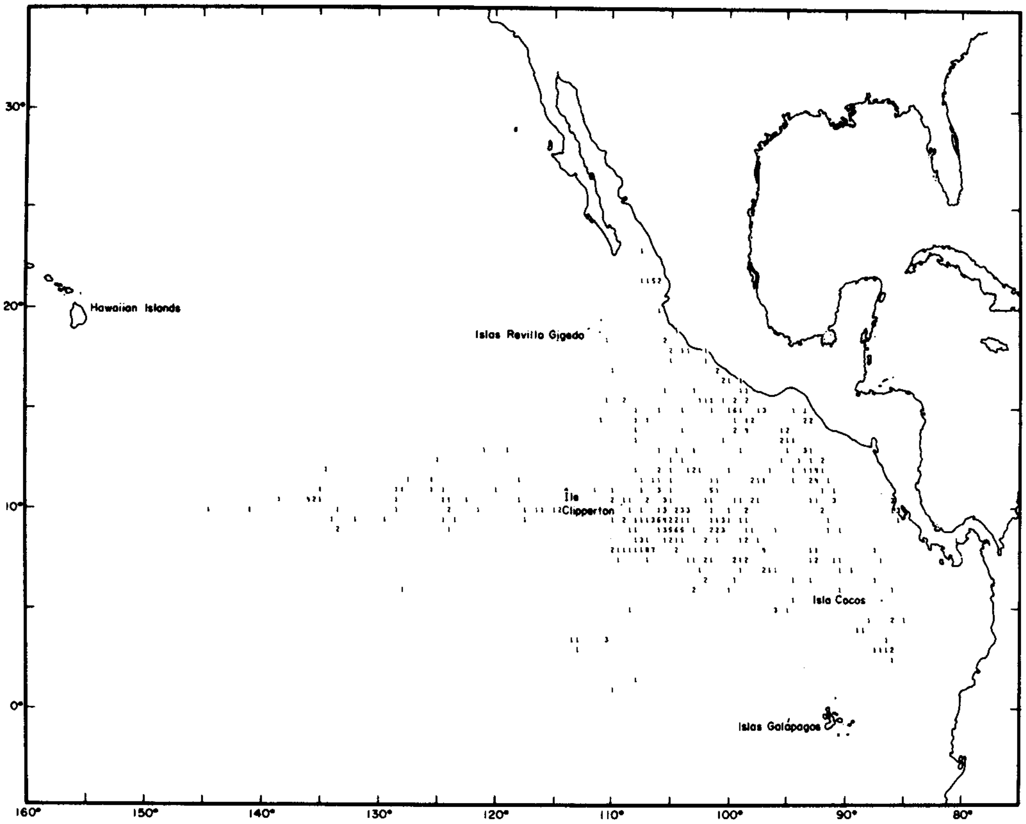


Figure 55. Distribution of records of spinner porpoise in the eastern tropical Pacific including collection localities of museum specimens, sightings from research vessels, and sightings by scientists aboard commercial fishing vessels. Numbers represent records per 1/2-degree square.

high and turned round not less than three times in the air, as if they had been on'a spit" (from 1773 translation). This spinning behavior has been well described by Hester, Hunter, and Whitney (1963) and is exhibited in the wild only by "spinners" (*Stenella longirostris* sensu Hershkovitz, 1966), around the world (Tomich, 1969; Caldwell et al., 1971).

The taxonomy of the spinners is very confused, because all the holotypes involved are from unknown localities (save one, that of *Delphinus roseiventris*, from Malaysia), and because of much confusion by early workers of spinners with long-snouted species of *Delphinus*.

The skull of the spinner porpoise of the eastern Pacific (described below in section on variation), and of spinners from other parts of the world, has a long, attenuate rostrum (approximately four times as long as broad at the base), from 45 to 61 teeth in each row, very shallow palatal grooves, and very small posttemporal fossae (29-47 mm high; 7.2-11.8% CB length). These criteria are used below as background aids.

Gray in 1828 described *Delphinus longirostris,* on the basis of a skull of unknown provenance in the private museum of D. Brookes, as having "*Osse palatino carinato, postice convexo; rostro longissimo attenuato, supra depresso, lineâ mediâ elevatâ; dentibus parvis utrinque* $\frac{48-50}{48-50}$." He clearly differentiated it from *D. delphis* in having the "palate bone more strongly keeled." The specimen was not figured. In the same paper he described *D. capensis,* apparently from a stuffed or preserved whole animal from the Cape of Good Hope. The description includes no skeletal characters except a tooth count of "circiter $\frac{50}{50}$" and consists entirely of measurements and color notes obviously taken from a whole specimen. Although he stated that "this dolphin is at once distinguished by the shortness of his beak," he obviously meant "length," as the measurements and a figure of external appearance clearly indicate that a long-snouted animal is involved.

The Brookes collection was broken up in 1828 and in part purchased by the Leiden Museum. Schlegel (1841) described and figured under *Delphinus longirostris* a skull he said was used by Gray as the basis for *D. longirostris.* According to Flower (1884) the specimen was one of two purchased by the Leiden Museum and was listed in the original list of items purchased as "*Phocaena longirostris.*" The skull is evidently of a spinner, judging from the relatively flat palate, small cranium, long attenuate snout, very small posttemporal fossae, and high tooth count (55). This skull has been reexamined by many subsequent workers (Flower, 1883, and van Bree, 1971*b*, among others) and definitely does not have a palate "more strongly keeled" than that of *D. delphis* but, as noted by Schlegel himself (1841), it lacks palatal grooves. Schlegel (in Temminck and Schlegel, 1844) stated that the proper tooth count for the skull was 55, and that Gray had counted only 48-50 on each side because the anterior end of the cranium was mutilated and some teeth were missing. Gray was very explicit, however, about the carinated palate of *D. longirostris,* including it in the Latin description; one must conclude that the specimen sold to the Leiden Museum may not have been the type specimen used by Gray, but rather one belonging to a different species.

The Leiden Museum possessed several crania from the Cape of Good Hope "*absolument sembable à celui de la collection de Brookes*" (Temminck and Schlegel, 1844), and Schlegel for this reason synonymized Gray's *D. capensis* (described from external characters only) with *D. longirostris.* He did this in spite of the strong conflict between the description of *D. longirostris* and the nature of the purchased skull from the Brookes Museum. He also stated that the *D. longirostris* of Dussumier (in G. Cuvier, 1829) was also the same species. He referred a specimen from Japan to Gray's *D. longirostris* as well. Only a painting was collected of this specimen, and it obviously belonged to a species of *Delphinus* (sensu stricto) as noted by Takemura, Yoshida, and Mizue (1967).

The only thing clear emerging from this muddle in terms of original taxonomy is that *D. longirostris* Gray was described from a skull with strongly carinated palate and that the type specimen has probably been lost, the opinions of Schlegel and Flower notwithstanding. It must be noted that Gray in his subsequent works on Cetacea (1846, 1850, 1866*a*, 1866*c*, 1868*b*) retained *D. longirostris* Gray ("The Cape Dolphin") as a long-snouted species with deeply grooved palate and embraced the synonymy that Schlegel erected probably correctly but for the wrong reason. He did not include in the same section of *Delphinus* the species (*D. microps, stenorhynchus,* and *alope*) based on skulls from unknown localities and found by later workers to be similar to the Leiden specimen

(Flower, 1883) and from spinners, but placed them in a separate section *Clymene* (Gray, 1866*c*) with "Palate flat behind." It is evident that he assumed that Schlegel was correct in thinking that the Leiden Museum possessed the type of his *D. longirostris* and did not know that the specimen in question had a flat palate rather than a deeply grooved one.

The question of the fate of the holotype of *D. longirostris* Gray, 1828 will never be resolved satisfactorily. In view of this, it would seem best to designate the Leiden specimen as a lectotype of *D. longirostris* of Schlegel, 1841, and take Schlegel's figure and description as the earliest ascertainable starting point of the taxonomy of the spinners. This is the usage of Lütken (1889). It is also my usage here. As this strategy by implication resurrects *D. longirostris* Gray, 1828 as a species of *Delphinus* (sensu stricto), the trivial name *longirostris* may technically become unavailable for the spinners, and the next name applied to the species dealt with by Schlegel would have priority. Whether this would be *microps,* Gray, 1846, *alope* Gray, 1846, or *roseiventris* Wagner, 1846, would depend on the outcome of comparison of the holotypes with each other and with adequate series from around the world. Hershkovitz listed only one species of spinner, *S. longirostris* (Gray) including all the above names, but, aside from the problem discussed above, as van Bree (1971*b*) noted, this probably correct synonymy should be held in abeyance until the group is better known. The skeletons, color patterns, and external proportions of spinners from many parts of the world have not yet been adequately described. Another possible approach would be to conserve the long used name *longirostris* for the spinners, as *longirostris* Schlegel,1841, and suppress *longirostris* Gray, 1828 because of its uncertain status. Formal nomenclatural moves such as these must await more definitive knowledge of the spinners. The usage here is strictly provisional.

Gray (1850, 1866*a*) referred specimens from the "Coast of Brazils" and "near mouth of Rio de La Plata" to *D. microps.* He then (1866*c*) placed *microps, alope,* and *stenorhynchus* in *Clymene,* and subsequently (1868*a*) emended *Clymene* to *Clymenia,* giving the habitat of *C. alope* as Cape Horn.

Van Beneden and Gervais (1868-1880) placed *Clymenia* in their new genus *Prodelphinus.* Flower (1884), in line with his above-discussed views, placed *Clymenia stenorhyncha, microps,* and *alope* in a "section" (synonymy of ?) under *C. longirostris* (Gray). Later (1885), Flower recognized *Prodelphinus alope, microps,* and *longirostris,* but placed *D. stenorhynchus* in the synonymy of *P. longirostris.*

Lütken (1889) mistakenly referred specimens to *P. alope;* these were spotted porpoise.

True (1889) agreed with Flower's earlier (1884) conclusions regarding the synonymy of *P. longirostris* (Gray).

One hundred eighty-four years elapsed between publication of Pernetty's (1769) observations of what were probably spinners off West Africa and the first publication of a firm record of an Atlantic spinner. Moore (1953) referred to *Stenella longirostris* (Gray) a specimen harpooned in 1930 from a school "of several thousand" about 45 miles off Miami Beach, Florida. In recent years several additional records of spinners in the Atlantic have appeared.

Cadenat and Doutre (1958) reported on a specimen ("un *Prodelphinus*? indéterminé") from off Senegal that probably was a spinner, judging from the published photograph (triangular dorsal fin, thin light line from eye to posterior insertion of flipper, high cape with greatest development behind the dorsal fin). Unfortunately, the specimen was not saved. The tooth counts $\left(\frac{37}{42}\middle|\frac{39}{42}\right)$ are low for a spinner but were taken on the fresh specimen, and anterior teeth may have been embedded in the gums. The same authors later (1959) referred tentatively to *Prodelphinus longirostris* (Gray) four spinners from off Senegal (14°35'N, 17°48'W) that in coloration and body form were very similar to the eastern Pacific spinners. The skull of one of these specimens was figured by van Bree (1971*b*).

A large herd of spinners was stranded on a small island a few miles off the coast of Florida in the Gulf of Mexico in 1961. Layne (1965) compared the skull of one directly with the type of *S. longirostris* (Gray) and concluded that they were of the same species. These animals in shape and coloration were more like the Hawaiian spinner than the eastern Pacific or eastern Atlantic (as illustrated by Cadenat and Doutre) spinners. Caldwell et al. (1971) recorded occurrence of a "long-snouted or spinner dolphin belonging to the '*longirostris-roseiventris*' group of *Stenella*" from Saint Vincent in the Lesser Antilles and published a photograph of an animal that also strongly resembles the Hawaiian spinner in coloration, even to the dip in the ventral margin of the cape over the eye (see Perrin, 1972). Van Halewijn and van Bree (1972) reported a skull from Venezuela that they referred to *S. longirostris.*

The other, earlier records from the Atlantic, as of *D. microps* from "the coast of Brazil" by Gray, 1850, and from Rio de La Plata by Gray, 1866*a*, must be regarded as questionable, because of imprecise locality in the first instance and lack of substantiation by a specimen in the second.

Indian and Pacific Oceans

Dussumier painted watercolor sketches of several animals captured by him in 1828 and 1829. These excellent sketches remained unpublished until very recently (Arvy, 1972). Two of the specimens appear to have been spinners. One, a male, was captured on May 2, 1829 at 6°S and 85°E (about 600 miles southeast of Sri Lanka). The other, "female dolphin, no. 6," was caught "a few leagues to the east of the Maldive Islands, 73°E, on July 31, 1829." Specimens from Sri Lanka have been referred to *Stenella alope* (Gray) by Ellerman and Morrison-Scott (1951).

To the east, Hombron and Jacquinot in their atlas (1842-1853) of specimens collected during the voyage of the *Astrolabe* and *Zélée* illustrated the external appearance and skull (of the same individual?) of an animal they called "dauphin à ventre rose" from "la Mer des Molugues" (Jacquinot and Pucheran, in Hombron and Jacquinot, 1853). The color pattern shown is very similar to that of the adult Hawaiian spinner (Perrin, 1972), but the small size (1.18 m) indicates that the specimen may have been a calf. Wiegmann (in von Schreber and Wagner, 1846) published a figure (with no text) based on the plate of Hombron and Jacquinot and attached the name *Delphinus roseiventris.* Jacquinot and Pucheran (Hombron and Jacquinot, 1853) published an account of the specimen, with external measurements, and acknowledged Wagner as the author of the species. Van Beneden and Gervais (1880) placed the species in their new genus *Prodelphinus* and illustrated the skull of the holotype (?)–the skull figured by Jacquinot and Pucheran in the Paris Museum. Flower (1884) stated (that the Paris skull) "except in its smaller size, closely resembles the original *longirostris* of Gray. It is certainly the same as *microps*

[Gray, 1846]." Lütken (1889) placed the species in the synonymy of *Prodelphinus longirostris* (Schlegel). True (1889) disagreed with this view, preferring to "leave [*Delphinus roseiventris*] in the genus to which it was originally assigned, as distinct from *longirostris, microps, alope,* and *stenorhynchus*" which he considered to belong to a single species in *Prodelphinus.* Iredale and Troughton (1934) erected the new genus *Frettidelphis* for *D. roseiventris* Wagner, a dubious contribution that has generally been ignored. Rice and Scheffer (1968) tentatively recognized two species of spinners, "*Stenella longirostris* Gray, 1828 [sic] and *Stenella roseiventris* Wagner, 1853 [sic]." They stated that the "two forms differ markedly in body form and color pattern," but in point of fact the external appearance of spinners of the population from which the holytype of *S. longirostris* came can only be guessed at, since the type was a skull from an unknown locality. Of the holotypes, only that of *roseiventris* is of known external appearance, which is of little use because the specimen may have been a calf. Coloration changes during development (Perrin, 1972). Specimens have been referred to *longirostris* and *roseiventris* on a rather willy-nilly basis (see below), and there exists in the literature no valid justification for separating the species on the basis of coloration. As with the spotted porpoises, the definitive taxonomic and nomenclatural decisions must be based on large series of specimens from precisely known localities, with correlated data on external appearance and proportions.

According to True (1889), the specimen of *P. longirostris* described by Lütken (1889) was "from Australia," and very recently a specimen was collected in Queensland (G. Heinsohn, personal communication).

Spinners occur in Japanese waters. Aoki (1913) listed *Prodelphinus longirostris* (Gray) from Japan ("Madara iruka"), but was referring to the record published by Temminck and Schlegel (1844), which was of a species of *Delphinus* (sensu stricto). Ogawa (1932) referred a specimen to *Delphinus roseiventris,* but the accompanying photograph shows what appears to have been a young spotted porpoise. The first real record of a spinner from Japan was that of Ogawa (1936) of a specimen from Nagasaki that he referred to *Prodelphinus longirostris* (Gray). The clear photographs of the head show an animal with visible color pattern like that of the Hawaiian spinner and the spinner of the western Pacific, Caribbean, and Gulf of Mexico, but unlike that of the spinners of the far eastern Pacific (see Perrin, 1972). Kuroda (1952, fide Nishiwaki, 1972) described a subspecies *Stenella longirostris kunitomoi* based on a specimen collected off Nagasaki. He stated (fide Nishiwaki) "that this subspecies differs from the holotype [of *S. longirostris*] by lacking fine spots." This argument is specious for the reasons discussed above re the statement of Rice and Scheffer (1968). Mizue, Yoshida, and Sonoda (1964) reported on four specimens from near Goto [Island] in Nagasaki [Prefecture]. According to them, the Japanese name of this animal is "*Hashinaga iruka*," as opposed to "*Madara iruka*" (spotted porpoise) and "*Ma iruka*" (*Delphinus* sp.). They disagreed with Ogawa's choice of *Prodelphinus longirostris,* concluding that the skulls and vertebral counts were sufficiently different to justify considering them to belong to an undescribed species. Van Bree (1971*b*) disagreed, tentatively referring the specimens to *S. longirostris* (Gray, 1828). The color pattern as illustrated again is in every respect like that of the Hawaiian and Atlantic spinners, as is the shape of the dorsal fin.

The Hawaiian spinner has been variously identified: as *Stenella roseiventris* (Wagner) by Fraser, according to Morris and Mowbray, 1966; as *Stenella* cf. *roseiventris* (Wagner) by Brown, Caldwell, and Caldwell, 1966; and as *Stenella longirostris* by Nishiwaki, 1967, and by Tomich, 1969.

I have discussed above the distribution and taxonomic history of spinners in the eastern Pacific, where they have been referred variously to *S. microps* (Gray 1846) and *S. longirostris* (Gray 1828).

There exist, then, populations of spinners in tropical waters of the eastern Pacific, Hawaii, western Pacific, Indian Ocean, eastern Atlantic, and western Atlantic, with an unknown degree of continuity between them. The several holotypes are all from unknown localities, except that of the juvenile *roseiventris* from Malaysia, and were of unknown adult coloration and external proportions.

VARIATION

Coloration

I have previously described development and variation of the color patterns of the eastern Pacific and Hawaiian spinner porpoise (Perrin, 1972). Ontogenetic change is less drastic than in the spotted porpoise, which begin life unspotted, but geographical variation is much more pronounced (fig. 26 in Perrin, 1972). The patterns can be analyzed in terms of discrete component systems, and most geographical variation appears to be in a "dorsal field system" overlying a basic general pattern. The overlay is darkest and most extensive in the easternmost form considered and lightest and least extensive in the Hawaiian form. I defined the geographical variants "eastern" and "whitebelly" on the basis of coloration and external morphology (Perrin, 1972), and a third eastern Pacific form, "Costa Rican" is defined below on the basis of skull morphology (section on skeletons).

The only available data concerning the external appearance of the Costa Rican animal are underwater photographs in the possession of Scott MacVay (personal communication) of several very slim, long-snouted animals encountered off San Salvador, El Salvador. What can be seen of the color pattern appears to be similar to that of the "eastern spinner" (Perrin, 1972), except that no genital or axillary light areas can be seen, a possible artifact of the lighting. The cape (terminology of Perrin, 1972) is very faintly apparent in some of the photographs.

The color patterns of the whitebelly and Hawaiian spinners are very similar (Perrin, 1972). The main difference between them is that the whitebelly spinner distinctively has the ventral margin of the overlay (the lateral dark field) not entire, but speckled. Also, in the Hawaiian spinner, there is a dip in the ventral margin of the cape over the eye, a feature not present in the whitebelly form. The color pattern of the whitebelly spinner is the more variable of the two; some individuals are much more like the Hawaiian type than others. The differences between the two forms are most pronounced in large adults.

External Morphology

No data other than total lengths have previously been published on the external proportions of spinner porpoise from the eastern Pacific or Hawaii. Published measurements of total length (Harrison, Boice, and Brownell, 1969*b*; Pilson and Waller, 1970; Perrin, 1972) range from 75 to 186 cm. In this section I present the results of investigations of morphometrics of large series of spinners from the tuna fishery and compare them with data for Hawaiian spinners.

The same external measurements were made as for the spotted porpoise (fig. 1 & 2). Some difficulty was encountered in obtaining repeatable measurements of height of dorsal fin, because in large males the fin is canted forward (see below); hence, that measurement was dropped from consideration. For some specimens (11), only total body length and depth of body at center of ventral hump were measured.

Development

The spinner porpoise differs from the spotted porpoise in ontogeny. The sample of measurements for analysis of ontogeny (and sexual dimorphism, described below) included 120 postnatal specimens and 21 fetuses from the tuna fishery.

Most of the lengthwise measurements of the anterior portion of the body exhibit the same pattern of growth as in the spotted porpoise: their relationship with total length is linear until total length reaches approximately 1500 mm, after which they increase much less rapidly, if at all, and vary markedly.

The pattern of change in the proportional dimensions of the appendages is, however, quite different from that of the spotted porpoise. The flippers continue to increase in length (fig. 56f) and width (fig. 56g) after puberty at an increased rate relative to increase in total length. The curve for flipper width, instead of leveling off at 1500 mm, turns slightly upward. Even more striking is the pattern of increase in fluke span (fig. 56h). The curve for the spotted porpoise (fig. 10d) is linear, but for the spinner it takes a sharp upturn at puberty. A possible explanation of this difference is that the absolute rate of growth (relative to time) of fluke span (and flipper length and width) is similar in both species, but that the spotted porpoise continues to grow in total length longer than the spinner after puberty (it does reach a greater size), causing a differential relationship between appendage size and total length in adult animals. Whatever the cause, the result is that adult spinners have proportionately larger appendages than do adult spotted porpoises (see section below on variation in adults).

A sexual difference exists in the pattern of increase of the snout to dorsal fin tip measurement and girth at the anus, resulting in sexual dimorphism in the adult (discussed below).

After completion of the analyses of development based on measurements relative to total length, the dentinal layers in the teeth of a subsample of the specimens were examined. The teeth were prepared as for the spotted porpoise. As demonstrated by plots for selected measurements (fig. 57), the results confirm the conclusions reached in the preceding analysis. Especially striking is the contrast between the spotted porpoise and

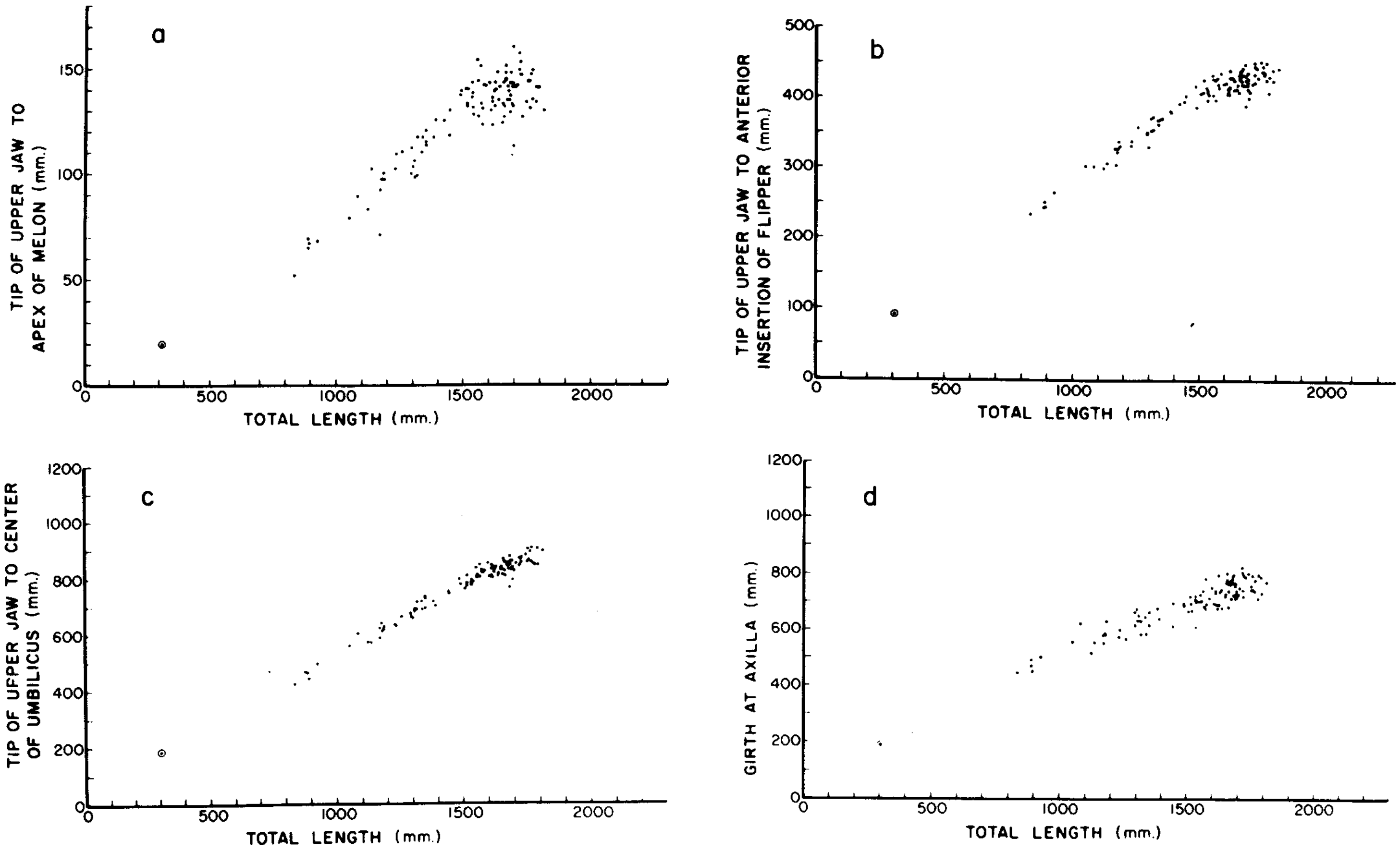


Figure 56. External development of spinner porpoise: scatterplots of external measurements on total length, demonstrating changing proportions (continued).

