

Abstract.—The spotted dolphin (*Stenella attenuata*) is found throughout much of the eastern tropical Pacific Ocean. A previous study evaluated morphological variation in skull morphology, but now specimens are available for a greater portion of the range. Also, corrections have been made in data and an assessment has been made evaluating repeatability of character measurements. We reassessed geographic variation in 30 cranial features (26 morphometric measures and 4 tooth counts) based on 611 museum specimens. All characters except two tooth counts showed statistically significant geographic variation, while 21 of the 30 characters exhibited significant sexual dimorphism. Males were larger in most characters; females were larger in some length measurements involving the rostrum and ramus. As in previous analyses, inshore *S. attenuata* were found to be very distinctive, so subsequent analyses focused on offshore spotted dolphins from 29° 5′ latitude-longitude blocks. Mantel tests and matrix correlations for 19 of the 30 features demonstrated significant “regional patterning,” whereas 22 of the characters were shown to have “local patterning.” Principal-components, canonical-variates, and cluster (UPGMA and function-point) analyses also were employed to assess geographic variation. In the eastern portion of the range, the subdivision between northern and southern offshore *S. attenuata* found in the previous investigation was confirmed. In general, blocks to the west (including one encompassing part of the Hawaiian Islands) were more like the southern blocks than those of the northeast. Morphological patterns were similar to those found in a number of environmental variables, particularly water depth, solar insolation (January), sea surface temperature (January and July), surface salinity, and thermocline depth (winter and summer). Present management units are inconsistent with the pattern of cranial variation; spotted dolphins from west of lat. 120°W probably should not be pooled with those to the east, as they show closer affinity with the Southern Offshore unit. In addition, the boundary between the Northern and Southern units should probably be moved north to about lat. 5°N.

Manuscript accepted 12 October 1993
Fishery Bulletin 92:324-346 (1994)

Reexamination of geographic variation in cranial morphology of the pantropical spotted dolphin, *Stenella attenuata*, in the eastern Pacific

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Spinner and spotted dolphins (*Stenella longirostris* and *S. attenuata*) have broadly overlapping ranges in the eastern tropical Pacific Ocean (Perrin et al., 1983). Information concerning geographic variation of these species is of both intrinsic scientific and practical interest. Dolphins in the region are killed as a result of purse-seining for yellowfin tuna (*Thunnus albacares*; Allen, 1985). The tuna often are found in association with these two dolphin species (or with *Delphinus delphis*), and fishermen set nets on the dolphin schools to capture tuna found below the dolphins. Estimates indicate that from 1985 to 1990 roughly 53,000 to 129,000 dolphins were killed annually as a result of fishing operations (Hall and Boyer 1987, 1988, 1989, 1990, 1991, 1992). Most recently the annual kill has dropped to approximately 15,000 to 27,000 (Hall and Lennert^{1,2}). Government regulations in the United States set limitations on U.S. vessels with respect to the

extent of dolphin mortality that will be permitted. Dolphins are managed by defining a series of management stocks. Data, such as those on skull morphology, can provide insight into the underlying population subdivision and may be of considerable value in defining geographic boundaries of biologically relevant management stocks (Dizon et al., 1992).

Douglas et al. (1992) have provided a detailed assessment of geographic variation in cranial morphology of spinner dolphins. For spotted dolphins, the most recent geographic-variation analyses using skull characteristics were by Douglas et al. (1984) and Schnell et

¹ Hall, M. A., and C. Lennert. 1992. Estimates of incidental mortality of dolphins in the purse-seine fishery for tunas in the eastern Pacific Ocean in 1991. Int. Whal. Commn. meeting doc. SC/44/SM6, 5 p.

² Hall, M. A., and C. Lennert. 1993. Incidental mortality of dolphins in the eastern Pacific Ocean tuna fishery in 1992. Int. Whal. Commn. meeting doc. SC/45/SM1, 5 p.

al. (1986). Numerous additional specimens have become available, particularly from the western portion of the range and Hawaii. The repeatability of 36 skull measures used in previous studies (Douglas et al., 1984; Schnell et al., 1986) was appraised, as was done previously by Douglas et al. (1992) for spinner dolphins. Also, some immature specimens had inadvertently been incorporated into the previous spotted dolphin analyses. For these reasons, we have undertaken a reassessment of geographic variation and sexual dimorphism of spotted dolphins from the eastern tropical Pacific. This study provides an opportunity to re-evaluate variation patterns previously described and to compare directly patterns of variation found in spotted and spinner dolphins.

Materials and methods

Overall, data-gathering and assessment procedures outlined by Douglas et al. (1992) were used. We measured 611 adult museum specimens (maturity evaluated on the basis of premaxilla fusion with maxilla at distal end of rostrum; Dailey and Perrin, 1973) of spotted dolphins (Fig. 1). These included 534 of 613 specimens used in earlier studies (Douglas et al., 1984; Schnell et al., 1986; 79 specimens previously used had been incorrectly aged or had inadequate locality data) along with 77 new specimens.

As was done with spinner dolphins (Douglas et al., 1992), the first specimen set was measured by M. E. Douglas and the new specimens by W. F. Perrin. In addition, Perrin remeasured 81 specimens of spinner and spotted dolphins measured by Douglas to determine whether measurements were repeatable. Initially, 36 characters were evaluated (illustrations and character definitions given in Schnell et al., 1985). Comparisons of measurements taken on the same specimens by the two investigators indicated that 6 of the original 36 measurements (i.e. width of left premaxillary [at midline of nares], width of right premaxillary [at midline of nares], separation of pterygoids, length of left tympanic cavity, length of right tympanic cavity, and width at pterygobasiooccipital sutures) should be deleted, because we were not able consistently to repeat these measurements. For some other measurements, there were differences between investigators, but the differences were consistent (e.g. one obtained measurements that were smaller than those reported by the other). Therefore, we calculated regression equations for each of the remaining characters based on the 81 jointly measured specimens. These regression equations were used to convert the measurements from the rest of the initial specimens to appropri-

ate values for inclusion with the measurements taken by Perrin. Through these procedures, we developed a data set of 30 characters (see Table 1) for the 611 specimens.

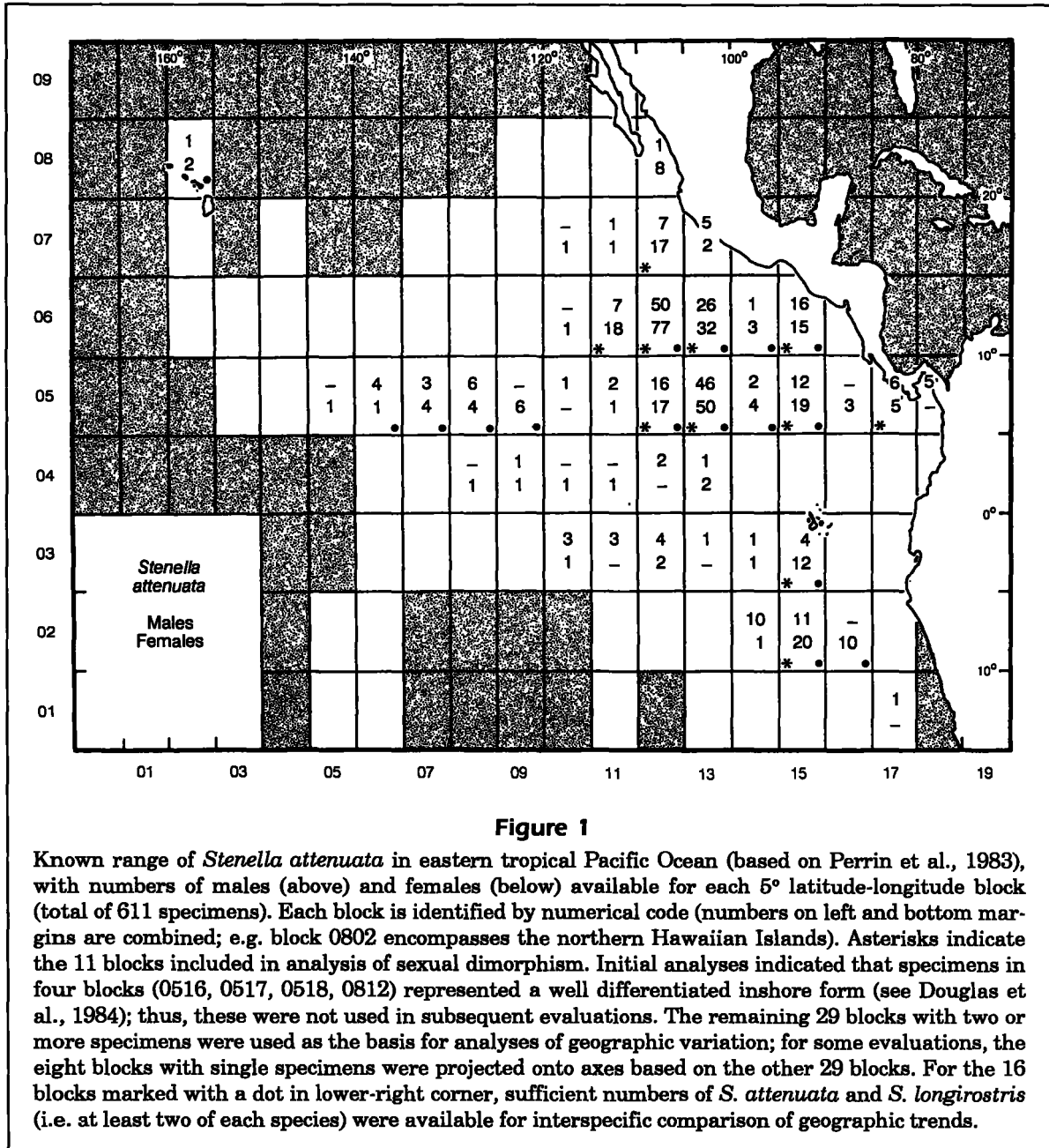
Specimens were not used if, because of damaged parts, we could not obtain most of the 30 measurements. Missing values (0.50% of total) for included specimens were estimated by linear regression³ onto the character that explained the greatest proportion of the variance for the variable being considered.

Animals were assigned to 5° latitude-longitude blocks and each geographic block assigned a numerical code (see Fig. 1). These codes were modified slightly from those employed by Schnell et al. (1986) to accommodate new specimens from more westerly blocks. We had specimens available from 41 blocks, 8 of which were represented by only a single specimen and 4 of which were inshore blocks (i.e. contained only specimens of the inshore form; Douglas et al., 1984). The 29 blocks that were not inshore blocks and had more than one specimen were used as the basis for most geographic variation analyses. While several of the 29 blocks have relatively small samples, geographic-patterning tests (described below) suggested that, in general, sample values are representative of what is expected for these blocks based on their geographic positions.

Schnell et al. (1985) showed *S. attenuata* to be sexually dimorphic for 23 of 36 characters. Because some specimens used in that analysis were removed and new specimens added (see above), we conducted a two-way analysis of variance (ANOVA) for block and sex, based on specimens in the 11 blocks with at least four of each sex (Fig. 1). Correction terms were obtained to adjust measurements of the larger sex downward and the smaller sex upward, thus producing sex-adjusted or "zwitter" measurements (method described in more detail by Schnell et al., 1985). As a result, we were able to combine specimens for both sexes in an overall analysis of geographic variation.

To assess whether combining specimens from different cruise sets within blocks confounded geographic patterns based on blocks, we performed a nested ANOVA for cruise sets within the 12 blocks for which two specimens were obtained from at least two cruise sets. Blocks employed in this analysis (with numbers of cruise sets in parentheses) were the following: 0215 (4), 0216 (3), 0312 (2), 0506 (2), 0507 (2), 0512 (9), 0513 (10), 0515 (2), 0612(6), 0613 (7), 0615 (3), and 0712 (2).

³ "Missing Data Estimator" program by Dennis M. Power, Santa Barbara Mus. Nat. Hist., pers. commun. 1975.



Correlation, ordination, and clustering

After conversion to zitters, characters were standardized (means=0, standard deviations=1). Product-moment correlations were computed among characters, and associations among characters were summarized by clustering characters (unweighted pair-group method with arithmetic averages; UPGMA). This technique is a type of hierarchical cluster analysis that also was used to summarize average distance coefficients (Sneath and Sokal, 1973) calculated for all pairs of blocks based on stan-

dardized data. Cophenetic correlation coefficients indicate the extent to which distances in resulting dendrograms accurately represented original inter-block morphologic distances.

