

Abstract. — Variation in color pattern, dorsal fin shape, and body length exhibit sharp north/south gradients centered at about 5–10°N latitude and east/west gradients at about 120–125°W longitude. A conservation zone with boundaries in these regions would provide protection for the morphologically unique eastern spinner dolphin *Stenella longirostris orientalis*. A radial pattern of geographic variation in the eastern Pacific and a complex pattern of discordant variation outside the core range of *S. l. orientalis* suggest that the present separate management of “whitebelly” spinner dolphins (which comprise a broad zone of hybridization/intergradation between *S. l. orientalis* to the east and the pantropical spinner dolphin *S. l. longirostris* to the west and southwest) north and south of the Equator may not be justified on the grounds of conservation of distinct populations.

Geographic Variation in External Morphology of the Spinner Dolphin *Stenella longirostris* in the Eastern Pacific and Implications for Conservation

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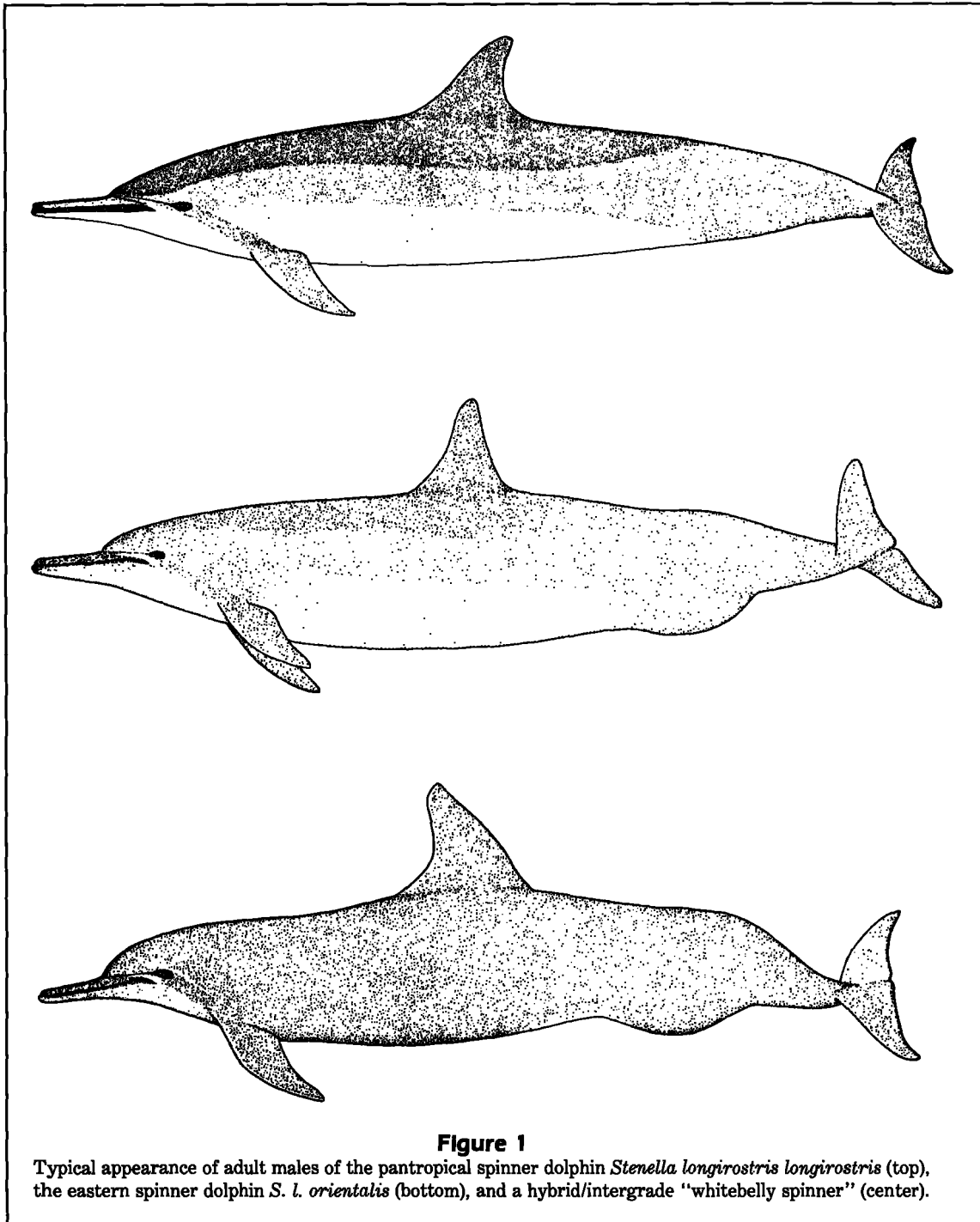
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Spinner dolphins in the eastern tropical Pacific vary geographically in color pattern (Perrin 1972), in external and skeletal size and shape (Perrin 1975, Perrin et al. 1979a, Schnell et al. 1982 and 1985, Douglas et al. 1986), and in reproductive seasonality (Barlow 1984). Perrin (1975) and Perrin et al. (1979a) described several forms that have served as stock units for management of populations of dolphins killed incidentally in the international purse-seine fishery for yellowfin tuna in the region (Perrin et al. 1985). Kills in recent years have been on the order of 100,000 annually. The management units have been known as the “Costa Rican,” “eastern,” “northern whitebelly,” and “southern whitebelly” spinner dolphins. The geographic ranges of the eastern and whitebelly forms overlap broadly (Perrin et al. 1985).

The model used in studies and, to a lesser degree, management of the species in the region has been one of several discrete, more-or-less reproductively isolated stocks with some geographic overlap. However, as more morphological data have accumulated, a different picture has emerged. For example, while the boundary between the present northern and southern whitebelly management stocks was drawn latitudinally,

the overall pattern of variation in the eastern Pacific now appears radial (Schnell et al. 1982 and 1985, Perrin et al. 1985). Further, the results of a genetic study indicate substantial exchange of at least mitochondrial DNA between and among the eastern and whitebelly forms (Dizon et al. 1991). Most recently, Perrin (1990) described two subspecies, *Stenella longirostris centroamericana* and *S. l. orientalis*, based on the Costa Rican and eastern forms, respectively, and concluded that the whitebelly “forms” (Fig. 1) collectively comprise a broad zone of intergradation or hybridization between the eastern subspecies and a third subspecies to the west and southwest, the pantropical spinner dolphin *S. l. longirostris*, a form occurring in the central and western Pacific, Indian and Atlantic Oceans (Perrin et al. 1981; Gilpatrick et al. 1987).

In this context, the purpose of the present study was to reexamine variation in external morphology on a finer geographical scale than had been used in earlier studies. Specimens previously identified as “Costa Rican,” “eastern”, or “whitebelly” based on the modal appearance of adult animals in the schools from which they came were pooled in the analyses. In this way we hoped to



gain a better understanding of the morphological gradients and other geographical patterning involved in the relationships among the Central American, eastern, and pantropical subspecies and to contribute to the development of approaches to conservation and management of the several populations.

Materials and methods

Source of the data

We examined variation in the ventral field and cape components of the color pattern (terminology of Perrin 1972), the shape of the dorsal fin, and body length.

The data on color pattern and dorsal fin were collected by biologists during the period 1974–88 aboard commercial tuna seiners (see Acknowledgments). The length data were collected in 1968–89. The biologists completed a field “life-history” form for each dead dolphin examined, recording basic information such as sex and length and (starting in 1974) sketching in the ventral field, cape (if prominently visible; see below), and dorsal fin on a preprinted generalized dolphin outline. When feasible, the observer also traced the dorsal fin on the back of the data form. Body length was measured to the nearest cm with calipers mounted on a 2-m wooden ruler. For male specimens, a testis with epididymis attached was preserved and weighed ashore. For females, the number of corpora in the ovaries was determined in the laboratory (methods described in Perrin et al. 1976).

The quality of the sketches varied greatly. Although a few color pattern sketches were discarded as totally unusable, the basic features of the color pattern could be discerned in relatively inexpert sketches. However, the fin sketches proved to be unreliable. We found that for the cases where the observer both sketched and traced the dorsal fin, the correspondence between fin shape in the sketch and tracing was often poor. Therefore we used only the fin tracings, which reduced the sample size for dorsal fin shape. We also examined photographs of the specimens if they were available.

The analyzed data consisted of body length in cm and coded values for ventral field, cape, and dorsal fin shape. These were accompanied by date and location of capture and reproductive data (weight of testis + epididymis for males; number of ovarian corpora for females).

