

Distribution and Differentiation of Populations of Dolphins of the Genus *Stenella* in the Eastern Tropical Pacific¹

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There are at least two races of spotted dolphin, *Stenella attenuata*, in the eastern Pacific, based on length, color pattern, and skeletal differences. The coastal form is provisionally called *S. attenuata graffmani*. The offshore form is distinct from a third, Hawaiian race. Likewise, at least three unnamed races of spinner dolphin, *S. longirostris*, occur in the eastern Pacific. Length, shape of adult male, color pattern, and cranial differences are used to distinguish a Costa Rican, an eastern, and a whitebelly race. An Hawaiian race is distinct from these. A distributional break may indicate two stocks of the striped dolphin, *S. coeruleoalba*.

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Il existe au moins deux races de *Stenella attenuata* dans le Pacifique oriental, se distinguant par la longueur, le motif de coloration et le squelette. Nous nommons provisoirement la forme côtière *S. attenuata graffmani*. La forme du large est distincte d'une troisième, la race hawaïenne. Semblablement, au moins trois races sans noms de *S. longirostris* se rencontrent dans le Pacifique oriental. La longueur, la forme des mâles adultes, le motif de coloration et les différences crâniennes servent à distinguer une race de Costa Rica, une race orientale et une race à ventre blanc. Une race hawaïenne est différente de celles-ci. Une discontinuité dans la répartition peut indiquer l'existence de deux stocks de *S. coeruleoalba*.

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THE purse seine fishery for tuna in the eastern tropical Pacific employs three species of *Stenella* (Perrin 1968, 1969; NOAA 1972). The purpose of this paper is to describe the distribution of the subpopulations of these three species and the grounds for separating them.

The involved species of dolphin are *Stenella attenuata* (Gray, 1846), called "spotted porpoise" by the American tuna fishermen, *S. longirostris* (Gray, 1828), called "spinner porpoise," and *S. coeruleoalba* (Meyen, 1833), called "streaker porpoise." The taxonomy of the genus is unsettled, and the nomenclature used here is provisional. *Stenella attenuata* is the most important of the three species to the fishery (Table 1). *Stenella longirostris* is next most important. Only a very few net sets are known to have been made on *S. coeruleoalba*. Other cetaceans involved in the fishery are the delphinids *Delphinus delphis* L.,

Tursiops sp., *Lagenodelphis hosei* Fraser, 1956, and *Steno bredanensis* (Lesson, 1828), the latter three to very minor extent.

Materials and Methods

Most of the distribution data and the specimens used for morphological studies were collected by scientific observers aboard commercial tuna seiners during the period 1968–74. I also surveyed available U.S. museum collections and the literature. Complete details concerning the specimens and methods used in the analyses of morphology have been previously presented (Perrin 1972a, 1973).

In tagging dolphins to delineate their ranges and migrations, several tagging methods and types of tags were used. Animals were tagged on the deck after being extricated from the net or separated from the catch of tuna, in the net during the "backing down" rescue operation (Perrin 1969; Coe and Sousa 1972), or as they rode the bow-wave of the vessel. Dart-type spaghetti tags of two types were used. Initially, an all-plastic tag was used (Mather 1963). Since 1971, a tag with a metal dart (Mather 1963) has been used. Animals on the deck or in the net were tagged with a short wand. Bow-riding animals were tagged with a long wand with a quick-release head (Beckett 1968) or with a crossbow (Evans et al. 1972). Some

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TABLE 1. Observed net sets on delphinids by tuna purse seiners, 1971-74.

Stock	Number of observed net sets (% of year's observed sets in parentheses)			
	1971	1972	1973	1974 ^a
<i>Stenella attenuata</i>	64 (94.1)	219 (90.5)	616 (81.5)	681 (84.4)
Coastal race	0	0	7 (1.0)	0
Offshore race	64 (94.1)	219 (90.5)	609 (80.6)	666 (82.5)
Unidentified to race	0	0	0	15 (1.9)
<i>S. longirostris</i>	40 (58.8)	138 (57.0)	311 (41.1)	313 (38.8)
Eastern race	28 (41.1)	70 (28.9)	147 (19.4)	286 (35.4)
Whitebelly race	12 (17.6)	28 (11.6)	43 (5.7)	49 (6.1)
Unidentified to race	11 (16.2)	6 (2.5)	117 (15.5)	1 (0.1)
<i>S. coeruleoalba</i> ^b	0	0	2 (0.3)	2 (0.2)
<i>Delphinus delphis</i>	2 (2.9)	26 (10.7)	97 (12.8)	110 (13.6)
Northern race ^c	0	0	15 (2.0)	0
Southern race ^c	2 (2.9)	26 (10.7)	82 (10.8)	110 (13.6)
<i>Tursiops</i> sp. ^b	3 (4.4)	7 (2.3)	5 (0.7)	34 (4.2)
<i>Lagenodelphis hosei</i>	1 (1.5)	0	0	0
<i>Steno bredanensis</i>	0	0	0	2 (0.2)
Total sets observed ^d	68	242	756	807

^aPartial data, as of March 25, 1974.^bMay be more than one stock.^cRaces *vide* W. E. Evans personal communication.^dDo not equal sum of species totals; some sets are on mixed herds.TABLE 2. Races of *Stenella attenuata* in eastern Pacific and Hawaiian waters. Length data previously unpublished; color pattern and skeleton data from Perrin (1972b). Sample sizes in parentheses.