Standardized data also were summarized by using a nonhierarchical *K*-group method (function-point cluster analysis; described in Katz and Rohlf [1973] and Rohlf et al. [1979]). Through use of this technique, blocks are assigned to subgroups at a specified level. A *w*-parameter value used in function-point clustering was varied. An hierarchical, but not necessarily nonoverlapping, system of clusters was

Table 1
Geographic variation and sexual dimorphism in *Stenella attenuata* evaluated for 30 characters.

Character ¹	F-value ²		Mean ³		Correction factor ⁴	Percentage difference ⁵
	Block	Sex	Male	Female		
1 Condylbasal L.	10.59***	1.94	397.0	398.2	-0.74	-0.30
2 L. Rostrum (from Base)	6.94***	13.49***	236.7	239.5	-1.55	-1.20
3 L. Rostrum (from Pterygoid)	6.88***	6.84**	278.5	281.0	-1.31	-0.87
4 W. Rostrum (at Base)	14.20***	25.13***	83.3	81.8	0.73	1.85
5 W. Rostrum (at 1/4 L.)	12.25***	51.82***	57.1	55.2	0.90	3.32
6 W. Rostrum (at 1/2 L.)	13.82***	47.61***	42.4	40.9	0.78	3.78
7 W. Premax. (at 1/2 L.)	8.51***	72.88***	23.6	22.4	0.60	5.25
8 W. Rostrum (at 3/4 L.)	8.65***	73.90***	29.9	28.0	0.96	6.66
9 Preorbital W.	16.92***	45.92***	149.5	146.6	1.43	1.97
10 Postorbital W.	22.46***	42.23***	167.8	165.1	1.31	1.63
11 Skull W. (at Zygomatic P.)	21.98***	51.05***	167.4	164.5	1.46	1.79
12 Skull W. (at Parietals)	5.73***	54.11***	129.6	136.4	1.58	2.34
13 Ht. Braincase	10.61***	53.87***	95.9	93.7	1.04	2.36
14 L. Braincase	15.67***	39.94***	113.1	111.2	0.95	1.71
15 Max. W. Premax.	8.89***	4.45*	66.2	65.7	0.27	0.85
16 W. External Nares	7.38***	0.03	42.5	42.5	0.01	0.02
17 L. Temporal Fossa	22.41***	16.79***	70.1	68.4	0.82	2.53
18 W. Temporal Fossa	20.60***	28.50***	55.2	53.2	0.93	3.72
19 Orbital L.	2.97**	0.06	47.4	47.4	0.02	0.10
20 L. Antorbital P.	8.33***	4.30*	36.9	36.4	0.24	1.43
21 W. Internal Nares	9.58***	12.80***	47.4	46.6	0.36	1.58
22 L. Up. Toothrow	6.20***	10.56**	204.3	206.7	-1.29	-1.16
23 No. Teeth (Up. Lf.)	0.96	1.54	41.4	41.2	0.10	0.47
24 No. Teeth (Up. Rt.)	0.98	0.65	41.3	41.1	0.07	0.33
25 No. Teeth (Low. Lf.)	2.89*	0.02	41.0	40.9	-0.01	-0.02
26 No. Teeth (Low. Rt.)	2.82**	1.02	40.8	41.0	-0.08	-0.36
27 L. Low. Toothrow	5.38***	11.63***	198.6	201.2	-1.40	-1.28
28 Ht. Ramus	16.13***	0.12	57.3	57.1	0.38	0.24
29 Tooth W.	12.14***	19.65***	3.4	3.3	0.06	3.55
30 L. Ramus	9.02***	8.86**	335.5	338.3	-1.48	-0.82

¹ Abbreviations: Ht. = height; L. = length; Lf. = left; Low. = lower; Max. = maximum; No. = number; P. = process; Premax. = premaxillary; Rt. = right; Up. = upper; W. = width.

² F-values from main effects two-way analysis of variance (5* block vs. sex) involving 11 blocks (*P < 0.05; **P < 0.01; ***P < 0.001). Total of 170 individuals. Degrees of freedom 10 for among-block variation and 1 for between sexes.

³ Unweighted mean for 11 blocks.

⁴ Added to all individual female measurements and subtracted from all individual male measurements to correct for sexual differences.

⁵ Difference between sexes (males minus females) multiplied by 100; the resulting value was divided by average of male and female means.

obtained by repeating the analysis at different clustering levels. Results are displayed in modified skyline diagrams (Wirth et al., 1966).

Using standardized data, we constructed scatter diagrams by projecting blocks onto the first two principal components (Sneath and Sokal, 1973) extracted from a matrix of correlations among the 30 characters. Canonical-variates analysis also was employed to obtain the subset of variables that shows the greatest interblock separation relative to

intra-block variation (Program P7M of BMDP statistical software; Dixon, 1990). Plots of the first two canonical variables show the maximum separation of blocks in two-dimensional space.

Mantel test for geographic patterning

A Mantel (1967) test was used to assess interlocality variation in each character and determine whether measures are geographically patterned or, alterna-

tively, vary spatially at random. The observed association between sets of character differences and geographic distances was tested relative to its permutational variance, and the resulting statistic compared against a Student's *t*-distribution with infinite degrees of freedom. We performed analyses using GEOVAR, a computer-program library for geographic variation analysis (written by David M. Mallis and provided by Robert R. Sokal, State University of New York at Stony Brook).

Character differences were compared first with actual geographic distances (in nautical miles) between centers of blocks and then with reciprocals of distances. In evaluations of reciprocals, where distances are scaled in a nonlinear manner, longer distances are considered effectively to be equal, and the portion of the scale involving smaller distances is expanded. Thus, use of reciprocals of distances increases the power of analyses to reveal geographic patterns that are "local" in nature (i.e. involving closely placed blocks), whereas tests involving nautical-mile distances evaluate "regional" trends. Positive associations of character differences and nautical-mile distances are indicated by positive *t*-values, while negative *t*-values denote such associations when using distance reciprocals. Douglas et al. (1992) provided a simplified example to demonstrate use of the Mantel procedure.

We also computed matrix correlations (Sneath and Sokal, 1973) between character differences and the associated geographic distances or reciprocals of distances between localities. The statistical signifi-

cance of these coefficients cannot be tested in the conventional way, because all pairs of localities were used and these are not statistically independent. However, the resulting values can be used as descriptive statistics indicating the degree of association of difference values.

Morphological-environmental covariation

We calculated product-moment correlations of block means for morphological characters with environmental variables. Data were available for 13 environmental variables for the eastern tropical Pacific Ocean (Table 2; data sources summarized in Douglas et al., 1992). The list of environmental variables used is somewhat different than that employed by Schnell et al. (1986), because data for some of the variables were not available for all blocks in the broader geographic range being considered in the current study. We also used UPGMA to summarize associations among these environmental variables for 51 blocks; since these two dolphin species have broadly overlapping distributions in the eastern tropical Pacific, the blocks used are representative of areas inhabited by *S. attenuata*.

In order to obtain summary variables reflecting overall environmental trends, we conducted a principal-components analysis of the 13 environmental variables for 51 blocks with specimens of *S. longirostris* (Douglas et al., 1992) or *S. attenuata* or both. Individual blocks were projected onto the resulting environmental principal components based

Table 2
Environmental measurements compiled for each 5° latitude-longitude block.¹

- 1 Sea Current (N., Winter)—Average northern component (in knots) of surface water current in winter.
- 2 Sea Current (W., Winter)—Average western component (in knots) of surface water current in winter.
- 3 Water Depth—Average sea depth (in m).
- 4 Solar Insolation (Jan.)—Average incoming solar radiation for January (in gm-cal/cm²).
- 5 Solar Insolation (Annual)—Average annual incoming solar radiation in gm-cal/cm².
- 6 Sea Surface Temp. (Jan.)—Average January sea surface temperature (in °C).
- 7 Sea Surface Temp. (July)—Average July sea surface temperature (in °C).
- 8 Sea Surface Temp. (Ann. Var.)—Average annual sea surface temperature variation (in °C).
- 9 Oxygen Min. Layer (Depth)—Annual mean depth (in m) of absolute oxygen minimum surface with respect to the vertical.
- 10 Surface Salinity—Average salinity (‰) of surface sea water.
- 11 Thermocline Depth (Winter)—Mean depths (in m) to top of thermocline for January, February, and March.
- 12 Thermocline Depth (Summer)—Mean depths (in m) to top of thermocline for July, August, and September.
- 13 Surface Dissolved Oxygen—Annual mean dissolved oxygen (mL/L) of surface sea water.

¹ Data sources listed in Douglas et al. (1992: table 2). Abbreviations: Ann. Var. = annual variation; Jan. = January; Min. = minimum; N. = north; Temp. = temperature; W. = west.

on standardized data. These environmental components served as composite environmental variables for comparisons with morphological variables.

Matrix correlations and Mantel tests were used to test for local and regional patterning of environmental variables. Also, differences between each pair of blocks for a given morphological variable were compared with those for an environmental variable.

Interspecific comparisons

The predominant trends in the data sets for each of *S. attenuata* and *S. longirostris* were summarized with principal components and canonical variables. Information is available for 16 blocks from which both offshore *S. attenuata* and *S. longirostris* were sampled (Fig. 1). These blocks are representative of the total geographic range investigated in our studies. In order to compare general patterns of variation in the two species, we calculated product-moment correlations, Mantel tests, and matrix correlations for individual morphological characters, principal-component projections, and canonical-variable projections of these 16 blocks.

In our analyses, average distances based on morphological characters were computed between each pair of localities. To evaluate the extent of similarity in geographic patterns, the original distance matrices for each species were modified such that only distances among the 16 localities common to both species were included. These matrices were then compared by using the Mantel test and computing the matrix correlation.

Results

Sexual dimorphism

Table 1 includes mean measurements for males and females based on 11 blocks. For two-way ANOVAs assessing geographic block and sex ($df=21, n=461$), all but 5 of the 30 were very highly significant ($P<0.001$). The probability was 0.02 for number of teeth (lower right) and 0.007 for orbital length. Two characters showed no significant variation (upper tooth counts) and one character (number of teeth [lower left]) was close to significant ($P<0.06$). Statistically significant interactions ($P<0.05$) between block and sex were found for five of the characters: condylobasal length; width of rostrum (at 1/4 length); width of rostrum (at 1/2 length); width of rostrum (at 3/4 length); and width of internal nares. Interaction denotes that the degree of sexual dimorphism differs among blocks for these characters.

Sexual dimorphism was significant for 22 of the 30 characters (Table 1). Females had longer ros-

trums, which is reflected in a number of characters (i.e. 2, 3, 22, 27, 30). In general, males had wider skulls and tended to be larger for nonrostral portions of the skull. Percentage differences between sexes are presented in Table 1. The average absolute difference (i.e. sign ignored) between the sexes for the 30 characters was 1.78%. For 8 characters where females were larger, the average difference was 0.75%, whereas for 22 characters where males were larger the average difference was 2.16%. The greatest differences were found for width of premaxillary (at 1/2 length) and width of rostrum (at 3/4 length)—5.25% and 6.66%, respectively.

Table 3 shows the results for the nested ANOVA for cruise sets within blocks. Twenty-three of the 30 characters showed highly significant or very highly significant block effects, whereas only three characters (those involving the temporal fossa and length of braincase) reflected highly significant or very highly significant effects for cruise set. Even in those three cases, block effects were more pronounced. Therefore, we conclude that combining cruise sets into blocks did not have an important confounding influence on geographic patterns found among blocks.

Correlation, ordination, and clustering

Most character pairs had positive correlations. An exception was tooth counts and temporal fossa measurements, which tended to have negative correlations with skull width measurements. The dendrogram in Figure 2 summarizes absolute correlations (i.e. sign of correlation ignored) among characters based on 29 blocks to provide an assessment of character covariation. The width of external nares was the character with the least association with other measures. Tooth characters join and are separated from the remaining morphometric characters. Braincase measures and skull width (at parietals) cluster in another relatively distinct group. The remaining characters are arranged in two groups. The cluster at the top of Figure 2 includes most length measurements and height of ramus. Width measurements along with length of antorbital process, orbital length, and length of temporal fossa are included in the adjoining major cluster (Fig. 2).