The ventral field received a code from 1 to 5 (Fig. 2). Code 1 is the state typical of the eastern subspecies; Code 5 is that typical of the pantropical subspecies (Fig. 1). Codes 2–4 are intermediate. In Code 1, the animal is gray laterally and ventrally, with white patches in genital and axillary regions. In Code 2, the separate genital and axillary white areas of Code 1 are joined by a speckled zone. In Code 3, the two areas are confluent, forming a white ventrum. In Code 4, the ventral field extends dorsally above the umbilical-genital region, yielding a stepped pattern in lateral view. In Code 5, the anterior portion of the ventral field extends dorsally to behind the eye, eliminating the step of Code 4. This variation is continuous, of course; a code was assigned for the state closest to that evident in the

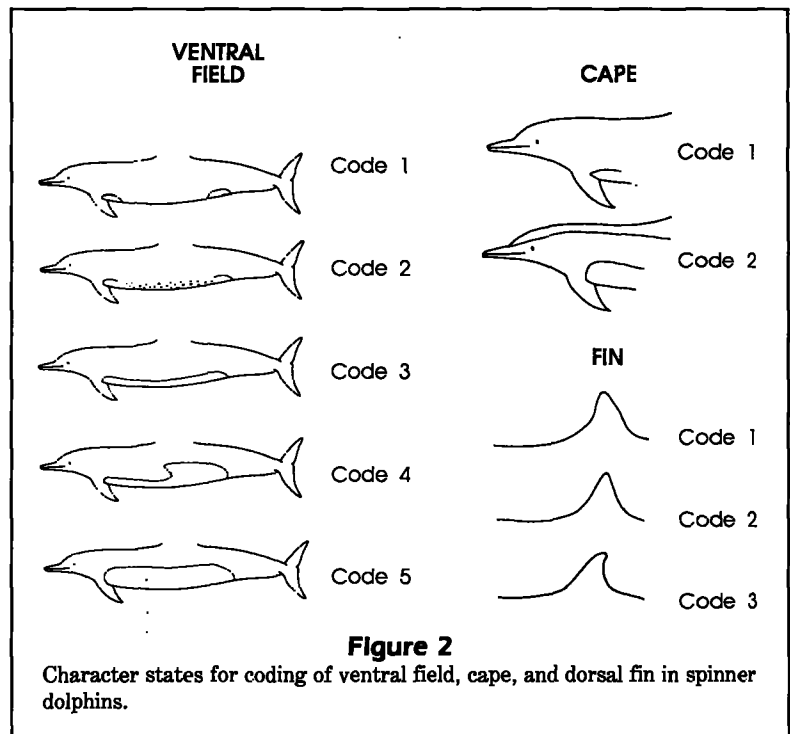


Figure 2
Character states for coding of ventral field, cape, and dorsal fin in spinner dolphins.

sketch. The sketches themselves already incorporated some artificial stratification. For example, in some animals the darker region yielding the step of Code 4 is only faintly evident. Some observers indicated the presence of this faint feature, leading us to code the animal as Code 4; others undoubtedly overlooked such faint markings or failed to record them, leading us to code the animals as Code 5. While such errors could be expected to blunt the resolving power of the analyses, there is no reason to suspect that they inject a systematic spatial bias that would affect the accuracy of the conclusions; the data were collected by a large number of observers working over large areas.

The cape (Fig. 2) was coded as “not noted in the sketch” (Code 1) or “noted in the sketch” (Code 2). In a living or freshly dead spinner dolphin, the cape can be discerned on close and careful inspection, if only very faintly, in all cases. In the eastern spinner, the dorsal overlay (terminology of Perrin 1972) is very dense, almost obliterating the underlying cape in even very fresh specimens. When a carcass of an eastern spinner has lain on the deck of a tuna boat for more than a few minutes, the dorsal overlay darkens to the point of completely obscuring the cape. In the live pantropical spinner, the dorsal overlay is less dense and the cape is sharply defined and obvious. It is detectable even in specimens dead for several hours, albeit more faintly. Thus the absence of the cape in a sketch means that the observer did not note it upon fairly cursory

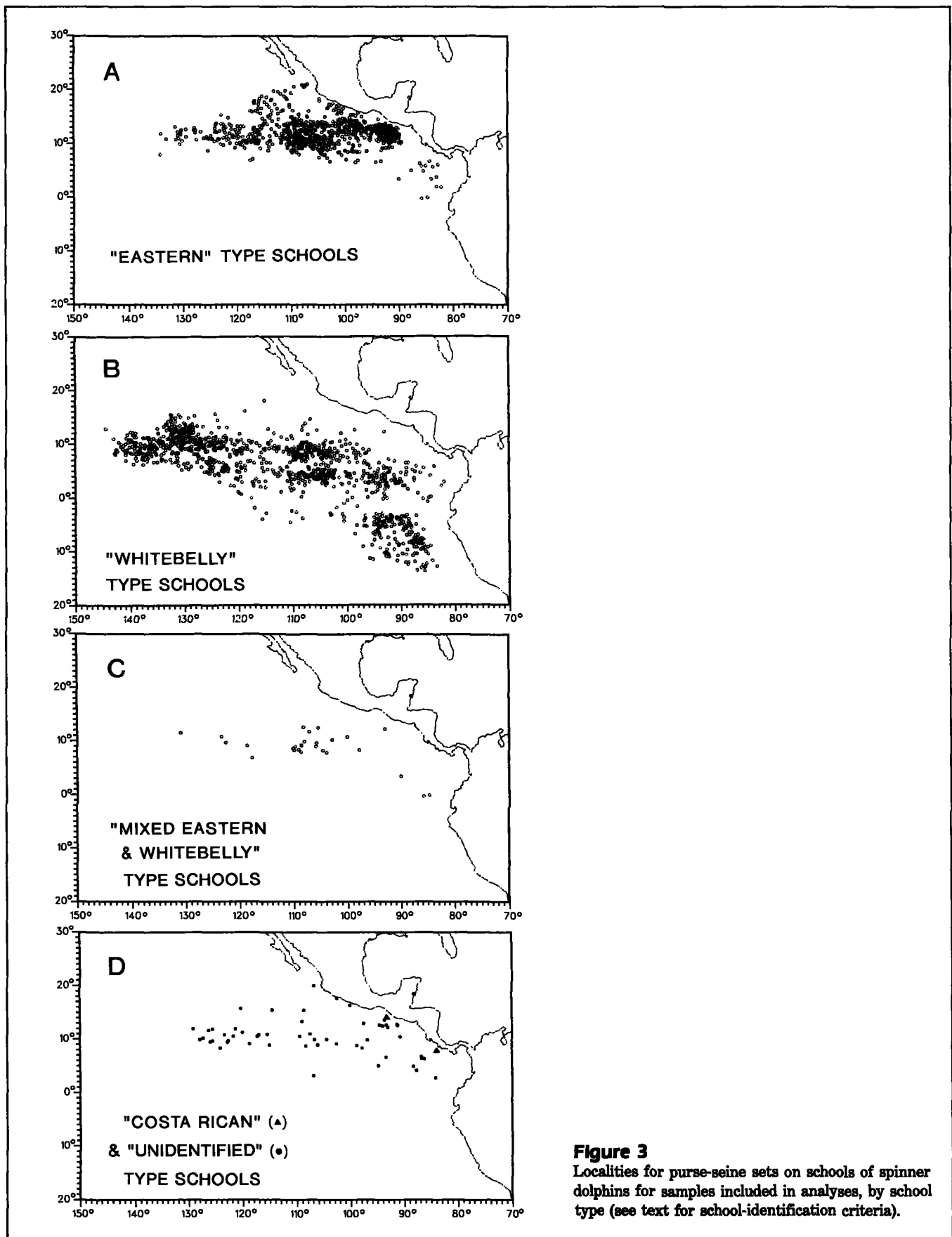


Figure 3
Localities for purse-seine sets on schools of spinner dolphins for samples included in analyses, by school type (see text for school-identification criteria).

inspection, not that it was not actually absent. Cape “presence” is a relative measure of the density of the dorsal overlay, with some precision lost due to post-mortem darkening. Again, under the assumption that time before examination of the carcasses and diligence of the observers did not vary with area, there should be no systematic bias.

The dorsal fin was coded to one of three states (Fig. 2): canted—closest to a right triangle with hypotenuse posterior (Code 1; most “eastern-like”), erect—isosceles triangle (Code 2), or falcate—right triangle with hypotenuse anterior (Code 3; most “pantropical-like”). Sources of error in this code include partial tracings of fins (part of the base of the fin not included) and injuries distorting the fin. The first was difficult to cope with and could not be resolved completely. Some tracings were discarded because of sharply anomalous shape obviously due to the fin being incomplete, but some small portion of the variation recorded is un-

doubtedly due to undetected errors of this sort. When a distal portion of the fin was missing due to injury, this was indicated in the observer’s sketch, and the tracing was not used. The tracing was also not used if a very large notch or gap was indicated. Small notches and holes do not affect the overall shape of the fin.

The total of the code scores for the three characters ranged from 3 (typical of the adult male eastern spinner) to 10 (typical of the adult male pantropical spinner).

The sample

The sample for color pattern and fin shape included 8350 specimens from 971 net sets on “eastern”-type schools, 1200 sets on “whitebelly”-type schools, 27 sets on “mixed eastern and whitebelly” schools, 2 sets on “Costa Rican”-type schools, and 54 sets on spinner dolphins of unidentified stock (Figs. 3 and 4). Not all