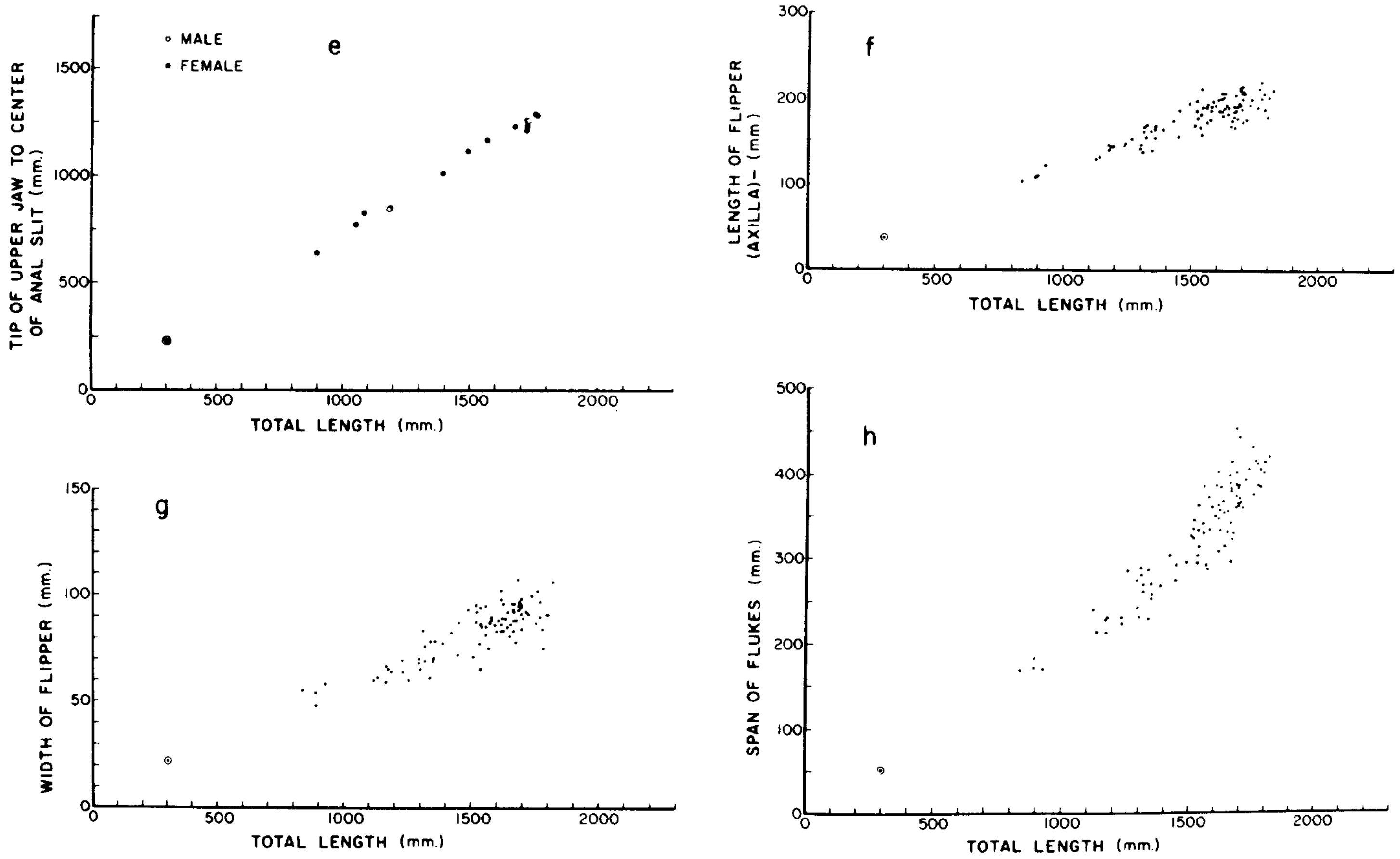


Figure 56 (continued). External development of spinner porpoise: scatterplots of external measurements on total length, demonstrating changing proportions.

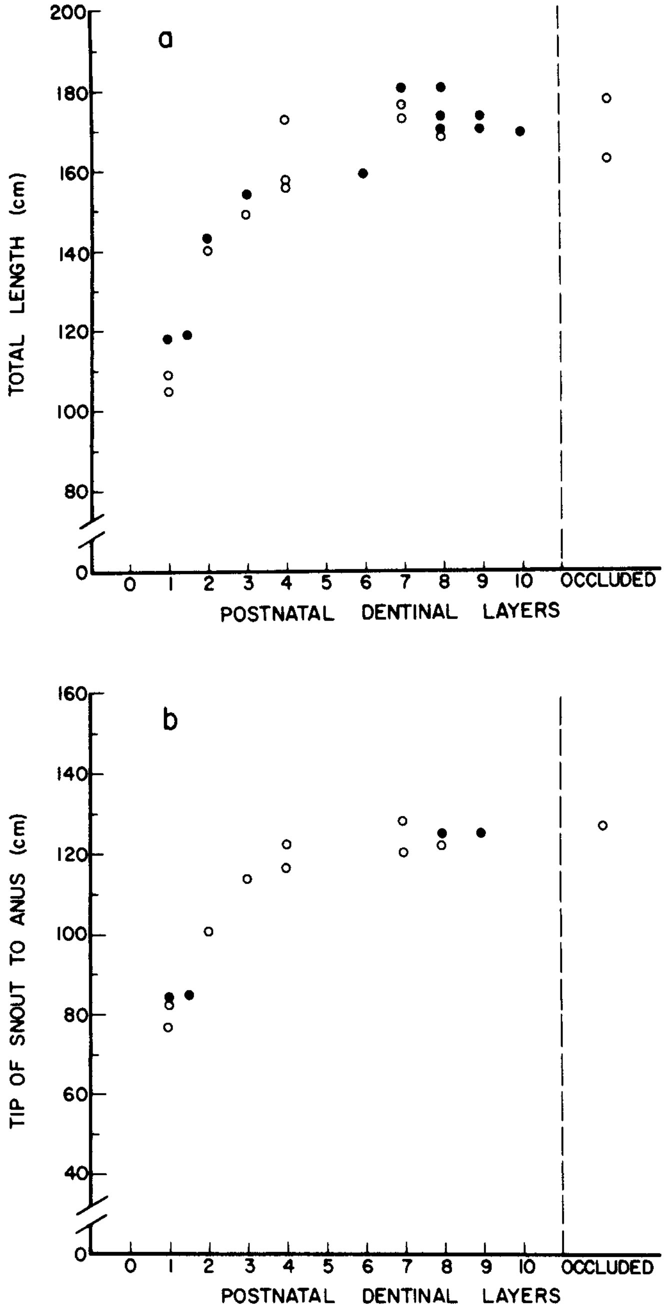


Figure 57. External development of spinner porpoise: scatterplots of external measurements on number of postnatal dentinal layers. Solid symbols are males, open symbols are females (continued).

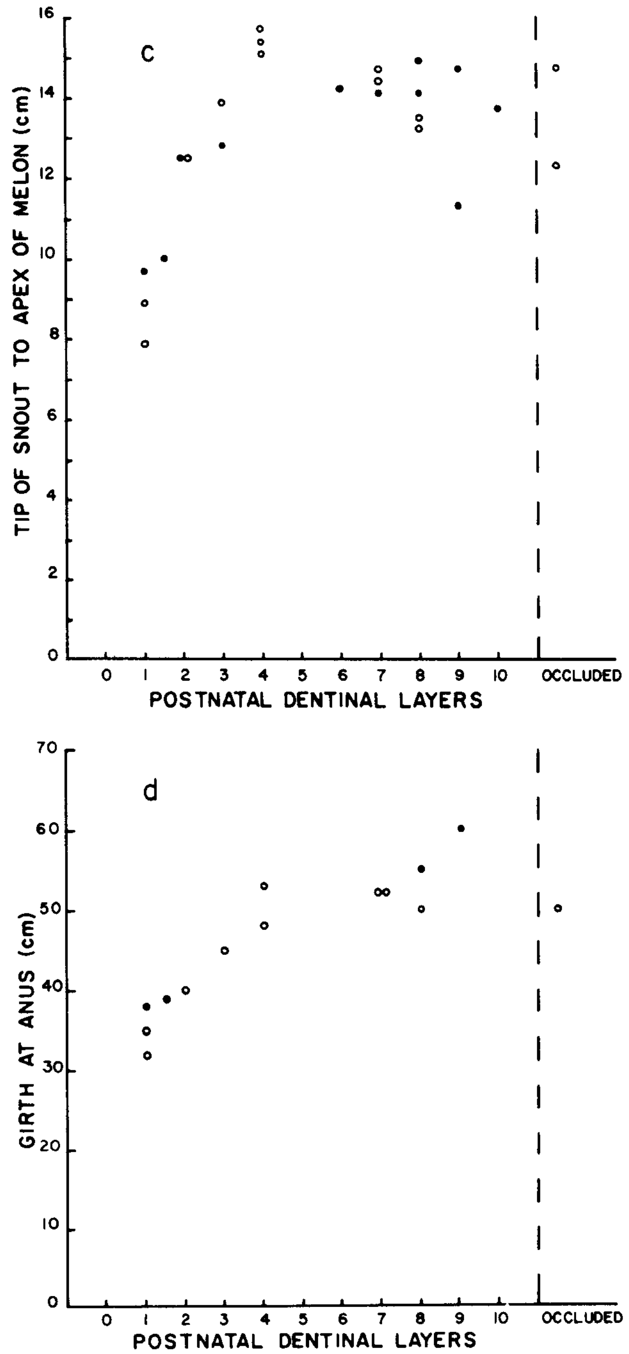


Figure 57 (continued). External development of spinner porpoise: scatterplots of external measurements on number of postnatal dentinal layers. Solid symbols are males, open symbols are females.

the spinner in the pattern of relation between dentinal numbers and total length. The curve for the spinner (fig. 57a) flattens off after about 5 or 6 layers, whereas the curve for the spotted porpoise continues to rise until at least 12 layers are reached. The contrast appears to be paralleled in the snout-to-anus measurements (figs. 11b and 57b). Snout length (figs. 11c and 57c), however, seems to show in the two forms a similar pattern of leveling off at puberty.

Sexual Dimorphism

Dimorphism exists in adults. Sexual maturity was determined by examination of gonads. The ovaries of 13 of 16 female spinners over 1600 mm in total length contained at least one corpus (corpus albicantium or corpus luteum). Ten of 11 males longer than 1625 mm were sexually mature (histologically showed spermatogenesis). These two breaking points were used to define adulthood for purposes of this analysis. Adults are defined as females longer than 1600 mm and males longer than 1625 mm.

Females have longer snouts, both absolutely (table 15) and relatively. This is also reflected in the other anterior measurements containing the snout.

The dorsal fins of adult male spinners in the eastern Pacific cant forward to varying degree (fig. 58), and the greater snout-to-dorsal-fin measurements for females reflects this feature. In some individuals the fin gives the impression of being reversed. Also evident in adult males is a more or less well-developed ventral keeled hump composed of connective tissue (see figures in Perrin, 1972). The two features are correlated in their development and are highly variable in their sexual dimorphism (figs. 58 and 59). The

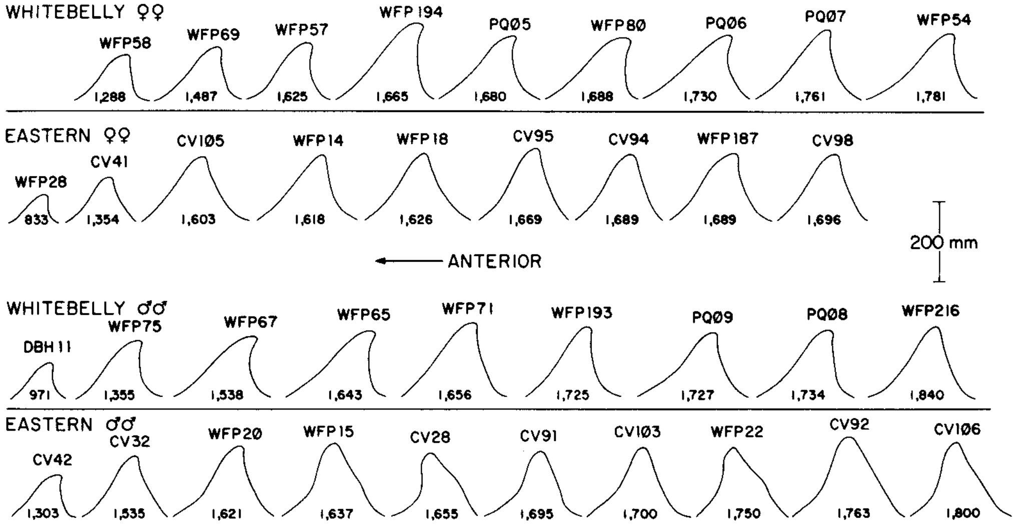


Figure 58. Developmental, sexual, individual, and geographical variation in size and shape of dorsal fin of spinner porpoise. Drawings from tracings of fins. Numbers above fins are field numbers. Total lengths in mm below fins.

Table 15. External measurements of adult male and female spinner porpoise, with statistical comparison of means

Measurements	Number of specimens	Males				Number of specimens	Females				Absolute value of significant t[c]
		Range (mm)	Mean (mm)	Standard deviation (mm)	CV $(100\ s/\bar{x})$		Range (mm)	Mean (mm)	Standard deviation (mm)	CV $(100\ s/\bar{x})$	
Total length	24[a]	1628-1818	1717	54.7	3.19	29[a]	1603-1830	1683	50.2	2.98	2.36
Tip of upper jaw to center of eye	24[a]	277-322	305	9.9	3.24	29[a]	287-325	308	9.6	3.12	
Tip of upper jaw to apex of melon	24[a]	113-149	136	8.4	6.18	29[a]	123-160	142	8.2	5.77	2.62
Length of gape	24[a]	237-276	265	9.1	3.43	29[a]	252-283	268	9.4	3.51	
Center of eye to center of blowhole	24[a]	109-124	116	3.5	3.02	29[a]	105-129	116	5.8	5.00	
Tip of upper jaw to blowhole	24[a]	277-319	305	9.3	3.05	28[a]	287-327	309	11.4	3.69	
Tip of jaw to anterior insertion of flipper	24[a]	392-455	431	16.5	3.83	29[a]	408-451	429	11.7	2.73	
Tip of upper jaw to tip of dorsal fin	24[a]	867-1050	948	37.6	3.97	29[a]	892-1058	973	40.6	4.17	2.31
Tip of upper jaw to midpoint of umbilicus	24[a]	760-902	848	31.4	3.70	29[a]	801-897	836	24.0	2.87	
Girth at axilla	24[a]	679-805	764	34.6	4.53	29[a]	679-821	737	32.3	4.38	2.93
Length of flipper, axilla to tip	21[b]	168-220	195	13.5	6.92	23[b]	167-215	194	13.2	6.80	
Width of flipper	21[b]	81-107	94	7.0	7.45	23[b]	75-102	89	6.2	6.97	2.51
Span of flukes	22[b]	314-453	391	36.3	9.28	24[b]	296-414	365	25.1	6.88	2.85

[a] Includes specimens from all collections.

[b] Frozen specimens not included.

[c] For comparison of means, Student's t was computed, after an F-test for homogeneity of variance at $\alpha = .05$.

Table 16. External measurements of Costa Rican, eastern, whitebelly, and Hawaiian spinner porpoise, with statistical comparison of eastern and whitebelly means

	Costa Rican		Eastern					Whitebelly					Hawaiian		Eastern vs. whitebelly: absolute value of significant t at $\alpha = .05$ between eastern and whitebelly
	Sample size	Range (mm)	Sample size	Range (mm)	Mean (mm)	Standard deviation (mm)	CV	Sample size	Range (mm)	Mean (mm)	Standard deviation (mm)	CV	Sample size	Range (mm)	
Total length (M)	2	1814-2164	24	1628-1818	1717	55.2	3.21	10	1643-1840	1730	58.8	3.40	2	1789-1854	—
(F)	3	1963-2033	30	1610-1786	1681	47.2	2.81	11	1625-1781	1723	53.6	3.11	3	1720-2007	2.44
Tip of snout to center of eye	4	320-351	54	264-309	292	9.6	3.29	21	265-309	295	11.8	4.00	6	318-350	—
Tip of snout to apex of melon (M)	2	143-158	24	112-153	134	8.8	6.57	10	136-148	142	5.1	3.59	2	174-178	2.68
(F)	2	158-168	30	122-161	142	9.0	6.34	10	134-157	148	6.9	4.66	3	178-191	—
Length of gape	4	283-305	54	225-269	254	9.1	3.58	21	230-276	257	10.6	4.12	5	300-311	—
Tip of snout to blowhole	4	311-360	53	265-313	294	10.5	3.57	21	266-310	294	10.3	3.50	6	315-381	—
Tip of snout to anterior insertion of flipper	4	445-472	54	367-426	401	12.2	3.04	21	388-439	413	13.6	3.29	4	420-502	3.70
Tip of snout to tip of dorsal fin (M)	2	954-1000	24	825-947	898	32.7	3.64	10	917-1014	954	31.9	3.34	1	1047	4.58
(F)	3	948-1006	29	848-1005	923	36.4	3.94	11	908-1006	959	30.1	3.14	2	1030-1168	2.92
Tip of snout to umbilicus	5	930-966	54	750-890	828	26.5	3.20	21	787-895	846	31.7	3.75	5	870-1010	2.50
Girth at axilla (M)	2	692-719	24	679-800	764	33.2	4.35	10	752-818	783	23.3	2.98	1	857	—
(F)	2	735-771	30	679-794	736	29.3	3.98	11	755-868	796	38.4	4.82	2	787-813	5.34
Flipper length to axilla	5	158-174	50	167-220	195	12.6	6.46	15	175-208	192	9.4	4.90	6	190-248	—
Fluke span (M)	2	399-402	24	314-453	391	34.8	8.90	7	334-442	396	34.2	8.64	2	394-400	—
(F)	2	381-442	28	296-444	368	28.0	7.61	8	323-410	379	26.7	7.04	3	380-425	—

Table 17. Skeleton measurements and meristics differing between adult male and female spinner porpoise, with statistical comparisons of means

Variable	Unit	Males					Females					Absolute value of significant t, at α = .05		
		Number of specimens	Range	Mean	Standard deviation	CV	Number of specimens	Range	Mean	Standard deviation	CV	Absolute measurements	Expressed as percentage of condylobasal length	Expressed as percentage of parietal width
1. Condylobasal length	mm	25	351-419	387.0	15.15	3.92	17	369-412	394.0	11.64	2.95			2.33
2. Rostrum length	mm	25	218-271	244.8	11.93	4.88	17	230-265	250.9	9.48	3.78			2.37
5. Rostrum width at mid-length	mm	24	38-47	42.7	2.39	5.59	16	37-46	41.1	2.64	6.31		2.19	
7. Rostrum width at 3/4 length	mm	24	27-36	32.0	2.46	7.69	16	27-35	30.3	2.62	8.66		2.63	
9. Rostrum tip to internal nares	mm	25	257-307	284.2	12.54	4.41	17	275-310	292.4	10.15	3.47		2.74	2.71
29. Occipital overhang	mm	26	0-11	4.7	3.17	68.21	21	3-12	6.8	2.81	41.54		2.08	2.51
44. Thyrohyal width	mm	16	15-23	17.4	2.03	11.68	20	13-22	17.7	2.21	12.50		2.31	
59. Axis lateral process length	mm	7	16-20	17.7	1.25	7.08	7	17-22	19.6	1.72	8.78	2.36		
69. First thoracic neural spine length	mm	7	12-22	17.3	4.31	24.93	7	17-28	23.6	4.08	17.29	2.81		

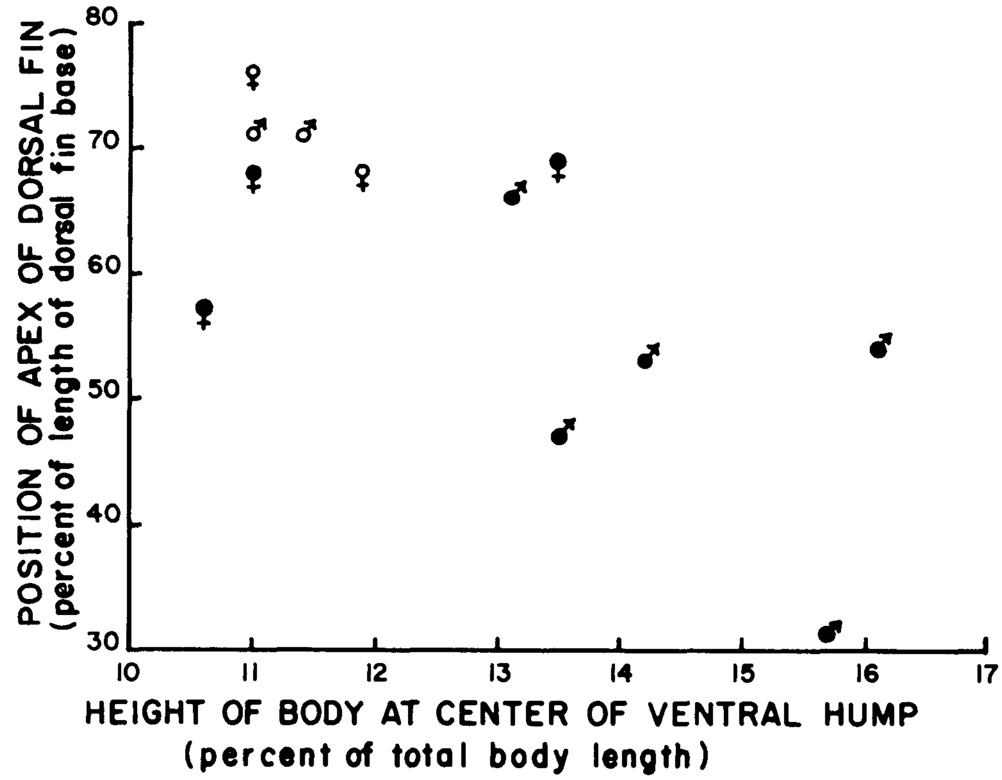


Figure 59. Relationship between forward cant of dorsal fin and development of ventral hump in spinner porpoise. Blackened symbols represent sexually mature specimens.

correlated features show great variation in degree of development. The possible functional significance of this sexually and geographically varying character complex as a species recognition signal in a mixed school has been discussed in another paper (Perrin, 1972).

Males exceed females in girth, width of flipper, and span of flakes (table 15), but these measurements are not different in males and females when taken as percentage of total length.

Individual Variation

In the spinner porpoise, as in the spotted porpoise, both males and females vary anteriorly most in the measurement of snout length (tip of upper jaw to apex of melon). This is indicated by the coefficients of variability for both the absolute measurements and the measurements expressed as percentage of total length. Also as for the spotted porpoise, the most variable measurements are the dimensions of the appendages: length and width of flipper and span of flukes. Individual variation in shape and size of the dorsal fin is great (fig. 58).

Geographical Variation

The spinner varies a great deal geographically. External measurements (table 16) are available for 4 adult "Costa Rican" spinners (unpublished data provided by David Waller) and 6 Hawaiian spinners (unpublished data provided by Robert L. Brownell, Jr., and Dale W. Rice: specimens "Momona" (name used at Sea Life Park) SLP-02-66 female, "Maka" female, OI-70-35 immature male, "Haina" sex unknown, "Opihi" male, MMBL 1194 female). In addition to the samples of measurements of 53 "adult" (males ⩾ 1625 mm, females ⩾ 1600 mm) mostly "eastern" spinners used in the above analyses of dimorphism, individual variation, and variation among schools, I have subsequently collected measurements of an additional 22 animals, for a total of 54 eastern and 21 whitebelly spinner specimens (fig. 60).