Table 4 includes character loadings on the first two principal components based on data for 29 blocks. Component I explains 45.0% of the total variance for the 30 characters, whereas component II summarizes an additional 16.8% (cumulative total of 61.8%). Projections of blocks onto the two components are depicted in Figure 3, and a map (Fig. 4) is included that renders geographic block projections onto the first component. Component I repre-

Table 3

Results of nested ANOVA (F -values) for different cruise sets within 12 latitude-longitude blocks of offshore *Stenella attenuata*.

Character ¹	F -value	
	Cruise set	Block
1 Condylbasal L.	1.28	3.03***
2 L. Rostrum (from Base)	1.34	3.25***
3 L. Rostrum (from Pterygoid)	1.65*	4.36***
4 W. Rostrum (at Base)	1.25	8.86***
5 W. Rostrum (at 1/4 L.)	1.60*	7.51***
6 W. Rostrum (at 1/2 L.)	1.12	8.34***
7 W. Premax. (at 1/2 L.)	1.29	5.25***
8 W. Rostrum (at 3/4 L.)	1.01	5.39***
9 Preorbital W.	1.25	10.87***
10 Postorbital W.	1.22	11.31***
11 Skull W. (at Zygomatic P.)	1.27	10.81***
12 Skull W. (at Parietals)	0.97	1.11
13 Ht. Braincase	1.55*	1.55
14 L. Braincase	1.83**	3.59***
15 Max. W. Premax.	1.22	4.01***
16 W. External Nares	0.95	3.00***
17 L. Temporal Fossa	2.13***	7.54***
18 W. Temporal Fossa	1.87**	9.48***
19 Orbital L.	1.29	1.24
20 L. Antorbital P.	0.82	5.00***
21 W. Internal Nares	1.09	3.47***
22 L. Up. Toothrow	1.33	2.67**
23 No. Teeth (Up. Lf.)	1.23	1.22
24 No. Teeth (Up. Rt.)	1.19	0.78
25 No. Teeth (Low. Lf.)	1.47*	2.57**
26 No. Teeth (Low. Rt.)	1.45*	2.57**
27 L. Low. Toothrow	1.63*	2.45**
28 Ht. Ramus	1.09	1.77
29 Tooth W.	1.31	1.45
30 L. Ramus	1.25	2.37**

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

¹ Abbreviations identified in Footnote 1 of Table 1.

Table 4

Principal component loadings for offshore *Stenella attenuata* involving character means for 29 latitude-longitude blocks.

Character ¹	Component ²	
	I	II
1 Condylbasal L.	0.812	-0.505
2 L. Rostrum (from Base)	0.786	-0.483
3 L. Rostrum (from Pterygoid)	0.795	-0.446
4 W. Rostrum (at Base)	0.867	0.206
5 W. Rostrum (at 1/4 L.)	0.923	0.157
6 W. Rostrum (at 1/2 L.)	0.855	0.308
7 W. Premax. (at 1/2 L.)	0.863	0.161
8 W. Rostrum (at 3/4 L.)	0.868	0.211
9 Preorbital W.	0.930	0.235
10 Postorbital W.	0.940	0.181
11 Skull W. (at Zygomatic P.)	0.938	0.173
12 Skull W. (at Parietals)	0.740	0.270
13 Ht. Braincase	-0.002	0.225
14 L. Braincase	0.508	-0.325
15 Max. W. Premax.	0.366	-0.059
16 W. External Nares	0.286	-0.311
17 L. Temporal Fossa	-0.544	-0.576
18 W. Temporal Fossa	-0.375	-0.541
19 Orbital L.	0.655	-0.018
20 L. Antorbital P.	0.805	0.203
21 W. Internal Nares	0.604	0.000
22 L. Up. Toothrow	0.705	-0.588
23 No. Teeth (Up. Lf.)	-0.137	-0.668
24 No. Teeth (Up. Rt.)	-0.112	-0.726
25 No. Teeth (Low. Lf.)	-0.301	-0.673
26 No. Teeth (Low. Rt.)	-0.341	-0.635
27 L. Low. Toothrow	0.680	-0.632
28 Ht. Ramus	0.608	0.355
29 Tooth W.	-0.129	0.118
30 L. Ramus	0.803	-0.528

¹ Abbreviations identified in Footnote 1 of Table 1.

² Relatively high loadings highlighted in bold as follows: (component I) $> |0.8|$; (II) $> |0.6|$.

sents general size, with relatively high character loadings (Table 4) for most characters, the exceptions being tooth characters and the two measurements of the temporal fossa. The specimens from blocks in the northeastern portion of the range tend to be small (Figs. 3 and 4), whereas those to the south and southwest typically are larger. The largest specimens were found in block 0802, which encompasses a portion of the Hawaiian Islands. Component II reflects tooth counts and measurements associated with toothrow length (Table 4). Blocks with relatively high values for these characters are found near the top of Figure 3, whereas those with low values tend to be near the bottom.

Blocks with single specimens were not used in the delineation of the principal components but have

been projected onto components calculated by using the 29 blocks (Fig. 3). In general, the single-specimen blocks fall close to where one would predict based on their geographic position; some exceptions are expected based simply on expected chance variation.

Interblock morphological differences are summarized in the phenogram in Figure 5. Two blocks (0312 and 0802) are loosely joined in the most disparate cluster. Remaining blocks are divided into two clusters. The one represented at the top of Figure 3 includes the blocks from the south, southwest, and west, whereas the other includes blocks from the northeastern portion of the range.

Clusters based on the function-point procedure are summarized in the modified skyline diagram in Figure 6A. The most distinctive block is 0802 (en-

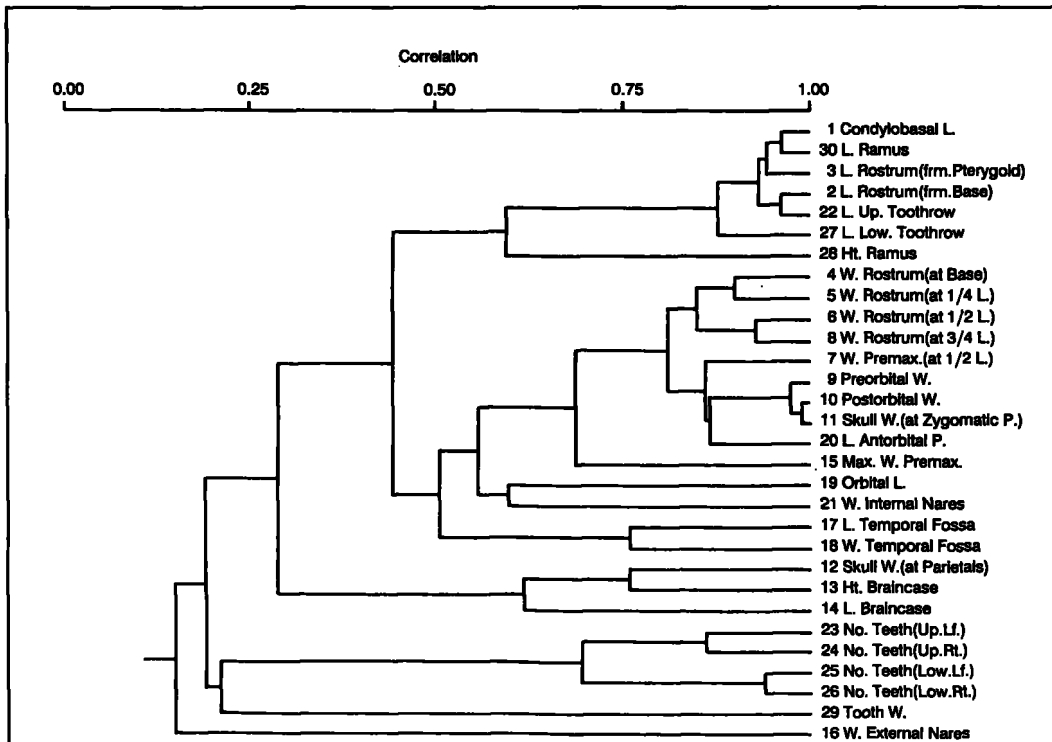


Figure 2

Correlations among characters based on character means for 29 latitude-longitude blocks. Clustering performed using UPGMA on absolute correlations among characters (i.e. negative signs removed). Cophenetic correlation coefficient is 0.87.

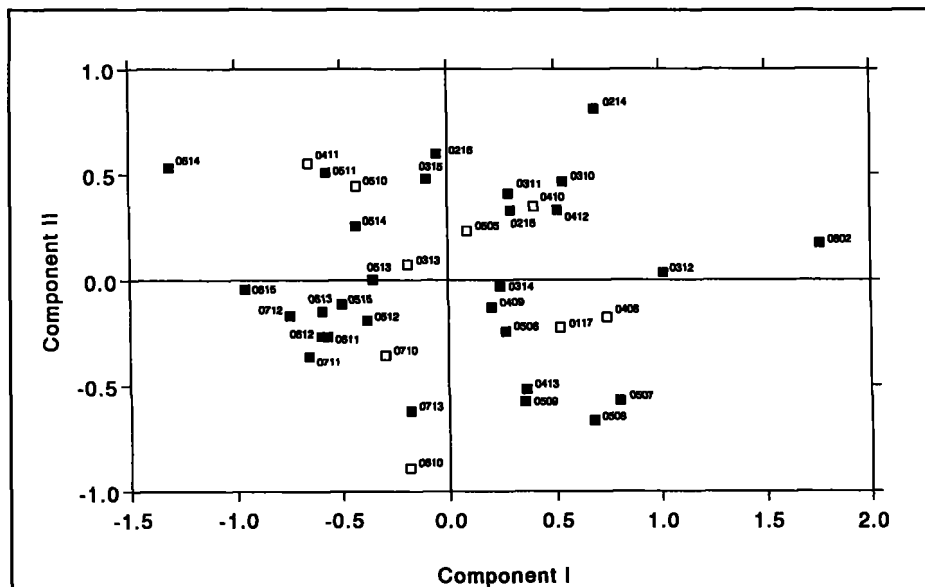
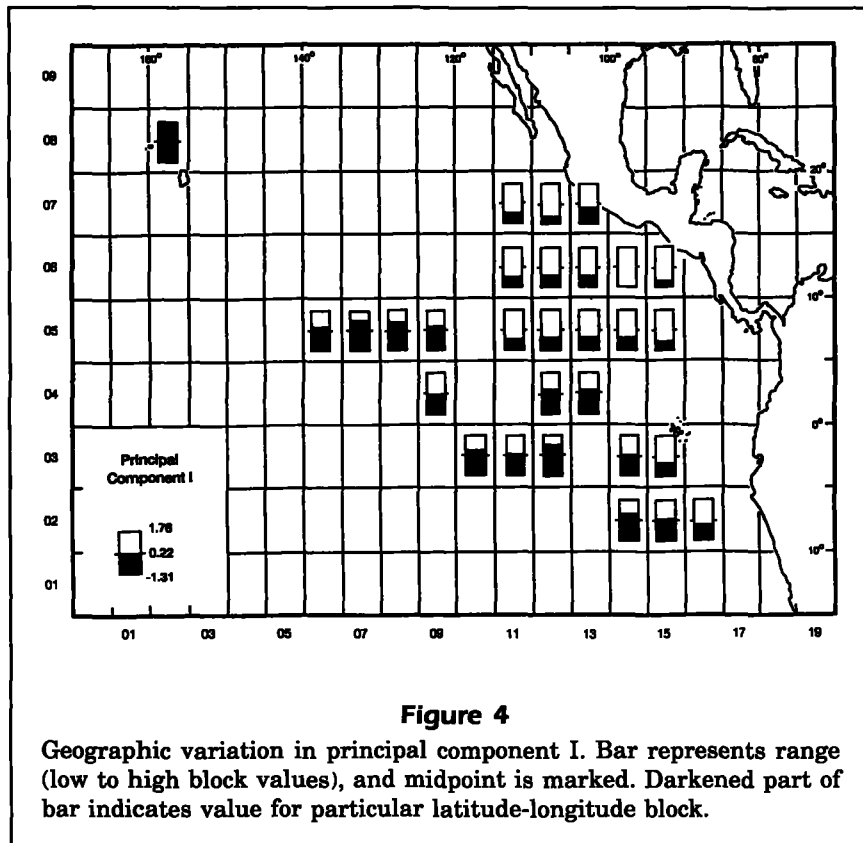


Figure 3

Projections of blocks onto first two principal components based on 30 characters. Solid symbols indicate 29 latitude-longitude blocks on which analysis was conducted. Open symbols represent blocks with only single specimens projected onto axes generated from 29 blocks with two or more specimens.



compassing part of Hawaiian Islands) at the right of the diagram. A number of single blocks (0312, 0314, 0311) are separated from the others at w -values of 3.10 and 2.87. Most of the blocks from the northeastern portion of the range were included in a single cluster at lower w -values, although some individual blocks were separated by themselves (e.g. 0614, 0711).