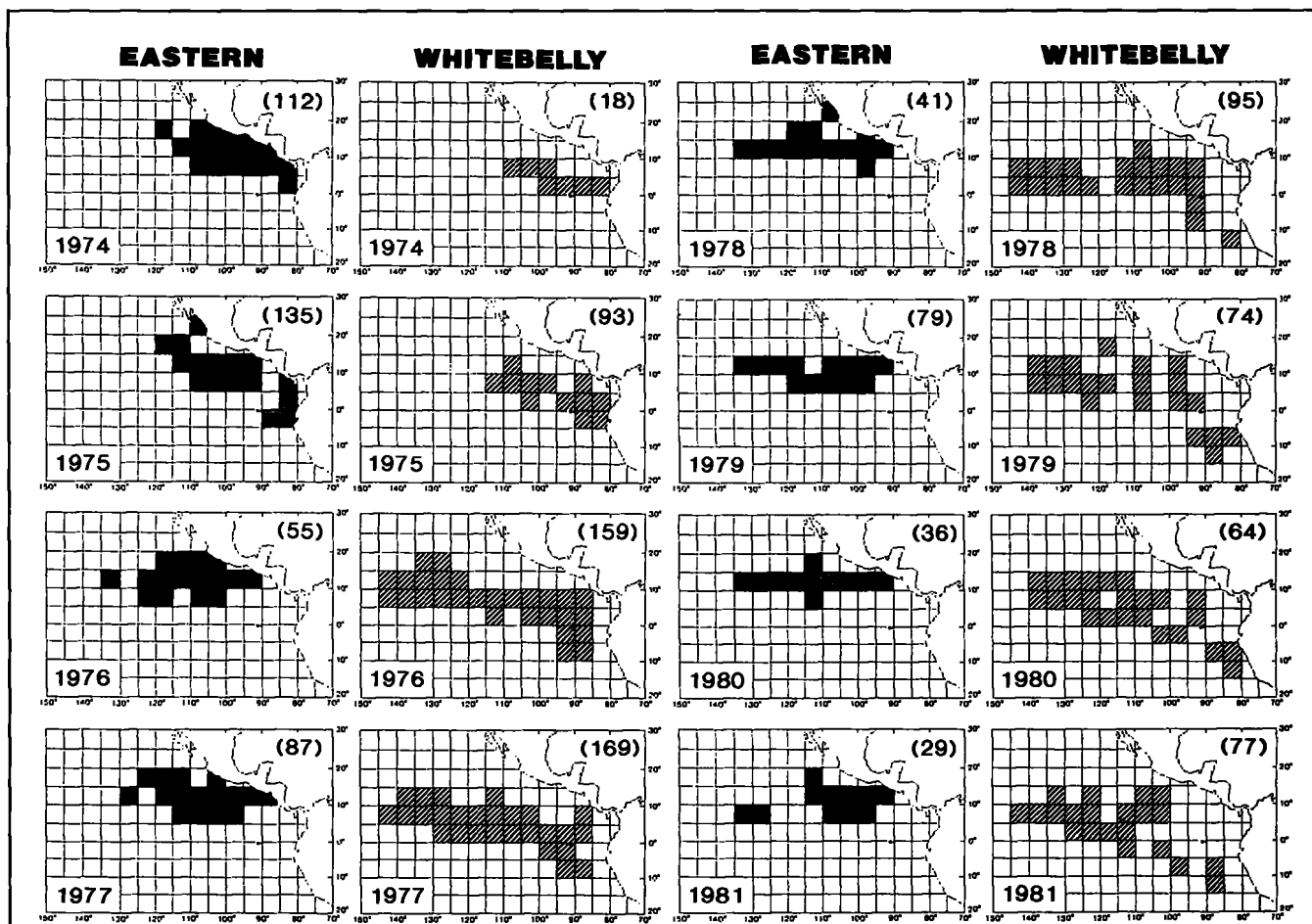


Figure 4

Distribution, by year, of purse-seine sets on “eastern” and “whitebelly” schools of spinner dolphins for samples included in analyses.

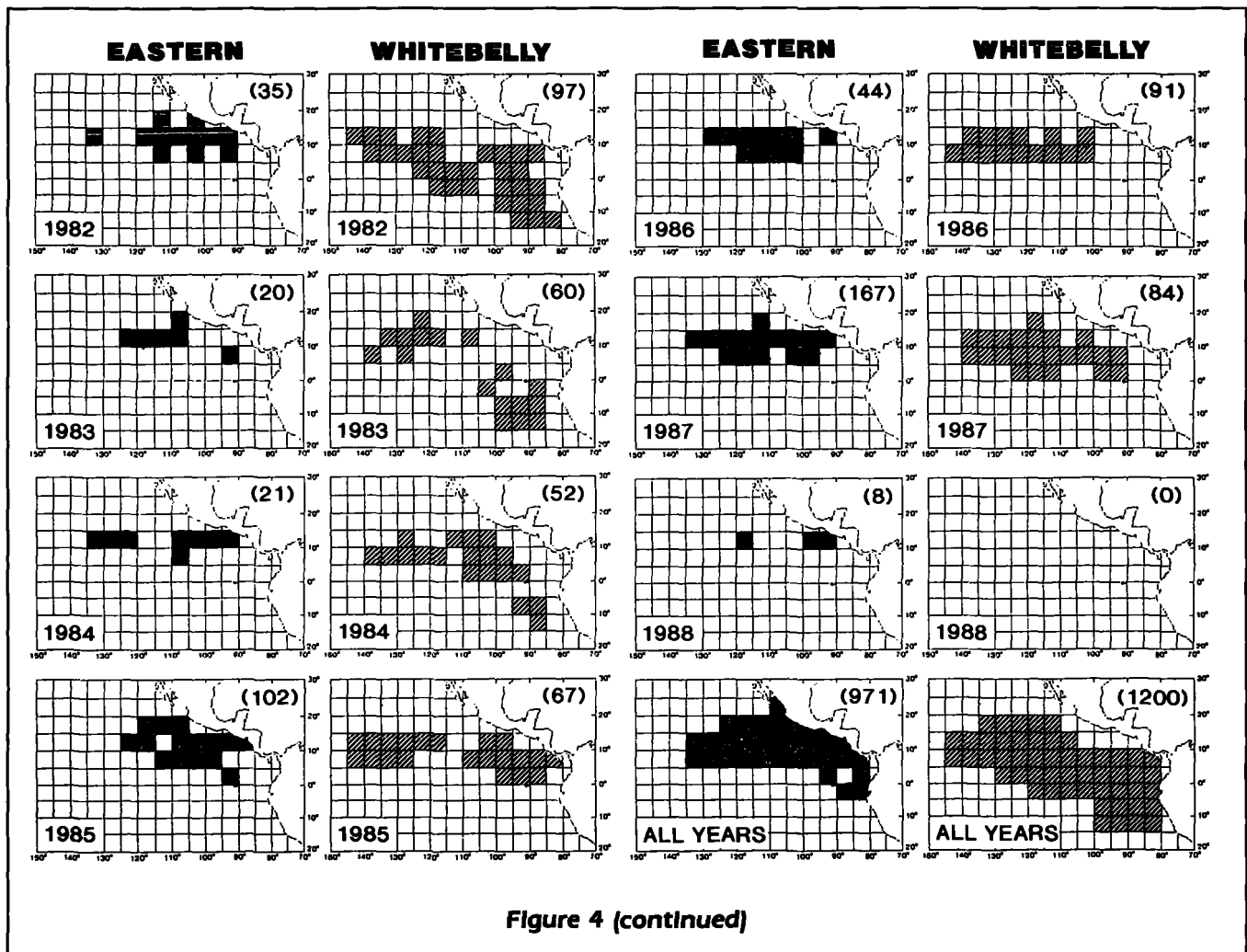


Figure 4 (continued)

of the characters were recorded for all of the specimens (Table 1). Body-length data were available for 3304 adult dolphins (1461 males and 1843 females). (Females with at least one ovarian corpus and males with testis/epididymis weight of 100g or more were considered adult, following Perrin et al. 1977.)

Analytical methods

Areal stratification For purposes of the analyses, we divided the study area into 60 5-degree blocks with boundaries at the Equator, 5 degrees, 10 degrees, etc., and 80 degrees, 85 degrees, etc. We experimented with 4-degree blocks and with different placement of the boundaries but obtained less consistent results (more embedded and peripheral anomalous blocks) than with the scheme adopted.

Effects of sexual dimorphism and development

Color pattern and fin shape are known to vary with

Table 1

Sample sizes for analyses of color pattern and fin shape of spinner dolphin in the eastern tropical Pacific Ocean.

Character	Males	Females	Total
Total individuals	4121	4229	8350
Ventral field	3377	3463	6840
Cape	3376	3462	6838
F'in shape	2053	2421	4474
Adults with all 3 characters	610	683	1239

sex or age or both (Perrin 1972). We endeavored to take into account these factors in the geographical analyses by considering males and females separately where necessary and by applying a minimum length or sexual-maturity criterion for specimens to be included in analyses of each of the characters separately.

Because they relate primarily to the methodology of the study, the results of analyses to establish the length/maturity criteria are presented here rather than below with the results of the analyses of geographical variation.

We found no difference between the sexes in extent of the ventral field but a statistically significant association between ventral field state and body length (contingency test of association with Peterson's chi-square, α 0.05; computer program BMDP4F in Dixon et al. 1990). As described by Perrin (1972), all calves tend toward the "whitebelly" color pattern (codes 4 or 5), with reduction in the ventral field in "eastern" spinners with age (to Codes 1, 2, or 3). The proportion in the overall present sample with Code-5 ventral field (most "whitebelly-like") declined with body length until about 120 cm, when it stabilized at about 30–35% (Fig. 5), and the proportion of individuals with Code 1 ventral field (most "eastern-like") behaved similarly but conversely. We therefore limited the analyses of ventral field to specimens of 120 cm or larger. (After about 170 cm, the proportion of Code-5 animals again climbed and Code-1 animals decreased; this is because most specimens above that length were "whitebelly" spinners—see analyses below of geographical variation in body length.)

Noted presence of the cape exhibited a similar pattern of change with growth (Fig. 6). Calves in all regions tend to exhibit a strongly defined cape, which is progressively obscured with development of the "eastern" pattern (Perrin 1972). Again, relative stability in the proportion of all animals for which the cape was noted was reached at about 120 cm in both sexes; the sample for the geographic analyses was limited to specimens of this length or greater.

We also found a slight association of expression of the cape with gender; the cape was noted for 10.1% of all females but only 7.8% of males (Fig. 6). In the geographical analyses, we used the average of male and female means in order to avoid effects of possible areal variation in sex ratio in the samples.

