Abstract.–The spinner dolphin *Stenella longirostris* is widely distributed in the eastern tropical Pacific Ocean. Geographic patterns in 30 cranial features were determined from 246 museum specimens grouped into 25 5° latitude-longitude blocks. Statistically significant sexual dimorphism was demonstrated for one-half of the cranial characters, with males generally being larger. ANOVAs, as well as principal components, canonical variates, and cluster (UPGMA and function-point) analyses demonstrated geographic variation in all characters. Patterns of geographic variation in morphology were evaluated for all *S. longirostris* specimens using Mantel tests and matrix correlations; 20 of 30 characters showed significant "regional patterning," while most (25 of 30) exhibited "local" patterning. The latitude-longitude block with specimens of *S. l. centroamericana* was distinctive in a number of features. Also, eastern spinner dolphins (*S. l. orientalis*) were smaller than spinners found to the south, southwest, or west. Many of the cranial characters exhibited a concentric pattern of geographic variation similar to that found by previous investigators for several external characters. Hawaiian specimens are the largest incorporated into this study and, typically, are more like those from southern localities than animals from geographically closer blocks. The association between morphological characters and 13 environmental measures was assessed with Mantel tests and product-moment correlations, revealing statistical concordance of morphological patterns for a number of cranial characters with those for water depth, sea surface temperature in January and July, surface salinity, thermocline depth, and surface dissolved oxygen. Several of these environmental variables manifest the same distributional pattern found in many of the cranial features.

Geographic variation in cranial morphology of spinner dolphins *Stenella longirostris* in the eastern tropical Pacific Ocean

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Information on geographic variation of dolphins in the eastern tropical Pacific is of intrinsic scientific interest, but also has practical implications because fishermen in the region kill dolphins in the course of purse-seining for yellowfin tuna (Allen 1985). Tuna in the region associate with schools of dolphins, primarily *Stenella* spp. and *Delphinus delphis*, and the fishermen set their nets on the schools to capture the tuna below them. In the process, many dolphins die, as many as 80,000–125,000 annually in recent years (Hall and Boyer 1988, 1989, 1990). The U.S. Government has used a series of management units, or stocks, in regulating this exploitation of the dolphins by U.S. vessels. For the spinner dolphin, these have been the eastern spinner, Costa Rican spinner, northern whitebelly spinner, and southern whitebelly spinner stocks (Perrin et al. 1985). These divisions are based on morphology, including body length and shape, color pattern, shape of the dorsal fin, and cranial characters. The Costa Rican form occurs close to the coast of Central America and is relatively large, with relatively long beak, erect to forward-canted dorsal fin, and monotonic gray coloration. The eastern form is smaller, with shorter beak; it also has the erect or canted fin and is gray overall, but with light patches in the axillary and genital areas. The whitebelly forms have a tripartite color pattern of dark gray, light gray, and (ventrally) white, and the dorsal fin is highly variable, ranging in adults from falcate to erect. The northern and southern stocks were divided based on modal differences in cranial measurements; the boundary is at the Equator. The eastern spinner and northern whitebelly spinner stocks overlap broadly; overlap between the eastern spinner and southern whitebelly spinner is very slight (Perrin et al. 1985). Dolphins killed in the fishery are identified to stock based on the modal appearance of adults in the school and, in the case of the two whitebelly stocks, location.

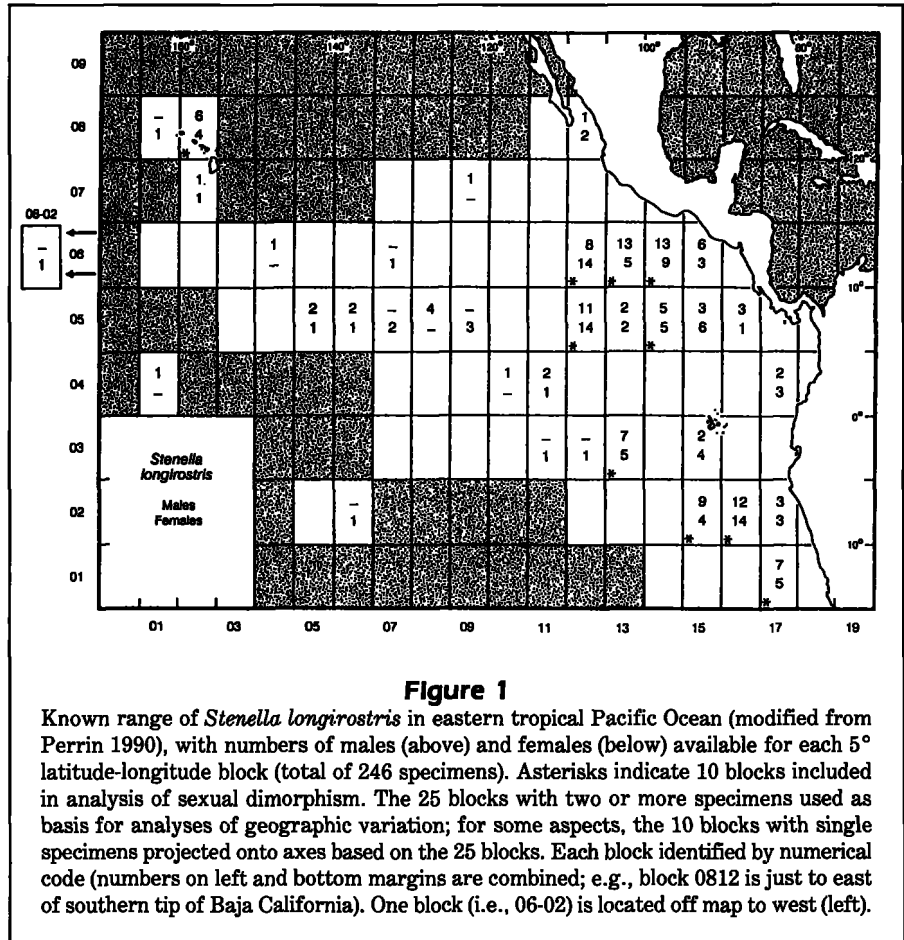Most recently, Perrin (1990) described three subspecies of *Stenella*

longirostris: the pantropical spin-
ner dolphin *S. l. longirostris*
occurring in the Central, South,
and Western Pacific, Indian, and
Atlantic oceans; the Central
American spinner *S. l. centro-
americana* endemic to the coast
of Central America and corre-
sponding to the Costa Rican spin-
ner management stock; and the
eastern spinner *S. l. orientalis*
endemic to the eastern tropical
Pacific off Mexico, Central Amer-
ica, and northern South America
and corresponding to the eastern
spinner management stock. He
concluded that the more offshore
whitebelly forms constitute a
broad zone of hybridization or
intergradation between the east-
ern and pantropical forms. This
view has support from results of
a genetic study; Dizon et al.
(1991) found no unique haplo-
types in a restriction-enzyme ex-
amination of mitochondrial DNA
of animals of the eastern and
whitebelly morphological types.

Perrin et al. (1991) reexamined
color pattern, body size and
shape, and dorsal fin shape with-
out *a priori* assignment of speci-
mens to subspecies or management stock. They com-
pared specimens from 5° geographic blocks. The re-
sults of their analyses support the taxonomic treatment
by Perrin (1990); the whitebelly forms constitute a com-
plex zone of highly variable animals intermediate be-
tween the eastern and pantropical types. Perrin et al.
(1991) concluded that the pattern of geographic varia-
tion does not justify separation of northern and south-
ern units on morphological grounds alone.

The purpose of the studies reported here was to carry
out a parallel analysis of geographical cranial variation
in the eastern Pacific, again making no *a priori* assign-
ment of specimens to subspecies or management stock.
We also examined relationships between cranial varia-
tion and environmental variables, in an effort to better
understand the ecologies of the several forms of spin-
ner dolphins.

Materials and methods

Data from 246 adult museum specimens (maturity
judged by evaluating fusion of premaxilla with the max-

Figure 1
Known range of *Stenella longirostris* in eastern tropical Pacific Ocean (modified from
Perrin 1990), with numbers of males (above) and females (below) available for each 5°
latitude-longitude block (total of 246 specimens). Asterisks indicate 10 blocks included
in analysis of sexual dimorphism. The 25 blocks with two or more specimens used as
basis for analyses of geographic variation; for some aspects, the 10 blocks with single
specimens projected onto axes based on the 25 blocks. Each block identified by numerical
code (numbers on left and bottom margins are combined; e.g., block 0812 is just to east
of southern tip of Baja California). One block (i.e., 06-02) is located off map to west (left).

illa at distal end of rostrum; Dailey and Perrin 1973)
of spinner dolphins were used in this investigation (Fig.
1). We purposely included all appropriate specimens
available, including those from the three named sub-
species recognized from the region (Perrin 1990); fur-
thermore, we did not differentiate between those with
different color patterns ("eastern" and "whitebelly";
Perrin et al. 1985, 1991), in order to focus simply on
cranial features. The animals used included 188 of 199
specimens used in the earlier study of sexual dimor-
phism (Douglas et al. 1986; the 11 remaining specimens
not used had been incorrectly aged or had inadequate
locality data) and 58 new specimens.

The first set of specimens was measured by M.E.
Douglas and the new specimens by W.F. Perrin. In
addition, Perrin remeasured 81 specimens of spinner
dolphins and spotted dolphins *S. attenuata* measured
by Douglas. This allowed a comparison to determine
whether measurements were repeatable. Initially, 36
morphometric and meristic characters were evaluated
(illustrations and character definitions given in Schnell
et al. 1985a). Comparisons of measurements taken on
the same specimens by the two investigators indicated

Table 1

Geographic variation and sexual dimorphism in *Stenella longirostris* evaluated for 30 characters.

Character[a]	F-value[b]		Mean[c]		Correction factor[d]	Percentage difference[e]
	Block	Sex	Male	Female		
1 Condylobasal L.	22.19***	0.05	405.9	404.6	0.22	0.32
2 L. Rostrum (frm.Base)	15.93***	0.50	258.9	259.4	-0.61	-0.21
3 L. Rostrum (frm.Pterygoid)	20.71***	0.01	299.6	299.3	-0.08	-0.11
4 W. Rostrum (at Base)	15.19***	2.88	74.2	73.1	0.37	1.44
5 W. Rostrum (at 1/4 L.)	10.17***	11.82***	52.1	50.6	0.67	2.84
6 W. Rostrum (at 1/2 L.)	9.97***	10.20**	44.2	42.8	0.65	3.16
7 W. Premax. (at 1/2 L.)	5.65***	8.31**	21.4	20.8	0.31	3.02
8 W. Rostrum (at 3/4 L.)	2.92**	24.96***	32.5	30.5	1.01	6.34
9 Preorbital W.	38.05***	8.67**	139.9	137.5	1.00	1.76
10 Postorbital W.	49.34***	8.19**	155.7	153.3	0.93	1.57
11 Skull W. (at Zygomatic P.)	49.11***	14.89***	154.4	151.3	1.27	2.04
12 Skull W. (at Parietals)	6.27***	20.36***	130.1	127.2	0.10	0.52
13 Ht. Braincase	16.56***	15.52***	89.1	87.1	0.89	2.28
14 L. Braincase	18.71***	8.09**	101.7	100.3	0.67	1.47
15 Max. W. Premax.	6.55***	0.22	62.9	62.6	0.04	0.36
16 W. External Nares	3.88***	0.09	41.6	41.5	1.40	2.27
17 L. Temporal Fossa	4.32***	9.27**	50.4	48.7	0.82	3.52
18 W. Temporal Fossa	9.24***	17.82***	40.2	38.2	0.96	5.16
19 Orbital L.	6.56***	0.00	40.7	40.6	-0.01	-0.13
20 L. Antorbital P.	12.41***	11.46***	42.7	41.4	0.67	3.27
21 W. Internal Nares	22.50***	3.85	43.5	42.7	0.31	1.81
22 L. Up. Toothrow	16.23***	1.12	224.3	225.5	-0.82	-0.54
23 No. Teeth (Up.Lf.)	3.39***	3.88	53.2	52.5	0.42	1.30
24 No. Teeth (Up.Rt.)	5.19***	1.15	52.7	52.3	0.21	0.76
25 No. Teeth (Low.Lf.)	2.33*	0.80	51.3	51.1	0.17	0.39
26 No. Teeth (Low.Rt.)	2.61**	0.34	51.0	50.9	0.11	0.29
27 L. Low. Toothrow	13.99***	1.00	218.4	219.5	-0.76	-0.51
28 Ht. Ramus	21.64***	13.02***	55.4	54.1	0.60	2.51
29 Tooth W.	3.74***	13.84***	2.6	2.5	0.07	5.10
30 L. Ramus	18.06***	0.04	346.8	345.6	0.20	0.35

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

[b] F-values from main effects two-way analysis of variance (5° block vs. sex) involving 10 blocks (*$P<0.05$; **$P<0.01$; ***$P<0.001$). Total of 170 individuals. Degrees of freedom 9 for among-block variation and 1 for between sexes.