Race	Adult length (see Fig. 2) (cm)		Adult color patterns	Skeleton		
	Males	Females		Adult condylobasal length (mm)	Adult tooth diameter (mm)	No. vertebrae
Coastal	203-257 (37)	184-227 (76)	Dorsal spotting light to heavy, but medium to heavy in most. Dorso-ventral contrast low.	419-460 (18)	3.4-5.7 (9)	77-79 (9)
Offshore	179-224 (332)	167-206 (1042)	Dorsal spotting light to heavy, but medium to light in most. Far offshore (> 800 km) animals lightly spotted.	356-411 (68)	2.7-4.0 (65)	77-83 (61)
Hawaiian	182-202 (6)	189-203 (3)	Dorsal and ventral spotting so obscure as to appear absent. Adult resembles neonate of offshore race (Perrin 1970).	395-440 (12)	—	79 (2)

plastic dorsal-fin tags (Norris and Pryor 1970) were also used.

Species Accounts

Stenella attenuata — There are at least two races of spotted dolphin in the eastern Pacific. They differ in several features (Table 2). A

coastal form is relatively large and robust, has heavy jaws and teeth, is heavily spotted, and is restricted to onshore waters from the Gulf of California to northern Peru (Fig. 1). An offshore race is relatively small and slender, has lightly built jaws and teeth, is spotted to varying degree, and occurs in offshore waters west to about 145°

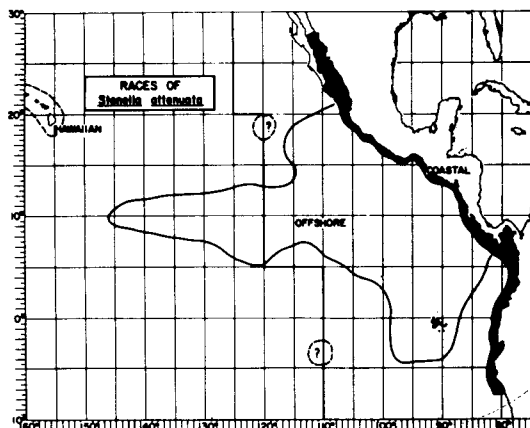


FIG. 1. Known ranges of races of *Stenella attenuata* in the eastern Pacific, based on collections and sightings by National Marine Fisheries Service observers aboard commercial tuna seiners and research vessels, museum collections and literature records. Boundaries are approximate only, and fluctuate seasonally and from year to year.

W long. The ranges of the two forms may overlap, or the boundary between them may move seasonally or from year to year. They have not been observed or captured together. In the central latitudes of the range the coastal form has been collected as far offshore as 50 km and the offshore form as far inshore as 20 km from the coast. The offshore form predominates in the fishery (Table 1). Another race inhabits the waters around Hawaii and may extend into the South Pacific and to the west. This form is also small and slender, but is less spotted.

The existence of two forms was first suspected upon comparison of a large series of skeletal specimens from the tuna fishery with the material available in museums, which consists mostly of animals harpooned on the coast and includes the type of *Stenella graffmani* (Lönnerberg, 1934). Both series included obviously very young and very old individuals. The skulls in the coastal series were longer, broader, and had proportionately larger posttemporal fossae and teeth than those in the series from the tuna fishery (Perrin 1972a). The skulls of the two forms differ mainly in those features that have to do with feeding. The coastal form appears to be adapted to feeding on larger, more substantial prey than does the offshore form. The offshore form feeds primarily on epipelagic squids and fishes (Perrin et al. 1973). No data are available on the diet of the coastal form. The two series of specimens are statistically separable on the basis of aspects of the skull related to feeding (Perrin 1972a). The

Hawaiian form is also separable on the basis of skull measurements. It has a longer, broader skull than does the offshore form but does not have the more massive feeding apparatus like that of the coastal race. Within the offshore race, an east-west cline may exist. Specimens from farthest west tend to be most Hawaiian-like.

The coastal form also has a larger, more massive postcranial skeleton than does the offshore form and, on the average, fewer vertebrae (Perrin 1972a). The range of vertebral counts for the coastal series is 77–79 (nine specimens), as opposed to 79–83 (48 specimens) for offshore animals taken from adjacent waters. Offshore animals from more than 800 km offshore tend again to have lower vertebral counts (77–82 in 13 specimens), supporting the concept of an east-west cline within the offshore race.