The four Costa Rican animals were very long. Both females were longer than any of the 30 eastern and 11 whitebelly females examined, and one male was longer than any

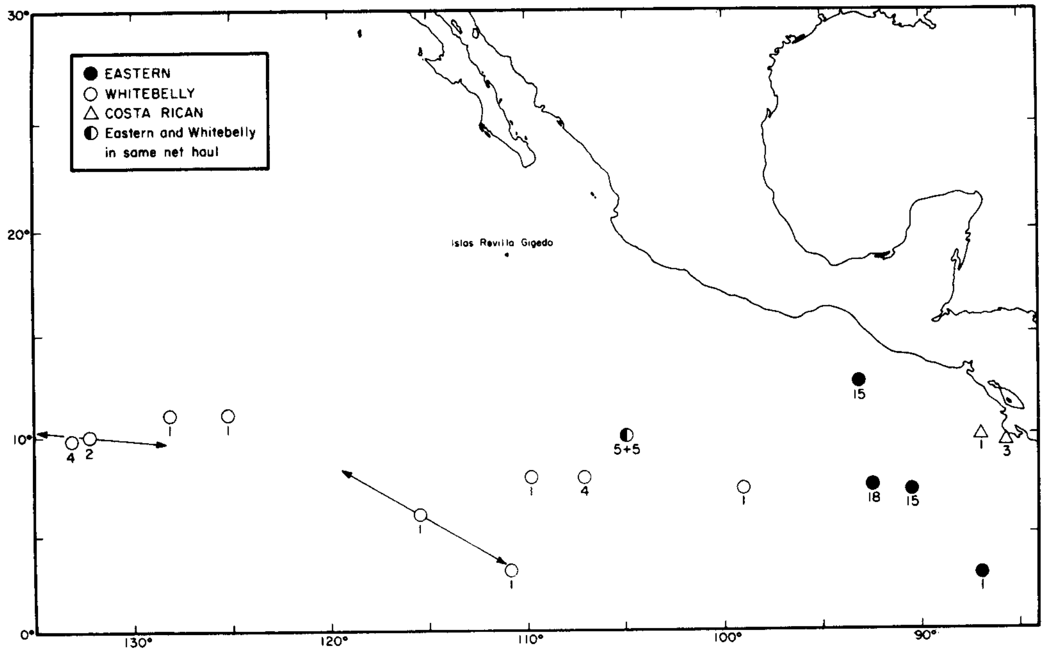


Figure 60. Provenance of 79 eastern Pacific specimens used in analysis of geographical variation in external proportions of spinner porpoise. The analysis also included specimens from Hawaii (see text).

of the 24 eastern and 10 whitebelly males. All four exceeded all the eastern and whitebelly spinners in the measurements tip of snout to center of eye, length of gape, tip of snout to anterior insertion of flipper, and tip of snout to umbilicus; and the overlap in other anterior and torso length measurements was slight. In flipper length, however, the overlap is extensive, and in fluke span and girth at the axilla the ranges for the Costa Rican series are entirely contained within the ranges for the eastern series. The resulting differences in proportions are striking. The Costa Rican animals were very slender; all four are below the ranges for the eastern and whitebelly series in proportionate girth. The same is true for proportionate length of flipper, although this may reflect a difference in measuring method. The mean value for proportionate fluke span is lower than for the other series, but the overlap is considerable. The dorsal fin tip is more anteriorly placed (or the postdorsal fin portion of the torso is proportionately longer) in both Costa Rican females than in any of the eastern or whitebelly females. The overall extreme slenderness of the Costa Rican animals is also apparent in the above mentioned underwater photographs of the spinners off San Salvador.

The whitebelly series differed from the eastern series in several measurements. The whitebelly females were on the average longest, the males had the longest snouts (consistent with the findings for length of the cranial rostrum), the measurements Tip of snout to tip of dorsal fin, and Tip of snout to umbilicus were greatest for both males and females, and girth at the axilla was greatest for females. When the measurements are considered in relation to total length, all but two of these differences disappear. The male whitebelly spinner on the average has the greatest proportionate girth at the axilla (fig. 61) and proportionately the greatest snout to dorsal fin tip distance, which reflects the greater forward cant of the fin in the male eastern spinner (fig. 58).

Adults of the Hawaiian spinner appear to be larger than whitebelly adults. The skull of MMBL 1194 (female, 172 cm) is of adult configuration (premaxillaries and maxillaries fused distally), but that of "Opihi" (male, 185 cm) is definitely of a subadult. OI-70-35 (male, 179 cm) was sexually immature (testes examined). The skulls of "Momona" (female, 201 cm), "Maka" (female, 183 cm), and "Haina" (sex unknown, 186 cm) are of adults. The three known females, (172-201 cm) were adults, but both males (179 and 185 cm) were subadults. This compares to ranges for whitebelly adults of 163-178 cm for females and 164-184 cm for males. The largest whitebelly male (of 10 measured) was smaller than one of the two Hawaiian subadults. The small sample (3) of Hawaiian animals known to be adult does not allow statistical comparison with the whitebelly series. Some differences are very clear-cut nonetheless. The greatest differences are in the anterior measurements, in particular the length of the snout. All the Hawaiian specimens, including the two subadult males, were greater than the whitebelly specimens in the distances tip of snout to eye, to melon, to angle of gape, to blowhole, and to flipper. There was overlap of the series in the long measurements to dorsal fin and umbilicus and in girth, but the Hawaiian specimens averaged larger. In flipper length and fluke span the overlap was nearly complete. When the measurements are considered as percentage of total length, the series are completely separated only in snout length (tip of snout to apex of melon). In summary, based on the few data available, the Hawaiian spinner is on the average longer than the whitebelly spinner and has a longer snout (more than 17 cm); the whitebelly spinner has a snout less than 16 cm long.

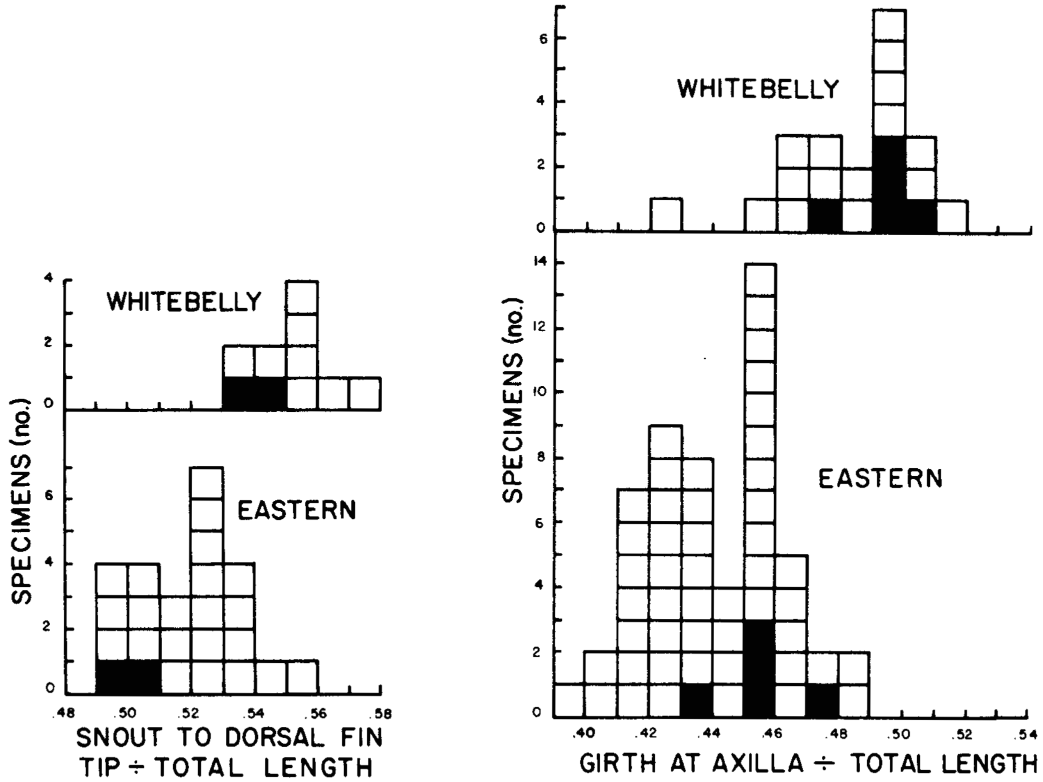


Figure 61. Geographical variation in (left) relative snout-dorsal fin length and (right) relative girth of spinner porpoise. Shaded squares represent specimens taken in a single net set and classified on basis of color pattern.

The dorsal fin of the Hawaiian spinner, while high and erect in large adult males, is always at least slightly falcate, but the fin of the whitebelly spinner ranges from slightly falcate in young animals and females to triangular in adult males, approaching the forward-canted fin of many large male eastern spinners (above, and Perrin, 1972).

Skeleton

No information on the skeletons of spinner porpoise from the eastern Pacific has previously been published.

Development

This account is based on 28 specimens: 16 eastern spinners collected in the tuna fishery aboard M/V *Carol Virginia* in 1968, 8 whitebelley spinners collected in the fishery aboard M/V *Pacific Queen* in 1969, and three small specimens (external appearance unknown) also from the fishery (LACM no. 27430, 27432, and 27433). Attention is given only to aspects of development in which this animal differs from the spotted porpoise. Additional available material from nearshore areas and from imprecisely known localities was not included. The series of 28 specimens comprises the following categories:

Class I.	Two newborn individuals, with no postnatal layers in the dentine (CB lengths 98 and 105 mm)
Class II.	Six calves, with one dentinal layer (CB length 121 to 128 mm)
Class III.	Six subadults, with 2 to 6 dentinal layers (CB length 134 to 145 mm)
Class IV.	Fourteen sexually mature adults, with 4 to > 10 dentinal layers (CB length 133 to 149 mm). Of these, seven are complete skeletons and make up a subsample for which degree of physical maturity can be determined. Of the seven, five (with 7 to > 10 dentinal layers, CB length 139 to 146 mm) are physically mature.

Note that these categories differ from those erected above for the spotted porpoise; they reflect the available material.

Cranial skeleton

The developmental series of crania of the spinner porpoise is shown in figure 62.

Braincase. Fusion of the interparietal with the supraoccipital appears to proceed more rapidly in the spinner than in the spotted porpoise. Fusion in one of the skulls with no postnatal layers has proceeded as far as in specimens of the spotted porpoise with 1 layer (Class II.5 in discussion of spotted porpoise). The telescoping process, however, does not seem to be accelerated. Proportions and relationships of the bones of the dorsal cranium are about the same in both species in specimens of presumed similar age. Closure of remaining occipital sutures is also affected. Of 17 specimens with 4 or more dentinal layers, in only 1 (with 5 layers) was any vestige of the parietooccipital sutural system visible outside the posttemporal fossa, whereas in the series of specimens of spotted porpoise examined such vestiges were common even among the oldest specimens.

The small, apparently nonfunctional foramina present in the occipital region of many specimens of spotted porpoise are not as common in the spinner series. Only one example was encountered in the 27 specimens, in an individual with 1 dentinal layer.

Growth of the cranium is not as protracted as it is in the spotted porpoise (fig. 63). It appears to cease after attainment of the adult plateau, when 3-4 layers have been laid down in the dentine.

Feeding apparatus. At birth the premaxillaries are in contact for approximately half the distance from the prenarial triangle to the tip of the rostrum. The extent of this contact remains constant throughout subsequent development, and in physically mature animals the two bones fuse along part or all of the zone of contact.

As in the spotted porpoise, distal fusion of the maxillaries and premaxillaries progresses variably, but begins roughly at puberty. In a subsample of 15 specimens, for which degree of sexual maturity was determined by histological examination of the gonads, in all the mature animals (5 males and 6 females with > 5 to > 10 dentinal layers) the maxillaries and premaxillaries have fused, whereas they have not fused in any of the

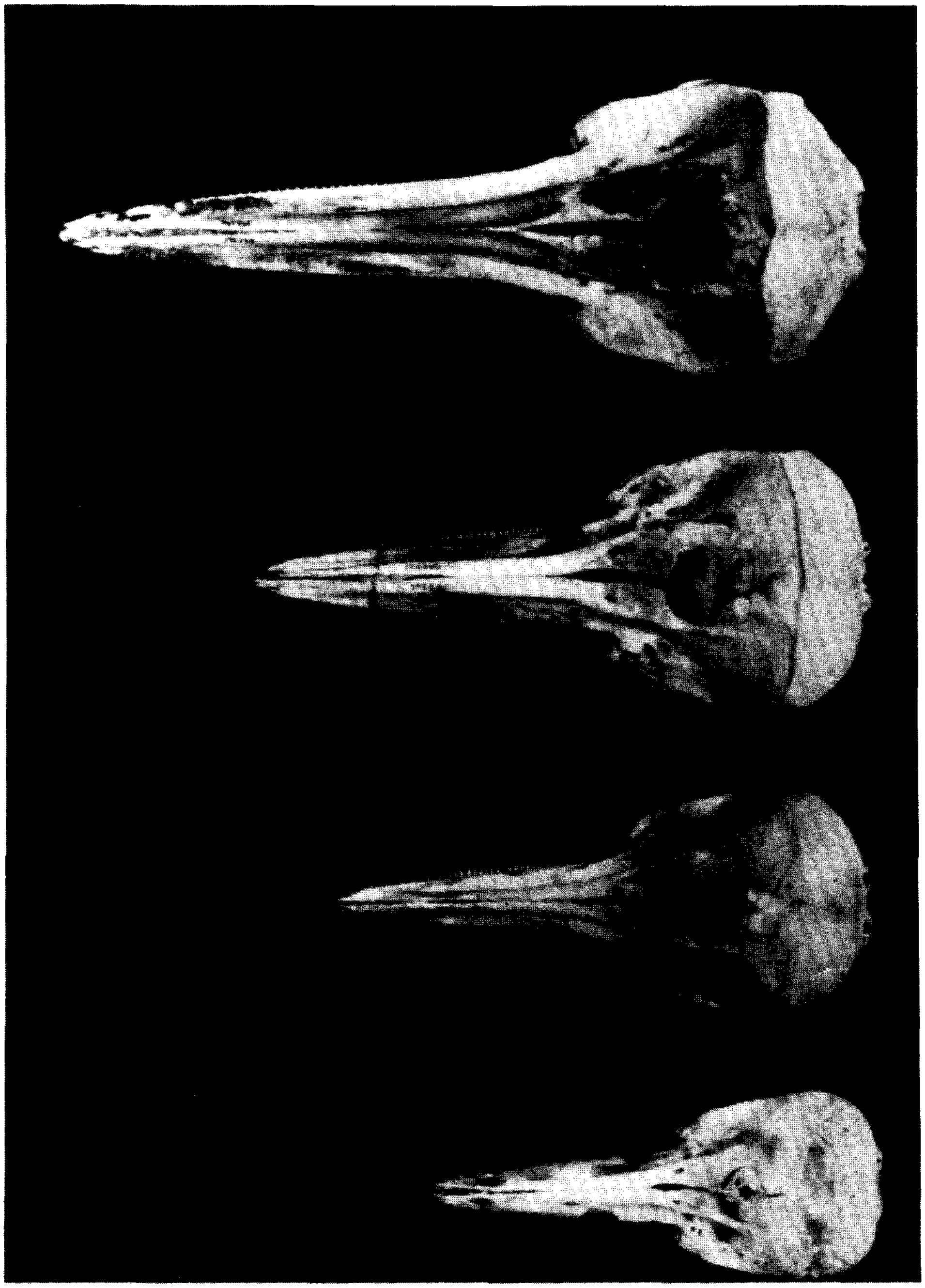


Figure 62. Dorsal views of crania of developmental series of spinner porpoise: (bottom to top) LACM no. 27430, calf of unknown sex, no postnatal dentinal layers, Class I; USNM no. 395601, immature female, one layer, Class II; USNM no. 395531, immature male, two layers, Class III. USNM no. 395396, physically mature female with occluded teeth, Class IV.

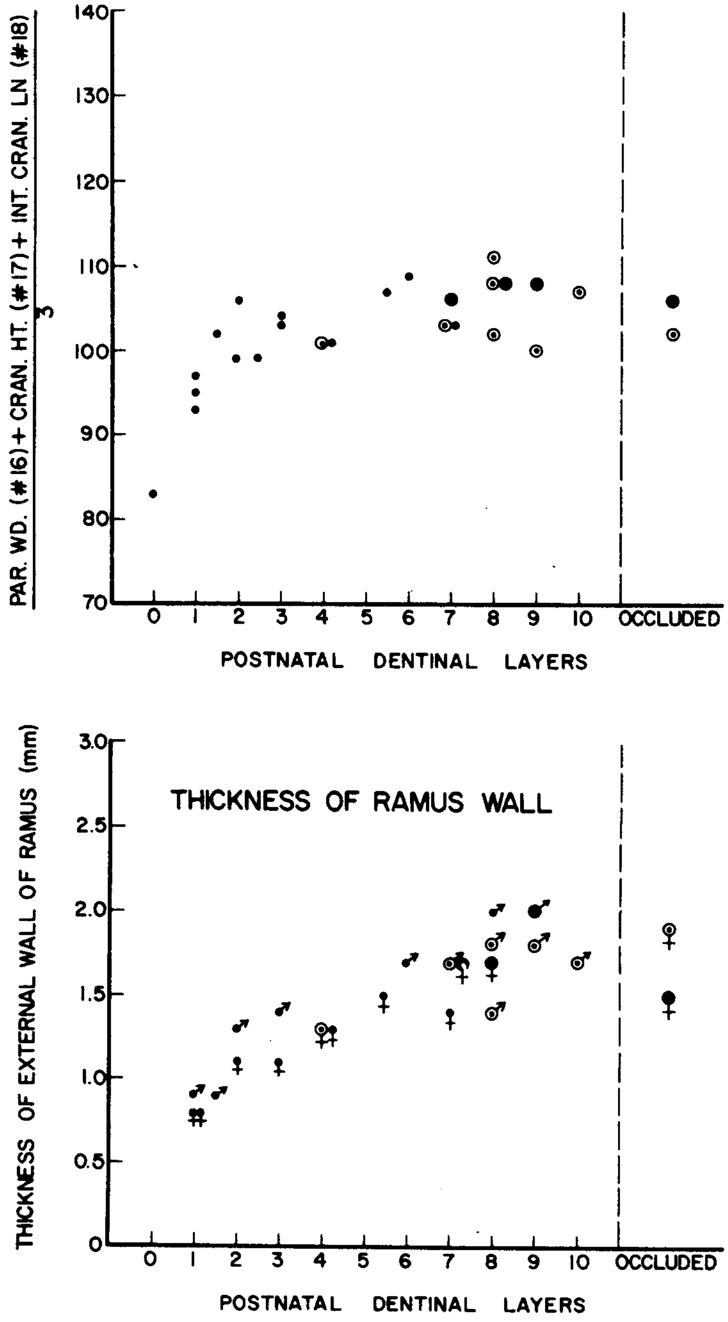


Figure 63. Development of skull of spinner porpoise: scatterplots of (top) average dimension of braincase and (bottom) thickness of ramus wall on number of postnatal dentinal layers. Small symbols are physically immature specimens. Large solid symbols are mature. Circled symbols are specimens of unknown degree of maturity.

4 large subadults (2 males and 2 females, with 2-4 dentinal layers). In some specimens in which fusion has occured, including some very old ones, a trace of the former juncture of the bones remains in the form of a groove extending to the end of the rostrum; in other specimens all traces of the juncture are obliterated in the distal 4 or 5 centimeters of the rostrum. The obliteration does not appear to be at all correlated with age.

Although with age the maxillaries and premaxillaries thicken slightly at the tip of the rostrum, such thickening is not nearly as extensive as in the spotted porpoise, in which physically mature specimens have noticeably heavier and blunter snouts than younger, though sexually mature, specimens. Some subadults have appreciably more attenuate snout tips, but most development of the rostrum and mandible tips appears to be accomplished before puberty.

Thickness of the external wall of the ramus, measured at the last tooth and at mid-height, increases with age (fig. 63), and mandibles of physically mature specimens are usually perceptibly heavier than those of younger specimens. One of the stoutest mandibles encountered in the series examined, however, was that of a physically immature male with only 8 layers in the dentine, indicating that the correlation is not a very close one.

The alveoli, especially in the maxillaries, do not develop at the same rate along the entire length of the tooth row; as a result the more distal teeth remain very insecurely anchored in quite large specimens. Distal development of discrete alveoli appears to coincide approximately with the onset of distal fusion of the maxillaries and premaxillaries and the attainment of sexual maturity, as opposed to the situation in the spotted porpoise, in which development of the alveoli progresses at an even rate along the length of the tooth row and alveoli are discrete in large sexually immature subadults. Distal development of the alveoli in some spinners is even more protracted, however; one specimen with 5 1/2 postnatal dentinal layers exhibits distal fusion but has only a furrow distally for anchorage of the teeth.

The rostrum develops more precociously in the spinner than in the spotted porpoise (compare fig. 64 with fig. 17): adult lengths are attained in subadults with only 2-3 layers. The same is true for the other measurements related to length of the rostrum. These include the measurements to the external and internal nares (nos. 8 and 9), tooth row lengths (nos. 32 and 37), and the length of the ramus (no. 38).

The shape of the rostrum (rostrum length/rostrum width in fig. 64) changes more in early development of the spinner than it does in the spotted porpoise. This is because of the early lengthening of the rostrum and not because of a difference in the rate of development of width. This growth spurt is also reflected in the early instability of other ratios based on rostrum length (fig. 64).

Fusion of the hyals is much more rapid, and there is less variation in degree of fusion in the spinner than in the spotted porpoise (compare fig. 65 top with fig. 20).

Hearing and vision apparatuses. The hearing apparatus develops as in the spotted porpoise; adult configuration is achieved in individuals with 2 postnatal dentinal layers. The orbit also develops similarly; adult size is reached in animals with 2-4 layers.

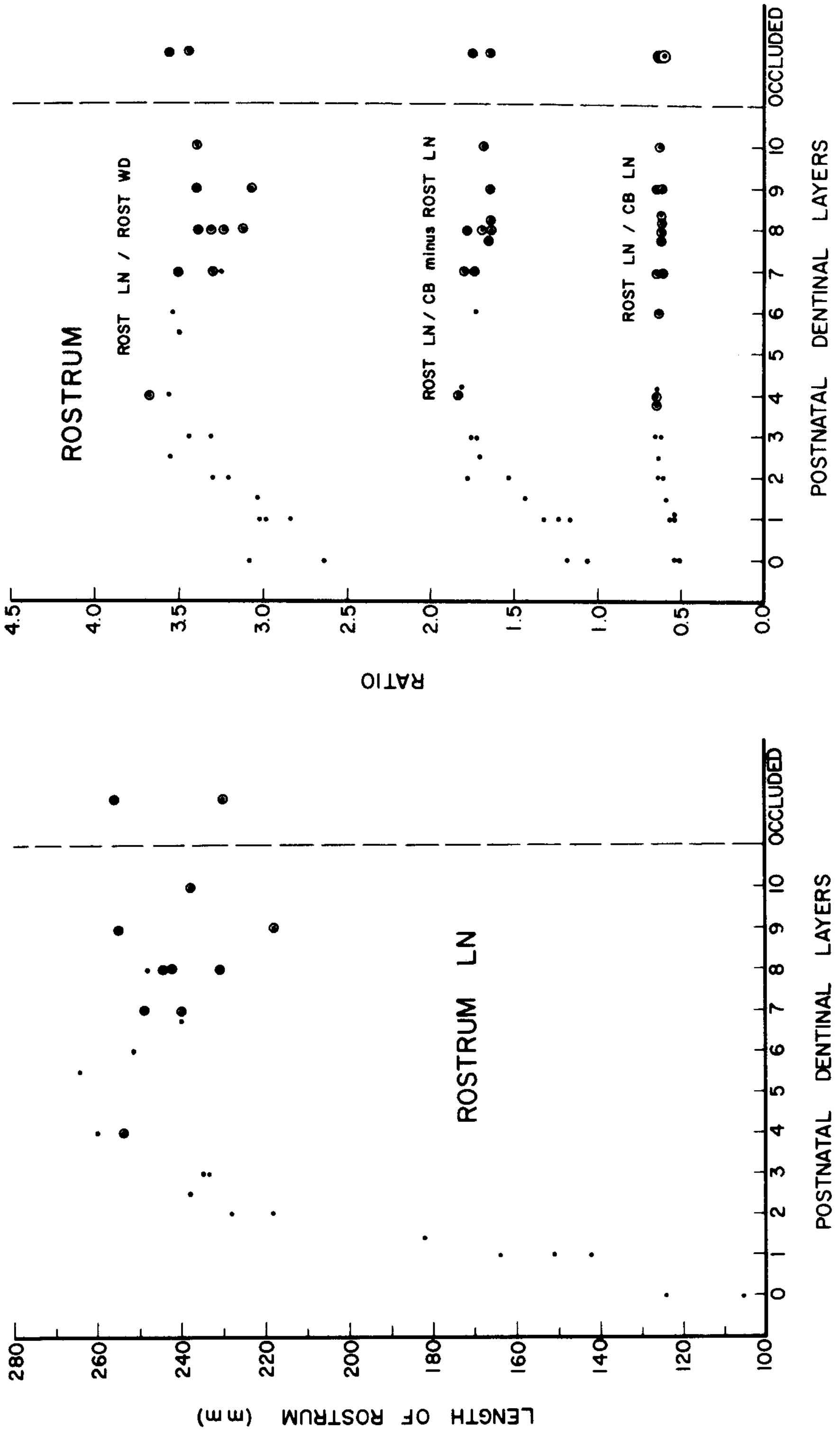


Figure 64. Development of skull of spinner porpoise: scatterplots of (left) rostrum length and (right) proportional rostrum lengths on number of dentinal layers. Larger solid dots are physically mature; circled dots are specimens of unknown degree of physical maturity.