[c] Unweighted mean for 10 blocks.

[d] Added to all individual female measurements and subtracted from all individual male measurements to correct for sexual differences.

[e] Difference between sexes (males minus females) multiplied by 100, with the resulting value divided by average of male and female means.

that 6 of the original 36 measurements (i.e., W. Lf. Premax. [at midline of Nares], W. Rt. Premax. [at midline of Nares], Separation of Pterygoids, L. Lf. Tympanic Cavity, L. Rt. Tympanic Cavity, and W. at Pterygobasioocipital Sutures; abbreviations used in these and other character names are listed in footnote a of Table 1) 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 appropriate values for inclusion with the measurements taken by Perrin. Through these procedures, we developed a data set of 30 characters (listed in Table 1) for 246 specimens.

Only specimens that were largely complete were included in the analysis. Missing values (1.34% of total) were estimated by linear regression ("Missing Data Estimator" program developed by Dennis M. Power, Santa Barbara Mus. Nat. Hist., pers. commun.) onto the character that explained the greatest proportion of the variance for the variable under consideration. Specimens then were assigned to 5° latitude-longi-

tude blocks, with each geographic block given a numerical code (see Fig. 1). We had specimens from 35 blocks, although 10 were represented by only a single specimen; the other 25 blocks were used as the basis for most analyses of geographic variation. While several of the remaining 25 blocks are represented by relatively small samples, tests for geographic patterning (described below) suggest that, in general, sample values are representative of what would be expected for these blocks based on their geographic positions. The 5° block size was selected, in part, because it was judged that available sample sizes would not permit detailed analysis of smaller geographic units. Furthermore, migratory movements and related factors were less likely to significantly influence results when these relatively large sampling areas were used.

Douglas et al. (1986) showed that *S. longirostris* in the eastern tropical Pacific was sexually dimorphic for 13 of 36 characters. Because some specimens used in that analysis were removed and new specimens added (see above), we reanalyzed the data with a two-way analysis of variance (ANOVA) for block and sex based on specimens in 10 blocks that had at least four of each sex (Fig. 1). We then produced a series of correction terms to adjust measurements of the larger sex downward and the smaller sex upward, thus producing sex-adjusted or "zwitter" measurements (for details on this adjustment, see Schnell et al. 1985a). These corrections enabled us to combine specimens for both sexes in an overall analysis of geographic variation.

Correlation, ordination and clustering

After conversion to zwitters, characters were then standardized so that means for blocks were zeros and standard deviations ones. Product-moment correlations were computed among characters, and the general associations among characters were summarized by clustering characters using the unweighted pair-group method with arithmetic averages (UPGMA).

This type of hierarchical cluster analysis also was performed to summarize average distance coefficients (Sneath and Sokal 1973) calculated for all pairs of blocks based on standardized data. Cophenetic correlation coefficients were computed to indicate the degree to which distances in the resulting dendrogram accurately represented original interblock morphologic distances.

In addition, we analyzed standardized data using a nonhierarchical *K*-group method called function-point cluster analysis (Katz and Rohlf 1973; described in Rohlf et al. 1979). Blocks are assigned to a series of subgroups at a specified level. The value for the *w*-parameter used by the function-point clustering method was varied. A hierarchical (but not necessar-

ily non-overlapping) system of clusters can be obtained by conducting the analysis at more than one clustering level. Results are presented in the form of a modified skyline diagram (Wirth et al. 1966) where, for a given *w*-value, blocks joined in a common line are in the same cluster.

Based on standardized data, we constructed scatter diagrams of blocks projected 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 applied to determine the subset of variables that show the greatest degree of geographic variation—in this case, those that provide the greatest interblock separation relative to the degree of intrablock variation (Program P7M of BMDP; Dixon 1990). Plots of the first two canonical variables show the maximum separation of blocks in two-dimensional space. The original variables, which in combination exhibited maximum interblock variability, were then subjected to additional analyses.

Mantel test for geographic patterning

Using a test devised by Mantel (1967) and described by Sokal (1979), we analyzed interlocality variation in each character to determine whether values are geographically patterned, or vary spatially at random. This procedure enabled us to determine whether differences in character values between all pairs of samples are statistically associated in a linear manner with corresponding geographic distances. The observed association between sets of character differences and geographic distances was tested relative to its permutational variance, and the resulting statistic was compared against a Student's *t*-distribution with infinite degrees of freedom. Computations were performed using GEOVAR, a library of computer programs for geographic variation analysis written by David M. Mallis and furnished 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 reciprocals of distances are used.

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

1   Sea Current (N., Winter)—Average northern component (in knots) of the surface water current in winter (Innis et al. 1979; their fig. 2.2).

2   Sea Current (W., Winter)—Average western component (in knots) of the surface water current in winter (Innis et al. 1979; fig. 2.3).

3   Water Depth—Average sea depth (in m) (Bartholomew 1975; fig. 122).

4   Solar Insolation (Jan.)—Average incoming solar radiation for January (in gm. · cal/cm²; Brunt 1934; table 2).

5   Solar Insolation (Annual)—Average annual incoming solar radiation in gm. · cal/cm²; Brunt 1934; table 2).

6   Sea Surface Temp. (Jan.)—Average January sea surface temperature (in °C; Robinson 1976: fig. 2 north of 5°S; Wyrtki 1974: fig. 2 south of 5°S).

7   Sea Surface Temp. (July)—Average July sea surface temperature (in °C; Robinson 1976: fig. 74 north of 5°S; Wyrtki 1974: fig. 8 south of 5°S).

8   Sea Surface Temp. (Ann. Var.)—Average annual sea surface temperature variation (in °C; Robinson 1976: fig. 148 north of 5°S; Wyrtki 1974: fig. 26 south of 5°S).

9   Oxygen Min. Layer (Depth)—Annual mean depth (in m) of the absolute oxygen minimum surface with respect to the vertical (Levitus 1982: fig. 52).

10 Surface Salinity—Average salinity (°/oo) of surface sea water (Levitus 1982: microfiche F-02, frames 2–5).

11 Thermocline Depth (Winter)—Mean depths (in m) to the top of the thermocline for January, February, and March (Robinson 1976: figs. 12, 24, and 36 north of 5°S; Cromwell 1958: fig. 1a south of 5°S).

12 Thermocline Depth (Summer)—Mean depths (in m) to the top of the thermocline for July, August, and September (Robinson 1976: figs. 84, 96, and 108 north of 5°S; Cromwell 1958: fig. 1c south of 5°S).

13 Surface Dissolved Oxygen—Annual mean dissolved oxygen (mL/L) of surface sea water (Levitus 1982: microfiche F-03, frames 2–5).

* Abbreviations: Ann. Var. = Annual variation; Jan. = January; Min. = Minimum; N. = North; Temp. = Temperature; W. = West.

As an example of the Mantel procedure, consider the 25 blocks for which two or more specimens were available (Fig. 1). The geographic distances (in nautical miles) between each pair of the 25 blocks (300 pairs total) are computed. We then obtain the mean value for a given morphological character for each block; consider a character with large mean values in northern blocks, a gradual change as one proceeds south, and the smallest means in the most southerly blocks. We calculate the absolute character difference for each pair of blocks (300 difference values); in general, for this hypothetical case, close blocks geographically exhibit small differences in character means, while blocks far apart (e.g., a northern and a southern block) have the largest morphological differences. We and the Mantel test would identify this morphological character as having a strong regional pattern. We also compare reciprocals of geographic distance for each block pair with corresponding morphological differences; this approach indicates whether, in general, geographically close blocks also are similar morphologically (a case of local geographic patterning). The examplar morphological character, thus, would be identified as displaying a strong local pattern (in addition to the strong regional pattern). In general, a character showing a regional pattern (as we have defined it) also will exhibit a local pattern, but the reverse is not necessarily true. For instance, if the morphological character was large in both the north and south, was small for blocks in the middle,

and had gradual changes between adjacent blocks, it would have a strong local pattern but no regional pattern (because many distant blocks are nearly identical morphologically). Detailed computational examples of the Mantel test can be found in Douglas and Endler (1982), Schnell et al. (1985b), and Manley (1985).

We also computed matrix correlations (Sneath and Sokal 1973) between character differences and the associated geographic distances or reciprocals of distances between localities. The significance of these coefficients cannot, however, be tested in the conventional way, because all pairs of localities were used and these are not statistically independent. However, the resulting values are useful as descriptive statistics indicating the degree of association of difference values.

Morphological-environmental covariation

Relatively little is known about the relationship (if any) of geographic variation in morphological characteristics of *S. longirostris* to differences in the environment. Therefore, as an initial exploratory analysis of covariation, we have 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). We also used UPGMA to summarize associations among these environmental variables for 51 blocks with specimens of *S. longirostris* or

S. attenuata or both; since these two dolphin species have broadly overlapping distributions in the eastern tropical Pacific, the blocks used are representative of areas inhabited by *S. longirostris*.

We conducted a principal components analysis of the 13 environmental variables for the 51 blocks in order to obtain summary variables that reflect overall environmental trends. Individual blocks were projected onto the resulting environmental principal components based on standardized data. These block variables were used as composite environmental variables for comparisons with morphological characteristics.

In addition to using matrix correlations and the Mantel procedure to test for local and regional patterning of variation in individual morphological characters, we compared difference patterns of selected morphological measures with those of environmental variables. In these tests, differences between each pair of blocks for a morphological variable were compared with those for an environmental variable.

Sources for environmental data are expanded over those used by Schnell et al. (1986: table 2) so as to accommodate the broader geographic representation resulting from increased numbers of specimens. Values for depth of the oxygen minimum layer were taken for all blocks from Levitus (1982). Data for sea surface temperatures and thermocline depths were not available in the previously used source for blocks west of 120°. Data for these and other blocks north of 5°S were taken from Robinson (1976). Overlapping blocks from the two sources for each environmental variable were used to produce regression equations. Previous data for blocks south of 5°S were converted using these regression equations. Overall, agreement of data for overlapping blocks from the two sources was relatively good. Correlations for sea surface temperatures were: January, 0.956; July, 0.951; annual variation, 0.929. Thermocline depth in winter had a correlation of 0.840, while that for summer values was lower (0.767). All correlations were statistically significant ($P < 0.001$), and the associations of values from the two sources were basically linear.
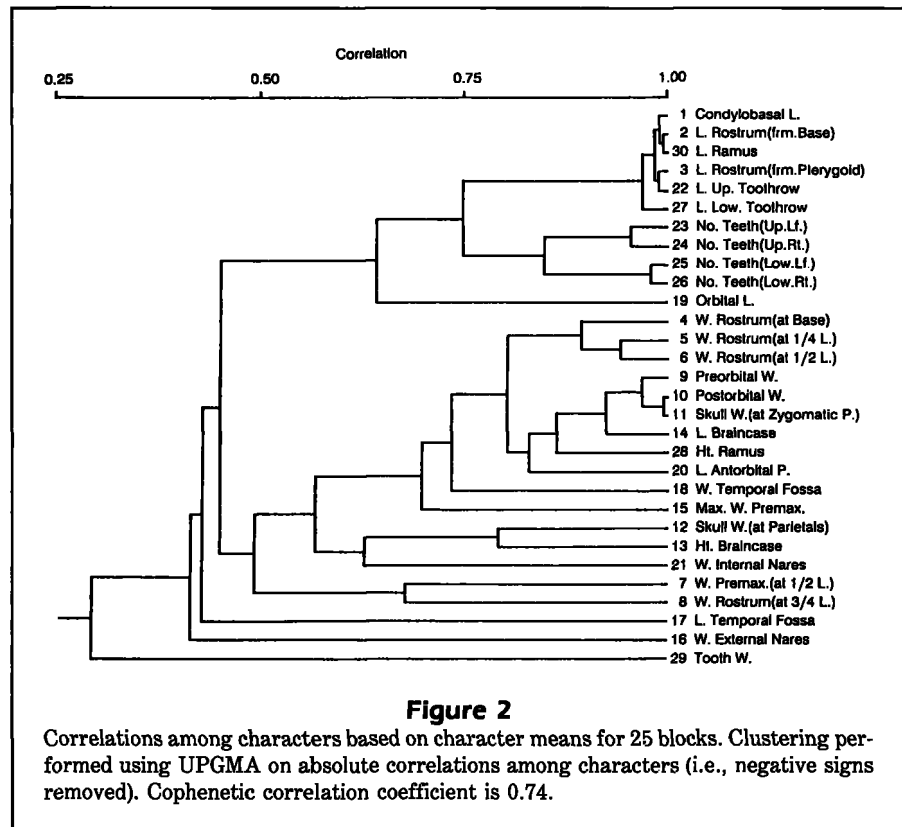

Figure 2
Correlations among characters based on character means for 25 blocks. Clustering performed using UPGMA on absolute correlations among characters (i.e., negative signs removed). Cophenetic correlation coefficient is 0.74.