In Figure 6B, a skyline diagram is included that is based on five characters: length of rostrum (from pterygoid); preorbital width; length of braincase; length of temporal fossa; and width of temporal fossa. These variables were identified by using canonical-variates analysis (reported below) as those that in combination provided the greatest discrimination among blocks. The use of function-point clustering on these selected characters provided clusters that persisted through several clustering levels. At the w -value of 1.38, four clusters were formed. The Hawaiian Island block (0802) is in a group by itself (on left side of Fig. 6B). The blocks to the south, southwest, and west are in a second assemblage (i.e. 0214 through 0506), while the northeastern blocks form the other major cluster (i.e. 0513 through 0713). Block 0711 is separated into its own group. At w -values less than 1.38, the second cluster is subdivided and the southern blocks are included with some from the southwest.

Canonical-variates analysis selected five characters (Table 5). Blocks are projected onto the first two canonical variables resulting from this analysis (Fig. 7), whereas Figure 8B shows geographically the distribution of geographic variation projections onto canonical variable 1. The eigenvalue for canonical variable 1 is 1.00, while that for variable 2 is 0.19. The two together summarize 82.4% of the variance in the five characters. In the scatter diagram (Fig. 7), blocks with only single specimens are projected onto the canonical variables generated by using the other 29 blocks. As indicated in Table 5, the most important character in the canonical-variates analysis was postorbital width. (Fig. 8A). It has relatively small values in the northeastern portion of the range, and considerably larger values in other areas to the south, southwest, and west. The largest postorbital width measurements are found in specimens taken near the Hawaiian Islands (0802). The geo-

graphic configuration of this character is very similar to the general pattern exhibited by the first canonical variable (Fig. 8B). Canonical variable 1 and principal component I (Fig. 4) have similar geographic patterns. Canonical variable 2 does not reflect any particular geographic pattern. It basically contrasts three blocks (0711, 0802, and 0311) with the others, as indicated by these three being separated in the upper portion of Figure 7 from other blocks.

Mantel test for geographic patterning

Results of Mantel tests and matrix correlations comparing interblock character differences with geographic distances (in nautical miles) and with the reciprocals of geographic distances are presented in Table 6. Regional patterning, as indicated by a significant association with geographic distance, was found for 18 (60.0%) of the 30 characters. In these characters, the localities the farthest apart tended to exhibit the greatest morphological difference. Local patterning, which is judged based on a significant negative association between geographic distance-reciprocals and morphological differences, was found in 22 (73.3%) of the characters. Not unexpectedly, virtually all characters (i.e. all but one) exhib-

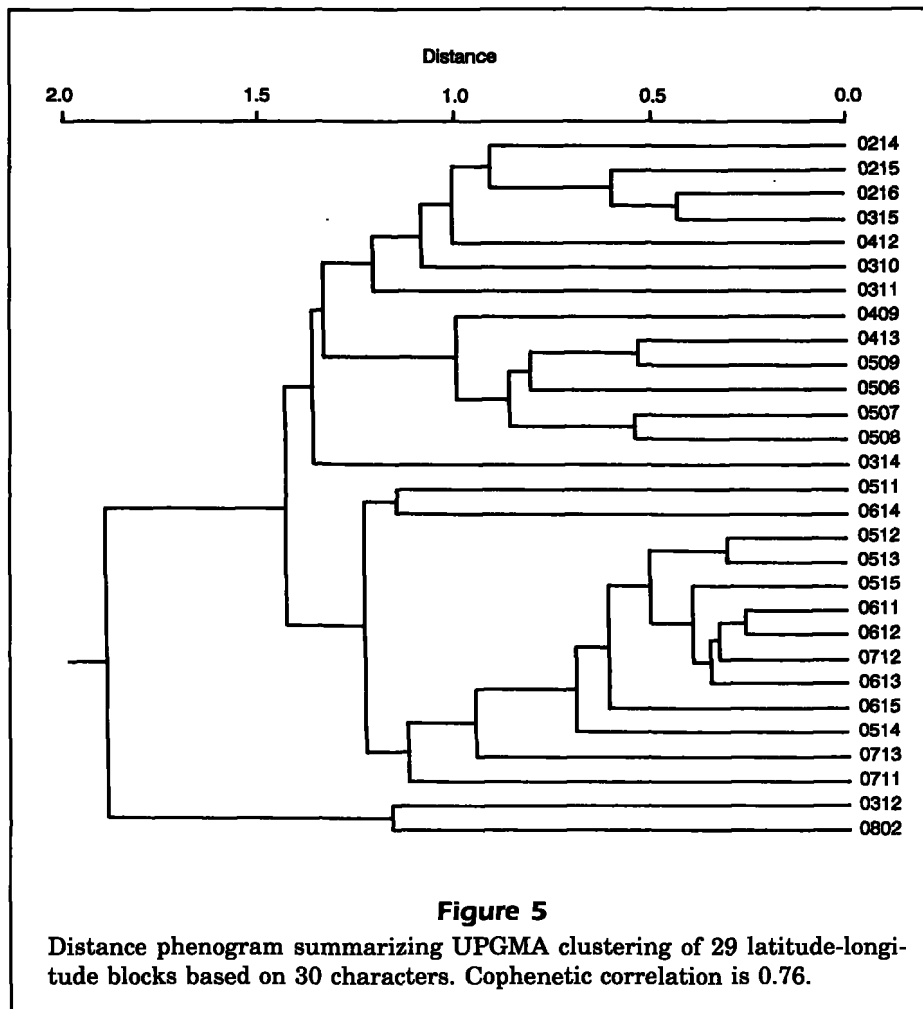


Table 5
Canonical variates analysis of all specimens of *Stenella attenuata* from 29 latitude-longitude blocks.

Character ¹	F-value to enter	Order of entry	Coefficients ²			
			1		2	
3 L. Rostrum (from Pterygoid)	2.88	4	0.0062	(0.0665)	-0.0731	(-0.7900)
9 Preorbital W.	9.19	1	0.1932	(0.8774)	0.0031	(0.3650)
14 L. Braincase	2.53	5	-0.0266	(-0.0851)	0.2243	(0.7179)
17 L. Temporal Fossa	2.84	3	-0.1113	(-0.4674)	0.0895	(0.3759)
18 W. Temporal Fossa	7.22	2	-0.1167	(-0.4305)	-0.0812	(-0.2996)
Constant			-13.5670		-18.3837	

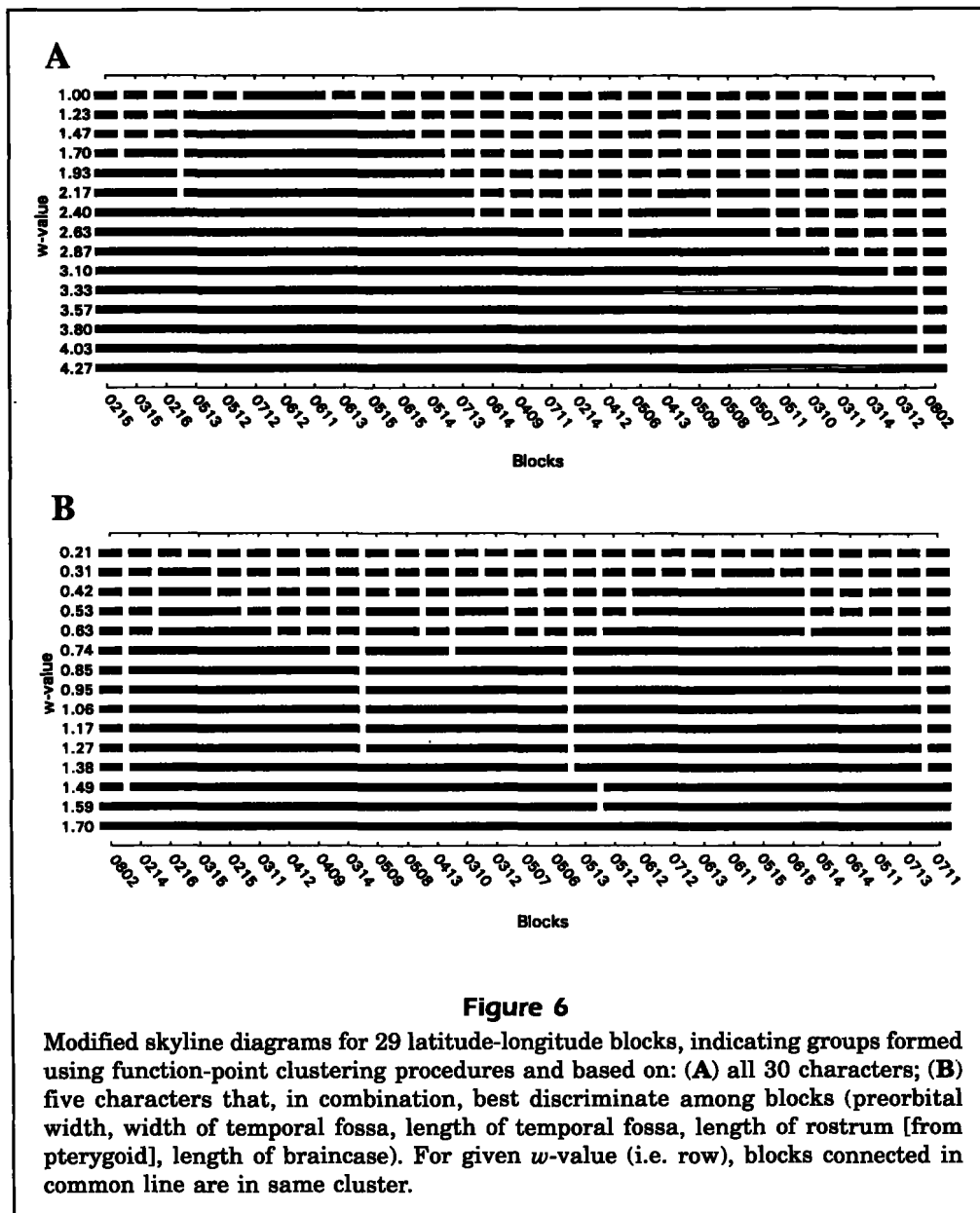
¹ Abbreviations identified in Footnote 1 of Table 1.

² Unstandardized coefficients (with standardized values in parentheses) for canonical variates.

iting a significant regional pattern also showed local patterning.

Our tests showed strong regional and local patterning for principal component I and canonical variable 1, whereas principal component II has sig-

nificant local patterning (Table 6). Mantel tests and correlations confirm a point made earlier—that canonical variable 2 does not exhibit a systematic geographic pattern.



Morphological-environmental covariation

Douglas et al. (1992: fig. 9) included a dendrogram summarizing absolute correlations among 13 environmental variables (listed in Table 2) for blocks having either *S. attenuata* or *S. longirostris* or both. These variables were partitioned into five clusters. Sea current (N., winter) is separated by itself, whereas sea current (W., winter) and oxygen minimum layer (depth) form a second cluster, which groups with an assemblage of five variables involving surface measures of temperature, oxygen, and salinity (variables 6, 7, 8, 10, and 13). The fourth cluster has the two solar insolation variables (4 and

5), while the fifth includes three measures indicating water and thermocline depths (variables 3, 11, and 12).

A principal-components analysis was conducted to obtain variables that would summarize general environmental trends; three components were presented from Douglas et al. (1992: table 6). Highest loadings for environmental variables on principal component I included those for sea surface temperatures (variables 6, 7, and 8), particularly July temperatures. The correlation with sea surface temperature (annual variable) is negative. The second component reflected thermocline depth (variable 11 and 12), as well as water depth and surface salinity. The

third had relatively high loadings with the two characters involving solar insolation (variables 4 and 5). A more detailed description of character associations with the principal components is available in Douglas et al. (1992).

Projection values for environmental principal component I are summarized in Figure 9A for the 29 blocks with larger samples of *S. attenuata*. It reflects the fact that sea surface temperatures are considerably higher in northern than southern blocks, and that the northern blocks exhibit relatively little annual variation in surface temperatures. Block projections on environmental principal component II are portrayed in Figure 9B, which summarizes the increases in thermocline depth, water depth, and surface salinity as one proceeds west and south.