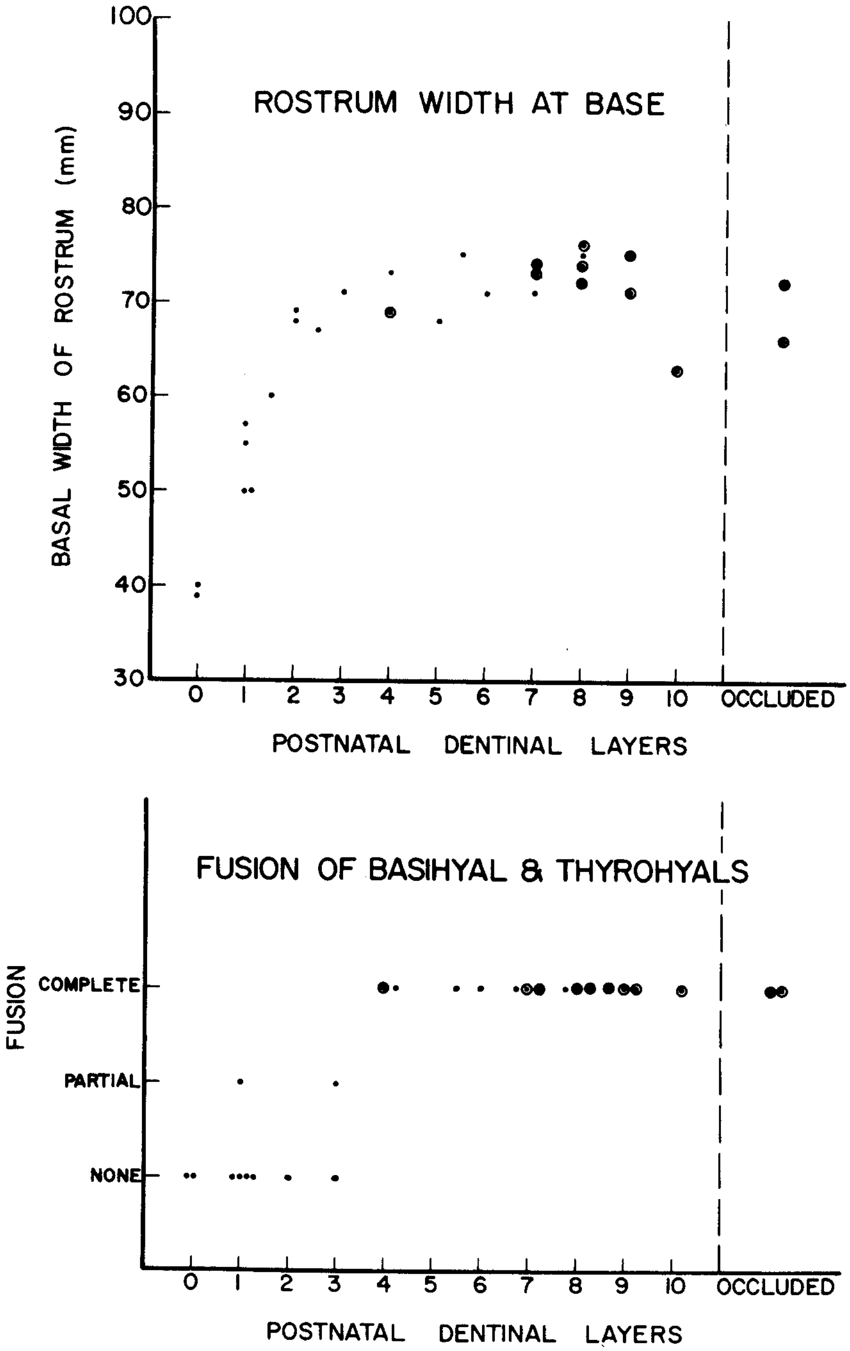


Figure 65. Development of skull of spinner porpoise: scatterplots (top) rostrum width and (bottom) degree of fusion of hyals on number of dentinal layers. Symbols same as figure 64.

Breathing and sound-producing apparatus. Facial telescoping proceeds faster in the spinner than in the spotted porpoise; adult configuration is attained in immature specimens with only 2 dentinal layers (fig. 66a), although widths of facial elements develop as in the spotted porpoise.

In specimens with more than 4 dentinal layers, the nasals are firmly fused to the frontals in all except one (with 6 layers). The outlines of the nasals are obliterated to varying extent with age.

Summary. Some functional elements of the skull of the spinner propoise, including the braincase, feeding apparatus, and breathing and sound-producing apparatus, grow more rapidly than they do in the spotted porpoise. Two alternative explanations exist: growth patterns are the same in the two forms and tooth layers are laid down at different rates, or tooth layers are laid down at the same rate in both forms but development in these features is faster in the spinner. The latter seems more likely, because the hearing apparatus and some features of the other systems, including the alveoli and parieto-occipital telescoping, develop at a similar or slower rate than in the spotted porpoise. In addition, no features in the spinner show the protracted growth into adulthood and physical maturity that exist in the spotted porpoise. I conclude, therefore, that developmental patterns are different in the two forms. The spinner is more precocious in most features. All skull with 4 or more postnatal dentinal layers, or with fused premaxillaries and maxillaries, are included below in the samples for analyses of sexual dimorphism and of individual and geographical variation.

Postcranial skeleton

The postcranial axial skeleton is shown in figure 67.

Axial postcranial skeleton. The anterior face of the atlas does not develop as precociously as it does in the spotted porpoise (compare fig. 66b with fig. 27d), but more resembles that of other features of the atlas, such as length of the neural spine. The growth continues at least until attainment of physical maturity.

Length of the 23d centrum (fig. 66c) shows a different pattern of increase than for the spotted porpoise (fig. 27). Although the small sample size precludes firm conclusions, it appears that growth of the torso is not so protracted as in the spotted porpoise, an interpretation again consistent with the external morphometric data. The pattern of fusion of vertebral epiphyses indicates that the onset of physical maturity in this species is on the average attained earlier than in the spotted porpoise (fig. 27) (with 7-8 layers, as opposed to 8-10 layers), a phenomenon consonant with earlier attainment of maximum total length.

The ribs and sternum (fig. 68) develop as in the spotted porpoise, with respect to the shape and fusion of the elements, but absolute growth posteriorly, as for other posterior thoracic and lumbar elements of the skeleton, stops earlier in the spinner than in the spotted porpoise (compare fig. 66d with fig. 22). Adult size is attained when 4-5 dentinal layers have been laid down.

As in the spotted porpoise, no developmental trend was noted in size of the manubrial foramen, but the largest foramen in 18 specimens examined was only 3 mm long. An

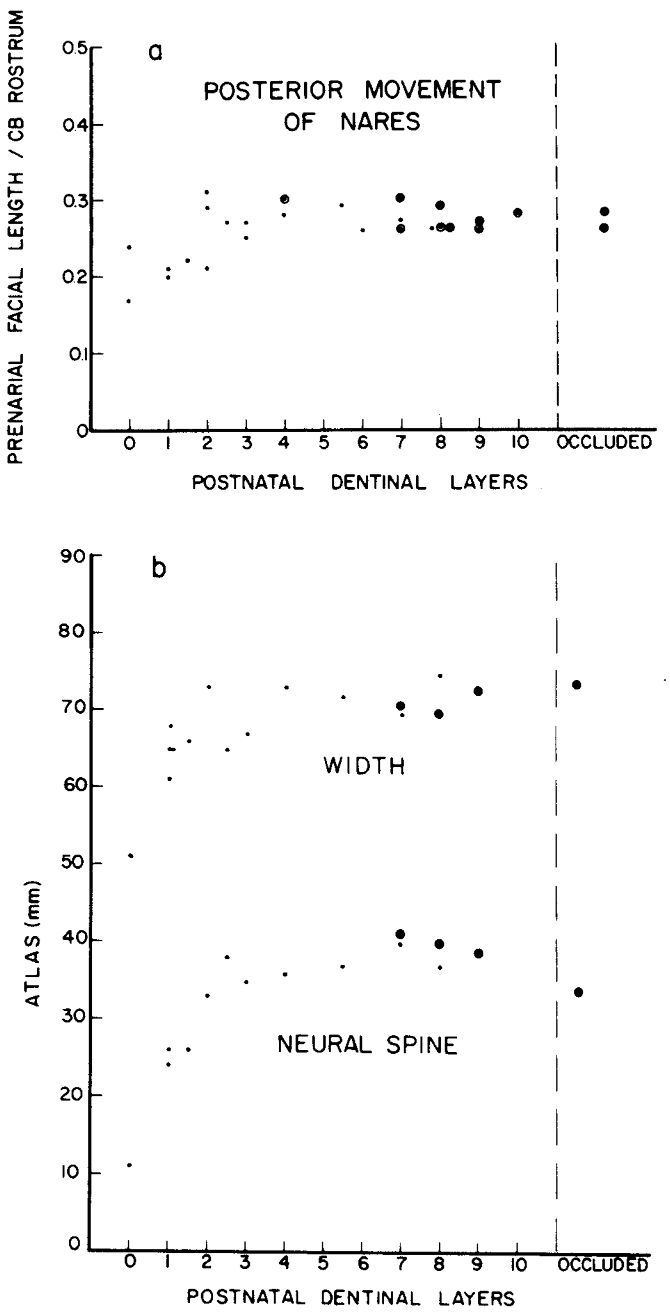


Figure 66. Development of skeleton of spinner porpoise: scatterplots of (a) prenarial facial length and (b) measurements of atlas (continued).

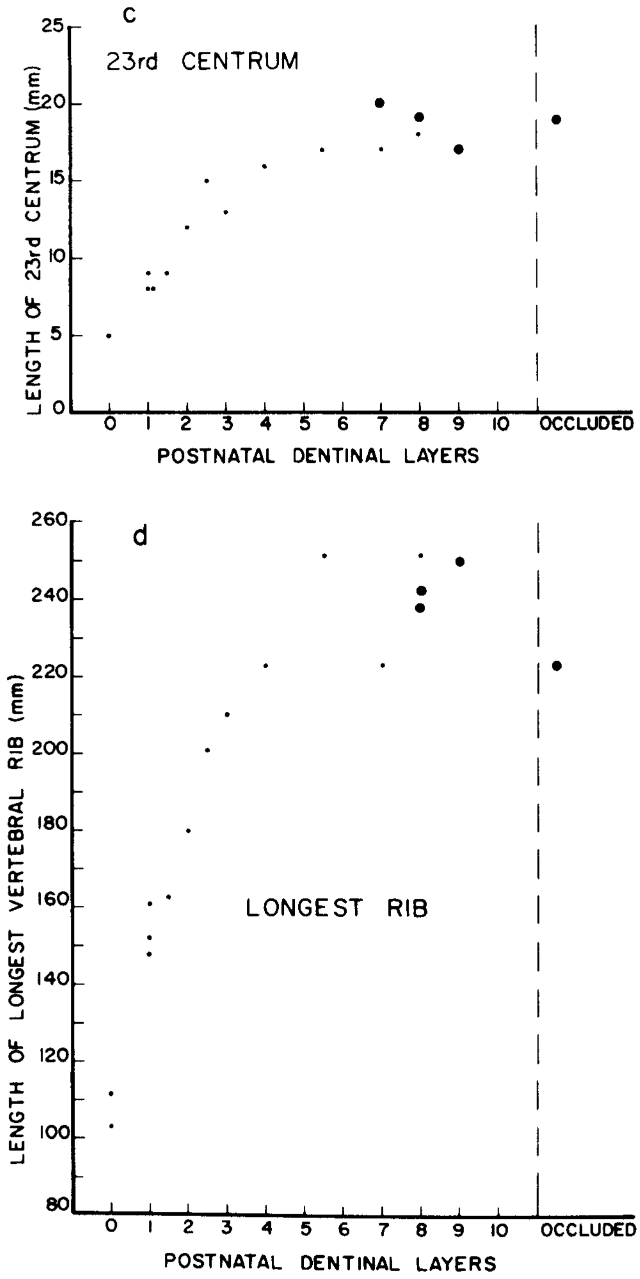


Figure 66 (continued). Development of skeleton of spinner porpoise: scatterplot of (c) length of 23rd centrum and (d) length of longest rib (continued).

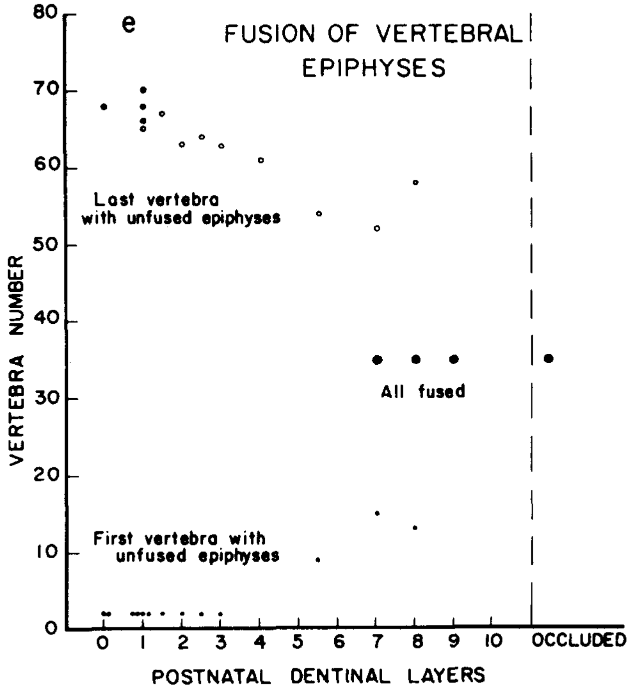


Figure 66 (continued). Development of skeleton of spinner porpoise: scatterplot (e) of progress of fusion of vertebral epiphyses on number of dentinal layers in spinner porpoise.

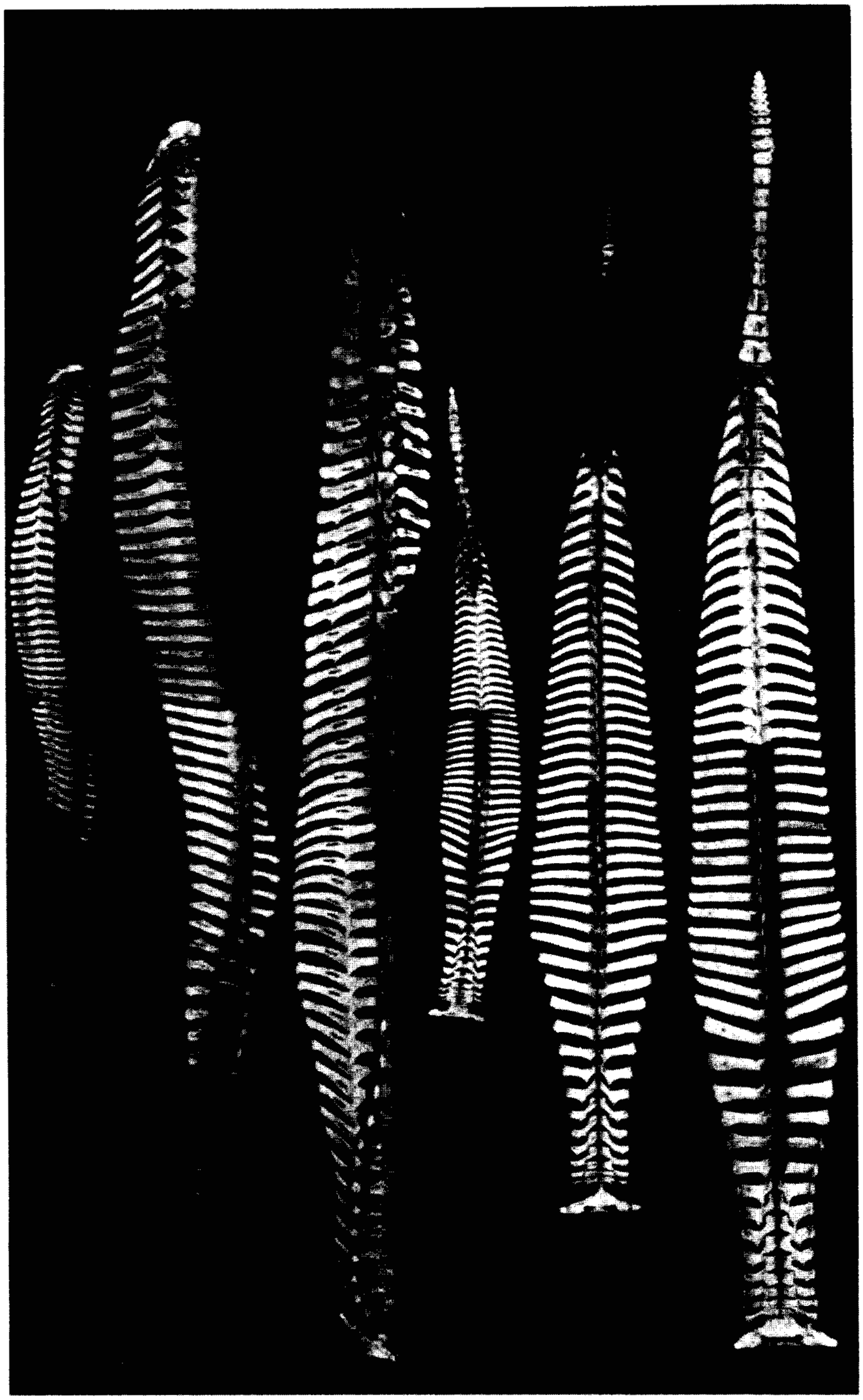


Figure 67. Development of postcranial axial skeleton of spinner porpoise: lateral and dorsal views of Class II (USNM no. 395601), Class III (USNM no. 395411), and Class IV (USNM no. 395396) specimens.

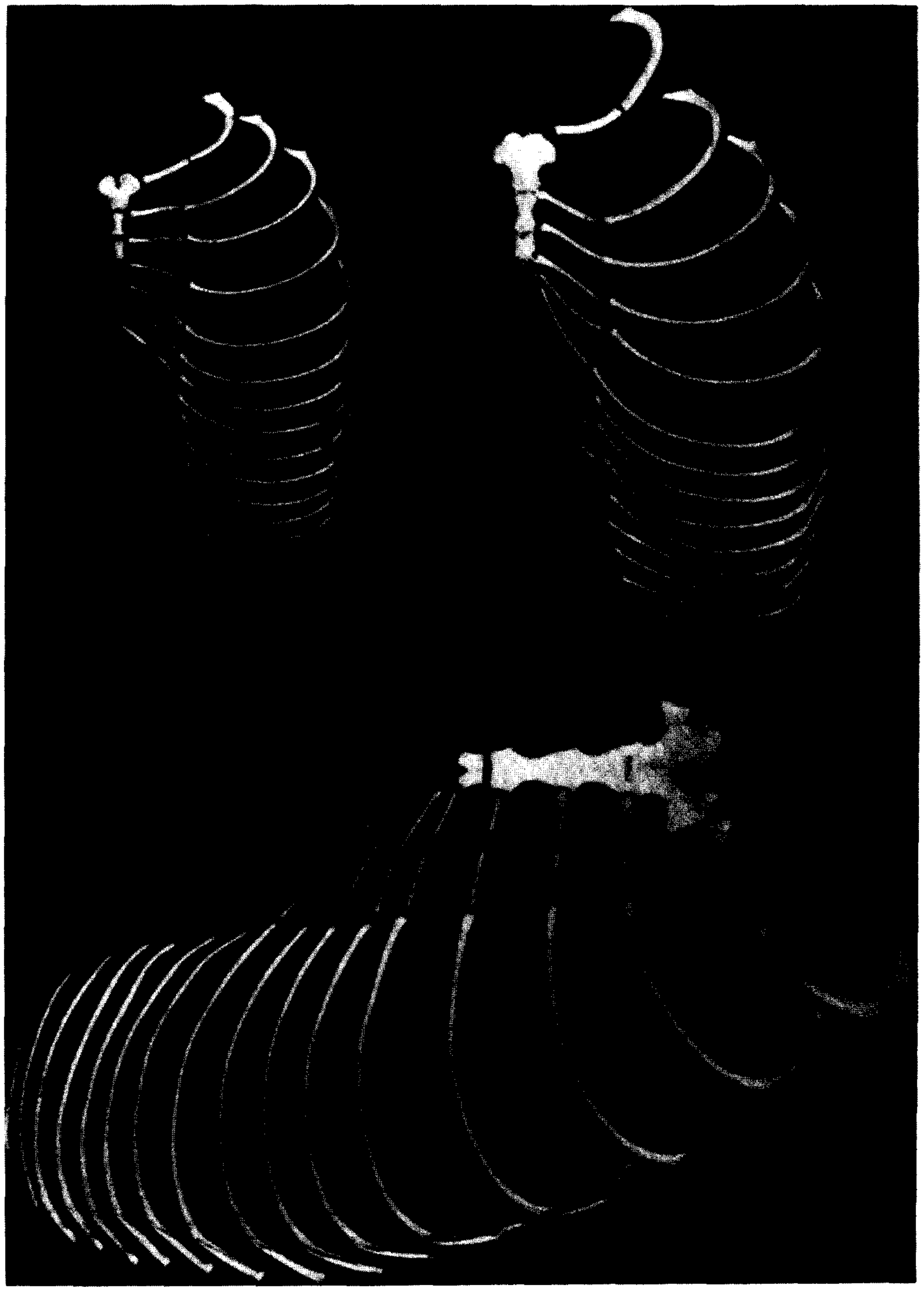


Figure 68. Ribs and sternae of specimens in figure 67.

adult specimen not in the developmental series had a foramen 10 mm long. It thus appears that ossification of the manubrium varies less than it does in the spotted porpoise.

Anterior appendicular skeleton. The scapula (fig. 69) and forelimb (fig. 70) develop as in the spotted porpoise, with some minor differences. In the specimens examined, the trapezium is ossified in neonatals, as opposed to its unossified condition in newborn specimens of the spotted porpoise. The element called the trapezoid by Fraser (1950) is not present in any specimen examined. The fifth metacarpal is also present in all young specimens examined, although absent in one manus of one adult.

None of the 18 specimens had ossified phalanges in the first digit. Hyperphalangy is more developed in the spinner than in the spotted porpoise in digits II and III (compare fig. 71 with fig. 33). There are 8 ossified phalanges at birth in digit II, with a maximum of 10 in older specimens. Digit III has 5 or 6 at birth, with a maximum of 7 in older animals. Digit IV is constant at 2-3 phalanges, and digit V has 0-2 ossified phalanges in adults as opposed to 0-1 in the spotted porpoise. Digits II, III, and V show change during development in number of ossified phalanges, with adult number attained in all three by the time 4 layers have been laid down in the teeth.

Figure 69. Scapulae of Class II (far left, LACM27430) specimen and same Class III and IV as specimens in figure 67.

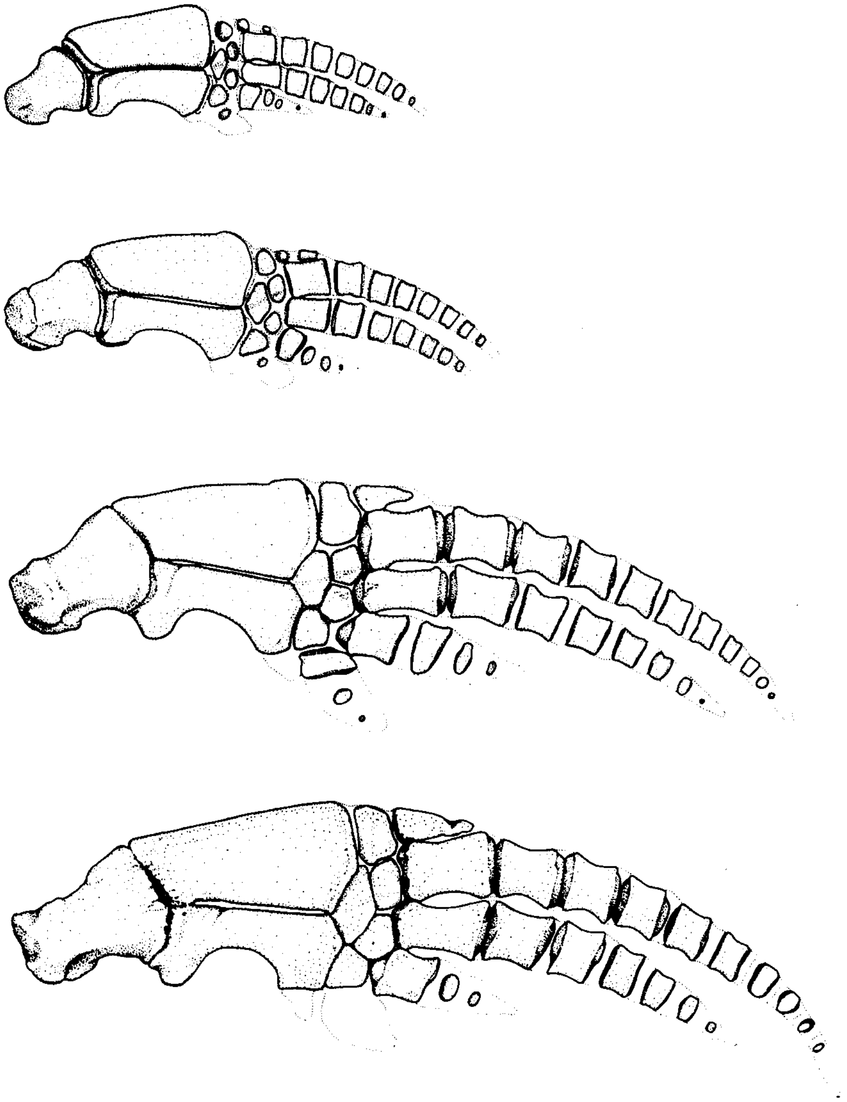


Figure 70. Development of forelimb skeleton of spinner porpoise: (top to bottom) Class I, II, III and IV specimens.