Results

Sexual dimorphism

In the two-way ANOVA for block and sex, only three measurements showed a significant interaction for block and sex (W. Rostrum [at Base], L. Temporal Fossa and No. Teeth [Up.Lf.]). All characters exhibited significant variation by block (i.e., geographic variation), and 15 of the 30 characters displayed significant sexual dimorphism (Table 1). For most characters, males are larger than females. Character differences between sexes range up to 6.34% (see Table 1), with the most dimorphic character being W. Rostrum (at 3/4 L.).

Correlation, ordination and clustering

Figure 2 summarizes associations among characters based on means for the 25 blocks. Virtually all of the intercharacter correlations were positive in sign; a few indicated weakly negative associations. For the cluster analysis, absolute character correlations were analyzed (i.e., sign of correlation ignored), because we wanted to assess simply the degree of covariation. The character showing the most distinctive pattern relative to

Table 3
Principal component loadings for *Stenella longirostris* involving character means for 25 blocks.

Character	Component* I	Component* II	Character	Component* I	Component* II
1 Condylobasal L.	0.914	−0.325	16 W. External Nares	0.573	−0.045
2 L. Rostrum (frm.Base)	0.872	−0.397	17 L. Temporal Fossa	0.575	0.040
3 L. Rostrum (frm.Pterygoid)	0.885	−0.396	18 W. Temporal Fossa	0.647	0.599
4 W. Rostrum (at Base)	0.856	0.083	19 Orbital L.	0.782	−0.064
5 W. Rostrum (at 1/4 L.)	0.838	0.242	20 L. Antorbital P.	0.849	0.108
6 W. Rostrum (at 1/2 L.)	0.880	0.248	21 W. Internal Nares	0.631	0.427
7 W. Premax. (at 1/2 L.)	0.578	0.044	22 L. Up. Toothrow	0.864	−0.426
8 W. Rostrum (at 3/4 L.)	0.508	0.504	23 No. Teeth (Up.Lf.)	0.608	−0.680
9 Preorbital W.	0.938	0.255	24 No. Teeth (Up.Rt.)	0.688	−0.593
10 Postorbital W.	0.917	0.344	25 No. Teeth (Low.Lf.)	0.600	−0.666
11 Skull W. (at Zygomatic P.)	0.916	0.359	26 No. Teeth (Low.Rt.)	0.652	−0.630
12 Skull W. (at Parietals)	0.331	0.659	27 L. Low. Toothrow	0.814	−0.467
13 Ht. Braincase	0.625	0.719	28 Ht. Ramus	0.872	0.219
14 L. Braincase	0.881	0.326	29 Tooth W.	0.216	0.752
15 Max. W. Premax.	0.811	0.042	30 L. Ramus	0.877	−0.366

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

other morphological characters is Tooth W. In addition, correlations of L. Temporal Fossa and W. External Nares with other characters are relatively low. The rest of the characters are placed in two groups. The first cluster (characters listed between 1 and 19 at top of Fig. 2) includes lengths involving the anterior portion of the skull, tooth numbers, and Orbital L. The second group (characters 4 to 8 as listed in Fig. 2) includes a variety of skull widths, dimensions of the braincase, and Ht. Ramus.

Character loadings of a principal components analysis using 25 blocks are presented in Table 3. The first component explained 57.0% of the total character variance and the second 18.5% (cumulative total of 75.4%). Projections of all blocks onto these components are shown in Figure 3, while Figure 4 is a map summarizing geographically the projections onto the first component. This component, which reflects general skull size, has relatively
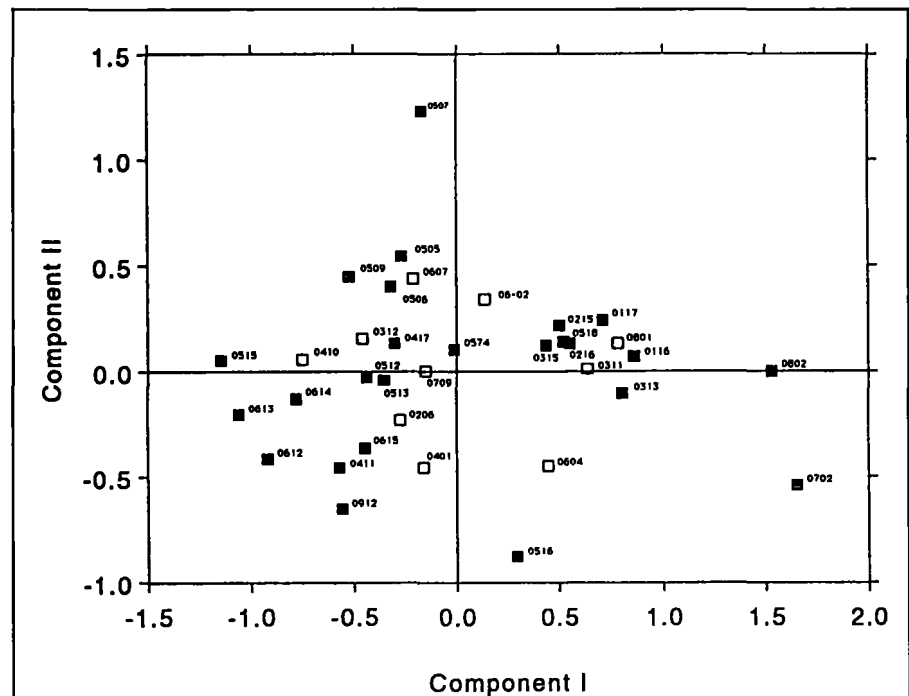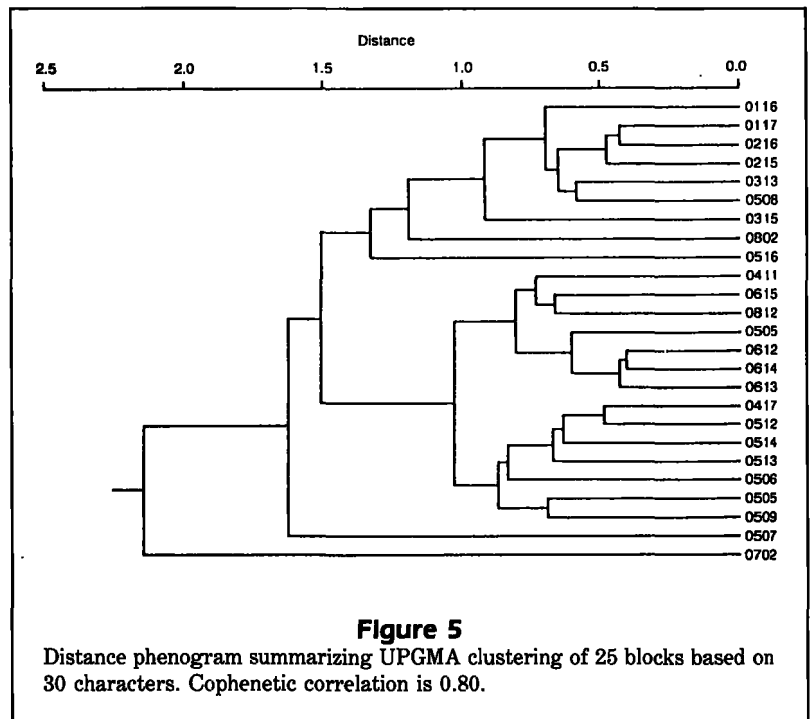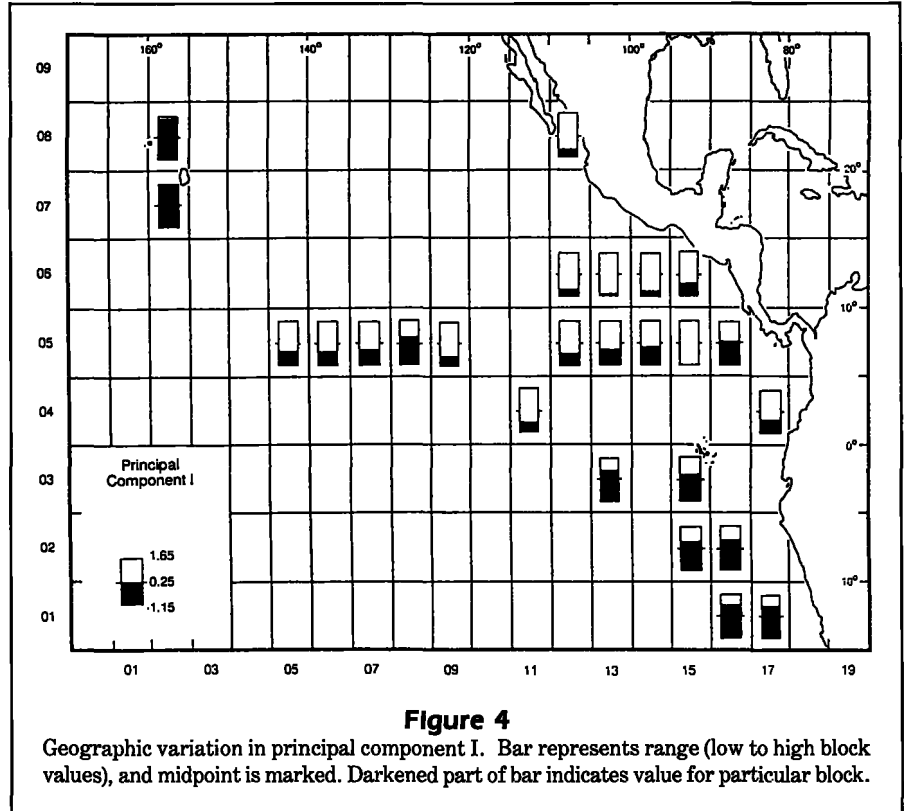

Figure 3
Projections of blocks onto first two principal components based on 30 characters. Solid symbols indicate 25 blocks on which analysis conducted. Open symbols represent blocks with only single specimens, which were projected onto axes generated from 25 blocks with two or more specimens.

high correlations (Table 3) with all characters except Tooth W. and Skull W. (at Parietals). Localities to the right in Figure 3 are from the Hawaiian Island area (0702 and 0802; see Fig. 4), where animals are larger. Specimens from southern blocks (e.g., 0116, 0117, 0313) also are larger than animals from other parts of the range. Blocks to the left in Figure 3, with negative loadings on component I, have smaller individuals. In general, *S. longirostris* from the northeastern blocks were the smallest (e.g., 0515, 0613, 0612).

Component II has its highest positive correlations with Skull W. (at Parietals), Ht. Braincase, and Tooth W.; it has negative associations with characters 23–26, which involve numbers of teeth. Block 0507 is the most extreme, with a positive projection on this component (see Fig. 3); animals from this block have relatively wide skulls and reduced numbers of teeth. In contrast, block 0516 is at the other extreme, with relatively narrow skulls and greater numbers of teeth.

Figure 5 is a dendrogram depicting results from a UPGMA cluster analysis of the 25 geographic blocks. Four main clusters are evident, with block 0702 being the most divergent and in its own cluster. Block 0507 also is in a cluster by itself. The first group in the diagram (i.e., blocks 0116 through 0516 at top of Fig. 5) includes predominantly southern and western localities. Those in the largest cluster (listed from block 0411 to 0509 in Fig. 5) are situated to the north and/or east.