Correlations of morphologic variables, principal components, and canonical variables with environmental variables and environmental principal components are summarized in Table 7. The sea current measures (variables 1 and 2) have virtually no statistical association with morphological characters, while water depth (variable 3) has positive correlations with lengths and widths of the rostrum, as well as principal component I and canonical variable 1 (Table 7).

Solar insolation (Jan.), the fourth variable, has larger values in the south; values become smaller to the north. It has significant positive correlations with nine morphologic variables, and negative associations with six others. The negative associations with the two temporal fossa measures are particularly strong (width of temporal fossa summarized in Fig. 10A). This environmental variable has relatively high correlations with canonical variable 1 and principal component II (Table 7).

Not unexpectedly, the fifth variable, solar insolation (annual) exhibits high values at the equator. Readings are lower for blocks closer to either pole. It has few significant statistical associations with morphologic characters, although the negative correlations with length of braincase and width of temporal fossa (Fig. 10A) are relatively high (Table 7).

The sixth and seventh environmental measures (surface temperatures in January and July) have negative associations with a number of width measurements, as well as with a few length variables (Table 7). They have very strong positive correlations with temporal fossa measures. Figure 10 summarizes the values for sea surface temperature (July), as well as for the closely associated width of

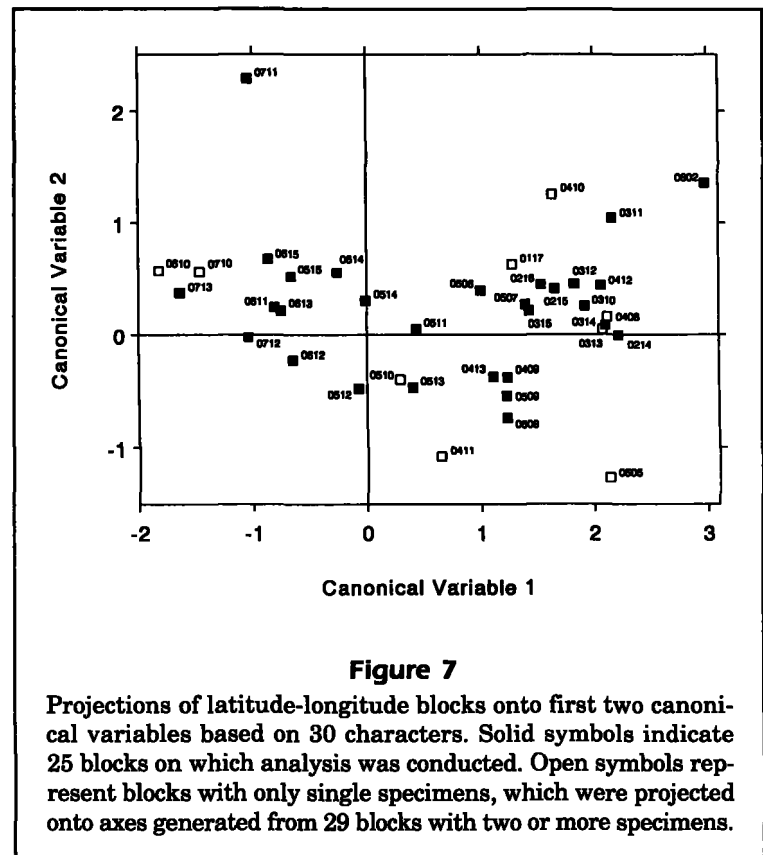


Figure 7

Projections of latitude-longitude blocks onto first two canonical variables based on 30 characters. Solid symbols indicate 25 blocks on which analysis was conducted. Open symbols represent blocks with only single specimens, which were projected onto axes generated from 29 blocks with two or more specimens.

temporal fossa ($r=0.799$; the highest correlation of an environmental and a morphological variable). Sea surface temperature (annual variable), the eighth environmental variable, has significant correlations with relatively few morphologic characters (Table 7), although its pattern has affinities with those summarized by principal component II and canonical variable 1. Environmental variable 9, oxygen minimum layer (depth), shows very few statistically significant correlations with morphological measurements (Table 7).

Surface salinity, variable 10, exhibits strong covariation with numerous measurements, particularly those involving the anterior portion of the skull (Table 7). It also has high correlations with principal component I (Fig. 4) and canonical variable 1 (Fig. 8B). Salinity, which was depicted in Douglas et al. (1992: fig. 13B) for *S. longirostris* blocks, shows east-west changes from lower to higher values at a given latitude, as well as a north-to-south trend of increasing values (below 15°N).

The eleventh variable, thermocline depth (winter), is summarized in Figure 11B. It has positive correlations with 12 morphological measures and a negative correlation with 1 character. The correlation of this environmental variable with skull width (at parietals), shown in Figure 11A, is 0.610. Variable

12, thermocline depth (summer), has strong positive correlations with a large number of variables, particularly those reflecting measurements in the anterior portion of the skull. Given its covariation with water depth, it is not surprising that thermocline depth (winter) has significant correlations with principal component I and canonical variable 1. Surface dissolved oxygen (variable 13) has only a few weak statistical associations with morphological characters.

Environmental principal component I (Fig. 9A) has a pattern similar to those for sea surface temperatures in January and July (variables 6 and 7). The highest correlation (0.733) of this component is with width of temporal fossa (Fig. 10A). The second environmental component (Fig. 9B) is strongly associated with numerous characters (Table 7), reflecting the general trends from the northeast to the west, southwest, and south. The third component, which is negatively associated with canonical variable 2 (Table 7), has only one strong association with a morphological variable, that being with tooth width ($r=-0.680$; Table 7). The third environmental component exhibits decreasing values as one moves away from the equator. Tooth width shows an opposite pattern, which is particularly emphasized with the relatively thick teeth in specimens from the Hawaiian Islands (block 0802).

In Table 8, Mantel t -values and matrix correlations are provided for associations of environmental variables (including environmental principal components) with the five morphologic characters selected for inclusion during the canonical-variates analysis. With this approach, covariation patterns are assessed on the basis of difference values between all block pairs. Preorbital width shows a strong association with water depth, the two measures of solar insolation, the sea surface temperatures in January and July, oxygen minimum layer (depth), and surface salinity (Table 8). It also exhibits a pattern that is statistically associated

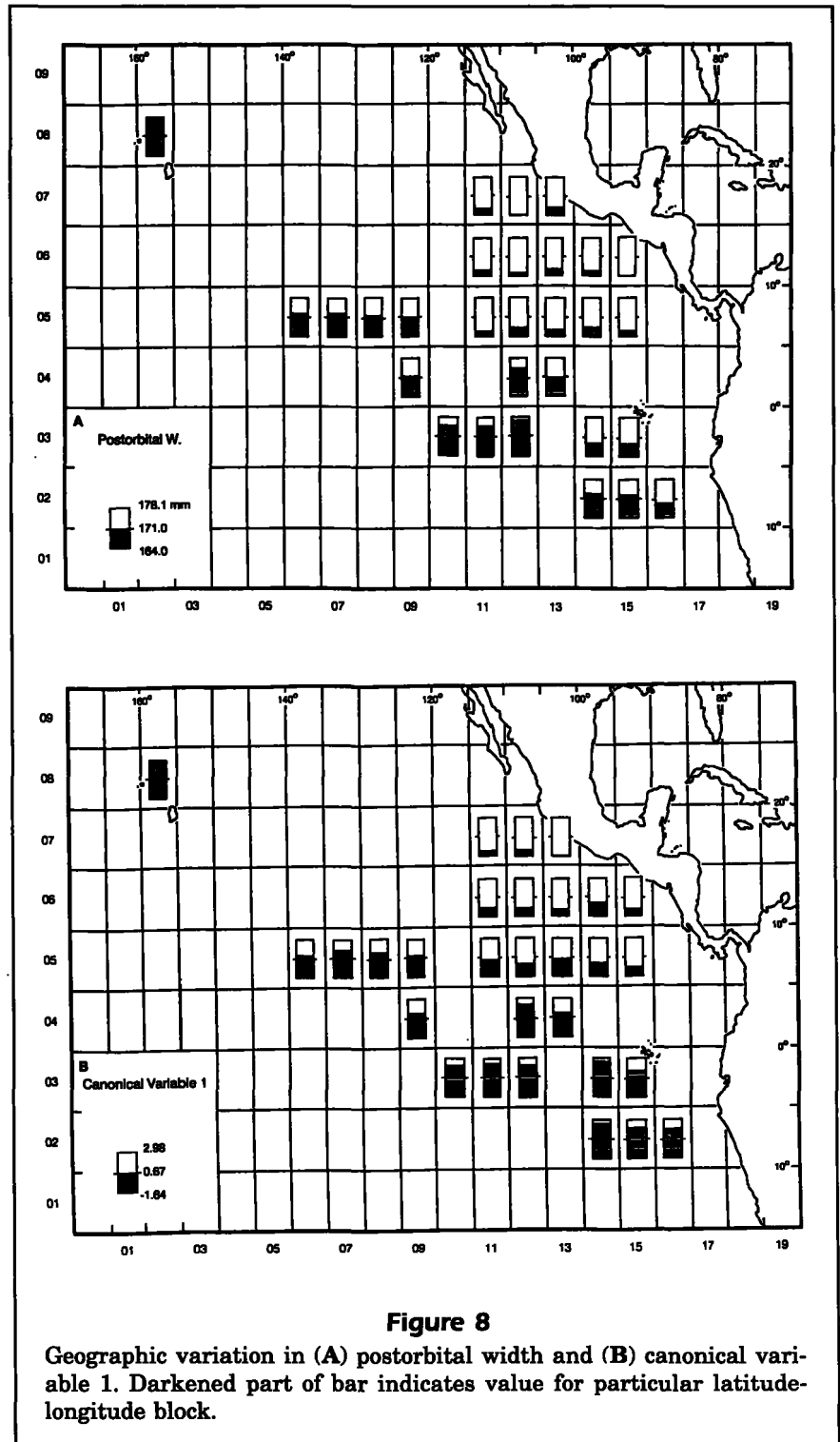


Figure 8

Geographic variation in (A) postorbital width and (B) canonical variable 1. Darkened part of bar indicates value for particular latitude-longitude block.

with all three environmental components. The two measures of the temporal fossa show concordance with patterns for solar insolation (January, as well as annual), all sea surface temperature measures, oxygen minimum layer (depth), surface salinity, and the first environmental principal component. The length of temporal fossa also has a weak statistical

association with environmental component III. Table 8 indicates that the pattern for length of rostrum (from pterygoid) is associated statistically with those for water depth and thermocline depth (summer). This morphologic character also is shown to have geographic patterning statistically similar to that exhibited by environmental components II and III. For length of braincase, the Mantel tests were significant (but weak) only for sea current (N., winter) and solar insolation (Jan.). The strongest association of length of braincase is with environmental component III; its pattern also is linked statistically to the second environmental component.

Interspecific comparisons

The study by Douglas et al. (1992) reported comparable statistical analyses on skulls of *S. longirostris*, a dolphin species that overlaps broadly with *S. attenuata* in the eastern tropical Pacific. The projections onto the first two principal components for *S. attenuata* were evaluated against projections on the two components obtained for *S. longirostris* (for summary information on these components, see Fig. 3 and Table 4 for offshore *S. attenuata*, and fig. 3 and table 3 of Douglas et al. [1992] for *S. longirostris*). A strong correspondence exists between the first principal components for the two species, as indicated by product-moment correlations, Mantel t -tests, and matrix correlations comparing the component projections. The second principal components for the two studies are not similar (Table 9); they summarize different general trends in variation.

A similar interspecific comparison was made of projections of the 16 blocks onto canonical variables (Table 9). The first canonical variable for *S. attenuata* and that for *S. longirostris* are virtually identical, reflecting highly concordant geographic patterns for the two species (Table 9). While block projections on the first canonical variables for the

Table 6

Association of interlocality character differences with geographic distances (in nautical miles) and the reciprocals of these distances. Results from Mantel tests (t) and matrix correlations (r) for offshore *Stenella attenuata*.