The epiphyses fuse to the humerus (fig. 71) earlier in the spinner than in the spotted porpoise (when 3-4, as opposed to 5-8 dentine layers have been formed), again prior to the fusion of the vertebral epiphyses.

Posterior appendicular skeleton. The available sample of pelvic rudiments is small (fig. 72), but it is obvious that while the trend is to increase in size with development, there is great variation in the course of development. For example, the smallest adult female pelvics are found in the oldest specimen. It appears that the adult female pelvics are in general less elaborate than in the spotted porpoise.

Summary. The postcranial skeleton of the spinner develops less precociously than the most anterior parts and the development is less protracted in its thoracic and lumbar regions than in the spotted porpoise, rendering overall growth more isogonic. It seems that adult configuration of the axial skeleton is attained earlier in the spinner than in the spotted porpoise, approximately coincidental with the attainment of sexual maturity. The small sample size of complete adult skeletons precludes a firm conclusion.

Sexual Dimorphism

Dimorphism at $\alpha = 0.05$ was found only in the braincase, feeding apparatus, and postcranial skeleton (table 17). The values of t, however, are all quite low, and it is likely that all or most of the "differences" result from chance alone, that is, from the large number of simultaneous tests. I therefore conclude that sexual dimorphism is negligible in the eastern Pacific spinner, except for the pelvics, and in any case is inadequate for determining the sex of specimens.

Individual Variation

The single-school series of osteological specimens available to me were not large enough to allow as detailed an examination of individual variation as was accomplished for the spotted porpoise. Three small series from the tuna fishery of 6, 7, and 5 specimens containing 4, 4, and 5 "adult" skulls, respectively, were available and the ranges for cranial measurements and, in one of the series, for both cranial and postcranial meristics, are presented (table 18).

Each of these short series shows a striking range of variation (figs. 73, and 76 and 77 below). These pairs are referred to below as "A" (figs. 76 and 77), "B" (fig. 73), and "C" (fig. 73).

In A, the differences are primarily in length; both the braincase and the rostrum are shorter in the smaller skull. Parietal width, however, is identical in the two specimens. In B, the smaller skull is both shorter and narrower than the larger. Most of the nonproportional difference in width of the postrostral portion of the skull is in development of the facial area. The narrow supraorbital shelf and premaxillary shield in the smaller specimen are notable (fig. 76). The smaller skull is from a large sexually mature male. The premaxillaries and maxillaries are fused dorsally the full length of the rostrum, but in size and proportions the skull is subadult (compare with Class III skull in fig. 62). This infantilism

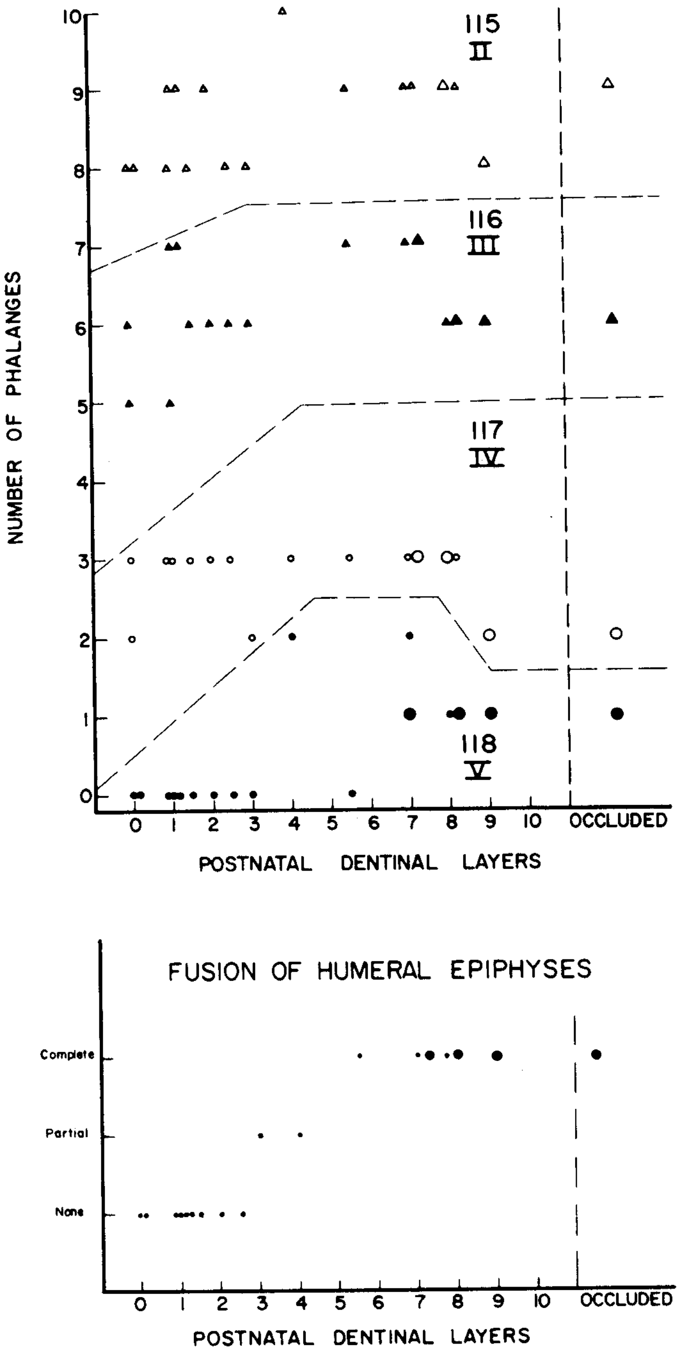


Figure 71. Development of forelimb of spinner porpoise: scatterplots of (top) number of ossified phalanges and (bottom) degree of fusion of humeral epiphyses on number of dentinal layers. Large symbols are physically mature specimens.

Table 18. Cranial measurements and meristics for three single-school series of spinner porpoise

	Variable	Unit	A		B		C	
			Number of specimens	Range	Number of specimens	Range	Number of specimens	Range
1.	Condylobasal length	mm	4	351-379	5	369-396	4	365-419
2.	Rostrum length	mm	4	218-240	5	230-254	4	227-271
3.	Rostrum width at base	mm	4	71-74	5	66-76	3	73-78
4.	Rostrum width at 60 mm	mm	4	46-50	5	47-53	3	52-57
5.	Rostrum width at midlength	mm	4	39-43	5	40-44	3	44-46
6.	Premaxillary width at rostral midlength	mm	4	16-20	5	17-21	3	21-24
7.	Rostrum width at 3/4 length	mm	4	29-34	5	27-33	3	34-36
8.	Rostrum tip to external nares	mm	4	252-282	5	269-296	4	265-308
9.	Rostrum tip to internal nares	mm	4	257-280	5	275-294	4	264-307
10.	Preorbital width	mm	4	128-136	5	127-136	4	138-145
11.	Postorbital width	mm	4	140-151	5	141-154	4	152-158
12.	Least supraorbital width	mm	4	125-136	5	125-136	4	138-141
13.	External nares width	mm	4	35-43	5	37-41	4	37-42
14.	Zygomatic width	mm	4	139-147	5	139-152	4	152-158
15.	Greatest width of premaxillaries	mm	4	49-63	5	58-62	4	60-66
16.	Parietal width	mm	4	121-124	5	121-132	4	130-138
17.	Braincase height	mm	4	85-88	5	83-92	4	87-92
18.	Braincase length	mm	4	95-99	5	98-108	4	94-108
19.	Posttemporal fossa length	mm	4	41-51	5	42-57	4	46-56
20.	Posttemporal fossa width	mm	4	32-36	5	30-38	4	40-44
21.	Temporal fossa major diameter	mm	4	29-30	5	30-32	4	30-34
22.	Temporal fossa minor diameter	mm	4	15-23	5	19-23	4	16-23
23.	Projection of premaxillaries	mm	3	14-20	5	15-25	—	—
24.	Nasals to crest	mm	4	22-36	5	25-44	4	26-31

25.	Orbit length	mm	4	38-40	5	38-41	4	41-42
26.	Antorbital process length	mm	4	39-40	5	39-43	4	38-41
27.	Internal nares width	mm	4	39-41	5	39-42	4	41-48
28.	Pterygzoid length	mm	4	45-59	5	54-61	4	54-60
29.	Occipital overhang	mm	4	0-6	5	2-11	4	0-11
30.	Bulla length	mm	4	25-28	4	27-29	4	26-30
31.	Periotic length	mm	4	24-26	5	24-25	4	26-27
32.	Upper tooth row length	mm	4	192-214	5	201-219	2	192-235
TEETH								
33.	Upper left	no.	6	51-57	4	49-52	4	51-55
34.	Upper right	no.	6	51-56	4	47-54	5	51-55
35.	Lower left	no.	6	49-53	5	45-50	5	50-53
36.	Lower right	no.	7	48-53	5	45-52	6	48-54
37.	Lower tooth row length	mm	4	188-219	5	191-218	3	190-234
38.	Ramus length	mm	4	301-321	5	309-336	4	308-360
39.	Ramus height	mm	4	47-53	5	50-55	4	50-60
40.	Mandibular fossa length	mm	4	80-89	5	83-91	4	84-95
41.	Deviation from symmetry	degrees	4	8-11	5	7-9	4	7-13
42.	Basihyal length	mm	4	26-32	5	25-31	4	27-31
43.	Basihyal width	mm	4	30-36	4	32-38	4	34-35
44.	Thyrohyal width	mm	4	13-19	4	15-18	4	16-23
45.	Thyrohyal length	mm	4	41-48	4	36-58	4	43-49
46.	Stylohyal width	mm	4	13-16	4	12-16	4	12-17
47.	Stylohyal length	mm	4	59-67	4	56-68	4	65-67

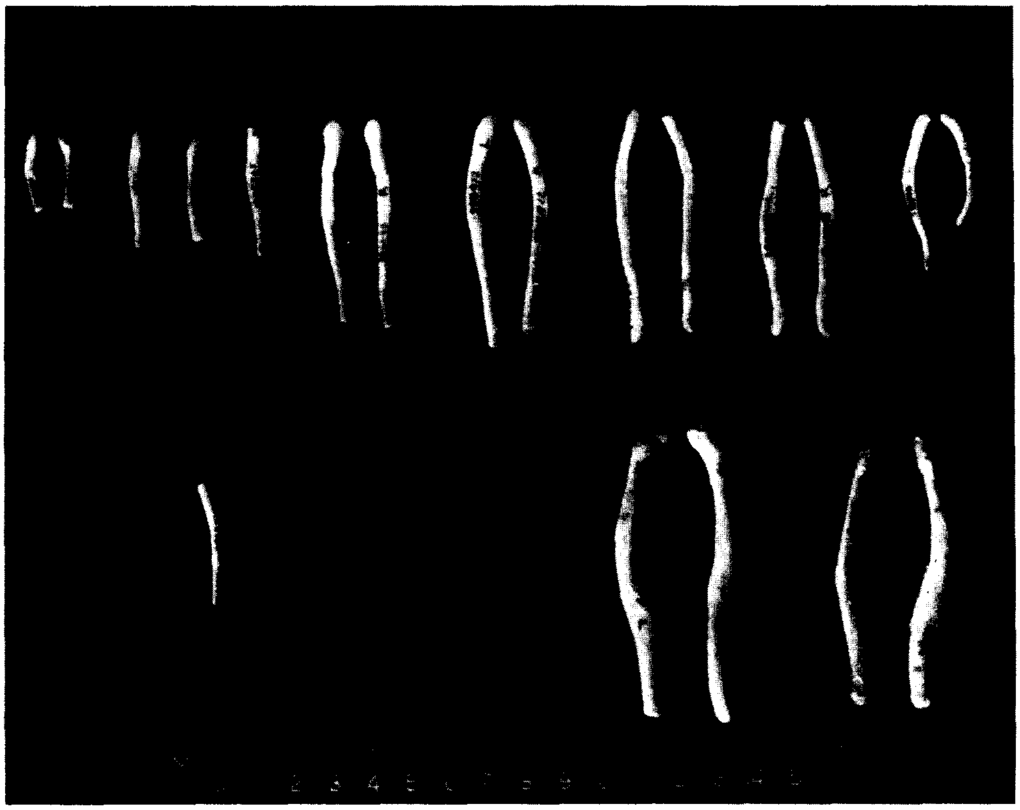


Figure 72. Development and variation of pelvic rudiments in spinner porpoise. Rightmost pair on top (females) and bottom (males) are from physically mature specimens.

is even more pronounced in the hearing system (fig. 74). The small skull is the only one of all those examined on which the occipital crest has a posteriorly directed overhang (approximately 1 mm). In C, as in A, the main difference between the two skulls is in length; the skulls are of nearly identical width. The larger skull is proportionately longer in the postnarial frontal region. In all three pairs of skulls, the size, shape, and orientation of the posttemporal fossae are notably disparate.

Geographical Variation

Pronounced geographical variation exists in the skeleton of the spinner porpoise. The available skeletal material from known localities in the eastern Pacific and Hawaii comprises 85 specimens. The area covered in the eastern Pacific extends from Tres Marias Islands in the north to Costa Rica and offshore to about 135°W longitude (fig. 75).

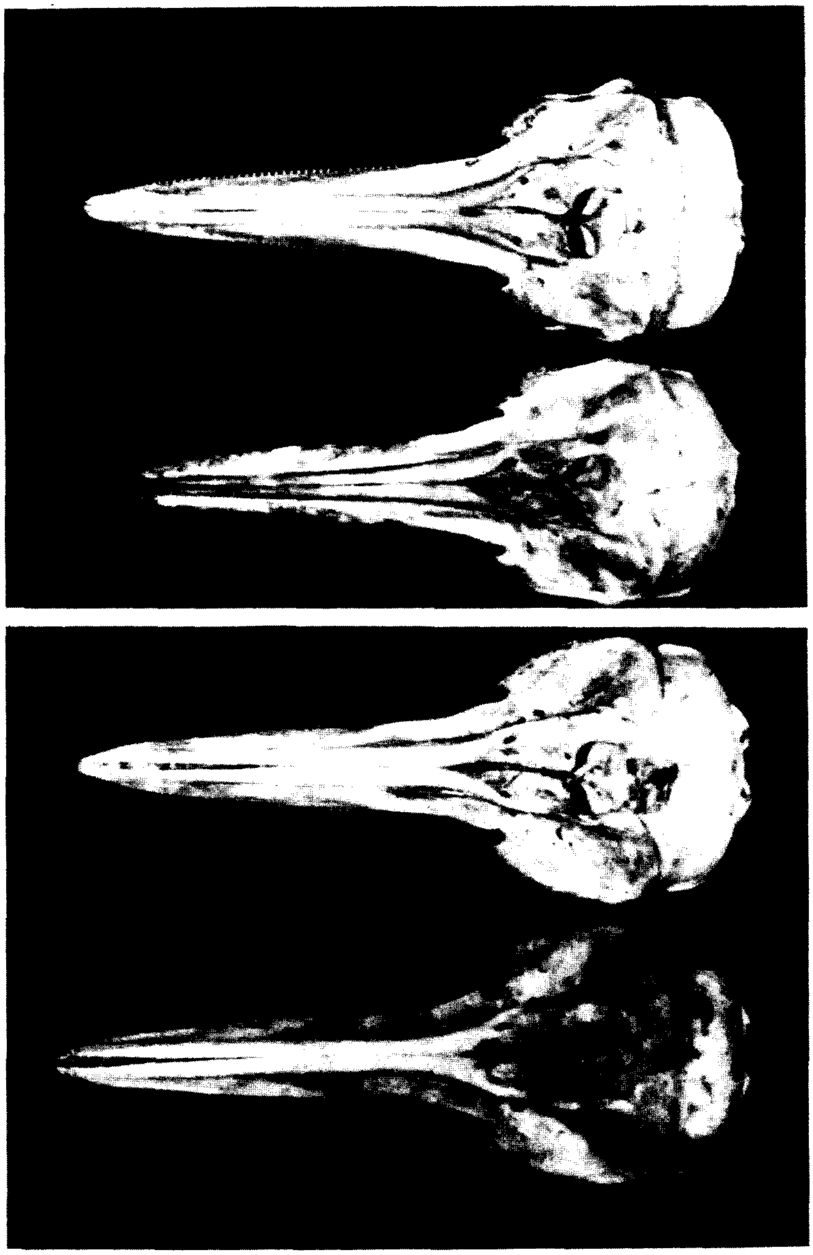


Figure 73. Individual variation of skull of spinner porpoise within school; dorsal view of cranium of spinner porpoise from each of two single-school series: pair B (bottom) SWFC no. CV 240 (pterygoids damaged), male, 8 layers, Class IV, and USNM no. 395275, male, 10 layers, Class IV; pair C (top) USNM no. 395271, male, 9 layers, Class IV, and USNM no. 395273, male, 7 layers, Class IV. See figures 76 and 77 for an additional pair of specimens (pair A: USNM no. 395031 and USNM no. 396170) from a single-school series (continued).

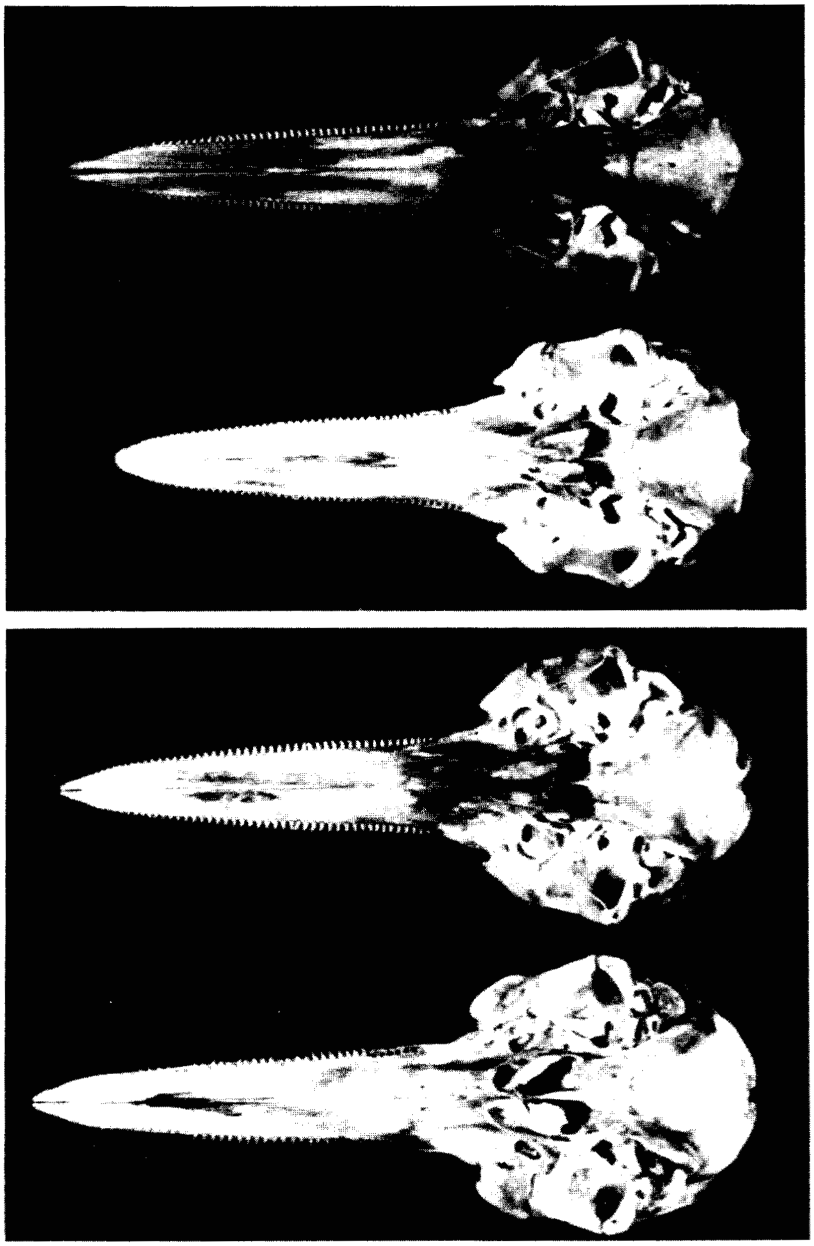


Figure 73 (continued). Individual variation of skull of spinner porpoise within school: ventral view of skulls on previous page.

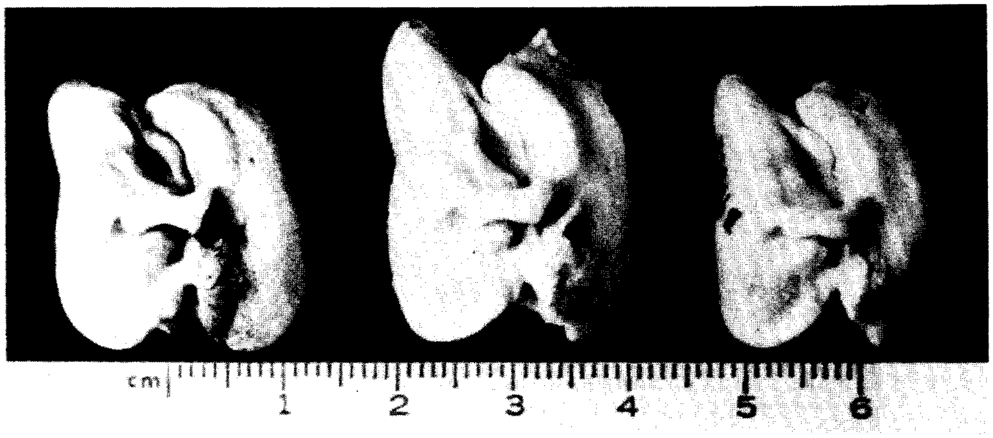


Figure 74. Tympanoperiotic bones of adult spinner porpoise USNM no. 395271 (on right) compared with those of normal adult (center) and calf (left) to illustrate infantilism.

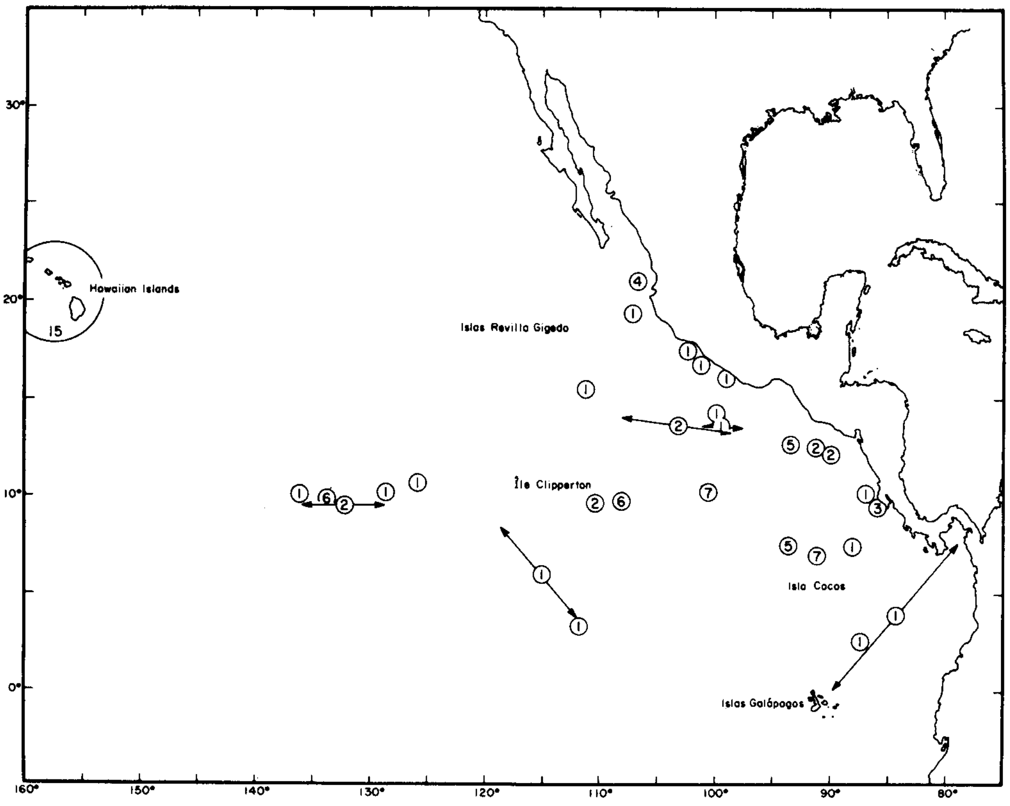


Figure 75. Provenance of specimens used in analysis of geographical variation in skeleton of spinner porpoise.