A modified skyline diagram (Fig. 6A) resulting from function-point clustering for 25 blocks based on 30 characters indicates an initial separation of block 0702 (which includes part of Hawaii) from the others. At a *w*-value of 3.50, there are three clusters: (1) block 0702; (2) the southern blocks in addition to blocks 0508 and 0802; and (3) the remaining northern and eastern blocks, including those just north of the Equator. Further sub-

Figure 4

Geographic variation in principal component I. Bar represents range (low to high block values), and midpoint is marked. Darkened part of bar indicates value for particular block.

Figure 5

Distance phenogram summarizing UPGMA clustering of 25 blocks based on 30 characters. Cophenetic correlation is 0.80.

division results with smaller *w*-values (see Fig. 6A).

A similar analysis (Fig. 6B) was conducted using the five characters—Postorbital W., L. Rostrum (frm.

Pterygoid), W. Internal Nares, W. Premax. (at 1/2 L.), and W. Rostrum (at Base)—that, in combination, were best for discriminating among blocks (based on canon-ical variates analysis reported below). With a w-value of 1.79, block 0702 is separated from the remaining blocks. Note that four groups were formed when using a 1.47 w-value; there are two single-block groups (i.e., 0702 and 0802). When the w-value was lowered to 1.37, the same groups were formed, except that 0315 was in its own group and 0802 joined with a group of predominantly southern localities. With a 1.26 w-value, the clusters are the same except that block 0505 joins the northeastern blocks instead of those from the south. Three groups were formed with a 1.15 w-value: (1) block 0702; (2) a group of eight blocks, including southern blocks in addition to 0508, 0505, and 0802; and (3) the northern and eastern blocks, including 0411 and 0417, as well as 0506, 0507, and 0509. At smaller w-values, there is further subdivision.

A canonical variates analysis, using as initial data the information on all 30 measurements for 25 blocks, incorporated the five characters listed in Table 4. A two-dimensional plot of the 25 block centroids on canonical variables 1 and 2 is included as Figure 7; although not used to generate the axes, 10 blocks with only single specimens also are projected onto these variables. The geographic pattern of canonical variable 1 is depicted in Figure 8B. The eigenvalue for canonical variable 1 is 2.93 and that for the second is 0.55, with the two summarizing 82.0% of the variance for the five characters. These five characters in combination show the
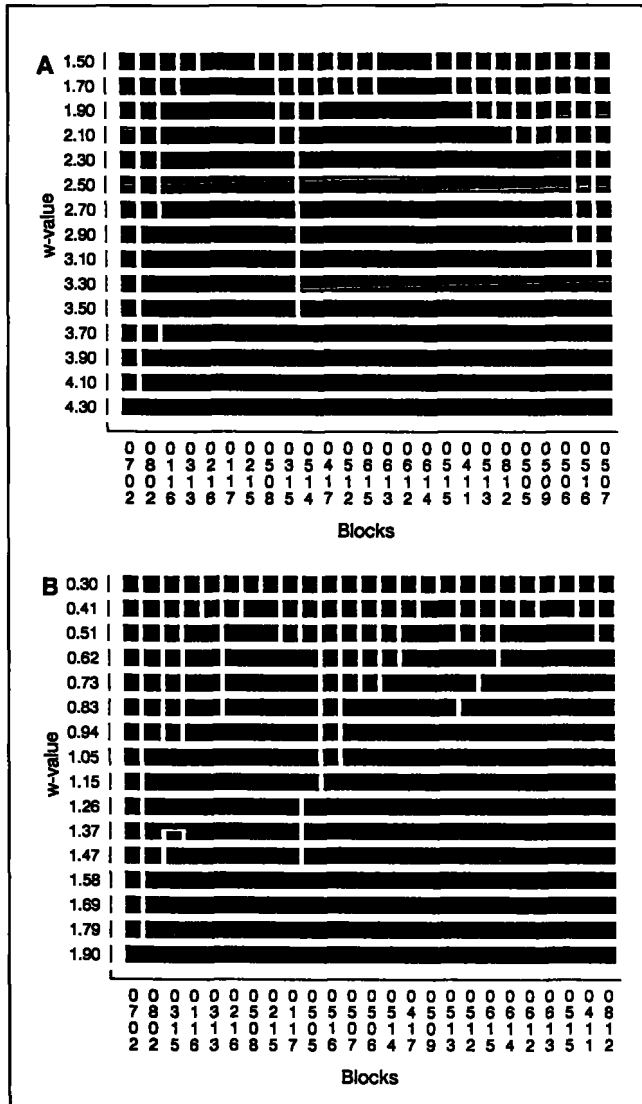
Figure 6

Modified skyline diagrams for 25 blocks, indicating groups formed using function-point clustering procedures and based on: (A) all 30 characters; (B) five characters that, in combination, best discriminate among blocks (Postorbital W., L. Rostrum [frm. Pterygoid], W. Internal Nares, W. Premax. [at 1/2 L.], and W. Rostrum [at Base]). For given w-value (i.e., row), blocks connected in common line are in same cluster.

Table 4
Canonical variates analysis of all specimens from 25 blocks.

Character	F-value to enter	Order of entry	Coefficients* 1	Coefficients* 2
3 L. Rostrum (frm.Pterygoid)	4.53	2	0.0242 (0.2830)	−0.0662 (−0.7734)
4 W. Rostrum (at Base)	2.38	5	−0.0603 (−0.1622)	−0.1912 (−0.5145)
7 W. Premax. (at 1/2 L.)	2.30	4	−0.0291 (−0.0393)	0.2419 (0.3273)
10 Postorbital W.	23.21	1	0.2113 (0.8570)	0.0648 (0.2628)
21 W. Internal Nares	2.88	3	0.0958 (0.1870)	0.3324 (0.6489)
Constant			38.9175	4.4931

*Unstandardized coefficients, with standardized values in parentheses, for canonical variates.

greatest among-group variability relative to that within groups and are used for more detailed comparisons with environmental variables (presented below).
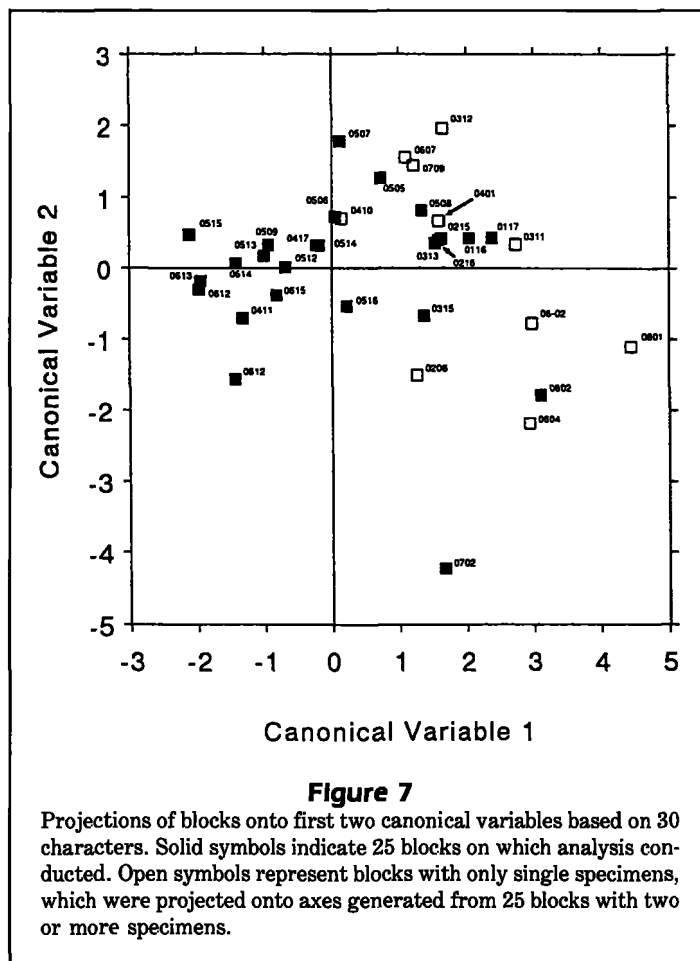
As indicated in Table 4, the first canonical variable is most influenced by Postorbital W. (Fig. 8A). In Figure 7, blocks that are large for this character are to the right, while those that are small are to the left. When considering only those blocks with more than one specimen (i.e., those shown with solid symbols in Fig. 7), the two blocks from the vicinity of the the Hawaiian Islands (0802 and 0702) are to the right, as are blocks predominantly from the southern portion of the range. The blocks with single specimens (which tend to be more westerly) also are to the right. Specimens from blocks to the north and east are smaller; they are depicted to the left in Figure 7. Some west-central blocks group with the southern blocks, while others are intermediate or group with those to the northeast. The second canonical variable contrasts blocks from the Hawaiian Island area (0702, 0802) with the others (see Fig. 7); in the characters reflected by this variable, values of block 0812 (which is northern, but to the east) show some similarities to those for 0702 and 0802.

Mantel test for geographic patterning

Individual characters were evaluated with respect to geographic patterning using Mantel tests, as well as matrix correlations that compare inter-block geographic distances (or reciprocals of these distances) and character differences between localities. Of the 30 characters, 66.7% (20) show statistically significant regional patterning indicating that geographic distances (in nautical miles) and interblock character differences are interrelated (Table 5). For measures showing significant *t*-values the greatest character differences tend to be between blocks that are farthest away from each other, while nearer localities are more similar.

Local patterning, as indicated by a significant negative association of distance reciprocals and character differences, was found in 83.3% (25) of the characters (Table 5). All characters that showed regional patterning also exhibited local patterning.
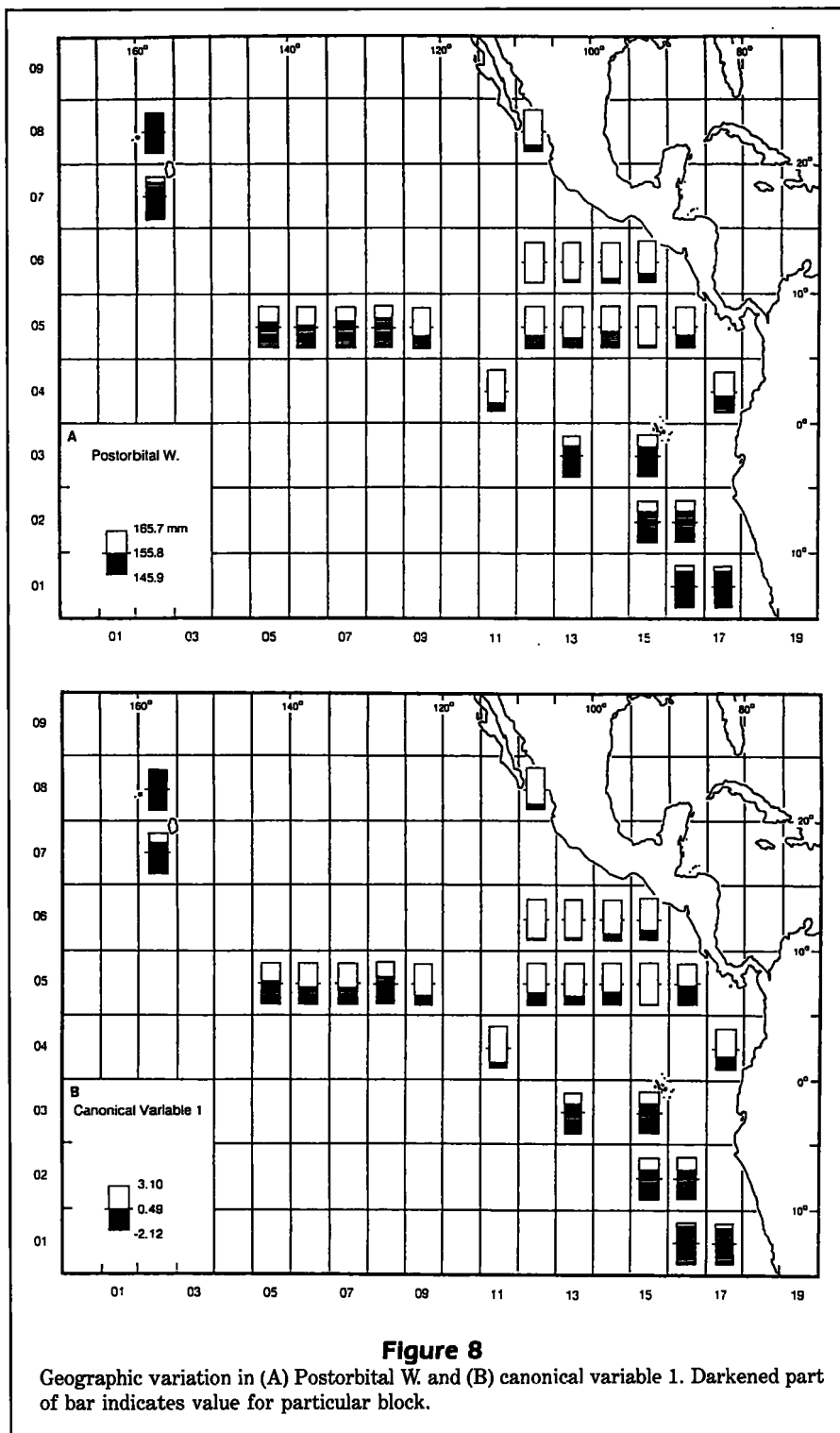
Principal component projections also were assessed in terms of geographic patterning. As indicated at the bottom of Table 5, component I (Fig. 4) has strong regional and local patterning; component II has significant local patterning. Canonical variables 1 (Fig. 8B) and 2 both exhibit marked regional and local patterning (Table 5).