The degree of sexual dimorphism in the shape of the dorsal fin varies geographically, ontogenetically, and individually (Perrin 1972). In the present sample, in schools classified as "eastern" (Fig. 7), about 60% of small calves of both sexes had erect dorsal fins (Code 2); the balance had falcate fins (Code 3). Beginning at about 135 cm, erect fins increasingly predominated, to more than 80% in large juveniles of both sexes and about 90% in adult females. In males, the first canted fins (Code 1) appeared at about 160 cm. They increased in frequency to about 70% in large adults of 180 cm or more. This corresponds roughly to the length at which about 80% (the asymptotic level) have achieved at least minimum testis-epididymis weight (94g) at which

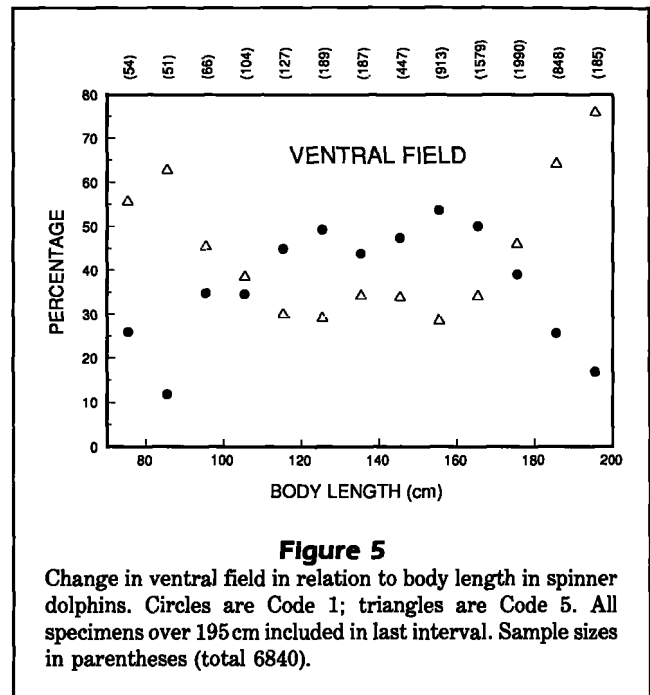


Figure 5

Change in ventral field in relation to body length in spinner dolphins. Circles are Code 1; triangles are Code 5. All specimens over 195 cm included in last interval. Sample sizes in parentheses (total 6840).

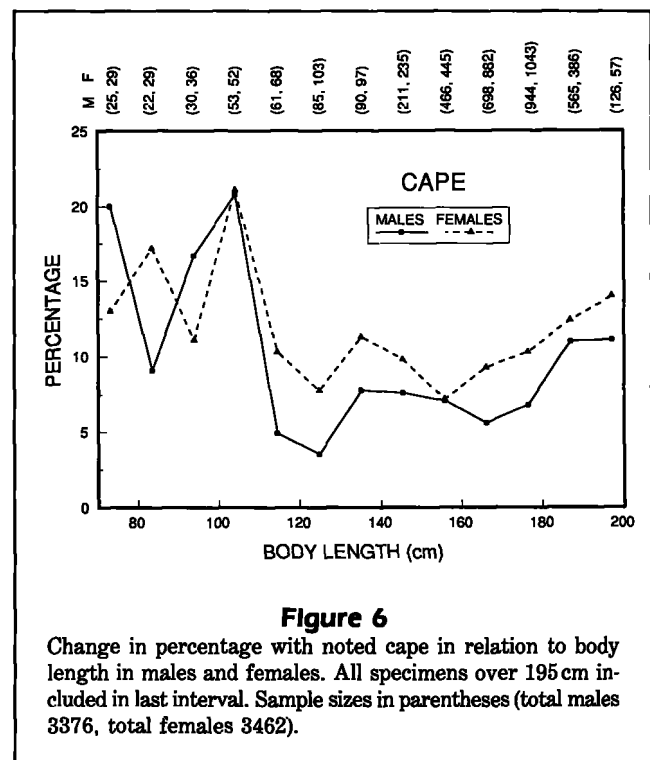
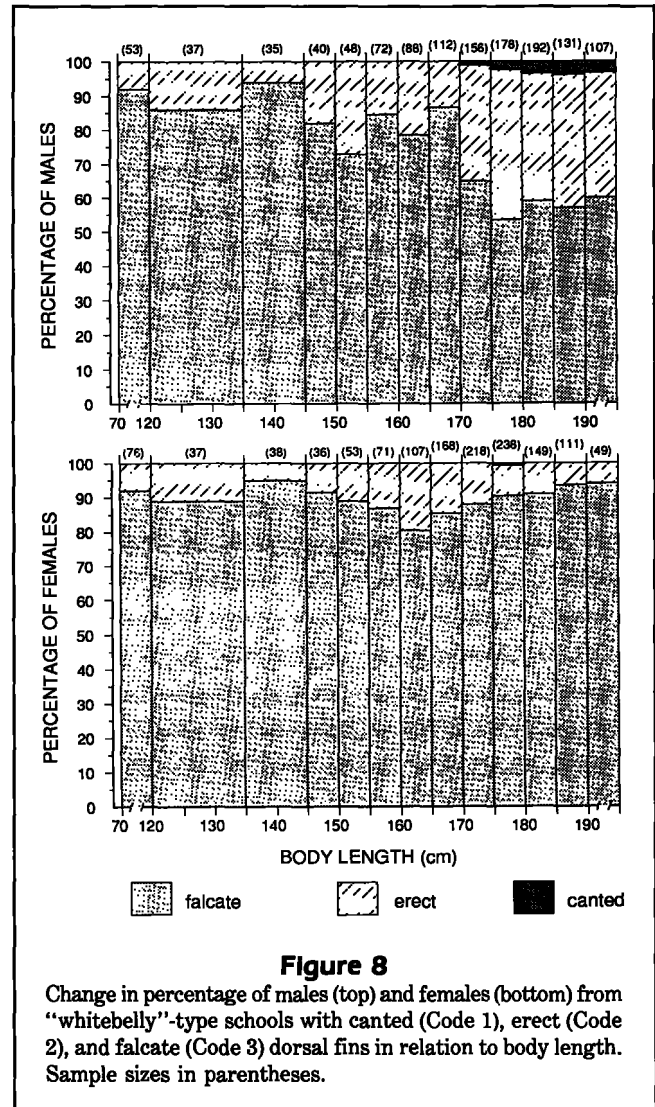
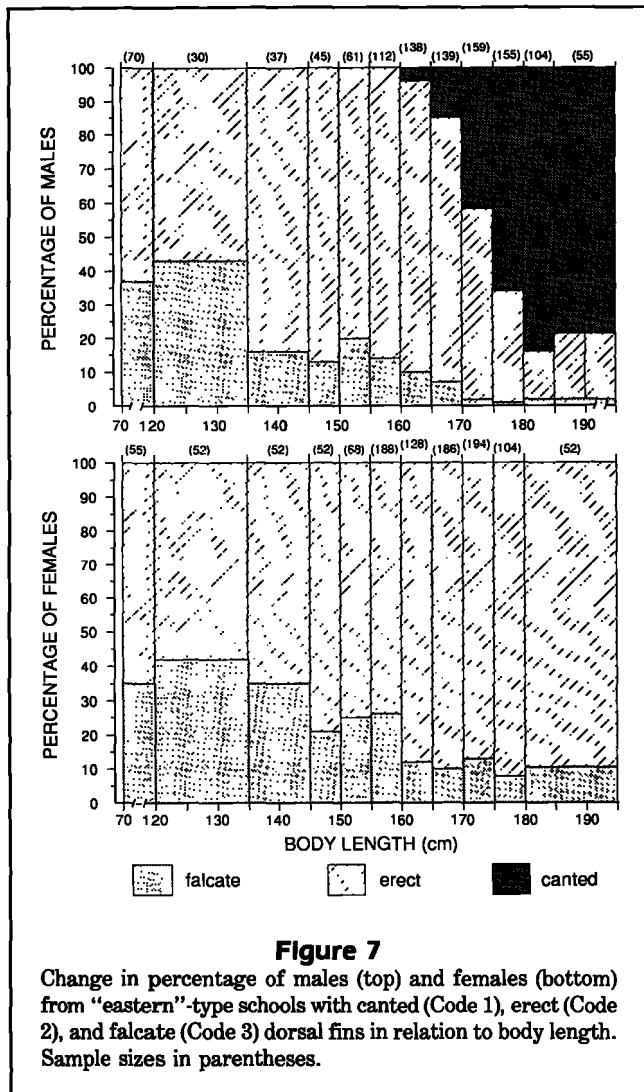


Figure 6

Change in percentage with noted cape in relation to body length in males and females. All specimens over 195 cm included in last interval. Sample sizes in parentheses (total males 3376, total females 3462).

spermatogenesis occurs (Perrin and Henderson 1984). Thus, the canted fin in the eastern-type animals was strongly associated with sexual maturity, although some mature males had erect fins.