Skeletal specimens included in analysis of geographical variation

Costa Rican–3 from 9°47′N, 85°42′W (USNM 395931-3), 1 from 9°58′N, 86°03′W (USNM 395934).

Eastern–4 from 12°51′N, 93°18′W (USNM 395396, 395531, 395533-4), 7 from 7°11′N, 90°32′W (USNM 395260, 395270-3, 395526, 395593), 5 from 7°20′N, 92°30′W (USNM 395274-5, SWFC - CV 240-1, SWFC - CV 245), 2 from ~21°16′N, 106°16′W (LACM - WAW 50, 55), 1 from ~18°N, 102°12′W (LACM - WAW 54), 1 from 14°30′N, 99°35′W (LACM - WAW 60), 1 from ~14°20′N, 107°20′W (LACM - RLB 405), 2 from 12°32′N, 91°04′W (USNM 324974-5), 1 from 16°15′N, 98°55′W (USNM 395930), 1 from 12°30′N, 92°53′W (SDMNH 21427), 1 from 13°30′-14°06′N, 98°-100°56′W (CAS 15665), 1 from 13°33′-14°02′N, 99°47′-102°02′W (CAS 15666), 1 from 13°33′-14°02′N, 99°-108°W (MVZ 140641), 7 from 9°50′-10°36′N, 99°47′-102°02′W (CAS 15667-9, MVZ 140642 and 140645, UCMP 86287, SWFC - LGB - WFP 28), 1 from ~3°N, 87°W (USNM 395026), 1 from 7°21′N, 87°14′W (USNM 396169), 1 from Pacific Ocean between Panama and Galápagos Islands (USNM 23302), 1 from ~21°35′N, 106°40′W (USNM 88976), 1 from ~17°N, 100°45′W (LACM - WAW 58), 1 from ~18°20′N, 106°40′W (SDMNH 21200), 2 from ~12°20′N, 80°50′W (CAS 13821, 13828), 1 from ~21°43′N, 10°47′W (MMBL 1967-102).

Whitebelly–2 from 7°40 - 8°N, 107°W (USNM 395409, 395411), 4 from 7°56′-8°N, 106°36′-50′W (USNM 395412-4, 395600), 2 from 8°N, 109°45′W (USNM 395599, 395601), 2 from 9°28′-55′N, 128°20′-136°08′W (USNM 396023, 396030), 6 from 9°47′N, 133°25′W (USNM 396017, 396021, 396031-2, 396036, 396170), 2 from ~11°N, 125°W (USNM 396035, 396168), 1 from 3°20′N, 110°44′W (USNM 396173), 1 from 3°20′N, 110°44′W or 8°19′N, 119°15′W (USNM 396174), 1 from 10°19′N, 135°38′W (USNM 396020).

Hawaiian–5 from Hawaiian waters (LACM 27095, LACM - RLB 240 and 242, TKO 050 and 295), 5 from Oahu (SWFC - WPSR01, LACM - "Maka",LACM 27093, MMBL 1194, CAS 10529), 2 from Molokai (LACM - "Momona"- SLP - 02-66, LACM - "Opihi"). USNM = U.S. National Museum, Washington, D.C., SWFC = Southwest Fisheries Center, La Jolla, Calif., LACM = Los Angeles (Calif.) County Museum, SDMNH = San Diego (Calif.) Museum of Natural History, CAS = California Academy of Science, San Francisco, Calif., MVZ = Museum of Vertebrate Zoology, University of Calif., Berkeley, UCMP = University of California Museum of Paleontology, Berkeley, MMBL = Marine Mammal Biological Laboratory, Sand Point NAS, Seattle, Wash., MCZ = Museum of Comparative Zoology, Harvard University, Cambridge, Mass., TKO = University of Tokyo.

Cranial skeleton

Geographical variation in the skull of the spinner porpoise is shown in figures 76-80. Measurements and meristics are shown in table 19.

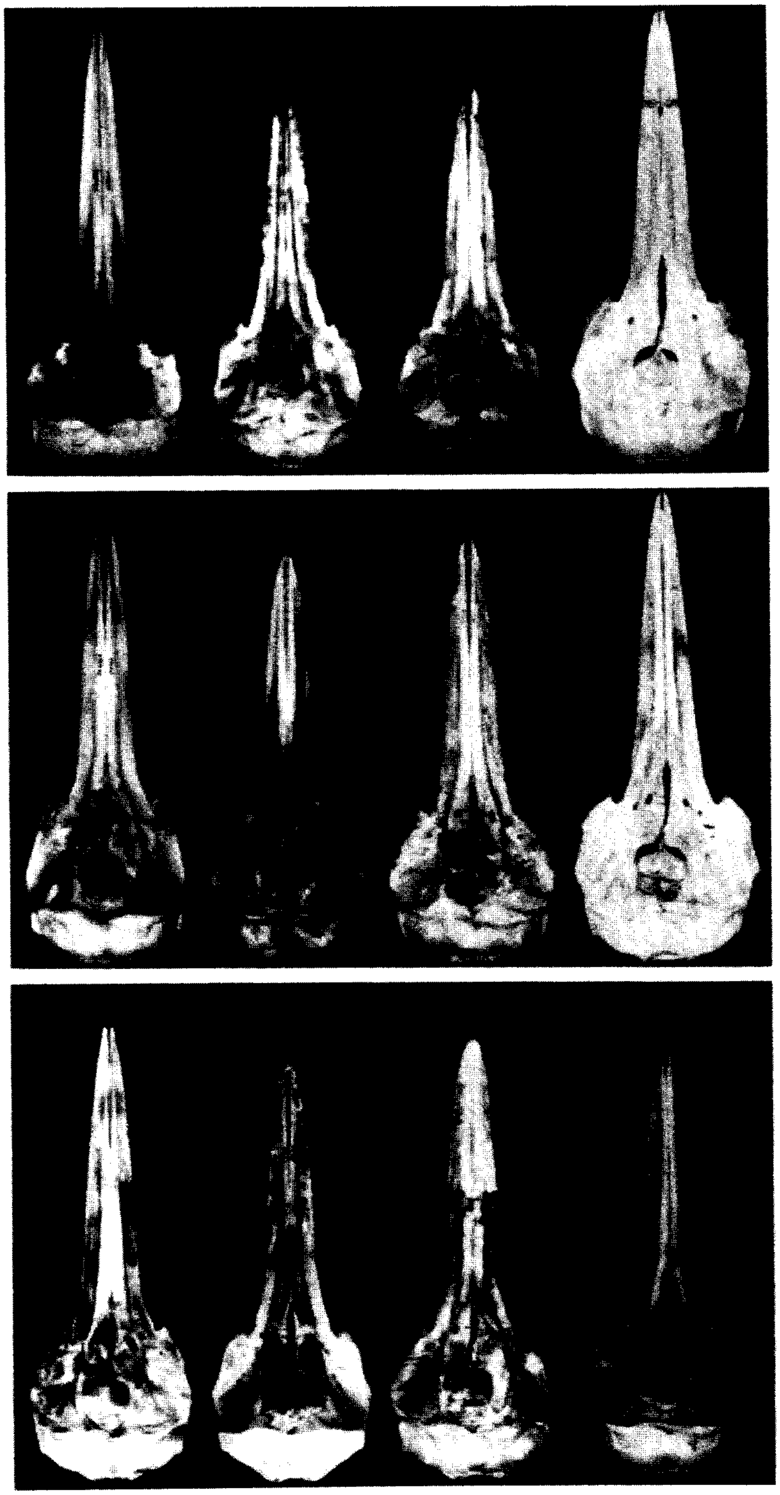


Figure 76. Geographical variation in skull of spinner porpoise: dorsal view of crania of (left to right) longest, modal and shortest intact skulls of (top to bottom) Costa Rican, eastern, whitebelly, and Hawaiian series. Costa Rican specimens are USNM nos. 395934, 395932, and 395931. Eastern specimens are USNM nos. 395271, 396026, and 395396. Whitebelly specimens are USNM nos. 395031, 395414, and 396170. Hawaiian specimens are TKO no. 050, LACM no. RLB 242, and TKO no. 295.

Figure 77. Ventral view of skulls in figure 76, in same order.

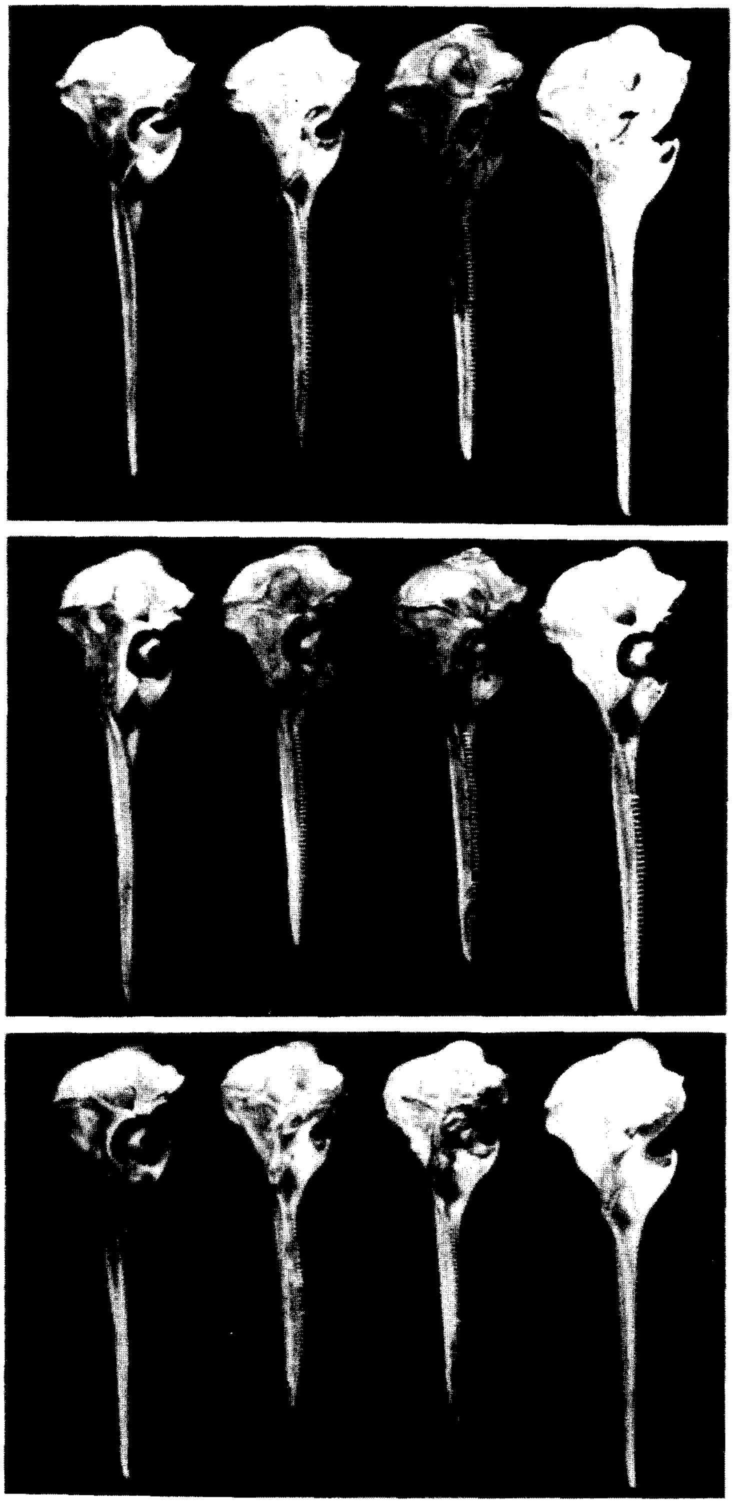


Figure 78. Lateral view of skulls in figure 76 (Costa Rican series at top, Hawaiian series at bottom); shortest skulls at top.

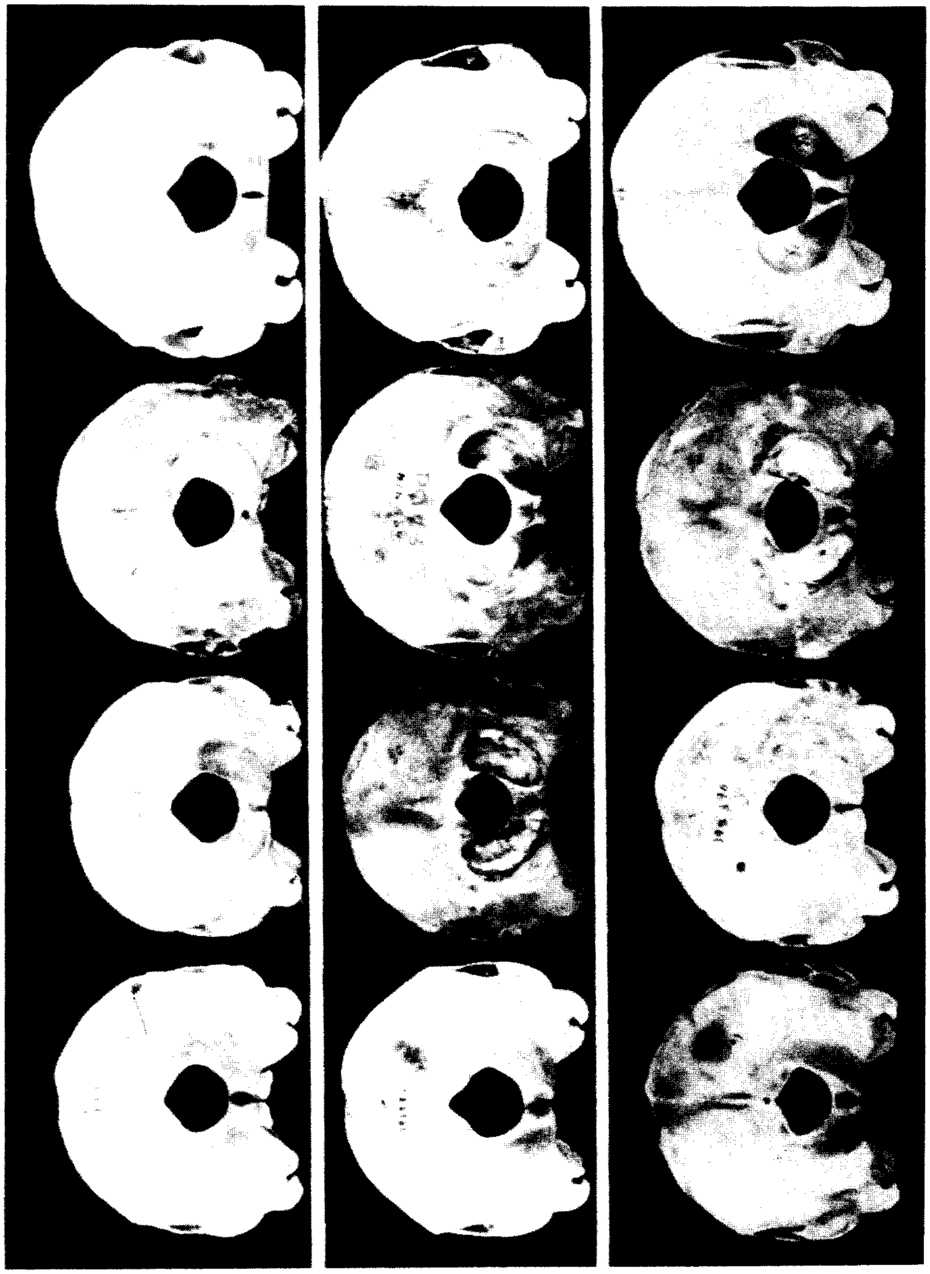


Figure 79. Occipital view of skulls in figure 76 (Costa Rican skulls at left; shortest skulls at top).

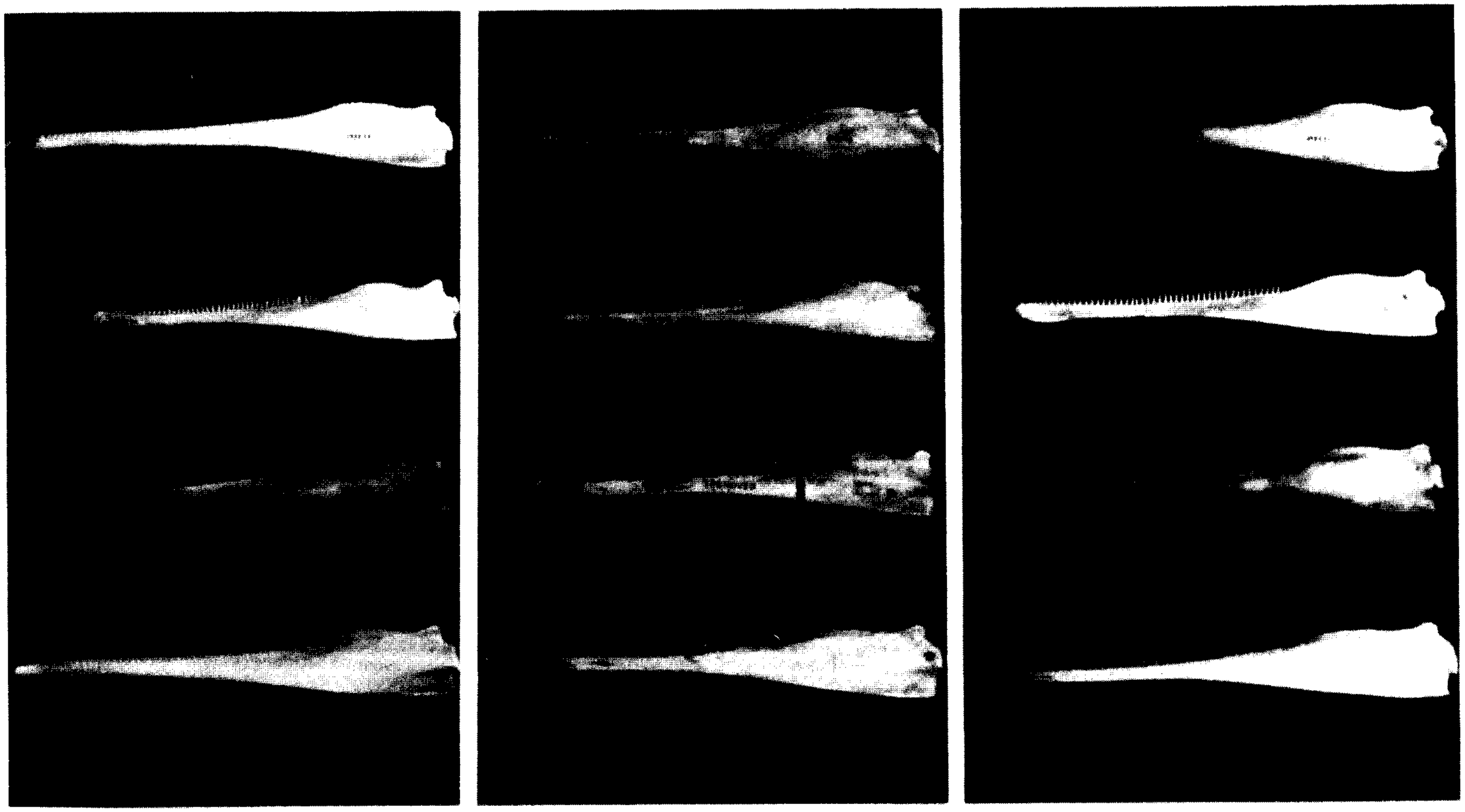


Figure 80. Lateral view of mandibles of skulls in figure 76, in same order as in lateral view (fig. 78). Note that mandible 395934 is erroneously labeled "395534."

Table 19. Skeleton measurements and meristics of Costa Rican, eastern, whitebelly, and Hawaiian spinner porpoise, with statistical comparisons (continued)

Variable	Unit	A. Costa Rican				B. Eastern				C. Whitebelly				D. Hawaiian				Absolute value of significant t, at α = .05		
		Number of specimens	Range	Mean	Standard deviation	Number of specimens	Range	Mean	Standard deviation	Number of specimens	Range	Mean	Standard deviation	Number of specimens	Range	Mean	Standard deviation	A/B	B/C	C/D
1. Condylobasal length	mm	4	416-437	426.0	11.05	26	351-407	386.5	13.51	13	365-419	396.0	13.35	10	431-464	441.7	10.76	5.54	2.08	8.83
2. Rostrum length	mm	4	269-288	276.8	8.18	26	218-262	245.5	10.83	13	227-271	251.5	11.89	10	277-304	288.2	8.94	5.51	—	8.14
3. Rostrum width at base	mm	4	70-77	72.8	3.10	29	66-77	72.1	2.61	14	69-78	73.7	2.43	10	76-84	80.4	2.41	—	—	6.68
4. Rostrum width at 60 mm	mm	4	49-53	51.3	1.71	29	46-54	49.8	2.34	14	48-57	51.6	2.59	10	52-60	56.7	2.40	—	2.28	4.90
5. Rostrum width at midlength	mm	4	39-43	41.8	1.89	26	37-47	41.6	2.45	11	39-46	42.8	2.04	10	45-49	47.0	1.41	—	—	5.43
6. Premaxillary width at rostral midlength	mm	4	21-22	21.5	0.58	26	16-22	19.6	1.70	11	17-24	19.9	1.87	10	20-22	20.6	0.70	2.19	—	—
7. Rostrum width at 3/4 length	mm	4	28-30	29.3	0.96	26	26-36	30.5	2.56	11	29-36	31.8	2.52	9	31-34	32.6	1.01	—	—	—
8. Rostrum tip to external nares	mm	4	317-335	328.5	8.27	26	252-304	284.6	12.51	13	265-308	289.4	11.86	10	319-349	331.3	9.78	6.74	—	9.04
9. Rostrum tip to internal nares	mm	4	313-331	322.0	7.75	26	257-310	285.5	12.47	13	264-307	291.8	11.85	10	319-352	330.8	11.08	5.64	—	8.02
10. Preorbital width	mm	4	131-138	134.0	3.16	29	127-138	132.3	3.54	14	132-146	138.2	4.28	10	150-157	153.5	2.32	—	4.78	10.24
11. Postorbital width	mm	4	149-152	151.3	1.50	29	140-154	148.1	3.86	15	148-158	153.9	3.39	10	164-171	167.4	2.46	—	4.92	10.81
12. Least supraorbital width	mm	4	131-155	133.0	1.83	29	124-137	130.3	3.88	15	130-142	135.1	4.10	10	139-155	149.9	4.72	—	3.82	8.33
13. External nares width	mm	4	39-41	40.0	0.82	29	35-44	40.2	2.15	15	37-42	39.7	1.71	10	40-45	42.3	1.95	—	—	3.52
14. Zygomatic width	mm	4	149-152	150.5	1.29	29	139-153	146.4	3.68	14	145-158	152.9	3.57	10	159-171	165.4	4.14	2.18	5.48	7.92
15. Greatest width of premaxillaries	mm	4	61-66	64.0	2.16	29	49-67	60.6	3.34	15	58-66	62.1	2.03	10	64-72	67.4	2.37	—	—	5.98
16. Parietal width	mm	4	129-130	129.3	0.50	29	119-132	125.9	3.67	14	120-138	130.0	4.33	10	126-138	132.4	3.95	—	3.24	—
17. Braincase height	mm	4	85-89	86.5	1.91	29	83-92	86.4	2.35	14	80-95	89.4	3.39	9	86-98	92.1	4.34	—	3.39	—
18. Braincase length	mm	4	97-103	100.0	2.94	29	95-108	100.0	2.99	14	94-108	102.1	3.50	10	103-110	106.6	2.76	—	2.04	3.38
19. Posttemporal fossa length	mm	4	46-50	47.8	1.71	29	41-57	48.5	3.69	14	43-56	49.4	3.78	10	45-56	50.3	4.37	—	—	—
20. Posttemporal fossa width	mm	4	34-36	35.0	0.82	29	29-47	36.6	3.65	14	32-46	39.9	3.93	10	38-50	42.0	4.06	—	2.71	—
21. Temporal fossa major diameter	mm	4	30-34	32.5	1.73	27	28-34	30.6	1.74	14	28-35	31.1	2.25	10	33-37	35.3	1.34	—	—	5.26
22. Temporal fossa minor diameter	mm	4	18-23	20.0	2.16	27	15-23	20.2	1.80	14	16-24	21.0	2.11	10	23-27	25.0	1.25	—	—	5.34
23. Projection of premaxillaries	mm	1	—	17.0	—	14	13-25	18.3	3.20	3	15-22	18.0	3.61	4	22-30	24.8	3.59	—	—	2.47
24. Nasals to crest	mm	4	23-31	25.3	3.86	29	22-44	30.3	5.31	14	23-42	32.7	6.07	8	24-36	28.5	4.38	—	—	—
25. Orbit length	mm	4	40-44	41.8	1.71	29	38-43	39.8	1.61	15	37-44	40.6	1.80	10	42-47	44.2	1.81	2.31	—	4.89
26. Antorbital process length	mm	4	41-45	42.5	1.91	29	33-45	39.9	2.82	15	35-45	40.9	2.67	10	42-50	45.3	2.83	—	—	3.94
27. Internal nares width	mm	4	42-46	44.3	2.06	29	38-45	41.2	1.99	14	39-48	43.2	2.39	10	42-49	45.0	2.11	2.91	2.89	—
28. Pterygoid length	mm	4	54-63	58.8	4.03	29	45-63	55.6	4.38	13	53-62	57.4	2.87	10	58-68	61.9	3.31	—	—	3.49