Figure 7

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

Morphological-environmental covariation

Figure 9 is a dendrogram indicating absolute correlations among the 13 environmental variables, subdividing them into five clusters. Sea Current (N., Winter) is in a group by itself and quite different from the others. Sea Current (W., Winter) and Oxygen Min. Layer (Depth) are in the second cluster, which joins with a group of five variables involving surface measures of temperature, oxygen, and salinity. The fourth cluster involves two measures of solar insolation, and the fifth reflects aspects of water depth.

The loadings of environmental variables on the first three environmental principal components are given in Table 6. The first component statistically explains 33.0% of the total character variance, the second 23.2%, and the third 15.8% (cumulatively 72.0%). Maps (Fig. 10) depict projections of the 25 blocks with two or more *S. longirostris* onto the first two environmental components. Environmental component I has relatively high values for blocks between 5° and 15°N, with intermediate values to the north and low values south of the Equator (Fig. 10A). Sea Surface Temp. (July)

Figure 8

Geographic variation in (A) Postorbital W. and (B) canonical variable 1. Darkened part of bar indicates value for particular block.

component has high values for the two blocks adjacent to the Hawaiian Islands (Fig. 10B), with intermediate values in other western blocks. Strong negative projections on this component are found for blocks along the coast of South and Central America just north of the Equator. The most substantial loadings on this component are for the two thermocline variables (Table 6), while Water Depth and Surface Salinity also exhibit relatively high positive projections for component II. Environmental component III reflects mainly Solar Insolation (Annual), with Solar Insolation (Jan.) also having a relatively high positive loading (Table 6). The most extreme negative projection for component III is for the northern block near the coast (i.e., 0812), with the highest positive projects for blocks in the west-central portion of the study area (i.e., 0505 through 0509). In general, other blocks have relatively high projection values, except for 0802 (which is somewhat lower). Other components beyond the first three tended to represent only single environmental variables.

Several of the environmental measures showed few or no statistical associations with morphological characters (and resulting principal components or canonical variables), while others exhibited significant covariation (Table 7). The first environmental variable, Sea Current (N., Winter), is not significantly correlated with any of the 30 morphological measures. The other character summarizing sea-current information, Sea Current (W.,Winter), has a geographic pattern showing relatively weak statistical concordance with eight of the morphological characters. Toothrow lengths and three of the four tooth counts are among those with significant associations.

has a high positive loading on component I, while that for Sea Surface Temp. (Ann. Var.) is negative. Five other variables have relatively high correlations with this component (Table 6). The second environmental

Table 5

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 *Stenella longirostris*.

Character	Distance		Reciprocal of distance	
	t	r	t	r
1 Condylobasal L.	4.49***	0.445	−4.86***	−0.348
2 L. Rostrum (frm.Base)	3.89***	0.395	−4.35***	−0.315
3 L. Rostrum (frm.Pterygoid)	4.26***	0.437	−4.67***	−0.340
4 W. Rostrum (at Base)	3.49***	0.435	−3.86***	−0.316
5 W. Rostrum (at 1/4 L.)	3.16**	0.327	−3.48***	−0.255
6 W. Rostrum (at 1/2 L.)	3.12**	0.297	−3.68***	−0.258
7 W. Premax. (at 1/2 L.)	−0.48	−0.046	0.23	0.017
8 W. Rostrum (at 3/4 L.)	0.33	0.028	−1.98*	−0.132
9 Preorbital W.	4.59***	0.403	−6.36***	−0.429
10 Postorbital W.	3.57***	0.262	−5.97***	−0.373
11 Skull W. (at Zygomatic P.)	3.43***	0.255	−5.98***	−0.357
12 Skull W. (at Parietals)	1.83	0.199	−2.19*	−0.165
13 Ht. Braincase	1.51	0.146	−3.89***	−0.275
14 L. Braincase	3.62***	0.323	−4.85***	−0.329
15 Max. W. Premax.	2.05*	0.209	−3.58***	−0.260
16 W. External Nares	−0.48	−0.047	−0.38	−0.027
17 L. Temporal Fossa	1.87	0.193	−2.74**	−0.201
18 W. Temporal Fossa	3.84***	0.362	−4.69***	−0.327
19 Orbital L.	3.01**	0.325	−3.68***	−0.276
20 L. Antorbital P.	2.93**	0.229	−4.32***	−0.277
21 W. Internal Nares	0.56	0.047	−3.43***	−0.226
22 L. Up. Toothrow	3.96***	0.392	−4.47***	−0.319
23 No. Teeth (Up.Lf.)	3.46***	0.411	−3.61***	−0.286
24 No. Teeth (Up.Rt.)	3.46***	0.434	−3.30***	−0.271
25 No. Teeth (Low.Lf.)	1.62	0.178	−1.38	−0.105
26 No. Teeth (Low.Rt.)	1.52	0.158	−1.28	−0.093
27 L. Low. Toothrow	3.00**	0.285	−3.46***	−0.242
28 Ht. Ramus	3.03**	0.237	−4.77***	−0.306
29 Tooth W.	−0.55	−0.067	−0.13	−0.011
30 L. Ramus	3.91***	0.375	−4.47***	−0.314
Component I	3.77***	0.363	−4.64***	−0.327
Component II	1.13	0.134	−2.72**	−0.214
Canonical Variable 1	2.77**	0.220	−5.08***	−0.327
Canonical Variable 2	4.05***	0.520	−4.12***	−0.343

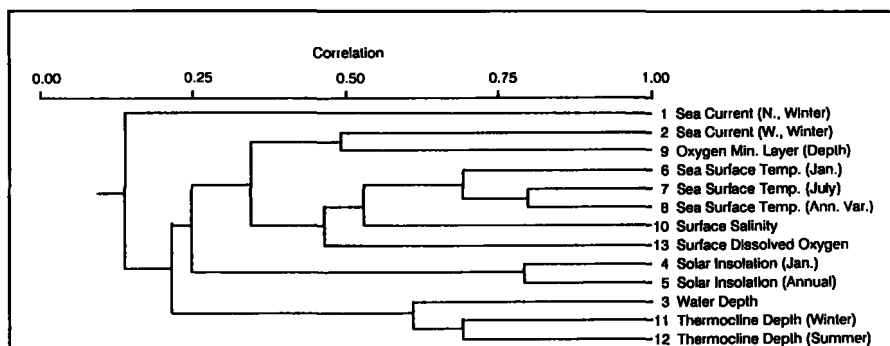*$P<0.05$; **$P<0.01$; ***$P<0.001$.

Figure 9

Clustering by UPGMA on absolute correlation values among environmental variables. Cophenetic correlation of 0.75.

Table 6

Principal component loadings for environmental variables.

	Environmental variable	Component[*]		
		I	II	III
1	Sea Current (N.,Winter)	−0.126	0.307	0.431
2	Sea Current (W.,Winter)	−0.495	−0.037	−0.091
3	Water Depth	−0.279	**0.783**	0.279
4	Solar Insolation (Jan.)	−0.683	−0.227	**0.627**
5	Solar Insolation (Ann.)	−0.274	−0.291	**0.872**
6	Sea Surface Temp. (Jan.)	0.768	−0.255	0.380
7	Sea Surface Temp. (July)	**0.942**	0.014	−0.101
8	Sea Surface Temp. (Ann.Var.)	**−0.848**	−0.224	−0.304
9	Oxygen Minimum Layer (Depth)	0.675	0.442	0.157
10	Surface Salinity	−0.608	**0.600**	−0.046
11	Thermocline Depth (Winter)	0.172	**0.888**	−0.269
12	Thermocline Depth (Summer)	−0.044	**0.836**	0.363
13	Surface Dissolved Oxygen	−0.596	0.089	−0.380

[*] Relatively high loadings highlighted in bold as follows: (component I) > |0.8|; (II and III) > |0.6|.

Table 7

Product-moment correlations of block means for morphological variables and components versus environmental variables and components based on 25 blocks of *Stenella longirostris*.[a]

| Character	Environmental variable[b]													Environmental component		
	1	2	3	4	5	6	7	8	9	10	11	12	13	I	II	III
1 Condylobasal L.						− −	− −						+ +	−		
2 L. Rostrum (frm.Base)						− −	−	+	+				+	−		
3 L. Rostrum (frm.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		−		+ +	+ +							− −				+ +

Table 7 (continued)

[a] Blanks indicate nonsignificant correlations. Individual symbols refer to significant positive or negative correlations ($P<0.05$; >0.396); double symbols indicate highly significant correlations ($P<0.01$; >0.505); and triple symbols represent very highly significant correlations ($P<0.001$; >0.620).

[b] 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.