Character ¹	Distance		Reciprocal of distance	
	t	r	t	r
1 Condylbasal L.	4.19***	0.460	-4.19***	-0.303
2 L. Rostrum (from Base)	4.34***	0.449	-4.45***	-0.310
3 L. Rostrum (from Pterygoid)	3.59***	0.352	-4.10***	-0.276
4 W. Rostrum (at Base)	4.53***	0.493	-5.07***	-0.365
5 W. Rostrum (at 1/4 L.)	4.11***	0.446	-4.84***	-0.348
6 W. Rostrum (at 1/2 L.)	3.76***	0.413	-4.73***	-0.343
7 W. Premax. (at 1/2 L.)	1.28	0.134	-2.88**	-0.203
8 W. Rostrum (at 3/4 L.)	3.14**	0.347	-4.11***	-0.300
9 Preorbital W.	5.00***	0.464	-6.83***	-0.445
10 Postorbital W.	4.61***	0.397	-6.66***	-0.416
11 Skull W. (at Zygomatic P.)	4.22***	0.380	-6.21***	-0.398
12 Skull W. (at Parietals)	4.81***	0.583	-4.34*	-0.336
13 Ht. Braincase	1.81	0.227	-1.81	-0.143
14 L. Braincase	2.60**	0.339	-1.85	-0.151
15 Max. W. Premax.	1.64	0.159	-3.53***	-0.236
16 W. External Nares	0.78	0.066	-1.38	-0.085
17 L. Temporal Fossa	1.49	0.152	-3.13**	-0.216
18 W. Temporal Fossa	0.90	0.097	-2.86**	-0.206
19 Orbital L.	-0.25	-0.031	-0.35	-0.027
20 L. Antorbital P.	0.89	0.078	-3.65***	-0.229
21 W. Internal Nares	0.44	0.046	-1.09	-0.077
22 L. Up. Toothrow	4.08***	0.422	-3.93***	-0.274
23 No. Teeth (Up. Lf.)	1.57	0.173	-1.68	-0.123
24 No. Teeth (Up. Rt.)	3.03**	0.296	-3.68***	-0.247
25 No. Teeth (Low. Lf.)	1.75	0.188	-1.89	-0.135
26 No. Teeth (Low. Rt.)	2.44*	0.283	-2.39*	-0.180
27 L. Low. Toothrow	2.99**	0.364	-3.20**	-0.249
28 Ht. Ramus	1.74	0.181	-1.69	-0.116
29 Tooth W.	3.36***	0.398	-3.82***	-0.292
30 L. Ramus	3.02**	0.361	-2.88**	-0.221
Component I	4.54***	0.474	-5.51***	-0.386
Component II	1.42	0.122	-2.75**	-0.172
Canonical Variable 1	3.76***	0.289	-6.69***	-0.393
Canonical Variable 2	1.11	0.143	-1.47	-0.119

* $P < 0.05$; ** $P < 0.01$, *** $P < 0.001$.

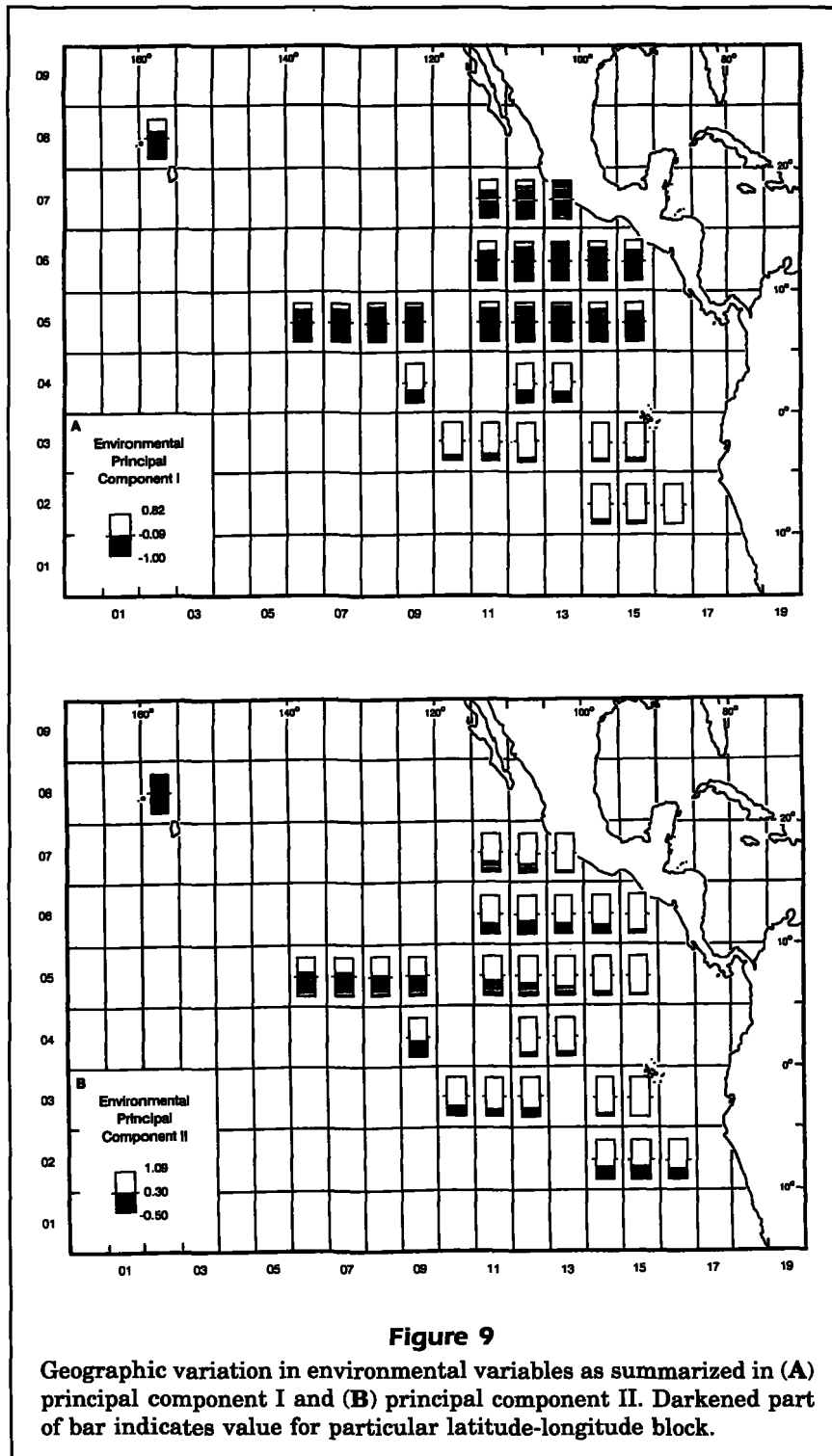
¹ Abbreviations identified in Footnote 1 of Table 1.

two species were very similar, the actual characters incorporated into the canonical variables are not the same (see our Table 5 and table 4 of Douglas et al. 1992). Of the five characters entered for each species, only length of rostrum (from pterygoid) was present in both character sets. However, the first and most important character entered into the analyses—preorbital width for *S. attenuata* and postorbital width for *S. longirostris* are highly correlated (see close association of these two characters in *S. attenuata* indicated in Fig. 2); because these two characters exhibit very similar variation pat-

terns, a canonical-variates analysis typically would not select both for inclusion, since they provide basically the same information for separating blocks.

The second canonical variables for the two studies also were compared (Table 9). They showed no statistical association.

Table 10 includes results of Mantel tests, matrix correlations, and product-moment correlations of interspecific comparisons for individual morphological characters. Thirteen of the 30 *t*-values for Mantel tests of interlocality differences for the same character in the two species were significant, while 15 of 30 product-moment correlations indicated statistical associations. Nine of 11 characters with positive correlations were width measures. Furthermore, a tenth (length of antorbital process) is essentially a width character as well (for illustration of measurement, see Schnell et al. 1985). The two characters involving upper tooth counts, as well as length of temporal fossa, exhibited significant negative correlations. For *S. attenuata*, upper tooth counts tend to be higher for the western blocks (but not for the Hawaiian Island block), whereas in *S. longirostris*, higher upper tooth counts are found in the Hawaiian and eastern blocks. The length of temporal fossa is greater in northern localities of *S. attenuata* (Fig. 10A), whereas the shorter fossae are found in northeastern blocks for *S. longirostris* (see Douglas et al. 1992: fig. 11).



Discussion

Sexual dimorphism

Schnell et al. (1985) conducted the most recent analysis of sexual dimorphism of *S. attenuata* in cranial morphology. They found statistically significant dimorphism for 23 of 36 characters. Our analyses used many of the same specimens, with some added and some deleted, and 30 of the same characters. For the 30 characters we analyzed, Schnell et al. (1985) found the same 22 to have statistical differences between sexes (one statistically significant character analyzed earlier was not used in our analysis). Results from the two studies on sexual dimorphism are essentially the same. Thus, for *S. attenuata*, our current findings simply update information in Schnell et

Table 7

Product-moment correlations of block means for morphological variables and components versus environmental variables and components based on 29 latitude-longitude blocks of offshore *Stenella attenuata*.¹

Character ²	Environmental variable ³													Environmental component		
	1	2	3	4	5	6	7	8	9	10	11	12	13	I	II	III
1 Condylbasal L.			++							+	++	+++				+++
2 L. Rostrum (from Base)			++								++	+++				+++
3 L. Rostrum (from Pterygoid)			++							+	+	+++				++
4 W. Rostrum (at Base)			++			--	-			+++	++	+++				+++
5 W. Rostrum (at 1/4 L.)			++			---	--			+++	+	++		--		++
6 W. Rostrum (at 1/2 L.)			+	+		---	---	+		+++		+		--		+
7 W. Premax. (at 1/2 L.)			+	+		--	--			++		+		--		
8 W. Rostrum (at 3/4 L.)			++	+		--	--			+++		+		-		+
9 Preorbital W.			+++	+		---	---			+++	+	++		--		++
10 Postorbital W.			+++	+		---	---			+++		++		--		++
11 Skull W. (at Zygomatic P.)			++			---	---	+	-	+++		++		---		+
12 Skull W. (at Parietals)											+++					++
13 Ht. Braincase											++					
14 L. Braincase						--	---				++					---
15 Max. W. Premax.				+		--	--			++		++		-		
16 W. External Nares																
17 L. Temporal Fossa				---	-	+++	+++	--		---		-	---	+++		
18 W. Temporal Fossa				---	---	+++	+++	---		---				+++		-
19 Orbital L.						-	-			++				--		
20 L. Antorbital P.				++		---	---	+	--	+++		+		---		
21 W. Internal Nares						---	--	+	-	++				-		
22 L. Up. Toothrow				-	+						++	+++				+++
23 No. Teeth (Up. Lf.)	++													-		
24 No. Teeth (Up. Rt.)														-		+
25 No. Teeth (Low. Lf.)							++				-			+		
26 No. Teeth (Low. Rt.)							+				-			-		
27 L. Low. Toothrow				+							+	++				++
28 Ht. Ramus																
29 Tooth W.				-	-	--										---
30 L. Ramus				+							++	+++				++
Component I				++			---	---		+++	+	+++		-		++
Component II					++		--	--	+++	+			++	--		
Canonical Variable 1				+++	+++	+	---	---	++	+++		++		---		+
Canonical Variable 2							-									---

¹ Blanks indicate nonsignificant correlations. Individual symbols refer to significant positive or negative correlations ($P < 0.05$; greater than 0.367), double symbols indicate highly significant correlations ($P < 0.01$; greater than 0.470), and triple symbols represent very highly significant correlations ($P < 0.001$; greater than 0.580).

² Abbreviations identified in Footnote 1 of Table 1.

³ Environmental variables: (1) Sea Current (N., winter); (2) Sea Current (W., winter); (3) water depth; (4) solar insolation (Jan.); (5) solar insolation (annual); (6) sea surface temp. (Jan.); (7) sea surface temp. (July); (8) sea surface temp. (ann. var.); (9) oxygen min. layer (depth); (10) surface salinity; (11) thermocline depth (winter); (12) thermocline depth (summer); and (13) surface dissolved oxygen.

al. (1985) to reflect a modified sample size and a reduced character set.

Douglas et al. (1992) analyzed sexual dimorphism in skull measures for *S. longirostris* from the eastern tropical Pacific. They found 15 of the 30 characters to be statistically different between sexes. Since *S. longirostris* samples are somewhat smaller,

one might expect fewer significant differences in this species simply due to sample size. Nevertheless, inspection of the results indicates support for the conclusion reached by Douglas et al. (1986: 542–543) “that the degree of sexual dimorphism in spotted dolphins is greater than in spinner dolphins.” They also pointed out that “the trends are basically the same for both species, suggesting

that common behavioral and/or ecological factors are influencing sexual dimorphism in these dolphins.”