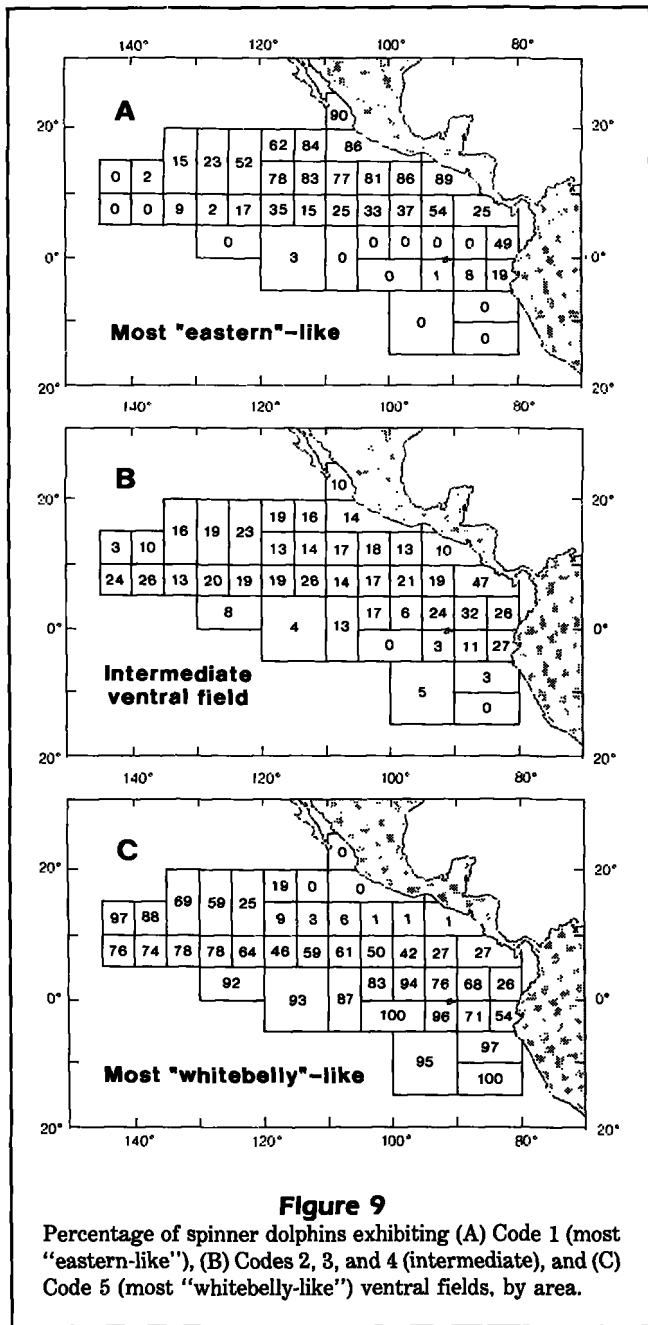
In the "whitebelly" schools (Fig. 8), roughly 90% of calves, juveniles, and adult females had falcate dorsal fins and about 10% erect fins. One adult female had a canted fin. In adult males, the frequency of erect fins increased to about 40% in individuals of 175 cm or more (2.3% had canted fins). Again, this is about the length at attainment of sexual maturity (*loc. cit.*). We limited the analyses of dorsal fin shape in the pooled samples to sexually mature dolphins and considered males and females separately.

We followed the same procedure for analyses of body length, limiting the sample to sexually mature animals and analyzing males and females separately.

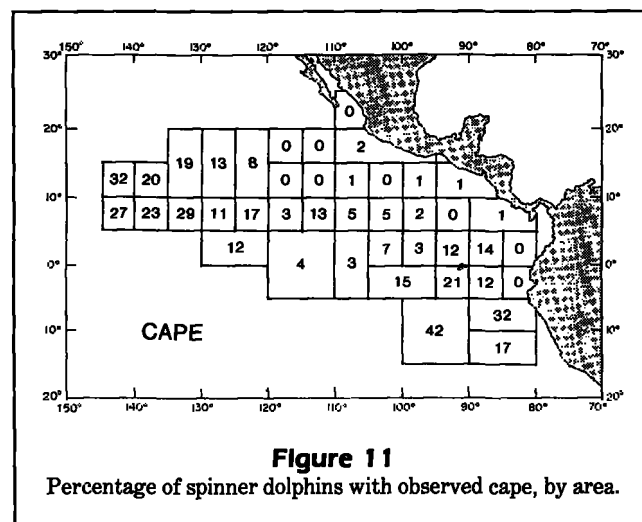
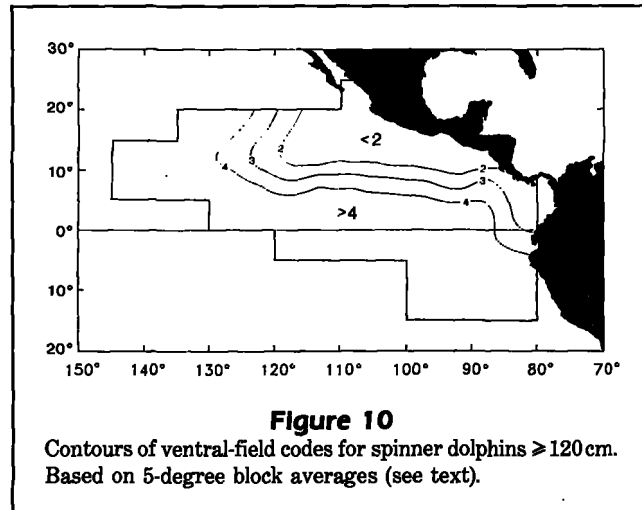
Effects of seasonal variation The apparent overlap of collection localities for the two kinds of schools is not an artifact of seasonal migrations. The region of substantive overlap of "eastern" and "whitebelly"

schools is between 8° and 12°N and 95° and 125°W (Fig. 3). We examined the data by quarter of the year and found overlap in this region in all four quarters.

Pooling to obtain adequate sample sizes Sample sizes in many cases were very small for some of the peripheral 5-degree blocks. In these cases we pooled the samples over two or more blocks, to achieve a minimum sample size of 25. In the pooling we attempted to approximate the apparent radial pattern of variation, i.e., pooling was mainly longitudinal in the south and mainly latitudinal in the west. To the extent possible, we maintained the same pooling scheme from analysis to analysis, although in some cases differential pooling was required for males and females. The sample sizes and pooling schemes for the various analyses are given in the Appendix.



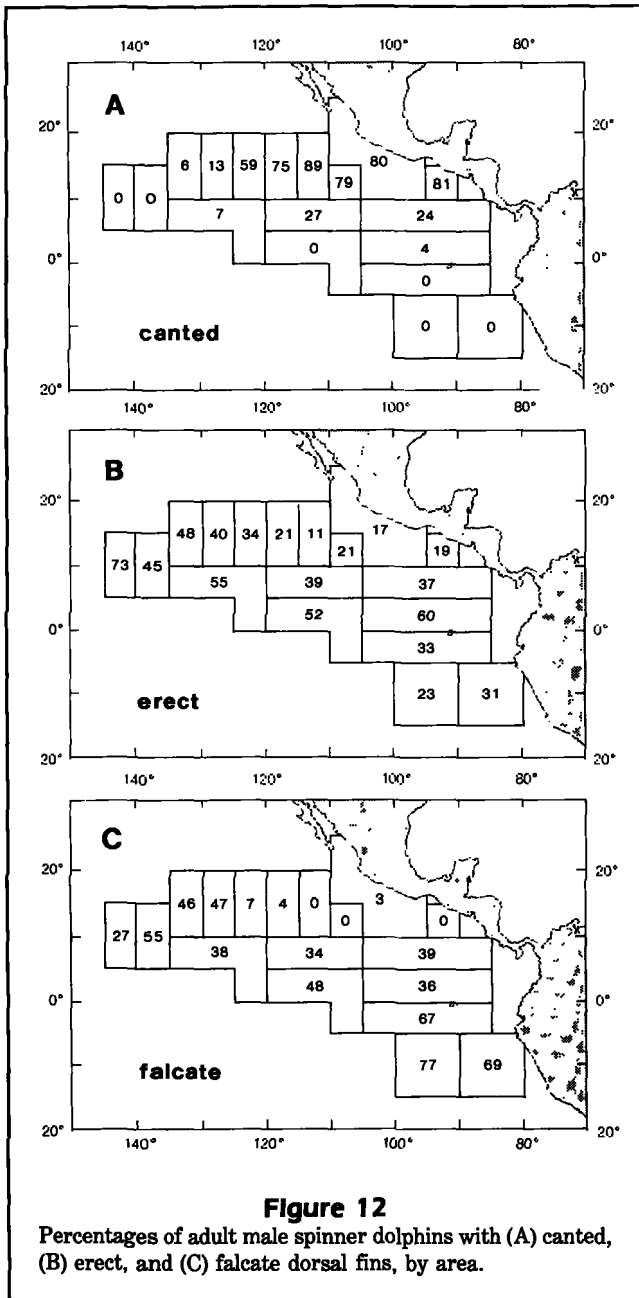
Contouring We used the ZSMTH, ZGRID, and ZCSEG subroutines of the PLOT88 graphics software package (Young and Van Woert 1987) to generate contours of ventral coloration scores for unweighted 5-degree blocks. The center of a block was used as the position for the mean ventral coloration score of specimens collected within the block. We used ZGRID with the "cay" parameter set at 5 and "nring" set at 4 to generate a data grid for contouring. ZSMTH with "nsm" set at 1 was used to smooth the grid. Contour lines were generated using ZCSEG with "ndiv" set at 4.



Results

Ventral field

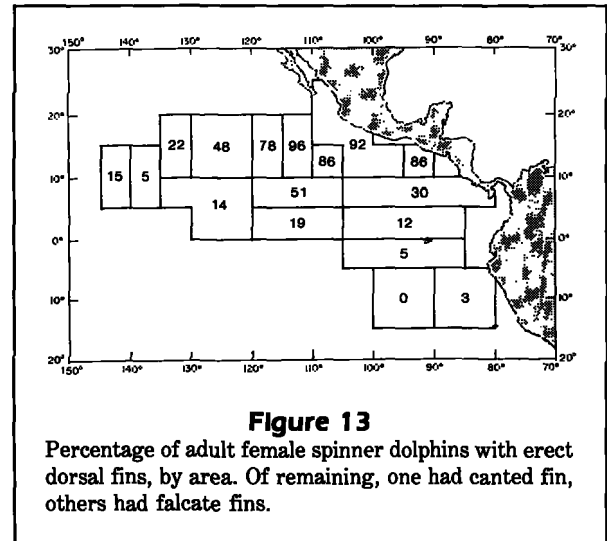
The pattern of disjunct axillary and genital white areas (Code 1) occurred at high frequencies ($\geq 75\%$) in a relatively small part of the study area, in 12 5-degree blocks north of 10°N and east of 120°W (Fig. 9A). It was totally absent south of 5°S and absent from most of the peripheral blocks between 15°N and 5°S . It occurred at intermediate frequencies near Central America and northern South America, between 10°N and 5°S . The steepest gradient would appear to have been at about 10°N , extending from the coast out to possibly beyond 125°W . This pattern was mirrored in the relative distribution of the Code-5 ventral field (most "whitebelly-like"), which was absent or nearly absent from most of the northeastern blocks where the Code 1 pattern predominated and occurred at frequen-



cies above 75% in a broad band encompassing the study area south of 15°N (Fig. 9C). Again, *per force*, the steepest gradient was at about 10°N.