Figure 10

Geographic variation in environmental variables as summarized in (A) principal component I and (B) principal component II. Darkened part of bar indicates value for particular block.
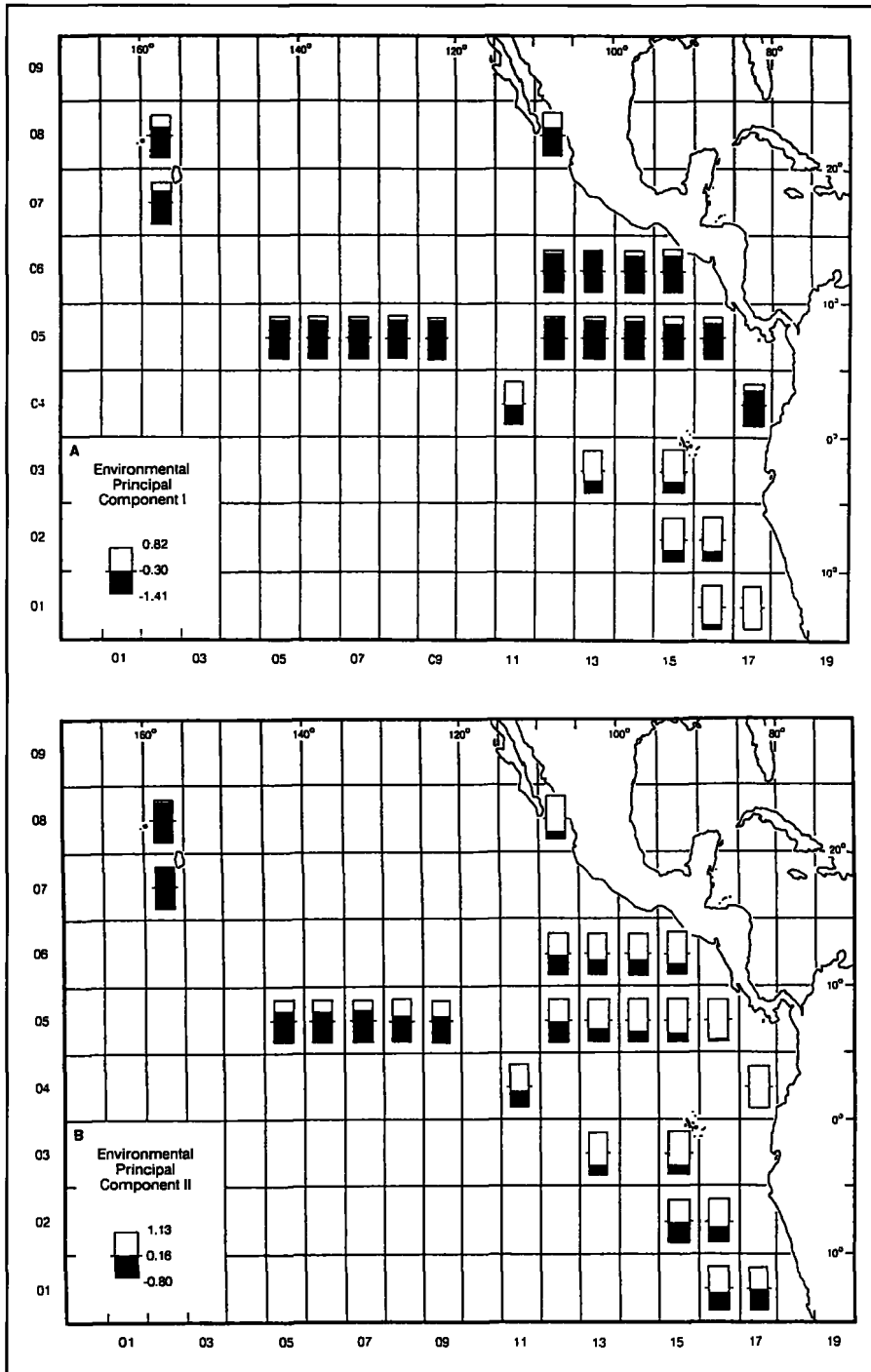
Water Depth (variable 3; Fig. 11B) is positively correlated with 13 morphological measures, two of which (L. Braincase and W. Temporal Fossa) are very highly significant ($P<0.001$). The block values for W. Temporal Fossa (which have a 0.755 correlation with Water Depth values) are shown in Figure 11A. For the 13 variables, relatively large values typically were recorded in block 0117 and those in the vicinity of the Hawaiian Islands (0702 and 0802), all of which have relatively deep waters, while more shallow localities like 0516 and 0812 had individuals that were smaller for these characters.

The fourth environmental measure, Solar Insolation (Jan.), changes from high to low values uniformly from north to south. It is statistically associated with only one character, W. Internal Nares, which has small values for 0812; values tend to get higher as one proceeds south, but there are exceptions (such as 0802, which is relatively high). Canonical variable 2 has a pattern statistically similar to this environmental variable (bottom of Table 7).

Annual solar insolation (variable 5) has high values at the earth's Equator, with decreasing values as one proceeds toward either pole. Only two morphological variables have significant correlations with this envi-
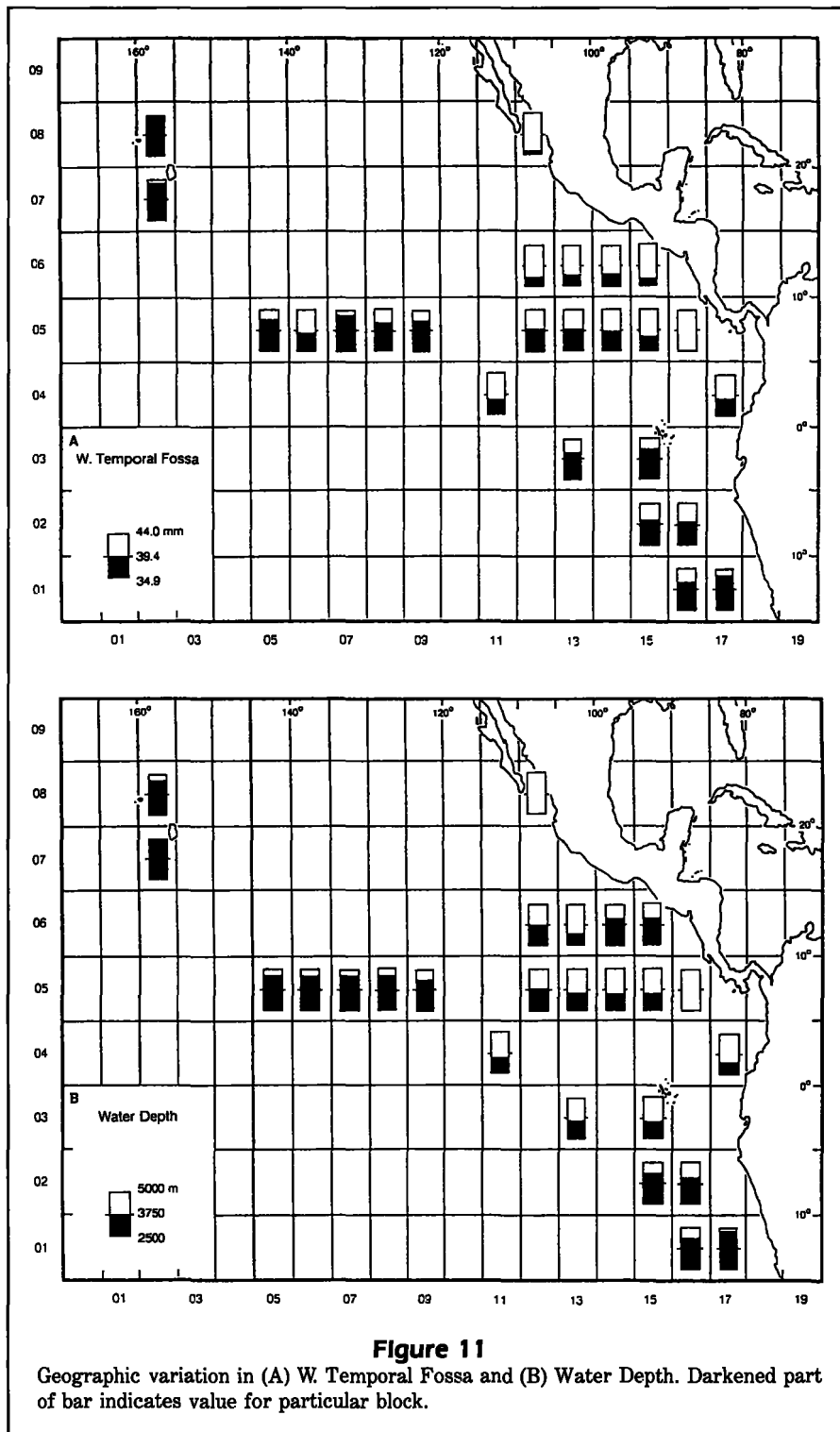
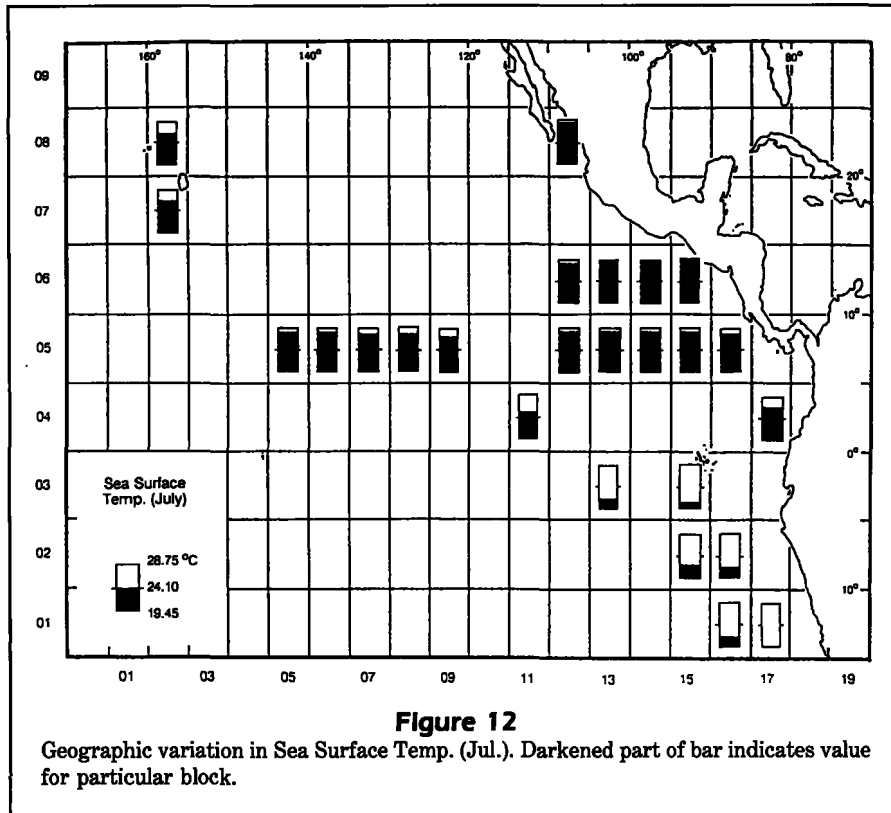ronmental factor (Table 7), each of which are negative and relatively weak.

The sixth environmental variable, Sea Surface Temp. (Jan.), has significant negative correlations with 22 morphological characters, as well as principal component I (Fig. 4) and canonical variable 1 (Fig. 8B). Variable 7, which is Sea Surface Temp. (July) (Fig. 12), has a relatively high number (21) of significant negative associations with morphological measures, as well as with principal component I (Fig. 4) and canonical variable 1 (Fig. 8B). Postorbital W. (Fig. 8A) has the strongest correlation (−0.681) of any of the morphological characters with Sea Surface Temp. (July).

The eighth environmental variable, Sea Surface Temp. (Ann. Var.), exhibited relatively weak geographic concordance with six morphological characters, one of which was a negative association (Table 7). Also, only weak negative correlations of five morphological variables were found with depth of the oxygen minimum layer (variable 9).

Fourteen of the 30 morphological measures are significantly correlated with environmental variable 10, Surface Salinity (Fig. 13B). In addition to east-west changes from lower to higher values at a given latitude, salinity also exhibits a north-to-south trend of increasing values (below 15°N). The highest correlation (0.661) is with L. Braincase (Fig. 13A).

Thermocline Depth (Winter), variable 11, was positively associated with 13 morphological variables (Table 8), while Thermocline Depth (Summer), variable 12, has statistically significant positive correlations with 11 morphological traits. The final variable, Surface Dissolved Oxygen, covaries with 16 morphological variables. As suggested in the dendrogram in Figure 9, this environmental variable has a

Figure 11

Geographic variation in (A) W. Temporal Fossa and (B) Water Depth. Darkened part of bar indicates value for particular block.

Figure 12

Geographic variation in Sea Surface Temp. (Jul.). Darkened part of bar indicates value for particular block.

pattern with similarities to those for sea surface temperatures.

Table 7 indicates that the pattern of correlations of environmental principal component I with cranial measures is similar to that of Sea Surface Temp. (July) (variable 7), which is expected given the strong loadings of this environmental variable on this component (see Table 6). Environmental principal component II has positive correlations with most skull-width measures (Table 7). The third environmental component has relatively few significant correlations with morphological characters; its strongest association is with one of the summary morphological variables, canonical variable 2.

In Table 8, we have summarized Mantel *t*-values and matrix correlations between selected

Table 8

Results of Mantel tests (*t*) and matrix correlations (*r*) for *Stenella longirostris*. Comparison of interlocality differences for 13 environmental variables and 3 environmental components against those for 5 morphological variables selected in canonical variates analysis.