Geographic variation

From an initial group of specimens, Perrin et al. (1979a) described differences between dolphin skulls available from southern areas and those from more northerly locations. Schnell et al. (1986), based on larger sample sizes, indicated that available information “strongly implies a significant degree of isolation between northern and southern forms.” They did not have specimens from west of 125°W and called for additional material from west of 120°W to help clarify the relationship between southern *S. attenuata* and other populations, particularly in light of the notation by Perrin et al. (1979a) of similarities of specimens from the southern group with those from Hawaii. In the eastern portion of the range, the subdivision between northern and southern offshore *S. attenuata* found previously by Perrin et al. (1979a) and Schnell et al. (1986) was confirmed by our analyses with a geographically expanded specimen base. In general, blocks to the west (including those from the waters adjacent to Hawaii) are more like the southern blocks than blocks of the northeast. We found a general concentric pattern of geographic variation (see Fig. 8B), much like that established by Douglas et al. (1992) for the broadly overlapping *S. longirostris*. This also was suggested by Perrin et al. (1985).

Reilly (1990) provided some insight as to possible reasons why samples of *S. attenuata* and *S. longirostris* from the south, southwest,

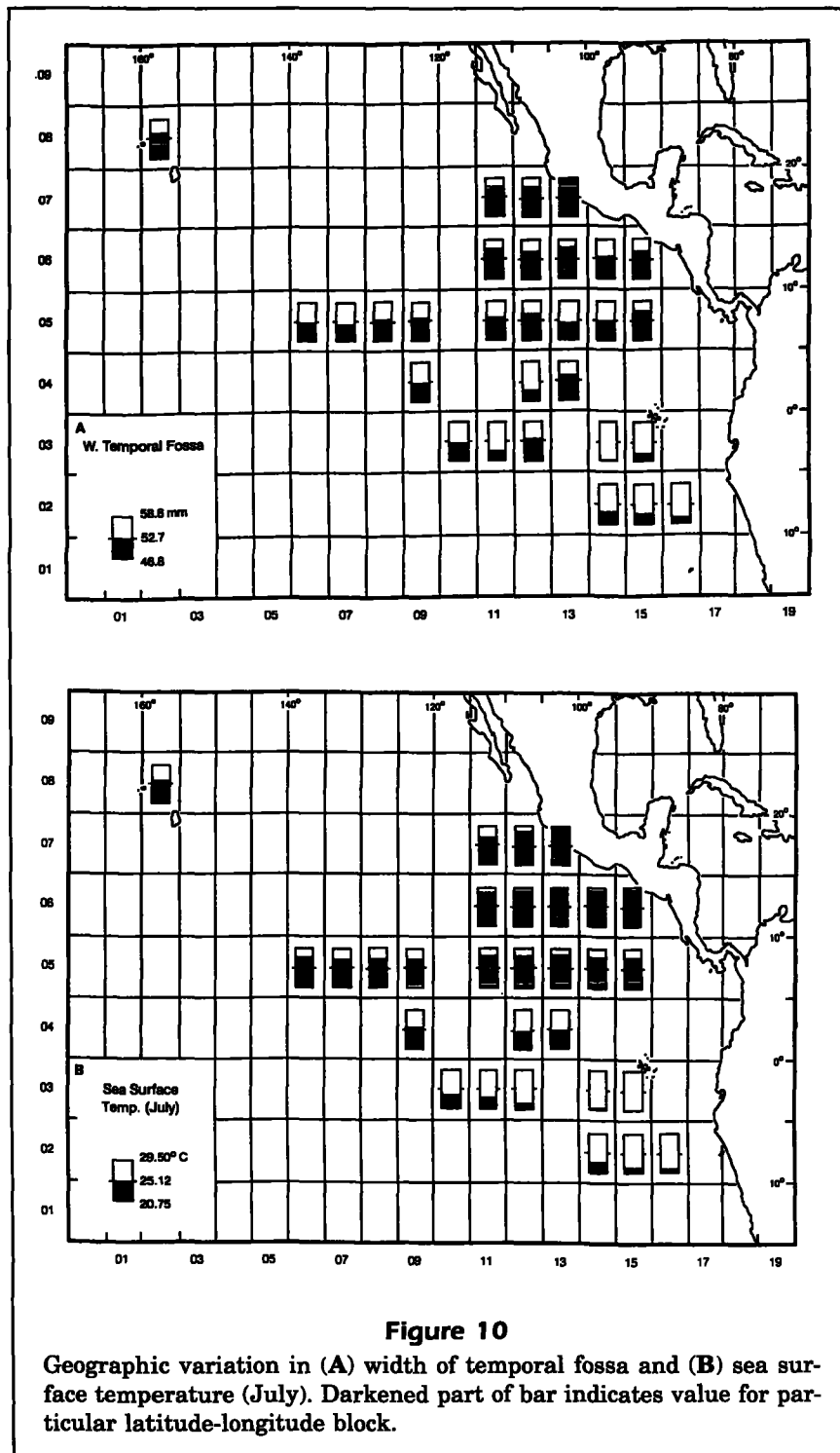


Figure 10

Geographic variation in (A) width of temporal fossa and (B) sea surface temperature (July). Darkened part of bar indicates value for particular latitude-longitude block.

and west would show close morphologic affinities. He analyzed large-scale dolphin distribution patterns and environmental patterns based on research-vessel surveys conducted in the eastern tropical Pacific from June through November, comparing his results with those of Au and Perryman (1985).

Reilly's (1990) distributional comparisons between seasons indicated that along 10°N *S. attenuata* and *S. longirostris* occur in relatively high density west of 120°W during the summer. Furthermore, they were not in high densities along 4°N between 90 and 120°W, and along 6°N between 88 and 110°W—regions with relatively high concentrations of these two species in the winter (Au and Perryman, 1985). Reilly (1990) indicated that "One hypothesis suggested by these complementary changes is an intraregional, seasonal movement." Data from mark-recapture efforts (Perrin et al., 1979b; Hedgepeth⁴) are consistent with respect to the hypothesized direction of such migrations, although the distances are greater than those suggested by the very limited data from these studies. Reilly (1990) also noted that the suggested movement patterns are at least partially explainable based on seasonal atmospheric and oceanographic changes in the region.

Morphological-environmental covariation

In the earlier study of *S. attenuata*, Schnell et al. (1986) assessed environmental-morphological covariation for a similar, although not identical, set of environmental parameters. Since their investigation was restricted largely to eastern blocks, different findings with respect to covariation are possible. Schnell et al. (1986) noted that the strongest morphological-environmental associations involved solar insolation (Jan.). Sea surface temperatures also co-

varied with a number of morphological characteristics, as did oxygen minimum layer (depth).

The environmental principal components indicated that a number of environmental measures have a north-south component (see Fig. 9A), while others (particularly thermocline depth and water

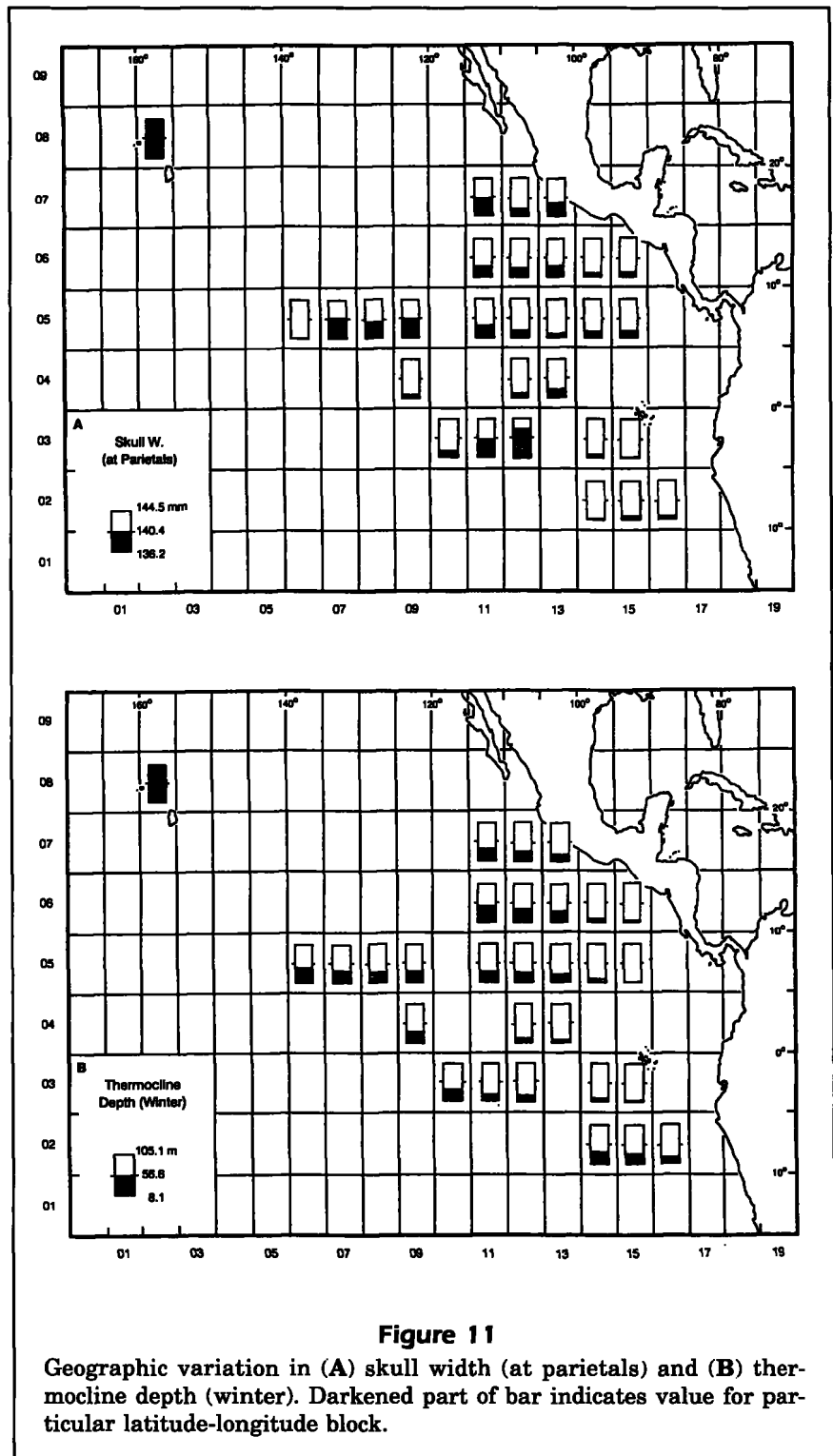


Figure 11

Geographic variation in (A) skull width (at parietals) and (B) thermocline depth (winter). Darkened part of bar indicates value for particular latitude-longitude block.

⁴ Hedgepeth, J. B. 1985. Database for dolphin tagging operations in the eastern tropical Pacific, 1969–1978, with discussion of 1978 tagging results. Southwest Fisheries Center Admin. Rep. No. LJ-85-03, 40 p.

Table 8

Results of Mantel tests (t) and matrix correlations (r) for offshore *Stenella attenuata*. Comparison of interlocality differences for 13 environmental variables and 3 environmental components against those for five morphological variables selected in canonical-variates analysis.