Dolphins with intermediate ventral fields (Codes 2-4) were least frequent in the peripheral blocks to the south and southwest and most frequent in a region off Central America below 10°N (Fig. 9B).

Contouring of the ventral-field data based on 5-degree block averages (Fig. 10) yields a clear pattern of extensive, largely Code-1 and Code-5 regions divided by a steep gradient.



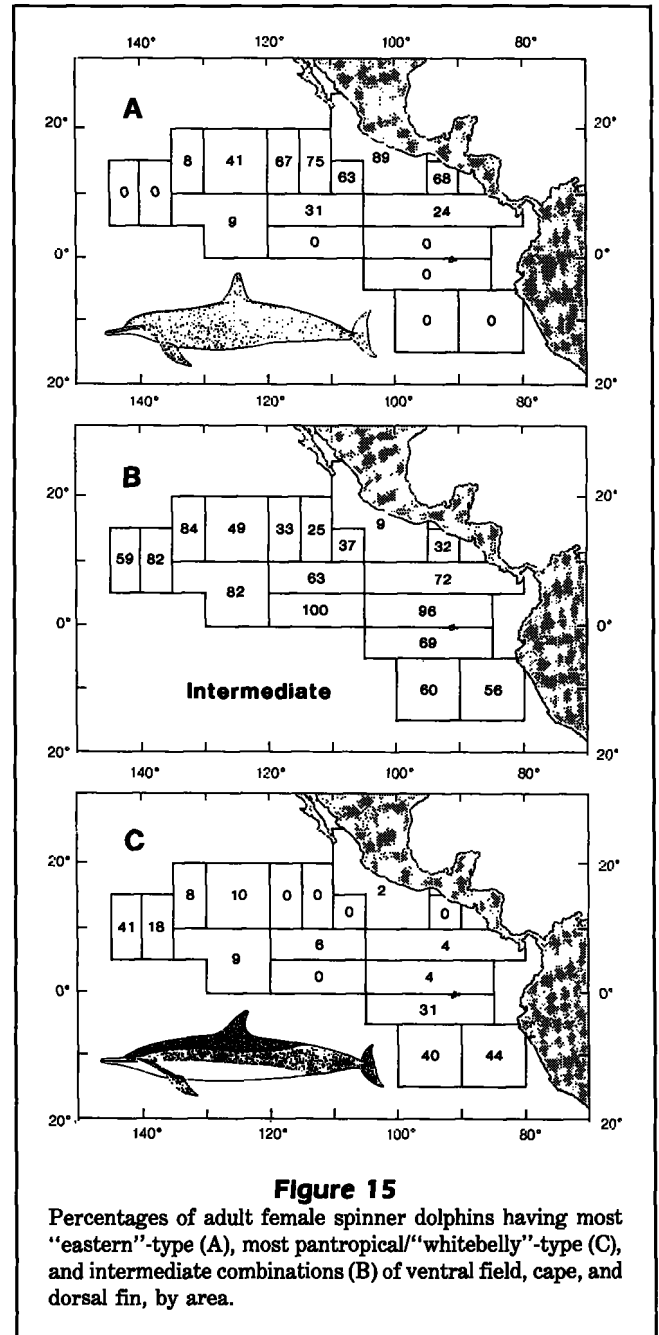
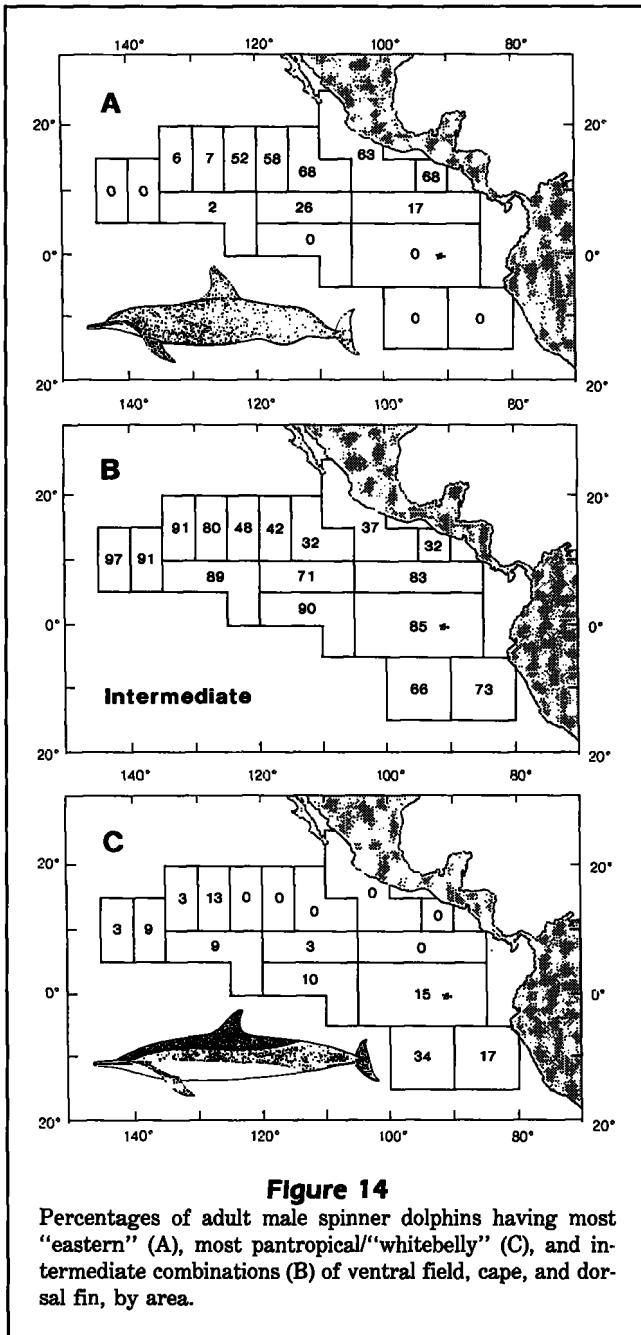
Cape

The percentage of dolphins with observed cape was highest in the far south and far west (Fig. 11). This pattern differs from that for the ventral field. For the ventral field (Fig. 9C), the zone of high frequency of Code-5 fields was continuous along a southeast-northwest axis, whereas for the cape the two regions of relatively high frequency in the south and north were separated by a broad zone of relatively low frequency. In addition, the north-south gradient in expression of the cape was not as steep (at 10°N) as for the ventral field.

Dorsal fin

Because of sexual dimorphism and the need to restrict the analyses to sexually mature animals, sample sizes were very much smaller for this character than for the cape and ventral field, necessitating more extensive pooling. Parts of the areas off northern South America and in the southwestern portion of the study area that were included in the coverage for the color pattern characters are not covered in the fin samples.

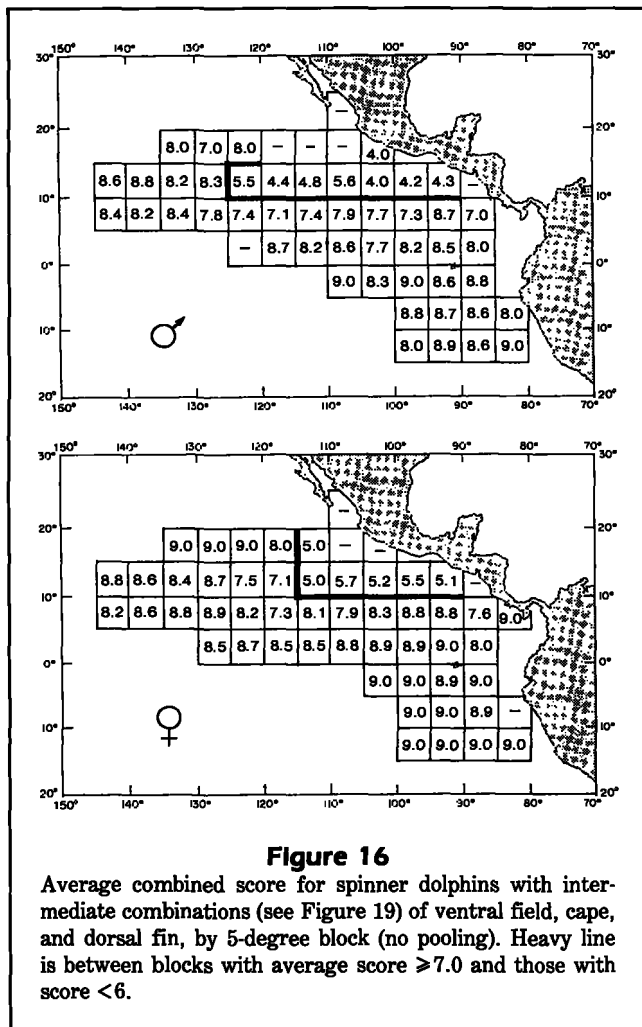
Despite the reduced resolution in the analyses of dorsal fin variation, some patterns are evident (Figs. 12, 13). In the males the sharp gradient at about 10°N (Figs. 12A, C) is concordant with the pattern for the ventral field (Fig. 9); the canted fin, like the disjunct ventral field, occurred at high frequency ($\geq 75\%$) only in a region bounded approximately by 10°N and 120°W. The same is true of the erect fin in the female (Fig. 13). The falcate fin in males was more common south of the Equator; 90 of 127 males (71%) in the three southernmost cells that contained no males with canted fins had falcate fins, but only 25 of 66 (44%) in the