Environmental variable	Postorbital W.		L. Rostrum (frm.Pterygoid)		W. Internal Nares		W. Premax. (at 1/2 L.)		W. Rostrum (at Base)	
	t	r	t	r	t	r	t	r	t	r
1 Sea Current (N.,Winter)	-0.56	-0.050	-0.59	-0.083	1.99*	0.215	-0.56	-0.073	-0.79	-0.141
2 Sea Current (W.,Winter)	-1.38	-0.092	0.12	0.010	-0.72	-0.053	0.59	0.048	-0.44	-0.044
3 Water Depth	3.23**	0.235	1.27	0.128	2.25*	0.186	-0.76	-0.073	2.22*	0.271
4 Solar Insolation (Jan.)	4.46***	0.339	2.60**	0.283	4.49***	0.393	0.77	0.079	1.81	0.241
5 Solar Insolation (Ann.)	2.14*	0.176	1.95	0.241	1.86	0.180	-0.54	-0.062	1.43	0.219
6 Sea Surface Temp. (Jan.)	5.47***	0.371	3.71***	0.327	3.63***	0.271	0.53	0.045	1.63	0.170
7 Sea Surface Temp. (July)	4.82***	0.353	1.73	0.176	4.65***	0.387	2.55*	0.244	0.64	0.079
8 Sea Surface Temp. (Ann.Var.)	1.64	0.114	1.22	0.113	3.80***	0.294	1.40	0.123	-0.40	-0.044
9 Oxygen Minimum Layer (Depth)	1.22	0.077	2.12*	0.158	3.54***	0.236	1.62	0.116	-0.61	-0.051
10 Surface Salinity	4.57***	0.323	0.37	0.035	1.03	0.082	0.06	0.005	0.62	0.072
11 Thermocline Depth (Winter)	2.92**	0.241	4.42***	0.548	-0.96	-0.093	-0.55	-0.063	3.87***	0.598
12 Thermocline Depth (Summer)	2.52*	0.172	1.63	0.146	-0.15	-0.001	-0.35	-0.030	3.41***	0.362
13 Surface Dissolved Oxygen	2.52*	0.204	1.43	0.172	1.88	0.179	0.93	0.105	-0.18	-0.027
Environmental Component I	3.63***	0.268	1.68	0.174	4.09***	0.345	2.02*	0.197	0.11	0.014
Environmental Component II	2.75**	0.212	3.85***	0.429	-1.11	-0.099	-0.75	-0.078	3.70***	0.508
Environmental Component III	1.39	0.120	1.19	0.160	1.99*	0.207	-0.97	-0.121	0.32	0.054

*P<0.05; **P<0.01; ***P<0.001.
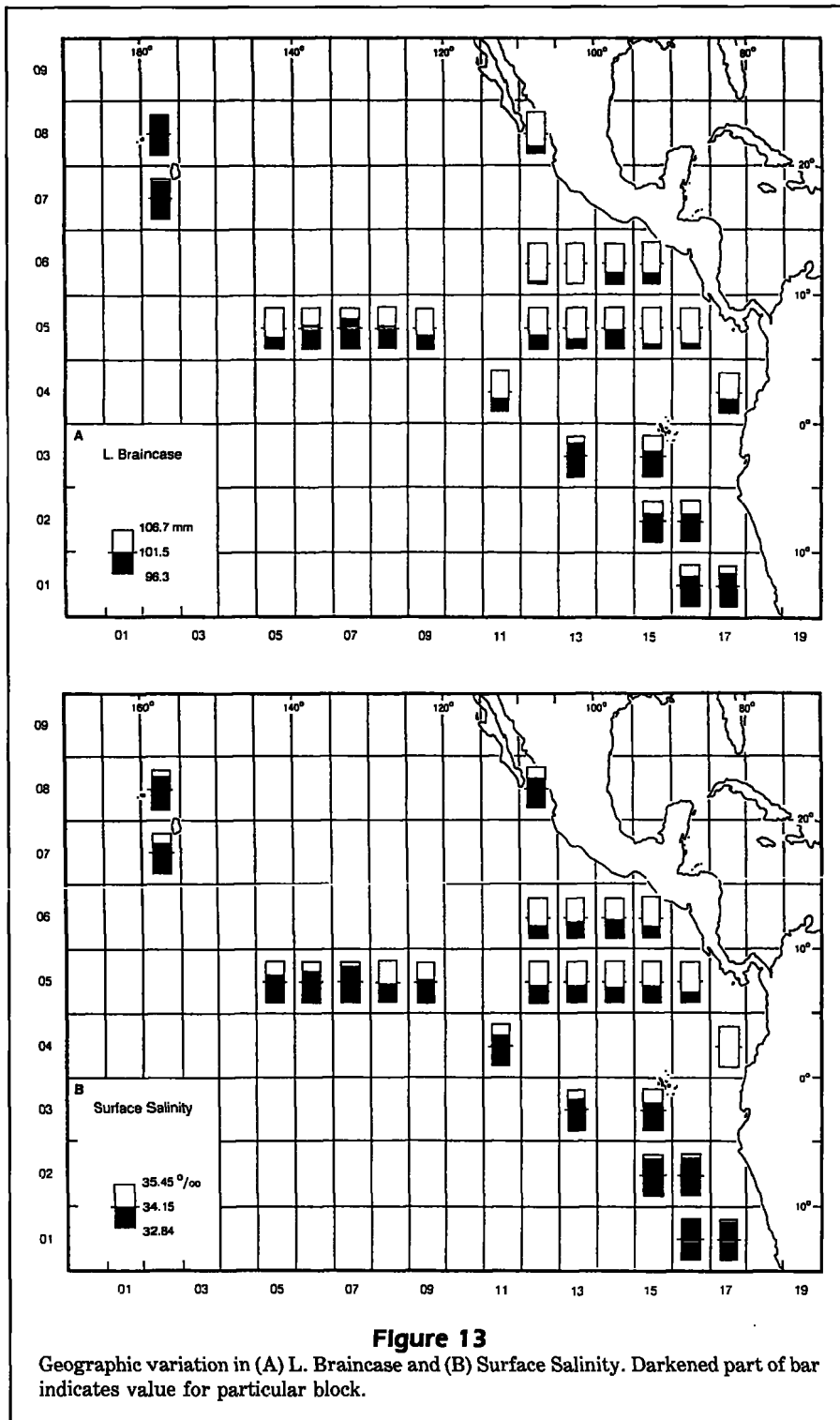
Mantel test (Table 8), with Sea Surface Temp. (Jan.) being the highest. The seven environmental variables displaying correlations in Table 7 with Postorbital W. also are judged concordant using the Mantel test. In addition, based on interblock difference values, there are statistically significant associations with the two measures of solar insolation (variables 4 and 5; see Table 8). The concordance with these two environmental variables is primarily on the strength of pattern similarities in the eastern portion of the range. Postorbital W. also shows significant associations with the first two environmental principal components.

Based on correlation tests for block means (Table 7), L. Rostrum (frm.Pterygoid) exhibited a geographic distribution of mean block values that was statistically associated with those for six environmental measures. Four significant associations were identified using the Mantel test (Table 8), only two of which were found by both tests (Sea Surface Temp. [Jan.] and Oxygen Minimum Layer [Depth]). It has a significant association with environmental component II.

In Table 8, a total of seven significant associations of difference values are recorded for W. Internal Nares with environmental variables, including the three listed in Table 7 as having statistically significant associations based on means. Difference values for environmental components I and III significantly covary with those of W. Internal Nares.

Using difference values, W. Premax. (at 1/2 L.) has only a weak correlation with a single environmental variable (Table 8); only a single significant association was found using correlations of mean values, and this was with another environmental variable (see Table 7). W. Premax. (at 1/2 L.) is weakly associated with environmental component I.

Figure 13

Geographic variation in (A) L. Braincase and (B) Surface Salinity. Darkened part of bar indicates value for particular block.

morphological and environmental variables. Assessing difference matrices using these techniques represents an alternate method with which to evaluate covariation of geographic patterns. For Postorbital W. (Fig. 8A), there are nine significant associations using the

The W. Rostrum (at Base) exhibits covariation with three of the environmental variables based on the Mantel test (Table 8), two of which involve thermocline depth. The matrix correlation (Table 8) for W. Rostrum (at Base) with Thermocline Depth (Winter) is substantial (0.598), as it is with environmental component II (0.508). Mean values also showed an association of W. Rostrum (at Base) with the thermocline variables and Water Depth, as well as with three other environmental variables (Table 7).

Discussion

Sexual dimorphism

Our analysis of sexual dimorphism extends the studies of Douglas et al. (1986) in terms of additional specimens and minor adjustments in previously collected data. We found 15 of 30 variables were statistically dimorphic. Douglas et al. (1986) identified 13 of these as showing sexual differences, the increase of two characters (Postorbital W. and Tooth W.) being due primarily to increased numbers of specimens available. In five characters, including two rostral and two toothrow lengths, measurements for females were slightly larger than for males, although the differences were not statistically significant. For all other measures, males are larger than females, including all 15 where statistical significance was found.

Geographic variation

In 1889, when the existence of spinner dolphins in the eastern tropical Pacific was not yet known, True indicated that the absence of adequate samples made very difficult the task of taxonomically evaluating species in the genus *Stenella*. By the 1970s, Perrin (1975b) had available considerably more material for a monographic treatment of *S. attenuata* and *S. longirostris* from the eastern tropical Pacific and was able to make significant advances with respect to our understanding of morphological variation of *Stenella*. However, his work on *S. longirostris* also was hindered by the paucity of skeletal material from parts of the range. For our study, many additional specimens of *S. longirostris* were available. On the whole, our results are strongly supportive of those obtained by Perrin (1975b) for cranial characteristics, but we also have been able to substantially extend his analyses.

Perrin (1972) conducted an initial analysis of geographic variation in color patterns of *S. longirostris* in the eastern Pacific Ocean. He found geographic variation, particularly in the "dorsal field system" of coloration, which overlies a basic general pattern.

These and other data suggested differentiation into eastern, whitebelly, and Hawaiian forms. The differences were analyzed further by Perrin (1975a,b), who indicated that the whitebelly form was in some ways similar to the Hawaiian form, but had a proportionately smaller beak. Perrin (1975b) described but did not name four races—the three mentioned above plus a Costa Rican form which occurs off the coast of Central America. Perrin et al. (1979b) evaluated possible differentiation in *S. longirostris* involving animals found south of the Equator in the eastern Pacific Ocean. They concluded that these *S. longirostris* are morphologically distinct from those to the northeast; characteristics showing such a trend include coloration, size, shape, and skeletal measures.

Recently, Perrin (1990) named and described three subspecies: *S. l. longirostris* (Gray's spinner dolphin), *S. l. orientalis* (eastern spinner dolphin), and *S. l. centroamericana* (Central American spinner dolphin). In our geographic variation assessment, we purposely included all adult specimens available, without an attempt *a priori* to differentiate previously described forms. However, the differences among the named forms are reflected in our results for cranial characteristics.

In our analyses, the Central American spinner dolphin of Perrin (1990) is shown to be different from other *S. longirostris* by the positioning of block 0516 on principal component II; it had the lowest value of any of the blocks (see Fig. 3). Three of the four specimens in block 0516 exhibit characteristics of Central American spinners (as does one of the nine from 0615). Character associations with the second principal component—summarized in Table 3—suggest that, after taking into account general size (summarized in and mathematically removed by component I), animals of this subspecies have relatively longer toothrows, greater numbers of teeth, a narrower skull at the parietals, and a shallower braincase than *S. longirostris* from other areas. Perrin (1990: table 2) provided comparative measurements and counts for *S. l. longirostris* and *S. l. centroamericana*, which show the Central American form to have longer toothrows and greater numbers of teeth. He did not include data on Ht. Braincase, but did characterize the Central American form as having a relatively long and narrow skull. While Skull W. (at Parietals) is slightly greater for *S. l. centroamericana* than *S. l. longirostris* (Perrin 1990: table 2), the former has a relatively narrow skull given its considerably greater length. Additional *S. l. centroamericana* specimens are needed, since the diagnosis and understanding of cranial variation in this subspecies still is based on very few animals.

Perrin (1990) suggested the existence of a zone of hybridization/intergradation between *S. l. longirostris*

and *S. l. orientalis* that may be about 2000 km wide. *Stenella l. orientalis* is found primarily in the northeastern blocks we assessed. Our analyses confirm that, in general, adult spinner dolphins from this region are smaller than those from areas to the south, southwest, and west (for general trends, refer to block projections onto canonical variable 1 in Fig. 8B). The nominate subspecies, *S. l. longirostris*, of Perrin (1990) subsumes a series of broadly distributed populations. He indicated that *S. l. longirostris* likely includes areal entities (outside the eastern Pacific) worthy of formal taxonomic recognition, but to date these have not been evaluated properly because of a paucity of specimens from major portions of the range.