29. Occipital overhang	mm	4	2-10	7.0	3.56	29	0-12	5.7	3.28	15	0-11	5.6	3.44	9	8-13	9.6	1.81	—	—	—
30. Bulla length	mm	0	—	—	—	23	25-29	27.6	0.94	15	26-30	28.1	1.05	7	28-31	29.8	1.04	—	—	3.54
31. Periotic length	mm	0	—	—	—	22	24-26	25.2	0.59	15	24-27	25.8	0.68	7	25-28	26.2	0.97	—	2.86	—
32. Upper tooth row length	mm	4	238-255	243.8	7.68	25	192-229	212.2	9.95	11	192-235	218.5	12.73	10	241-263	249.9	7.84	6.03	—	6.72
TEETH:																				
33. Upper left	no.	4	50-58	55.3	3.59	32	46-59	52.7	2.94	16	50-55	52.8	1.48	13	50-59	53.2	2.95	—	—	—
34. Upper right	no.	3	51-59	55.3	4.04	32	46-61	52.6	3.41	17	47-55	52.5	2.18	13	48-59	53.2	3.34	—	—	—
35. Lower left teeth	no.	4	52-59	56.3	2.99	34	45-56	50.8	2.28	16	47-54	51.1	1.81	13	48-55	51.8	1.79	4.43	—	—
36. Lower right teeth	no.	4	51-59	56.3	3.59	37	45-56	50.5	2.49	17	48-54	50-9	1.90	14	47-54	51.1	2.09	4.25	—	—
37. Lower tooth row length	mm	4	237-244	240.3	3.30	24	188-229	209.8	10.74	11	190-234	212.8	12.30	10	234-250	241.0	5.87	5.56	—	—
38. Ramus length	mm	4	358-378	367.3	8.30	27	301-348	329.1	12.28	15	308-360	335.1	13.11	10	365-399	379.4	10.64	5.98	—	8.89
39. Ramus height	mm	4	53-57	55.3	1.71	29	47-57	52.3	2.09	15	50-60	54.3	2.58	10	58-64	60.1	1.79	2.73	2.77	6.17
40. Mandibular fossa length	mm	4	87-98	93.5	4.80	27	78-97	86.9	4.81	15	79-97	89.9	5.11	10	88-108	98.5	6.26	2.56	—	3.77
41. Deviation from symmetry	degrees	4	6-9	7.8	1.26	29	4-13	8.3	1.98	14	6-13	8.4	2.06	9	8-15	11.1	2.47	—	—	2.84
42. Basihyal length	mm	4	27-34	31.5	3.11	23	20-33	28.5	3.01	14	25-32	29.3	2.19	5	28-32	29.8	1.48	—	—	—
43. Basihyal width	mm	4	31-36	33.5	2.08	22	25-40	33.5	3.69	15	29-37	34.4	2.06	5	34-38	36.2	1.48	—	—	—
44. Thyrohyal width	mm	4	16-21	19.0	2.16	23	9-21	16.5	2.82	15	15-23	17.8	2.11	5	13-21	17.6	2.97	—	—	—
45. Thyrohyal length	mm	4	45-50	46.8	2.36	23	28-58	43.1	6.37	15	42-29	44.5	2.42	5	42-48	45.0	2.24	—	—	—
46. Stylohyal width	mm	4	14-15	14.8	0.50	25	10-18	14.4	1.68	15	12-17	14.8	1.66	5	11-16	13.8	1.92	—	—	—
47. Stylohyal length	mm	4	65-66	65.5	0.58	25	51-69	61.6	4.65	15	55-71	64.8	3.65	5	64-77	67.0	5.61	—	—	—
48. Thoracic vertebrae	no.					16	14-17	15.4	0.72	19	14-16	15.5	0.61	2	14			—	—	
49. Lumbar vertebrae	no.					10	15-20	18.0	1.41	17	15-18	16.7	0.92					—	—	
50. Caudal vertebrae	no.					9	32-36	34.0	1.22	18	33-36	34.1	1.02					—	—	
51. Total vertebrae	no.					13	73-76	74.3	1.38	20	72-76	73.8	1.29	2	70-72			—	—	
52. Fused cervical vertebrae	no.					6	—	2.0	0	8	—	2	0	3	2			—	—	
53. Atlas width	mm					6	67-74	69.7	2.58	8	65-74	70.5	2.88					—	—	
54. Atlas height	mm					6	40-47	43.0	2.37	8	40-46	43.3	1.98					—	—	
55. Atlas lateral process length	mm					6	16-21	19.0	2.00	8	17-25	20.3	2.71					—	—	
56. Atlas neural spine length	mm					6	34-42	38.2	3.49	8	34-42	38.8	2.66					—	—	
57. Atlas dorsal ridge height	mm					6	1-2	1.3	0.53	8	1-2	1.3	0.46					—	—	
58. Atlas dorsolateral spine length	mm					6	0-1	0.5	0.55	8	0-4	1.4	1.41					—	—	
59. Axis lateral process length	mm					6	17-21	18.7	1.51	8	16-22	18.6	2.00					—	—	
60. Cervical vertebrae incomplete	no.					6	0	0.2	1.01	8	0-2	0.3	0.96	2	0			—	—	
61. Greatest ventrolateral cervical process	no.					5	5.5*-6	5.9	1.14	8	—	6.0	0	2	6			—	—	
62. First vertical foramen on	no.					16	47-54	50.3	1.74	20	48-53	49.9	1.46	2	50			—	—	

*On nos. 5 and 6.

Table 19 (continued). Skeleton measurements and meristics of Costa Rican, eastern, whitebelly, and Hawaiian spinner porpoise, with statistical comparisons

		A. Costa Rican				B. Eastern				C. Whitebelly				D. Hawaiian				Absolute value of significant t, at α = .05		
Variable	Unit	Number of specimens	Range	Mean	Standard deviation	Number of specimens	Range	Mean	Standard deviation	Number of specimens	Range	Mean	Standard deviation	Number of specimens	Range	Mean	Standard deviation	A/B	B/C	C/D
63. First vertebra with reduced metapophyses	no.					14	27-33	30.1	1.79	20	27-33	30.5	1.72	2	31			—	—	
64. Last transverse process on	no.					15	56-59	56.8	0.94	20	55-58	56.5	0.83	2	54-55			—	—	
65. Last neural spine on	no.					16	61-65	62.0	1.10	20	60-63	61.6	0.94	2	59			—	—	
68. First caudal with vertical spine	no.					16	55-59	56.3	1.23	20	55-58	56.0	1.00	2	54			—	—	
69. First thoracic neural spine length	mm					6	12-22	16.7	4.13	8	16-28	23.3	4.06					—	2.99	
70. Second thoracic neural spine length	mm					6	33-38	35.8	1.83	8	34-42	38.0	2.78					—	—	
71. Tenth thoracic neural spine length	mm					6	54-58	56.0	1.41	8	53-61	56.5	2.45					—	—	
72. Last thoracic neural spine length	mm					6	57-65	62.7	3.14	7	61-68	65.3	2.21					—	—	
73. First thoracic vertebra height	mm					6	36-39	37.3	1.21	8	35-43	38.9	2.47				—	—		
74. First thoracic vertebra width	mm					6	67-80	72.5	4.72	8	66-77	72.5	3.55				—	—		
75. First lumbar vertebra height	mm					6	39-41	40.3	0.82	7	38-43	41.3	1.70				—	—		
76. First lumbar vertebra width	mm					6	162-171	166.0	3.58	8	162-171	166.8	3.58				—	—		
77. 23rd centrum length	mm					3	19-20	19.7	1.35	8	17-22	19.9	2.00				—	—		
78. Left vertebral ribs	no.					15	14-17	15.4	0.74	18	14-16	15.4	0.62	2	14		—	—		
79. Right vertebral ribs	no.					14	14-17	15.4	0.76	18	14-16	15.4	0.62	2	14		—	—		
80. Left 2-headed ribs	no.					18	5-7	5.4	0.61	20	5-7	5.5	0.69	2	5-7		—	—		
81. Right 2-headed ribs	no.					18	5-7	5.4	0.70	20	4-7	5.5	0.76	2	5-7		—	—		
82. Left floating ribs	no.					13	1-2	1.2	0.38	18	0-2	1.4	0.70	2	0		—	—		
83. Right floating ribs	no.					12	1-2	1.2	0.39	18	0-2	1.4	0.70	2	0		—	—		
84. Left sternal ribs	no.					15	8-11	9.3	0.80	19	8-11	9.6	0.76	2	9-10		—	—		
85. Right sternal ribs	no.					15	8-11	9.3	0.82	18	8-11	9.6	0.70	2	9		—	—		
86. First vertebral rib length	mm					6	90-105	96.8	5.56	8	96-113	104.1	5.19				—	—	2.53	
87. First vertebral rib width	mm					6	16-18	16.7	0.82	8	16-22	10.0	1.69				—	—	3.05	
88. Longest vertebral rib length	mm					6	217-229	222.8	5.00	8	228-261	243.1	9.77				—	—	4.62	
89. First sternal rib length	mm					6	64-72	68.8	2.64	8	65-73	70.6	2.77				—	—		

90. *Manubrium width*	*mm*					3	82-91	85.3	4.93	8	80-91	86.4	3.42				—	—		
91. Manubrium length	mm					5	47-57	53.2	4.27	8	46-63	54.5	5.04				—	—		
92. Manubrium notch depth	mm					5	6-10	8.4	1.67	8	77-11	8.6	1.51				—	—		
93. Manubrium foramen length	mm					5	0-10	2.8	4.09	8	0-1	0.8	0.46				—	—		
94. Mesosternal elements	mm					5	2-3	2.8	1.20	8	2-4	2.9	1.09	2	2		—	—		
95. Mesosternals fused	no.					5	1-3	2.0	1.00	8	1-3	2.0	0.53	2	0		—	—		
96. Chevron bones	no.					5	25-29	26.7	1.32	11	26-28	27.3	0.82				—	—		
97. Chevron bones fused in first series	no.					3	—	0	0	8	0-3	1.8	1.58				—	—		
98. First chevron on	no.					10	40-43	41.6	0.84	17	39-42	40.5	0.87				—	—	3.21	
99. Last chevron on	no.					11	64-70	66.9	1.87	13	65-68	67.1	0.95				—	—		
100. First chevron length	no.					3	5-12	7.7	3.79	8	8-12	9.9	1.55				—	—		
101. Longest chevron length	mm					6	39-46	43.2	2.93	8	38-46	42.8	2.43				—	—		
102. Last chevron length	mm					3	—	2.0	0	5	—	2.0	0				—	—		
103. Scapula height	mm					6	99-110	101.8	4.17	8	98-114	106.0	5.42				—	—		
104. Scapula length	mm					6	87-104	97.8	5.74	8	87-113	97.5	8.60				—	—		
105. Coracoid length	mm					6	28-54	36.3	9.00	8	30-39	33.8	3.37				—	—		
106. Coracoid width	mm					6	18-25	22.5	2.74	8	19-30	23.9	4.05				—	—		
107. Metacromion width	mm					6	35-57	44.3	7.55	7	29-48	41.9	6.49				—	—		
108. Humerus length	mm					6	43-47	45.2	1.33	8	44-50	47.3	2.12				—	—		
109. Humerus width	mm					6	31-37	34.5	2.26	8	33-40	36.3	2.49				—	—		
110. Radius length	mm					6	64-71	67.5	2.74	8	64-70	67.3	2.38				—	—		
111. Radius width	mm					6	31-36	32.7	1.75	8	31-35	33.4	1.39					—	—	
112. *Ulna length*	*mm*					6	54-61	56.7	2.50	8	54-60	57.3	2.12					—	—	
113. Carpal row width	mm					6	51-60	55.5	2.95	8	55-61	57.8	2.38					—	—	
PHALANGES:																				
114. Digit I	no.					17	—	0	0	19	—	0	0	1	0			—	—	
115. Digit II	no.					18	8-9	8.5	0.78	14	7-10	8.5	0.76	3	7			—	—	
116. Digit III	no.					17	5-7	6.2	1.87	14	5-7	6.1	0.66	2	5-6			—	—	
117. Digit IV	no.					15	2-3	2.5	0.84	14	2-3	2.8	0.43	0	—			—	—	
118. Digit V	no.					18	0-2	0.4	1.32	15	0-2	0.6	0.63	2	0-1			—	—	
119. Pelvic length (left) (M)	mm					4	69-81	72.5	7.37	3	68-74	71.3	—					—	—	
(F)	mm					2	42-60	—	—	5	53-62	57.6	—					—	—	
120. Pelvic length (right) (M)	mm					3	68-82	73.7	7.47	3	65-74	70.3	—					—	—	
(F)	*mm*					2	31-60	—	—	4	53-61	57.5	—					—	—	

Braincase. The Costa Rican series does not differ from the eastern series in size or shape of the braincase.

The means of the cranial dimensions of the whitebelly series are greater (at $\alpha = 0.05$) than those for the eastern series, but the differences are very small (4.1 mm, 3 mm, and 2.1 mm, for width, height, and length, respectively), and the series overlap nearly completely.

The whitebelly and Hawaiian series do not differ in breadth or height of the braincase and only slightly in braincase length.

Feeding apparatus. All four of the Costa Rican specimens possess longer rostra than any of the eastern specimens (fig. 81). The situation is different from that of the coastal spotted porpoise compared to the offshore form, in that the rostrum is not larger and more massive in the Costa Rican than in the eastern form, but only longer and more attenuate. The posttemporal fossae are not larger in Costa Rican specimens, indicating that jaw-closing musculature is not more developed in the longer-snouted animal. Width of the premaxillaries at midlength of the rostrum, and zygomatic width (nos. 6 and 14) are greater, but the overlap is extensive. The ramus is on the average higher (no. 40), but the disparity between means is very slight compared to that for ramus length, yielding a proportionately slenderer ramus. The longer feeding apparatus produces a change in overall proportions of the skull (fig. 81).

Tooth counts in the lower jaw (nos. 35 and 36) are on the average higher in the longer-snouted form, although individual variation in this character is wide, and the ranges overlap by about 50%. Further overlap might be expected were a larger sample of the Costa Rican form available.

The eastern and whitebelly series are very similar in size of the feeding apparatus and show no differences in proportions of the complex. The whitebelly skull is on the average slightly larger in some widths and heights in the feeding system (nos. 4, 11, 14, 20, 39), but the overlap is wide, and the differences disappear when the measurements are considered as percentage of condylobasal length or parietal width, indicating identity of proportion.

The Hawaiian spinner skull is strikingly larger than the whitebelly spinner skull in length and in facial breadth (figs. 76-80). The series do not overlap in the measurements of condylobasal length, rostrum length, rostrum tip to external and internal nares, preorbital and postorbital width, zygomatic width, length of upper tooth row, and length of ramus. The differences in length measurements reflect primarily differential development of the feeding apparatus of a different sort from that in the spotted porpoises, where the main component of geographical variation is in the area of origin of the temporal muscle (the "posttemporal fossa"). The Hawaiian and whitebelly series do not differ in dimensions of the muscle origin (nos. 19 and 20) but rather in the cross-sectional dimensions of the fossa proper (nos. 21 and 22). This is reflected also in the nonoverlap in postorbital and zygomatic widths. In a scatterplot of zygomatic width on ramus length (fig. 82), the Hawaiian series is clearly separable from the whiteblly series and even more different from the eastern and Costa Rica series. The Costa Rican specimens also have very long snouts but do not exhibit the increased massiveness of the posttemporal aspects of the feeding apparatus and the concomitant increased facial breadth. The relative positions of the Hawaiian and Costa Rican series in figure 82 demonstrate again that more than

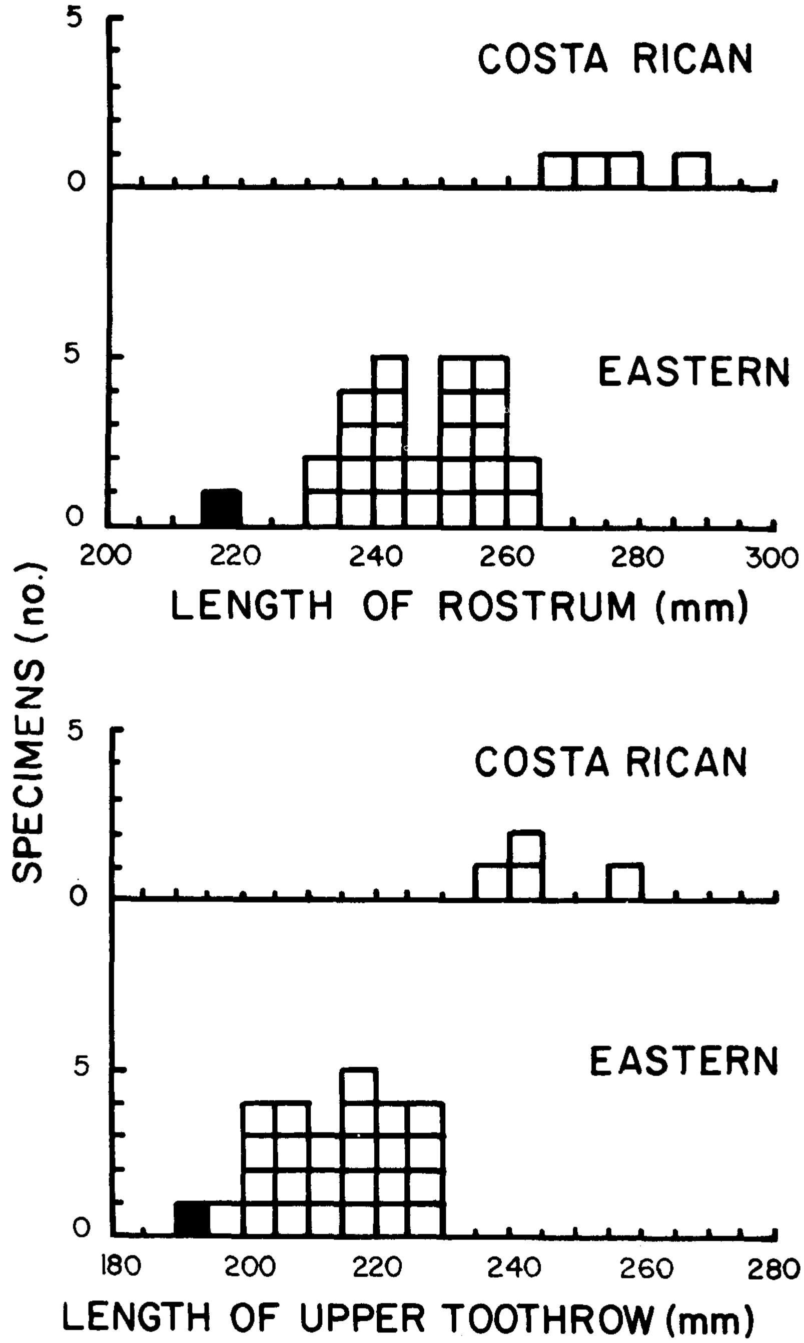


Figure 81. Geographical variation in skull measurements and proportions of spinner porpise, Costa Rican versus Eastern series: (top) length of rostrum (bottom) length of upper tooth row. Blackened square is infantile specimen discussed in text (continued).

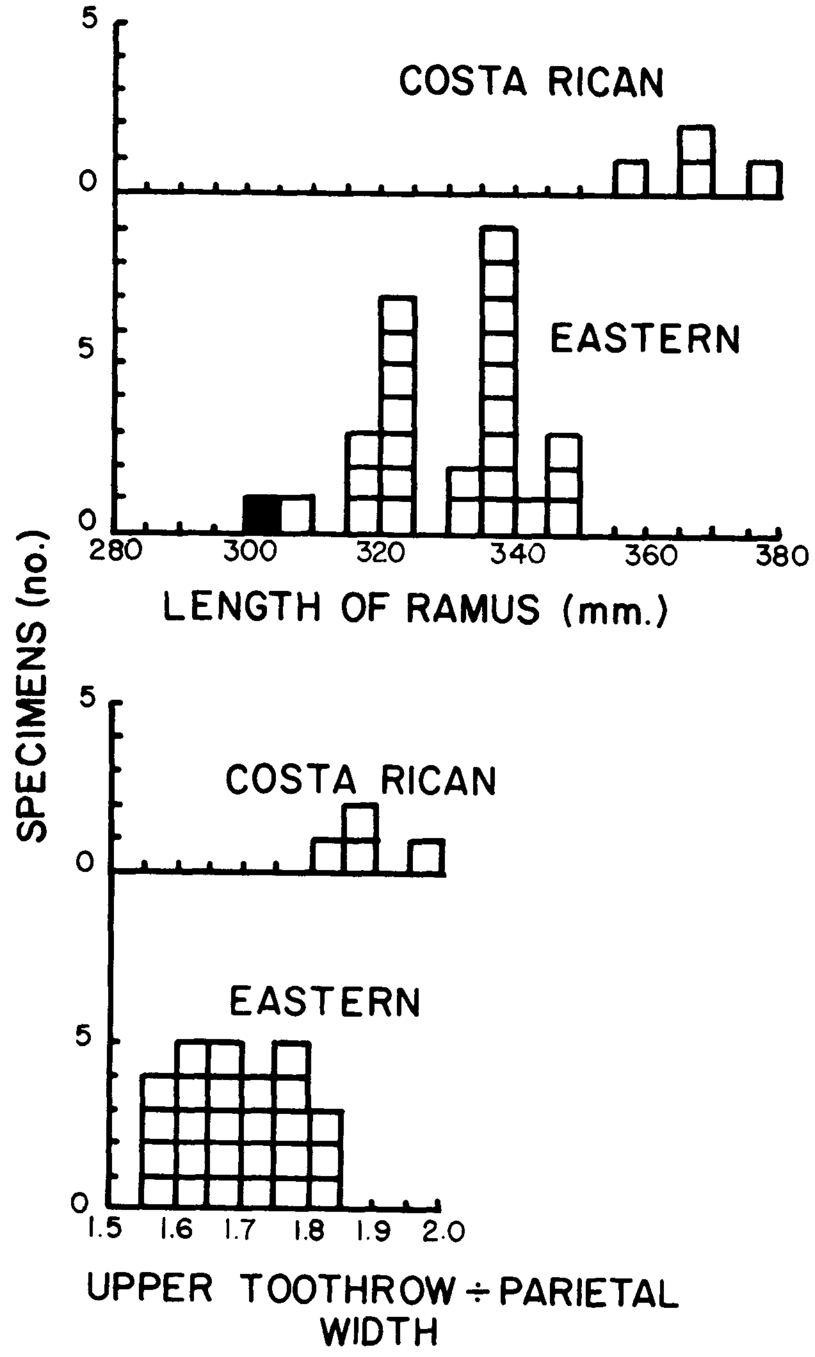


Figure 81 (continued). Geographical variation in skull measurements and proportions of spinner porpoise, Costa Rican versus Eastern series: (top) length of ramus, (bottom) relative length of tooth row. Blackened square is infantile specimen discussed in text.

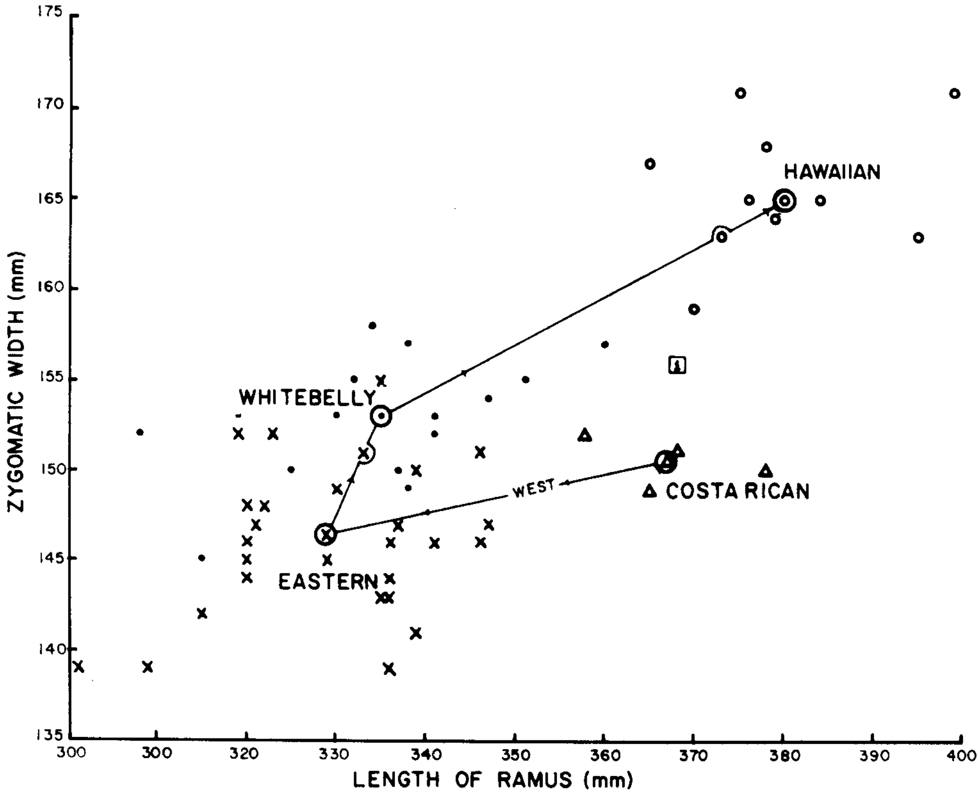


Figure 82. Geographical variation in the skull of the spinner porpoise in eastern tropical Pacific and Hawaiian waters: zygomatic width plotted on length of ramus. Circled symbols are series means. Square with numeral 1 is holotype of *S. longirostris* (Gray).

mere allometric growth is at work. The differing proportions must be responses to differential, and to some degree antagonistic, selection pressures on the various functional systems of the skull.