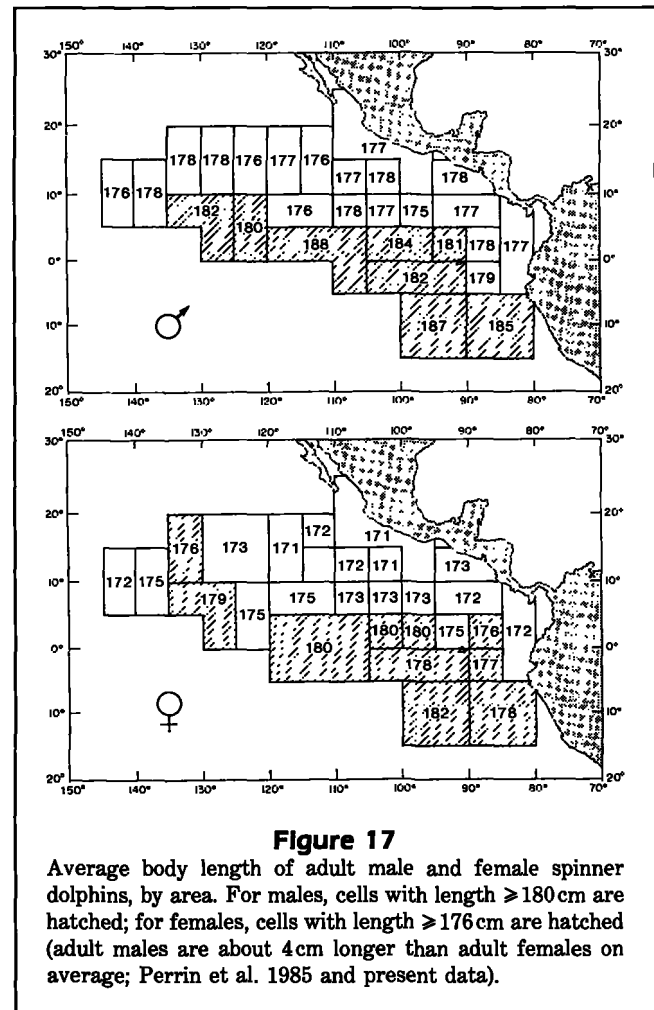
two westernmost cells had falcate fins. This difference is statistically significant ($P < 0.0001$: Fisher's exact test, two-tailed). The frequency of falcate fins in the two southwestern cells between 10°N and 5°S was intermediate (Fig. 12B). In females, the falcate fin was also most common in the south, although in this case the frequency there was not statistically different from that in the two westernmost cells at $P = 0.05$.

Combined characters

Data on all three characters (ventral field, cape and dorsal fin) were available for 610 sexually adult males and 683 females. The distributions of the extreme expression of eastern character combinations (a total score of 3 for males and 4 for females) and pantropical combinations (10 for both males and females) were similar for males and females (Figs. 14, 15). Only the extreme eastern combination predominated (more than 50%) in any area, in a region bounded by 10°N and



125°W for males (Fig. 14A) and 10°N and 120°W for females (Fig. 15A). It was absent in the cells south of 5°N and east of 120°W and in the cells west of 135°W. The extreme pantropical combination reached only 34% in males, in the southernmost region (Fig. 14C), and 44% in females (Fig. 15C). It was absent (except for one female) from the cells in which the eastern combination predominated (north of 10°N and east of 120–125°W). It was present only at low levels in the southwestern region, about the same as just to the south and west of the core eastern region. Except in the core eastern region, the majority of dolphins were intermediate (combined scores of 4–9 for males and 5–9 for females (Figs. 14B, 15B); in some cells between 0° and 15°N, over 95% of the adults were intermediate. The degree of intermediacy was not uniform, however. For both sexes, there was a very steep latitudinal gradient in average scores of intermediate animals at about 10°N (Fig. 16). There was

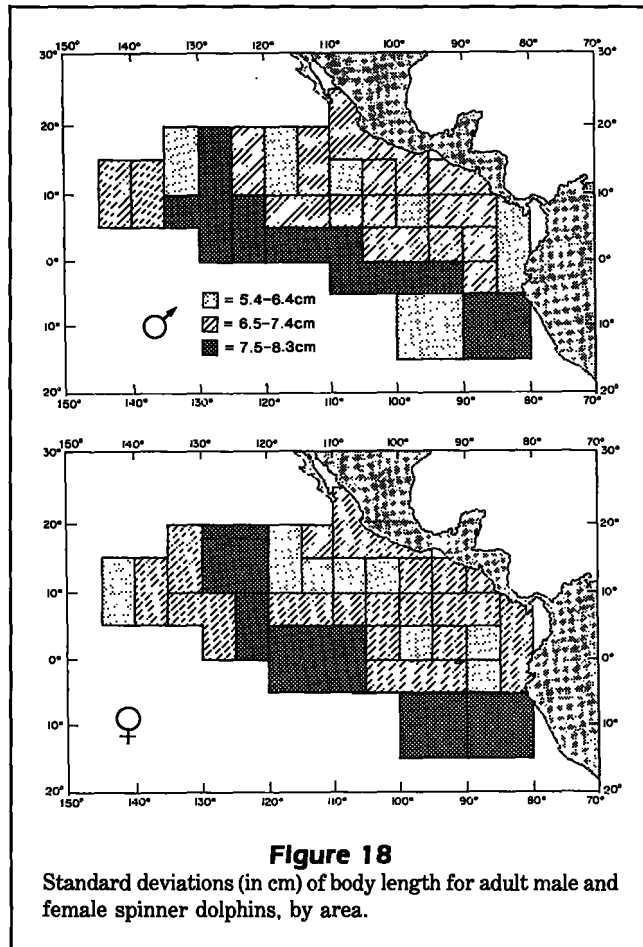


also a steep longitudinal gradient, at about 125°W for males and 115°W for females. Outside this sharply bounded core "eastern" region, variation in intermediate scores was very much less, with only slight N/S and E/W gradients and most animals relatively close to the pantropical extreme.

Proportionately more adult females than adult males in the westernmost cells (west of 140°W) were of the extreme pantropical combination (Fisher's exact test, $P < 0.01$), whereas this was not as true in the southernmost cells ($P > 0.10$).

Body length

The major shift in average adult length of both males and females (Fig. 17) was at about 5°N, rather than at about 10°N as for the other characters (e.g., compare with Figs. 14–16). The region of smaller animals extended south along the coast of northern South America to about 5°S. Animals from the far west were



more closely associated in average length with those in the east than those in the far south (below 5°S).

Body length is more variable in the regions of greater body length, in both males and females (compare Figures 17 and 18; Table 2).

Discussion

Year-to-year variation and home range

The patterns of distribution of the eastern spinner and the "whitebelly" intergrades/hybrids appear to be relatively stable year to year, although analysis of the present data is complicated by the fact that they come from incidental kills in a very mobile pelagic tuna fishery. The cumulative maps of specimen localities (Figs. 3, 4) show the locations where tuna boats made purse-seine sets that killed spinner dolphins. It reflects only co-occurrence of tuna boats, spinner dolphins, and yellowfin tuna. In addition, the spinner dolphin is not the main target dolphin species in the fishery; the pantropical spotted dolphin *Stenella attenuata* is relative-

Table 2

Variability of body length in sexually adult spinner dolphins of eastern (combined scores of 3 for males or 4 for females) and pantropical (combined score of 10 for both males and females) morphology (ventral field, cape, and dorsal fin) from the eastern Pacific.

	Eastern		Pantropical	
	Males	Females	Males	Females
Sample size	136	195	47	78
Average length (cm)	178.9	172.7	181.9	177.2
SD (cm)	6.30	5.90	7.46	7.84
CV	3.52	3.42	4.10	4.43

ly more often found together with tuna. The sets on spinner dolphins are largely sets on mixed schools of spotted and spinner dolphins; in some areas, especially in the southern and southwestern regions of the study area, spinner dolphins are not often associated with spotted dolphins and seldom are with tuna (Au and Perryman 1985).

Not all regions represented by capture localities in the cumulative maps (Fig. 3) are represented in the maps for individual years (Fig. 4). Possible reasons for this are (1) the dolphins moved around from year to year, (2) the tuna vessels moved around, (3) the yellowfin tuna moved around, and, most likely, (4) some combination of (1), (2), and (3). For some years (e.g., 1985-87), the samples included no spinner dolphins from south of the Equator, but dolphin research survey cruises in that region in 1986 and 1987 made numerous sightings (Holt and Jackson 1987, 1988). That particular hiatus in the maps of localities for at least some years therefore represents the absence of tuna vessels and possibly yellowfin tuna associated with dolphins, not an absence of spinner dolphins. On the other hand, the pattern of paired latitudinal bands of high density of localities for "whitebelly" schools in the cumulative map (Fig. 3) was not apparent in annual plots. It resulted mainly from relatively large numbers of specimens from the area of the upper band in 1975 and 1984-87 and from the lower band in 1977 and 1978. "Eastern" schools were sampled from the region of the northern band in all years. Again, research surveys in 1986 and 1987 sighted comparable numbers of "whitebelly" spinner schools in the two regions. In this case, it is possible that the pattern or degree of association of tuna with the two forms varied interannually. However, the numbers of sightings of spinner dolphins during all the research cruises were relatively small, and it remains possible that some portion of the patterning in the cumulative distribution represents inter-

annual variation in distribution; i.e., the northern boundary of the main "whitebelly" distribution may fluctuate year to year by about 5 degrees of latitude. This would be consistent with some of the results of the present study; for example, the intermediate percentages of the extreme "eastern" and "whitebelly" character states in the band between 5° and 10°N (Figs. 9–10, 12–15).