Extensive data on geographic variation in external morphology of *S. longirostris* in the eastern tropical Pacific were assessed by Perrin et al. (1991). They evaluated color patterns, dorsal-fin shapes, and total lengths for *S. longirostris* from throughout the geographic range covered in our study. Some external characters (e.g., ventral field coloration pattern) exhibited a "radial" or concentric pattern of variation, where spinners to the south, southwest and west were similar, but markedly different from those to the northeast. This pattern also was prevalent among cranial variables (e.g., see values for Postorbital W. [Fig. 8A], canonical variable 1 [Fig. 8B], and L. Braincase [Fig. 13A]).

We were able to incorporate specimens into our analyses from the general vicinity of the Hawaiian Islands. Perrin (1975b) evaluated Hawaiian specimens for cranial features and concluded that, in general, they were strikingly larger than other spinners. However, at the time, few specimens were available from southern localities. When these southern blocks are incorporated into the analysis, the Hawaiian specimens are not quite as extreme, although for most characters the Hawaiian specimens remain the largest (see Postorbital W. [Fig. 8A], W. Temporal Fossa [Fig. 11A] and L. Braincase [Fig. 13A], as well as principal component I [Figs. 3 and 4] and canonical variable 1 [Figs. 7 and 8B]). Also, for many of the characters the Hawaiian specimens are more similar to far-southern ones than to those from geographically closer western blocks located between 5° and 10°N. When evaluating other western single-specimen blocks that are situated closer to the Hawaiian Islands, some analyses (e.g., canonical variates analysis; see Fig. 7) indicate that spinners similar to Hawaiian specimens are present; however, additional specimens will be needed in order to clarify the trends in variation in this part of the Pacific.

In some descriptive analyses (e.g., see Figs. 6 and 7), block 0702 to the south of the Hawaiian Islands is depicted as quite distinct from other blocks, including the adjacent block to the north (0802). This incongruity

is likely a statistical aberration related to the small sample size for 0702 (*n* 2), rather than to a biological difference. Checking the specimens from the two blocks indicated that they were taken in relatively close proximity, but were separated because of where the border between the blocks happened to be located. This apparent anomaly does not detract from the general conclusion that the spinners in the vicinity of the Hawaiian Islands are among the largest found in the overall study region.

Schnell et al. (1986) conducted an extensive analysis of geographic variation of offshore *S. attenuata*, a similar species that broadly overlaps in range with *S. longirostris*. The two species frequently are seen in mixed schools (Au and Perryman 1985, Reilly 1990). Reilly (1990) noted that 73% of the *S. longirostris* sightings from research vessels also included *S. attenuata*; 49% of the records of the more common *S. attenuata* involved schools that also had *S. longirostris*. While detailed comparisons evaluating interspecific geographic covariation in morphology are beyond the scope of this paper, our preliminary findings indicate that about one-half of the individual morphological characters show similar geographic patterns for blocks where both species are represented. However, two characters involving the temporal fossa (variables 17 and 18) exhibit negative correlations (the length correlation is statistically significant and the width nearly so)—localities where the fossa is larger in *S. attenuata*, it is smaller in *S. longirostris*. The temporal fossa reflects the size of muscles involved in the feeding apparatus. Also, the upper tooth counts show pronounced negative correlations interspecifically. Opposite trends in the two similar species for these characters may be an example of ecological character displacement related to differences in feeding and the types of food taken by the two species in given localities (Perrin 1984).

Genetic subdivision, management units, and implications of cranial variation

Considerable attention has been given to definition of stock units with a meaningful biological basis that can be employed to manage *S. longirostris* in the eastern Pacific (Perrin 1975a,b; Perrin et al. 1979b, 1985, 1991). One of the important questions with respect to the effectiveness or relevance of geographic management units is the degree to which the species is genetically subdivided. Perrin et al. (1991) noted a complex patchwork pattern of geographic variation in external and other characteristics in *S. longirostris* suggesting "that there is not a large amount of movement between the various regions." They pointed out that the complex geographic pattern of variation in the

zone of intergradation/hybridization of *S. l. orientalis* with *S. l. longirostris* is consistent with limited data on movements from tag returns (Perrin et al. 1979a), which indicate "a home range of a diameter of hundreds rather than thousands of kilometers."

Our findings strongly support these conclusions. All 30 characters studied showed geographic variation, with two-thirds having demonstrable regional patterning, and 25 of the 30 showing local patterning. These patterns emerge even though data are based on specimens pooled over season and for a number of years; consistent geographic patterns largely would be obscured if animals typically moved long distances within or between years. Clearly, as found by Schnell et al. (1986) for *S. attenuata*, in *S. longirostris* "there are notable patterns of geographic variation...indicating that geographic subdivision exists among populations."

We found concordance of geographic patterns in *S. longirostris* for a number of cranial characters as noted by Perrin et al. (1991) for external characters. Yet, some patterns are not concordant; in fact, there is a mosaic of patterns involving different characters and/or character suites. For example, many of the tooth counts, toothrow measurements, and rostrum and ramus lengths show very similar patterns of variation (as indicated in Fig. 2), while other characters like Tooth W. have a pattern among blocks that is not closely related to that of any other character. Not surprisingly, a number of skull widths covary. Overall, the findings for *S. longirostris* parallel the situation typically found in other mammals where geographic variation in morphological characters has been studied. Some observed patterns may be the consequence of action by selective forces, while others simply result from and are maintained because of isolation by distance. The findings are consistent with *S. longirostris* being genetically subdivided, stemming from individual animals or groups of animals having relatively limited home ranges.

For management stocks, Perrin et al. (1991) proposed an alternative management scheme where "an 'eastern spinner conservation zone' could be devised that would offer appropriate and unequivocal protection to the unique and coherent gene pool of the eastern subspecies." For instance, a zone bounded on the south by 10°N and and on the west by 125°W would encompass 84% of the schools that were identified in the field as being composed of "eastern" spinners, and would include very few "whitebelly" animals (Perrin et al. 1991). Based on the cranial measures we employed, spinners from the blocks in this portion of the range are very similar; the blocks typically were closely linked in cluster analyses and ordinations. Blocks from most other parts of the range did not show the same degree

of consistency and concordance. Our data also provide additional biological justification for establishing a geographically defined management zone for *S. l. orientalis* that, operationally, would be easily understood and more effective for management purposes.

Perrin et al. (1991) also concluded that data on external characters do not support the division of whitebelly spinners into northern and southern stocks for management purposes. For cranial features, if one considers only eastern blocks, it is possible to achieve a considerable degree of separation between northern and southern whitebelly spinners. However, the situation becomes notably more complex when more westerly blocks are added. For virtually all cranial characters, the western blocks group with the more southerly blocks even though they are at the same latitude as blocks to the east containing northern whitebelly spinners; the only possible exception is W. Internal Nares, which shows a strong north to south gradient involving all blocks except for one in the vicinity of the Hawaiian Islands (i.e., 0802). The addition of cranial specimens from western locations has provided a more sophisticated picture of geographic variation of *S. longirostris* in the region under study.

Morphological-environmental covariation

Considerable heterogeneity exists in environmental parameters over the range of *S. longirostris* in the eastern tropical Pacific (see examples of environmental variation in Figs. 11–13). With two circulatory gyres adjacent to the region, one to the north and the other to the south, the eastern tropical Pacific has an easterly-flowing equatorial counter-current from 3° to 10°N latitude, and a number of fronts and convergences (Wyrtki 1966, 1967). These coupled with latitudinal and other gradients result in substantial spatial differences in environmental characteristics.

Spotted dolphin/environmental comparisons
Schnell et al. (1986) evaluated covariation in a similar suite of environmental and cranial morphological features for offshore *S. attenuata* in the eastern tropical Pacific. The *S. attenuata* investigation was focused in eastern areas (only 1 of 19 blocks was west of 115°W). Our analysis of *S. longirostris* covers considerably more of the ocean, and includes areas around the Hawaiian Islands, which potentially could have substantially different marine environments. The importance of particular environmental variables, of course, could be quite different when different geographic levels and different-sized areas are considered. Furthermore, environmental influence could well vary between species. Yet it can be instructive to compare results of environmental-morphologic patterns for

these two dolphin species with broadly overlapping geographic ranges in the tropical Pacific Ocean.

Sea surface temperatures (variables 6 and 7; July values depicted in Fig. 12) have negative correlations with a large number of morphological features in both studies (Table 7 and Schnell et al. 1986: table 6), indicating a general trend of larger animals in warmer waters. Surface Salinity (Fig. 13B) exhibits relatively strong morphologic correlations in both studies, reflecting a pattern that has both east-west and north-south components. Also, Thermocline Depth (Summer), which has relatively low values in northern localities and higher numbers in blocks as one proceeds to the west and south, is positively associated with a number of morphological measures in S. longirostris (Table 7), and covaries with S. attenuata cranial features as well.

Solar Insolation (Jan.) registers a north-south gradient. Our S. longirostris study produced virtually no significant correlations with this measure, while there were numerous positive correlations in the S. attenuata investigation. In the eastern portion of the S. longirostris range, a number of cranial features have north-south gradients, but the overall statistical association is negated with the addition of the western blocks, where animals often (irrespective of latitude) exhibit characteristics similar to those found in southern areas. The same findings were obtained for Solar Insolation (Ann.).

Three environmental variables—Water Depth (Fig. 11B), Thermocline Depth (Winter), and Surface Dissolved Oxygen—are positively correlated with cranial measures in S. longirostris, but show few of these associations in S. attenuata. Again, the differences in findings simply may reflect the inclusion of a wider geographic range of blocks in the S. longirostris study.

Schnell et al. (1986) indicated that for S. attenuata it would be helpful to have additional samples, particularly from western locations. They suggested that "Such a geographic broadening of representation may enable investigators to separate, at least in part, environmental-morphological correspondences that reflect causal relationships from trends [in morphology] maintained primarily as a result of isolation by distance." For S. longirostris, where additional western blocks are now represented (albeit in some cases with very limited samples), it is clear that the gradients in a relatively large number of cranial characteristics are not simply north-south trends, but rather what Perrin et al. (1991) described as a radial pattern. From northeastern blocks, these characters in S. longirostris change more-or-less gradually as one moves to the south, the southwest, or the west. There are several environmental variables exhibiting this type of pattern (e.g., Surface Salinity; Fig. 13B). At the same time, the January and July sea surface temperatures (for July

values, see Fig. 12) have a predominantly north-south orientation (with the Hawaiian Island blocks being lower than expected, given their latitude) and are correlated with the largest number of cranial characters (see Table 7). When additional specimens of S. attenuata become available from westerly blocks not represented in samples available to Schnell et al. (1986), it will be of interest to determine whether patterns of cranial variation (and covariation with environmental measures) in this species will mirror those we have found for S. longirostris.

Significance of covariation with environmental measures

While previous literature has little information on the relation of environmental and cranial variation in S. longirostris, other investigators (Au and Perryman 1985, Reilly 1990) have evaluated physical environmental parameters with respect to distributions of S. longirostris and several other species in the eastern tropical Pacific. They pointed out that the highest school densities for S. longirostris are in the area off the Mexican coast, which also is the most tropical and least seasonally variable portion of the range. We have demonstrated notable associations of cranial variation with physical environmental characteristics. Analyses involving environmental-cranial correlations, by their very nature, are descriptive and do not provide direct information on causal factors per se. Nevertheless, they clearly indicate that between areas where animals are different cranially, there often are marked habitat differences involving the physical environment.

The first two environmental principal components (Fig. 10) describe independent, orthogonal environmental patterns: component I has a general configuration of high values between 5° and 15°N, slightly lower values further to the north, and low values to the south (Fig. 10A), which is overlain by basically an east-to-west trend summarized in environmental principal component II. The important individual environmental covariates with morphological characters include surface temperatures, salinity, and measures of water depth. The physical environmental differences reflected by the principal components, as well as by individual environmental measures, describe basic habitat differences and likely reflect, indirectly, geographic differences in available prey species and their abundances. Given the marked environmental differences exhibited in the range of S. longirostris, the most surprising result would have been if this species had been relatively uniform geographically in cranial features—clearly, this is not the case. Our initial assessment of morphologic-environmental covariation further underscores the appropriateness of treating different parts of the range of S. longirostris in the eastern tropical Pacific

separately for management purposes. In particular, a growing base of information suggests giving special attention to the spinners from the relatively uniform area of the Pacific just to the west of the Mexican/Central American coast, and viewing the pattern of morphologic variation as being broadly concentric in nature.

Acknowledgments

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