Vision apparatus. Mean orbit length in the Costa Rican series is slightly greater (2 mm) than in the eastern series, but overlap is nearly complete. The eastern, whitebelly, and Hawaiian series do not differ in size or proportions of the orbit.

Hearing apparatus. No ear bones are available for the Costa Rican forms. The whitebelly series exhibits mean periotic length 0.6 mm greater than that in the eastern series, but the ranges for the two series are nearly identical. The sample of ear bones from Hawaiian specimens is too small to allow comparison with the eastern Pacific forms.

Breathing and sound-producing apparatus. With the exception of a slightly greater average width of internal nares (no. 27), the Costa Rican and eastern series are not different in size and porportions of aspects of the breathing apparatus.

The eastern and whitebelly series are more divergent in proportions of the breathing and sound-producing system than in any of the other systems. All the widths encompassing the facial area are on the average greater in the whitebelly series, and the disparity in each case is greater than for condylobasal length (or, more precisely, CB length minus rostrum length), indicating proportional difference.

The Hawaiian form is broader facially than the whitebelly form.

Summary. The Costa Rican and eastern series are very different in size and proportions of the feeding apparatus but very similar in the other systems. The longer, more attenuate beak of the Costa Rican form is presumably an adaptation to local feeding conditions or prey items. The eastern and whitebelly series are very similar in size and proportions, with some slight divergence in proportions of the facial area in the hearing and sound-producing complex. The differences between these two series are slight indeed compared to those between the eastern and Costa Rican series or the whitebelly and Hawaiian series. The Hawaiian series diverges sharply from the whitebelly series in size of the feeding apparatus.

Postcranial skeleton

The sample for postcranial measurements is limited to physically mature specimens. No postcranial skeletons are available for the Costa Rican form and only 4 were available from Hawaii.

The mean values in the whitebelly series are greater than in the eastern series in length of the first thoracic neural spine (no. 69), length and width of the first vertebral rib (nos. 86 and 87), and length of the longest vertebral rib (no. 88). In length of the longest rib the two series very nearly do not overlap. In postcranial meristics, the eastern Pacific series differ only in placement of the first chevron bone, with an average difference of about one vertebra. Only 2 Hawaiian skeletons were sufficiently complete to allow collection of meristic data. The two had 70 and 72 vertebrae as opposed to the ranges of

72-76 for 20 whitebelly spinners, and 73-76 for 13 eastern spinners, indicating that the Hawaiian form may have fewer vertebrae than spinners in the eastern Pacific. The difference is in the precaudal series, as indicated by the positions of the first vertical foramen, last transverse process, and last neural process.

CLASSIFICATION AND DIAGNOSES

I conclude on the basis of the above evidence that the spinners of eastern Pacific and Hawaiian waters belong to a single geographically variable species. The name that should apply to this species is still a matter of question, for the reasons discussed above, but I provisionally use *Stenella longirostris* (Schlegel, 1841). The holotype of this species is from an unknown locality and does not fit well into the ranges of cranial measurements of any of the four geographical races defined above (fig. 82); therefore, the final disposition and nomenclature of the forms studied here must await the results of further discriminant analyses based on series covering more of the pantropical distribution of the spinners.

The four geographical races deserve subspecific status. The Costa Rican and Hawaiian series are separable from the eastern and whitebelly series, but I do not elevate the populations to specific rank because the series of adult skeletal specimens studied are quite small (4 and 10, respectively). The group of whitebelly specimens (24) for which color pattern data were available, moreover, is not sufficiently large to convince me that intergradation may not be encountered in larger series. The forms are very similar in cranial features, and even with discriminant analysis skeletal specimens can be separated only with 91% accuracy (table 20 and fig. 83). I therefore designate these forms also as subspecies only.

While the type of *D. longirostris* Schlegel obviously does not belong to the same subspecies as the eastern or whitebelly series (it may fall into the extremes of the Costa Rican or Hawaiian ranges), it is possible that further discriminant analyses may assign the types of *D. microps* Gray, *D. stenorhynchus* Gray, or *D. alope* Gray to one or the other of them, along with the names. I therefore do not name any of the four subspecies but designate them only as *S. longirostris* subspecies A, B, C, and D, recognizing that one of them (A or D) may be the type subspecies, and that applicable names may already exist for the subspecific portions of the trinomials for all or some of them.

Diagnoses of Subspecies of Spinner Porpoise, *Stenella longirostris* (Schlegel, 1841), of the Eastern Pacific and Hawaii

A. Costa Rican Spinner Porpoise, *Stenella longirostris* subsp. A (unnamed?).

Coloration. Poorly known, probably similar to that described by Perrin (1972) for the "eastern form" (B below).

External size and shape (based on 4 specimens). Adults 1.8-2.2 m long; tip of snout to apex of melon 14-17 cm, to flipper origin 44-47 cm, to dorsal fin tip 94-101 cm (46-53% body length); girth at axilla 69-77 cm (32-40% body length).

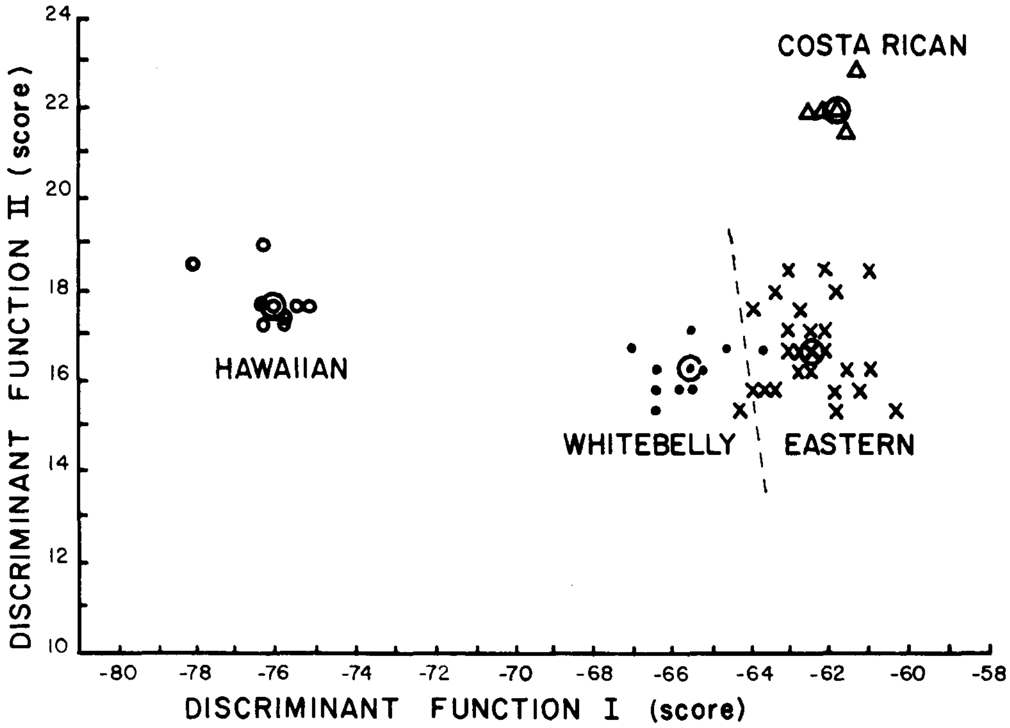


Figure 83. Geographical series of skeletal specimens of spinner porpoise plotted on first three discriminant functions (based on 25 measurements). Circled symbols are series means.

Skeleton. Condylobasal length 416-437 mm; rostrum length 269-288 mm (208-223% parietal width); rostrum width at base 70-77 mm; tip of rostrum to external nares 313-331 mm (75-80% CB length, 244-260% parietal width); postorbital width 149-152 mm (115-118% parietal width); major diameter of temporal fossa 30-34 mm, minor diameter 18-23 mm; length of upper tooth row 238-255 mm (185-198% parietal width); length of ramus 358-378 mm (278-293% parietal width); tooth counts $\frac{50-59}{51-59}$; no information on postcranial skeleton.

Range. Nearshore waters of Pacific coast of Central America. Recorded only from Costa Rica and El Salvador.

B. Eastern Pacific Spinner Porpoise, *Stenella longirostris* subsp. B (unnamed?).

Coloration. As described by Perrin (1972) for "eastern spinner."

External size and shape. Adults 1.6-1.9 m long, tip of snout to apex of melon 11-15 cm, to flipper origin 36-43 cm, to dorsal fin tip 83-95 cm in males (49-56% body length) and 85-101 cm in females (48-50% body length); girth at axilla 68-80 cm (40-49% body length). Canted fin and ventral hump as described by Perrin (1972 and above).

Table 20. Loading coefficients for first two discriminant functions separating Costa Rican, Eastern, Whitebelly, and Hawaiian series of crania of spinner porpoise. Measurements refer to figure 2

Number	Measurement	Discriminant Function I	Discriminant Function II
1	Condylobasal length	-.12411	-.04808
2	Length of rostrum	-.20709	-.16605
3	Width of rostrum at base	-.00716	-.00775
4	Width of rostrum at 60 mm	.49906	.32805
5	Width of rostrum at midlength	-.77836	-.45203
6	Width of premaxillaries at midlength of rostrum	.76464	.50564
7	Width of rostrum at 3/4 length	.73873	.19535
8	Tip of rostrum to external nares	.01450	.09391
9	Tip of rostrum to internal nares	.10828	.12807
10	Preorbital width	-.86583	-.17570
11	Postorbital width	.78164	.14861
12	Least supraorbital width	.20805	.00969
13	Width of external nares	-.08184	-.07997
14	Zygomatic width	-.72493	-.12731
15	Greatest width of premaxillaries	.32605	.14079
16	Parietal width	-.10273	-.00481
17	Height of braincase	.09109	.19587
18	Length of braincase	.06318	-.05494
19	Length of posttemporal fossa	-.07131	-.22892
20	Width of posttemporal fossa	-.06509	-.11738
25	Length of orbit	-.70907	-.11276
27	Width of internal nares	.20716	.11607
32	Length of upper tooth row	.23194	.05071
38	Length of ramus	.00695	.02887
39	Height of ramus	.10282	-.03908

Skeleton. Condylobasal length 351-407 mm; rostrum length 218-262 mm (180-213% parietal width); rostrum width at base 66-77 mm, tip of rostrum to external nares 252-304 mm (72-76% CB length, 208-246% parietal width); postorbital width 140-154 mm (110-124% parietal width); zygomatic width 139-153 mm (35-41% CB length, 109-123% parietal width); major diameter of temporal fossa 28-34 mm, minor diameter 15-23 mm; length of upper tooth row 192-229 mm (157-184% parietal width); length of ramus 301-348 mm (244-284% parietal width); tooth counts $\frac{46-61}{45-56}$; length of longest vertebral rib 217-229 mm; 73-76 vertebrae.

Range. Pacific coast of tropical North American from Tres Marias Islands south at least to Acapulco, and offshore approximately 800 km. Replaced on coast of Central America by the Costa Rican spinner (A, above).

This is the eastern Pacific form described or referred to (variously as *microps*) in Dailey and Brownell (1972), Daugherty (1966), Evans (1967), Evans, Sutherland, and Bell (1964), Fitch and Brownell (1968), Harrison (1969*a*, 1969*b*), Harrison, Boice, and Brownell (1969*b*), Harrison, Johnson, and Tedder (1967), Harrison, Johnson, and Young (1970), Hershkovitz (1966), Hester, Hunter, and Whitney (1963), Miller (1924), Miller and Kellogg (1955), Nelson (1899), Nishiwaki (1967 and 1972), Norris (1967), Perrin (1968, 1969, 1970*a*), Pilson and Waller (1970), Purves (1969), Rice (1967), Rice and Scheffer (1968), Scheffer and Rice (1963), True (1889), Van Gelder (1960) and Walker (1964).

C. Whitebelly Spinner Porpoise, *Stenella longirostris* subsp. C (unnamed?).

Coloration. As described by Perrin (1972).

External size and shape. Adults 1.6-1.9 m long; tip of snout to apex of melon 13-15 cm, to flipper origin 39-44 cm, to dorsal fin tip 91-102 cm (53-58% body length); girth at axilla 75-87 cm (43-52% of body length). Triangular fin and ventral hump as described by Perrin (1972 and above).

Skeleton. Condylobasal length 365-419 mm; rostrum length 227-271 mm (175-217% parietal width) rostrum width at base 69-78 mm; tip of rostrum to external nares 265-308 mm (71-75% CB length, 204-250% parietal width); postorbital width 148-158 mm (114-126% parietal width); zygomatic width 145-158 mm (37-42% CB length, 112-124% parietal width); major diameter of temporal fossa 28-35 mm; minor diameter 16-24 mm; length of upper tooth row 192-235 mm (148-189% parietal width); length of ramus 308-360 mm (237-282% parietal width); tooth counts $\frac{47-55}{47-54}$; length of longest vertebral rib 228-261 mm; 72-76 vertebrae.

Range. Far offshore tropical waters of eastern Pacific from approximately 800 km offshore to 140°W longitude.

This form has been previously described or referred to only in Perrin (1972) and Dailey and Perrin (1973).

D. Hawaiian Spinner Porpoise, *Stenella longirostris* subsp. D (unnamed?).

Coloration. As described by Perrin (1972).

External size and shape. Adults ⩾ 1.7-2.0 m long; tip of snout to apex of melon 17-19 cm, to flipper origin 42-51 cm, to dorsal fin tip 103-117 cm (58-60% body length); girth at axilla 71-86 cm (38-48% body length). Dorsal fin falcate, ventral hump absent except for slight development in large males.

Skeleton. Condylobasal length 431-464 mm; rostrum length 277-304 mm (206-241% parietal width); rostrum width at base 76-84 mm, tip of rostrum to external nares 319-349 mm (74-77% CB length, 238-277% parietal width); postorbital width 164-171 mm (122-130% parietal width); zygomatic width 159-171 mm (35-39% CB length, 119-130% parietal width); major diameter of temporal fossa 33-37 mm; minor diameter 23-27 mm; length of upper tooth row 241-263 mm (180-208% parietal width); length of ramus 365-399 mm (272-314% parietal width); tooth counts $\frac{48-59}{47-55}$; number of vertebrae 70-70 (2 specimens); no postcranial measurements available for physically mature specimens.

Range. Hawaiian waters. Specimens from Hawaiian waters that are referred in the literature to *Stenella longirostris* or *Stenella roseiventris* are of this subspecies.

Specimens from unknown localities in the eastern Pacific may also be classified by application of the discriminant functions in table 20 and comparisons of the scores with the scatterplot in figure 83.

Summary of Differences between the Subspecies

The Costa Rican form is longer and more attenuate, and has a proportionately longer, narrower skull than do the other three forms. The Hawaiian form is distinctive in its large, broad skull and sharply defined, tripartite color pattern. The eastern and whitebelly forms both have small skulls of intermediate breadth, but sharply different color patterns. The eastern form is largely dark, whereas the whitebelly form presents a two-tone appearance. The whitebelly form is also slightly more robust than the eastern form, and the correlated extreme development of ventral hump and forward cant of dorsal fin that is typical of adult eastern males is absent.

GENERAL CONCLUSIONS

Some generalizations relevant to the systematics of delphinids in general can be drawn on the basis of this examination of variation in *Stenella.*

1. Sharp geographical differentiation is to be expected over quite short distances, that is, hundreds or even tens of kilometers. In addition, less pronounced clinal variation is to be expected within the ranges of well-defined races.
2. Before progress can be made in revising any delphinid group (species, superspecies, genus), thorough studies must be made of variation owing to ontogeny, sexual dimorphism, and individual variability in that particular group. Few prior assumptions can be made about the sources of variation. This is demonstrated by the sharp differences in the patterns of variation of the two species studied here. For example, the spinner porpoise is sharply dimorphic in external proportions but only slightly so in skeletal features, whereas the exact opposite is true for the spotted porpoise. The spinner skull develops faster than the skull of the spotted porpoise. Patterns of relative growth of external features, for example, the flukes, differ sharply between the two species. The results of this study of large series are an adequate basis for evaluating variation in smaller series of the same two species from other parts of the world, but not necessarily for evaluation of geographical variation in series of other forms of other genera, for example, *Delphinus* or *Tursiops.*
3. The above caveat notwithstanding, some general tendencies in geographical variation are apparent. The rostrum and temporal fossae, that is, the feeding apparatus, vary most sharply in both forms studied, whereas the braincase varies least. Localized races with long versus short or with robust versus narrow snouts should be expected in other delphinid groups. Overall body size should also be expected to vary sharply over short distances.

SUMMARY

1. Spotted porpoise occur in coastal and offshore tropical waters in a triangularly shaped area of the eastern Pacific and in Hawaiian waters. The base of the triangle is the coastline from Cabo San Lucas, Mexico to Colombia, and the seaward apex is at about 10°N latitude, 145°W longitude.
2. Intensity of spotting varies along an east-west axis in the eastern Pacific. Coastal animals on the average are most heavily spotted, and those from the westernmost parts of the range are least spotted. Hawaiian animals are unspotted or sparsely spotted as adults.
3. Changes in external proportions of the spotted porpoise during development are owing primarily to a disproportionate rate of growth of the section of torso between the umbilicus and anus, combined with an early surge in growth of the snout. The snout apparently stops growing at puberty, but total body length continues to increase at least until the onset of physical maturity.
4. Adult female spotted porpoise average about 10 cm smaller than males but have relatively longer snouts, greater girth, and greater fluke span.
5. Individual variation in external proportions of the spotted porpoise is greatest in length of the snout. Of the appendages, the dorsal fin is most variable.
6. Spotted porpoise from very near the coast are larger than offshore specimens in all torso dimensions and in fluke span. The offshore animals have longer flippers. The Hawaiian form has a larger head than the offshore form.
7. The functional systems of the spotted porpoise skull have different patterns of postnatal development. The hearing apparatus is most precocious, followed by the vision apparatus, the braincase, the breathing and sound-producing apparatus, and the feeding apparatus, in that order. Skulls with 5 or more layers in the postnatal dentine can be considered "adult" for purposes of inclusion in taxonomic series.
8. The postcranial skeleton of the spotted porpoise develops more slowly than the skull, with the exception of its anteriormost elements. The scapula, vertebral centra, and long vertebral ribs show most protracted growth.
9. The sex of a spotted porpoise can be determined from measurements of the skull only if the specimen is physically mature. In general, males have larger braincases and shorter, broader rostra.
10. Individual variation in the skull of the spotted porpoise is greatest in the feeding apparatus, closely followed by the breathing and sound-producing apparatus. The remaining functional units of the skull are significantly less variable.
11. Geographical variation in the skeleton of the spotted porpoise indicates existence of distinct coastal and offshore forms. This confirms the results of the analysis of external size and shape. Of the functional systems of the skull, the two series are most disparate in the feeding apparatus, the offshore form having a shorter, more attenuate rostrum. Differences are smallest in the braincase. The coastal form is also larger in most postcranial measurements, but has on the average fewer vertebrae. Within the offshore series, there is an apparent east-west cline in absolute size; the most offshore animals are the largest. The Hawaiian spotted porpoise has a slightly greater parietal width, larger feeding apparatus, and more massive postcranial skeleton than the offshore form.

12. The taxonomy of the spotted porpoise is confused, but there appears to be only a single species in the Pacific. The name *Stenella attenuata* (Gray, 1846) is provisionally used for this species.

13. The eastern Pacific coastal, eastern Pacific offshore, and Hawaiian spotted porpoise deserve subspecific status within *Stenella attenuata.* Because many of the holotypes of spotted porpoise are from unknown localities, a trinomial can presently be assigned only to the coastal form, namely, *S. attenuata graffmani.* Skulls of unknown provenance within eastern Pacific and Hawaiian waters can be referred to one of the four forms with the help of discriminant functions.

14. The range of spinner porpoise in the eastern Pacific coincides that of the spotted porpoise almost exactly.

15. Patterns of developmental, sexual, and individual external variation differ between the spinner porpoise and the spotted porpoise. Attenuation in spinners is less during postpubertal development than in the spotted porpoise. Adults have proportionately larger appendages than juveniles. The dorsal fin is canted forward to varying degree in large males. Males and females do not differ in proportionate girth or size of appendages.

16. In external size and shape, as well as in coloration, the eastern Pacific specimens fall into three geographical series. "Costa Rican" (coast of Central America) spinners are longest and most attenuate. "Eastern" spinners (North American coast to about 800 km offshore) are greatest in girth and have the least canted dorsal fins. The Hawaiian spinner has a color pattern most like that of the whitebelly form but is larger.

17. The skeleton of the spinner porpoise develops in the same pattern as that of the spotted porpoise, except that cranial development proceeds more rapidly. The adult configuration is reached when 4 layers have been laid down in the dentine, and postpubertal elongation of the axial skeleton is less protracted, rendering overall growth more isogonic. Sexual dimorphism is negligible. Patterns of individual variation are similar to those in the spotted porpoise.

18. In skeletal features, the Costa Rican spinner is most divergent, having a very long, attenuate rostrum. Differences between the eastern and whitebelly series are comparatively slight. The Hawaiian spinner has a longer, broader skull than the eastern Pacific forms.

19. Taxonomy of the spinner porpoise is as confused as that of the spotted porpoise , but again there appears to be but a single species in the Pacific. The name *Stenella longirostris* (Schlegel,1841) is applied provisionally.

20. The Costa Rican, eastern, whitebelly, and Hawaiian spinners deserve subspecific status within *S. longirostris,* but trinomials cannot be assigned until the taxonomy has been adequately reviewed on a worldwide basis. Skulls of unknown provenance can be classified with discriminant functions.

ACKNOWLEDGMENTS

A very large number of people helped me in this study. I owe thanks to the members of my doctoral committee for their encouragements and criticisms. The cochairmen, Kenneth S. Norris and Carl L. Hubbs, made available to me all the pertinent data and study materials in their possessions and assisted me in innumerable ways. Dale W. Rice, Robert L. Brownell, Jr., and David W. Waller very generously turned over all their *Stenella* data and specimens to me. My colleagues Craig J. Orange, Gary D. Sharp, William E. Evans, Steve Leatherwood, and Susumu Kato collected specimens for me under trying conditions at sea. Assistance in collecting and processing data and specimens was furnished by several technicians in the Marine Mammals Assessment and Conservation Group of the Southwest Fisheries Center, including John La Grange, Robert L. Garvie, James M. Coe, David B. Holts, Charles W. Oliver, G. Michael Treinen, and A. Poshkus. Nancy K. Wiley, James R. Zweifel, and David Marston gave me indispensable help and advice in data processing. Lorraine C. Downing and Joanne Webber typed innumerable partial drafts from my scrawled manuscripts. Kenneth S. Raymond and Roy Allen prepared most of the illustrations. William E. Schevill gave me much help in locating references and citing them properly.

The National Marine Fisheries Service funded this work, and a succession of sympathetic and tolerant directors of the La Jolla Laboratory (of the Southwest Fisheries Center) and my immediate supervisors encouraged me to begin the studies and subsequently allowed me to continue them (and saw that they were supported) years beyond the time I had originally estimated the project would require. These were (in chronological order of entrapment) Richard R. Whitney, Roger E. Green, Frank J. Hester, Alan R. Longhurst, Paul E. Smith, and Izadore Barrett. The confidence placed in me by these men saw me through the many low points of the last several years.

Charles O. Handley, Jr., Ian McTaggart Cowan, Masaharu Nishiwaki, Richard G. Van Gelder, Donald R. Patten, and William E. Schevill very kindly allowed me to borrow museum materials in their charge. Charles O. Handley, Jr. and James M. Meade arranged for the difficult and costly preparation, at the U.S. National Museum, of the more than 100 skeletal specimens collected during the study. James Joseph, Director of Investigations of the Inter-American Tropical Tuna Commission, allowed me to use tuna boat logbook data collected by the commission.

To these people and others I have forgotten to mention, and especially to my long-suffering family, I express my deepest thanks.

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