Another possible explanation of the latitudinal pattern has to do with distribution of tuna-fishing effort. During the period 1976–79, the Inter-American Tropical Tuna Commission set a regulatory demarcation line at 5°N, between 95° and 110°W. During this period, when an annual areal quota of yellowfin tuna for the region north of the line was filled, the international fleet was forced to fish south of the line or to the west (Peterson and Bayliff 1985). A similar line was in force in 1973–75 at 3°N. The subsidiary latitudinal band of distribution records south of 5°N apparent in the spinner dolphin data is also present in data for the pantropical spotted dolphin *S. attenuata*, the principal target species of the tuna fishery (Perrin et al. 1983). Illustrations of the effect of the regulatory regime on the distribution of fishing effort are given in Punsley (1983); the effect was particularly pronounced in 1978.

Some of the morphological results speak against the hypothesis of large-scale latitudinal movements. Variation among sub-areas of the "whitebelly" range is discordant. For example, for the character "ventral field" (Figs. 9, 10), the far-western blocks, far-southern blocks, and southwestern blocks are similar in having relatively high frequencies of the Code-5 character state (most "whitebelly-like"), while for the "cape" (Fig. 11), the southwestern region differed from the west and south in having low frequencies of observed cape (they were most like the animals immediately to the north). For male/female dorsal fin shape (Figs. 12, 13), the southern blocks had higher frequencies of the falcate fin than did the western blocks. While in color pattern and in cranial characters (Schnell et al. 1985), the westernmost blocks were most like the southern blocks, in body length and variability of body length (Figs. 17, 18) they were most like the northern and central blocks. The blocks just north of the Equator were remarkable in having very high frequencies of females intermediate between the most "whitebelly" state and the most "eastern" state in combined character scores (Fig. 15); the highest frequencies of these in males were in the westernmost blocks. In body length in both males and females (Fig. 17), the steepest gradient was at about 5°N, whereas in combined ventral field, cape and dorsal fin (Figs. 14, 15), it was at about 10°N. In cape (Fig. 11) and body length (Fig. 17), the dolphins in the Panama Bight and just to the south were most like those in the core "eastern" region (lacking visible cape

and small in body size), but in ventral field (Fig. 9) they were intermediate between those to the north and south, having approximately equal frequencies of Code 1, Code 5, and summed Codes 2–4. This complex patchwork of variation suggests that there is not a large amount of movement between the various regions and that the year-to-year variation in the collection localities (Figs. 3, 4) reflects mainly movements of the tuna vessels and perhaps the tuna.

The complex geographical pattern of variation in the zone of intergradation/hybridization ("whitebelly spinners") is consistent with the limited information from tag returns (Perrin et al. 1979b), which suggests a home range of a diameter of hundreds rather than thousands of kilometers. This is also supported by the stability of the core eastern region between years and patterns of reproductive seasonality that suggest areal structure within the eastern region (Barlow 1984).

However, there may be mid-scale seasonal movements within an overall pattern of interannual stability, especially in the "whitebelly" areas outside the core range of the eastern spinner. Based on census surveys from dedicated research vessels, Reilly (1990) reported increases in abundance west of 120°W along 10°N coincident with seasonal shoaling of a thermocline ridge. Because of interannual variation in distribution of tuna fishing effort (discussed above), the coarse geographic strata used, and the relatively small sample sizes for the outlying strata, the present analyses probably could not be expected to detect such shifts, although the shifts might be expected to blur the perceived patterns of morphological gradients.

Taxonomic status and management of the "whitebelly" spinner dolphin

The "whitebelly" spinner has been managed as two "stocks" divided at the Equator, the northern whitebelly spinner and the southern whitebelly spinner, implying effective reproductive isolation between them and from the eastern spinner (e.g., Hall and Boyer 1990). The complex pattern of discordant geographic variation and the relatively higher standard deviations (of body length) in the range of the "whitebelly" spinner are typical of a hybrid zone resulting from what Mayr (1970) called allopatric hybridization, or "the formation of a secondary zone of contact and of partial interbreeding between two formerly isolated populations that had failed to acquire complete reproduction isolation during the preceding period of geographic isolation." The discordant pattern speaks against the earlier hypothesis of a locally adapted "whitebelly" population sharing features with populations to the east and west and defined by morphological clines. An

hypothesis of secondary contact after isolation (Perrin et al. 1985) and consideration of the patterns of variation led to the formal recognition of the eastern form as a subspecies, *Stenella longirostris orientalis*, and the "whitebelly" form as an hybrid/intergrade between that subspecies and the pantropical spinner dolphin *S. l. longirostris* (Perrin 1990). The hypothesis of genetic exchange between the eastern and "whitebelly" populations is also supported by results of analysis of mitochondrial DNA (Dizon et al. 1991); the presence of unique haplotypes that would be expected in isolated populations was not detected. Given this situation, a relatively higher priority should probably be given to protection of the eastern subspecies on the grounds that it is a distinctly and locally adapted form vulnerable to depletion and to genetic "swamping" from the larger and less-exploited population to the west. In any case, the understanding presented here of the complex pattern of variation within the "whitebelly" range does not support the present division into northern and southern stocks for management on grounds of population distinctness.

Conservation and management of the eastern spinner dolphin

There was generally good concordance between the patterns in the individual morphological characters and the relative distributions of the two kinds of schools as identified by modal appearance (Fig. 3). One exception was the region west of the Bight of Panama; here the very high frequency of morphologically intermediate dolphins and virtual absence of animals of the extreme "eastern" appearance indicate that these schools perhaps would have better been identified as "whitebelly" schools. Apart from this discrepancy, the concordance between the character patterns and the field identification of schools suggests that the modal appearance method of identification is largely effective. The substantial number of "mixed schools" and unidentified schools, however, indicates that the method can still offer difficulties. In addition, it is sometimes difficult to identify a school of spinner dolphins to "stock" (eastern or "whitebelly") before the seine is set. This can be due to poor viewing conditions (time of day, angle of sun, amount of wind, height of swell) or to the behavior of the dolphins (e.g., "laying low," precluding observation of ventral coloration).

An alternative management scheme based on geographic location would avoid the difficulties of field identification of schools. Although the working hypothesis for management of the eastern spinner and the "whitebelly" spinner (eastern/pantropical hybrids or intergrades) has been one of broadly overlapping ranges (e.g., Perrin et al. 1985), the actual transition

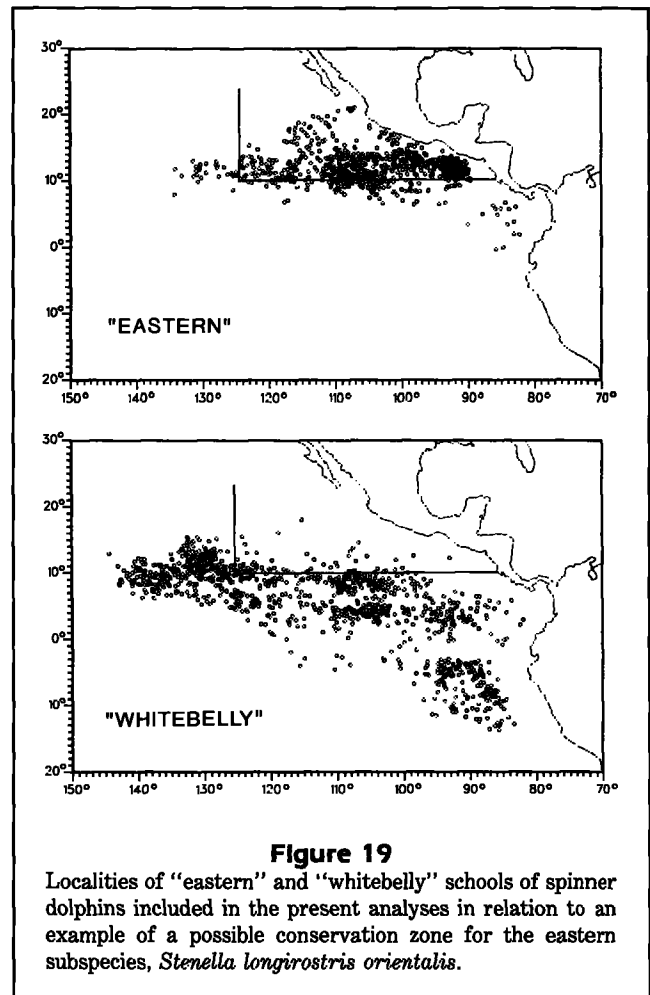


Figure 19
Localities of "eastern" and "whitebelly" schools of spinner dolphins included in the present analyses in relation to an example of a possible conservation zone for the eastern subspecies, *Stenella longirostris orientalis*.

between the two as indicated by gradients in the morphological characters and the field identifications (Fig. 3) is quite sharp. 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 example, such a zone bounded by 10°N latitude and 125°W longitude, the approximate latitude and longitude of the major gradients in the morphological characters, would have included 84% of the schools identified in the field as "eastern" (excluding those in the Bight of Panama, discussed above) and only about 5% of those identified as "whitebelly" (Fig. 19). Implementation of an international quota or prohibition for such a zone would be straightforward. The boundaries could be set based on a balance of considerations of conservation and operational practicality and should take into account seasonal and interannual variation in locations of concentrations of schools of the eastern spinner.

This scheme, of course, is only one of numerous possible alternatives to conservation and management of

the subspecies. Others include international application of a stock quota, complete bans on this type of fishing, and increased focus on technological efforts to reduce fishing mortality rates, to name a few.

The Central American spinner ("Costa Rican spinner")

The number of "Costa Rican" schools sampled was too small for meaningful separate analysis (2 of 1454; Fig. 3) and the effect on the analyses of including them in the pooled samples can be considered negligible. In any case, the range of the Central American spinner *S. l. centroamericana* as presently understood (a coastal strip about 50 nmi wide between about 13° and 7°N) does not overlap those of the eastern subspecies or the "whitebelly" hybrid/intergrade forms (Perrin 1990). This range could serve as a management unit for the subspecies.

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