Environmental variable	Preorbital width		Width of temporal fossa		Length of temporal fossa		Length of rostrum (from pterygoid)		Length of braincase	
	t	r	t	r	t	r	t	r	t	r
1 Sea Current (N., winter)	-1.34	-0.114	2.43*	0.318	-0.20	-0.026	0.67	0.085	2.41*	0.322
2 Sea Current (W., winter)	0.02	0.001	-1.95	-0.139	-1.68	-0.119	1.94	0.136	0.82	0.059
3 Water Depth	4.12***	0.259	-0.45	-0.033	-1.08	-0.080	3.24**	0.236	1.17	0.088
4 Solar Insolation (Jan.)	7.38***	0.466	6.39***	0.479	6.47***	0.481	-0.56	-0.041	-2.29*	-0.173
5 Solar Insolation (ann.)	7.58***	0.502	2.85**	0.238	2.91**	0.241	0.68	0.056	-0.84	-0.071
6 Sea Surface Temp. (Jan.)	5.53***	0.371	5.71***	0.493	4.70***	0.401	-1.15	-0.097	-1.43	-0.125
7 Sea Surface Temp. (July)	5.59***	0.369	6.97***	0.579	4.08***	0.335	-0.94	-0.076	-1.30	-0.109
8 Sea Surface Temp. (ann. var.)	1.69	0.114	6.23***	0.547	2.87**	0.249	-0.74	-0.064	-0.82	-0.073
9 Oxygen Minimum Layer (depth)	4.18***	0.236	3.60***	0.191	3.75***	0.200	-0.56	-0.030	-0.79	-0.042
10 Surface Salinity	9.52***	0.594	5.31***	0.386	4.66***	0.337	0.32	0.023	-1.20	-0.088
11 Thermocline Depth (winter)	0.40	0.026	0.90	0.070	1.88	0.144	0.20	0.016	-0.39	-0.031
12 Thermocline Depth (summer)	1.21	0.085	-0.07	-0.007	0.84	0.079	2.60**	0.240	0.00	0.000
13 Surface Dissolved Oxygen	-1.85	-0.147	0.76	0.089	1.83	0.211	-0.40	-0.045	-0.01	-0.001
Environmental Component I	3.71***	0.238	6.75***	0.476	4.57***	0.309	-1.69	-0.111	-1.31	-0.104
Environmental Component II	3.77***	0.364	-0.26	-0.030	0.39	0.041	3.45***	0.352	2.63**	0.359
Environmental Component III	4.64***	0.449	0.52	0.059	2.36*	0.252	2.22*	0.227	4.54***	0.623

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

depth) show trends from the east to the west, southwest, and south. Not unexpectedly, a mosaic of variation patterns is present in the suite of morphologic characters we assessed. Some, like width of temporal fossa (Fig. 10A), align closely with environmental variables—such as sea surface temperature (July) (Fig. 10B)—subsumed under environmental component I (Fig. 9A). Others, like skull width (at parietals) (Fig. 11A), display patterns similar to those of thermocline depth (winter) (Fig. 11B) and other environmental measures summarized by environmental component II (Fig. 10B). However, the overall, general morphological trend is reflected best

by projections onto the first canonical variable based on morphologic data (Fig. 4), which has a relatively strong negative correlation with environmental component I and a weaker positive one with environmental component II.

By adding the more westerly blocks to the analysis, environmental-morphological covariation patterns that emerged, in some cases, were different from those reported by Schnell et al. (1986). For example, the previous statistically significant correlations they found for several morphologic characters with sea current (N., winter) and sea surface temperature (annual variation) were not repeated

in our expanded study. Likewise, strong associations with measures of solar insolation were substantially reduced for all but a few characters (i.e. length of braincase, length of temporal fossa, and width of temporal fossa; Table 7). Some characters, such as sea current (W., winter) and oxygen minimum layer (depth), did not have variation patterns in either study that corresponded to those for morphologic variables. Water depth, however, has significant correlations with more characters now that western blocks have been added. At least three environmental measures—sea surface temperature (Jan.), sea surface temperature (July) (Fig. 10B), and surface salinity—had relatively strong covariation patterns that stayed relatively constant through the two studies.

Availability in the future of better information on environmental variation and, possibly, on other relevant parameters reflecting environmental heterogeneity will allow researchers to analyze dolphin-environmental covariation in a more meaningful way. For example, better environmental data and more comprehensive information on dolphin feeding ecology could provide a basis for testable predictions concerning why certain morphological characters covary with specific environmental variables. Our admittedly descriptive analyses demonstrate some striking cases of dolphin-environmental covariation and, thus, provide initial guidance in terms of possible causal relationships that may be examined with greater sophistication by future investigators.

Interspecific covariation

In this paper we have presented statistical data for trends in geographic covariation of *S. longirostris* and *S. attenuata* skulls from 16 blocks for which samples of both species were available (brief comments on covariation were included by Douglas et al. 1992). Geographic patterns in 13 of the 30 morphological characters showed statistical correspondence based on Mantel tests, whereas

Table 9

Comparisons of principal component and canonical variable projections for offshore *Stenella attenuata* and *S. longirostris* based on corresponding data for 16 latitude-longitude blocks.

Statistic	Principal component		Canonical variable	
	I	II	1	2
Product-moment correlation	0.745***	0.289	0.896***	-0.328
Mantel <i>t</i> -value	3.46**	0.32	6.65***	1.62
Matrix correlation	0.528	0.039	0.741	0.204

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. *P*-values for Mantel tests based on number of times permutational *Z*-values less than or equal to observed *Z*-values (one-tailed test).

Table 10

Results of Mantel tests, matrix correlations, and product-moment correlations for 16 overlapping latitude-longitude blocks of offshore *Stenella attenuata* and *S. longirostris*. Comparison of interlocality differences for 30 morphological variables.

Character ¹	Mantel <i>t</i> -value	Matrix correlation	Product-moment correlation
1 Condylbasal L.	1.21	0.184	0.256
2 L. Rostrum (from Base)	1.28	0.178	0.159
3 L. Rostrum (from Pterygoid)	0.55	0.074	0.150
4 W. Rostrum (at Base)	4.65***	0.626	0.837***
5 W. Rostrum (at 1/4 L.)	4.14***	0.337	0.693**
6 W. Rostrum (at 1/2 L.)	4.57***	0.495	0.775***
7 W. Premax. (at 1/2 L.)	-0.49	-0.066	0.351
8 W. Rostrum (at 3/4 L.)	1.01	0.120	0.540*
9 Preorbital W.	5.70***	0.737	0.865***
10 Postorbital W.	6.24***	0.693	0.861***
11 Skull W. (at Zygomatic P.)	6.37***	0.732	0.883***
12 Skull W. (at Parietals)	2.71**	0.446	0.616*
13 Ht. Braincase	0.60	0.093	0.294
14 L. Braincase	2.91*	0.494	0.613*
15 Max. W. Premax.	2.88**	0.318	0.675**
16 W. External Nares	-0.64	-0.073	0.224
17 L. Temporal Fossa	0.79	0.088	-0.499*
18 W. Temporal Fossa	0.62	0.077	-0.443
19 Orbital L.	0.92	0.148	0.383
20 L. Antorbital P.	4.10**	0.396	0.658**
21 W. Internal Nares	1.61	0.205	0.613*
22 L. Up. Toothrow	1.19	0.165	0.069
23 No. Teeth (Up. Lf.)	2.98**	0.501	-0.753***
24 No. Teeth (Up. Rt.)	2.99**	0.517	-0.691**
25 No. Teeth (Low. Lf.)	0.03	0.004	-0.223
26 No. Teeth (Low. Rt.)	0.66	0.104	-0.428
27 L. Low. Toothrow	0.59	0.090	0.015
28 Ht. Ramus	2.34*	0.298	0.408
29 Tooth W.	0.20	0.038	-0.260
30 L. Ramus	0.70	0.111	0.174

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. *P*-values for Mantel tests based on number of times permutational *Z*-values less than or equal to observed *Z*-values (one-tailed test).

¹ Abbreviations identified in Footnote 1 of Table 1.

product-moment correlations were significant for 15 characters. Some of these associations were very strong (i.e. correlations as high as 0.883; see Table 10). Given that we are comparing two species, entities that have independent gene pools, the most likely explanation for common positive trends in morphologic covariation is that the two species are being subjected to similar forces of natural selection.

However, we found several striking examples where covariation was negative. A significant negative association was found for length of temporal fossa, while the negative correlation for width of temporal fossa was nearly significant statistically. The number of upper teeth (characters 23 and 24) also show significant negative correlations (Table 10). Muscles associated with the feeding apparatus are positioned in the temporal fossa; obviously, tooth numbers could be related to prey types taken. One suspects that the presence of antithetical trends in these particular skull characteristics is a result of competitive interactions involving these two interacting species. This may be an example of ecological character displacement related to differences in feeding and food types taken (Perrin, 1984). Certainly, the two species are found in close association over much of the eastern tropical Pacific (Au and Perryman, 1985; Reilly, 1990); 49% of *S. attenuata* schools included some *S. longirostris*, while 73% of the schools of the less common *S. longirostris* included *S. attenuata* (Reilly, 1990).

The information available to date indicates that spinner and spotted dolphins may have different feeding habits or preferences in areas of co-occurrence in the eastern tropical Pacific. Based on analysis of stomach contents of spinner and spotted dolphins captured together in purse-seine hauls in the tuna fishery, Perrin et al. (1973) concluded tentatively that while some prey species are taken by both, spinner dolphins in the mixed-species associations specialize in small mesopelagic fishes (mainly myctophids and gonostomatids) and squids, whereas the spotted dolphins consume larger and more epipelagic species such as flying fishes, small scombroids (e.g. *Auxis* sp.), and larger squids. In addition, state of digestion of the stomach contents indicated that the spinner and spotted dolphins had fed at different times of the day. Stomachs of a spotted dolphin from Hawaii, where the two species do not school together, and from two spotted dolphins from the far western portion of the range in the eastern Pacific, where the mixed species associations are less common than in the core area of the tuna fishery off Mexico and Central America (Au and Perryman, 1985; fig. 11), contained a large proportion of small mesopelagic species like those eaten by

the spinner dolphin in the mixed species associations farther to the east. This geographic variation in feeding habits may reflect resource partitioning where the two species associate closely, which in turn may be manifested in morphological character displacement.

Genetic subdivision, management units, and implications of cranial variation

The results suggest that gene flow is not uniform throughout the range of *S. attenuata* in the eastern Pacific; the morphological heterogeneity probably reflects genetic subdivision, a conclusion also reached as a result of the earlier study by Schnell et al. (1986). A similar inference was drawn by Douglas et al. (1992) based on morphologic studies of *S. longirostris*. For *S. attenuata*, we found that 93.3% of the 30 morphologic characters had statistically significant geographic variation, with 60.0% exhibited regional patterning and 73.3% local patterning. This geographic partitioning of morphologic variance was demonstrable even with pooling of specimens taken over a number of months and years, a process that would tend to shroud such relationships.

The boundaries of management units presently employed (Perrin et al., 1985) are not fully consistent with the general pattern of morphologic variation described here. It appears that animals west of about 120°W longitude have greater affinity with those in the Southern Offshore management unit than they do with *S. attenuata* from the eastern portion of the present Northern Offshore unit, the unit in which they are presently included. Further, the present boundary between the Northern and Southern Offshore units, at 1°S latitude, is probably too far south; a boundary at about 5°N would be more consistent with the general pattern of cranial variation.

The proposed Northern Offshore unit bounded by 5°N and 120°W would be nearly congruent with the "conservation zone" suggested for *S. longirostris* (Perrin et al., 1991). This is to be expected based on the correlated trends of covariation with environmental variables; the two species, as they exist in this region, apparently are parts of an endemic fauna uniquely adapted to the far eastern tropical Pacific and, as such, are "evolutionarily significant units" (Dizon et al., 1992).

The cranial results are only one line of evidence useful for delineation of management units; others, such as patterns in movements, external morphology or life-history parameters, also should be taken into consideration. For example, other data may indicate that *S. attenuata* west of 120°W differ sig-

nificantly in some regard from those south of 5°N and should be managed separately (yielding three management units instead of the present two). Certainly, the specimens from the Hawaiian Islands are generally larger than those from the south, southwest, and west with which they have their closest morphologic affinity.

Note added in proof Based in part on the results and recommendations in this paper, the management unit boundaries for the offshore spotted dolphin in the eastern Pacific have been changed. The boundary of a new "Northeastern stock" runs south along the 120°W meridian to 5°N and then east to the mainland. Offshore spotted dolphins outside this zone to the west and south are now part of a "Western/Southern stock." February, 1994.

Acknowledgments

Support for aspects of this research was received by the University of Oklahoma through Contract 79-ABC-00167 from the U.S. Department of Commerce, National Oceanographic and Atmospheric Administration, and Purchase Orders 84-ABA-02177 and 40JGNF0532 from the National Marine Fisheries Service, Southwest Fisheries Science Center, La Jolla, CA. We thank individuals (listed in Douglas et al., 1992) who provided access to museum specimens. M. E. Douglas measured the initial set of specimens used in this study. Pamela A. Pogorelc assisted with preparation of some of the figures. Paul Fiedler, Steven Reilly, Michael Scott, and an anonymous reviewer provided useful suggestions on earlier drafts of this paper.

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