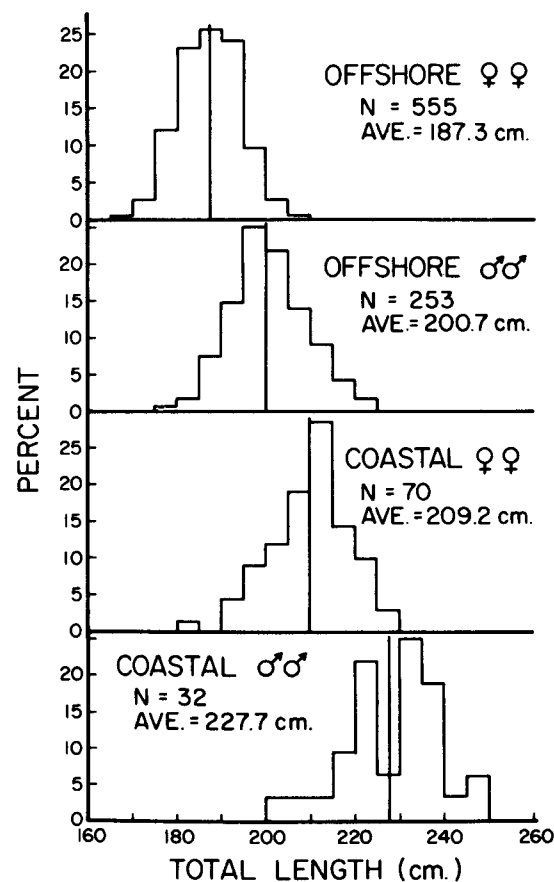


FIG. 2. Histograms of body lengths of spotted dolphins, *S. attenuata*, of two races, collected aboard tuna seiners in 1973. Specimens identified to race on the basis of locality of capture and range of lengths in sample.

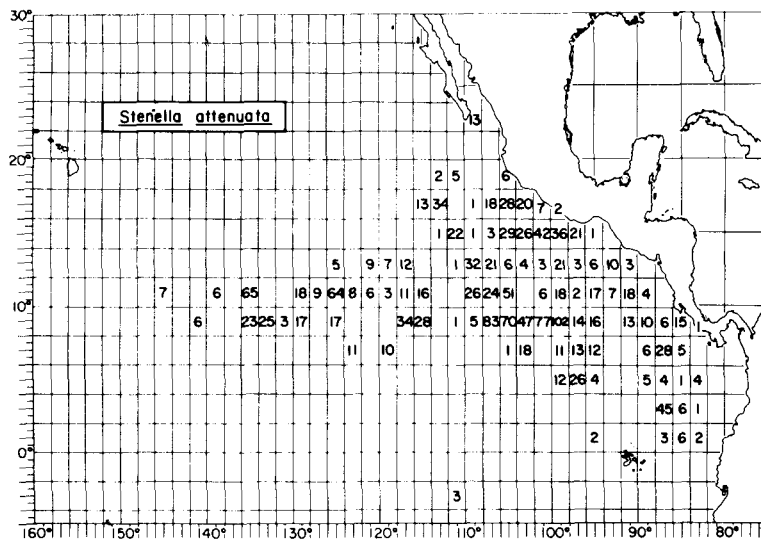


FIG. 3. Numbers of spotted dolphins, *S. attenuata*, tagged, 1969-74, by 2-degree square.

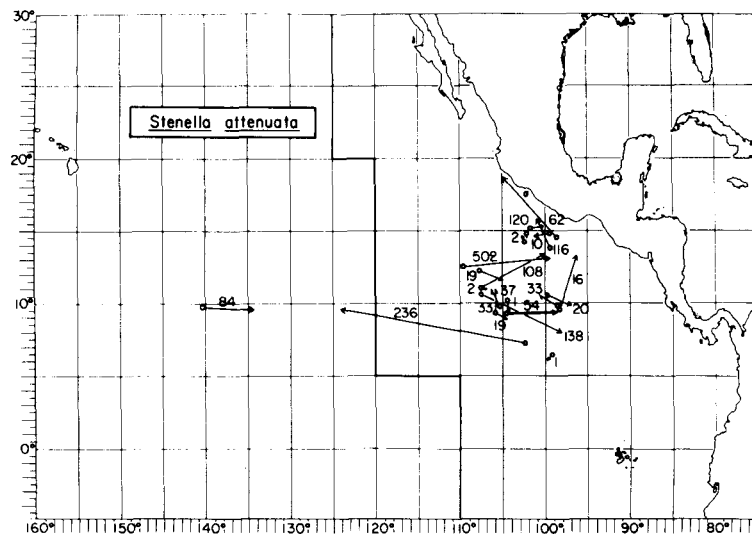


FIG. 4. Net movements of recovered tagged spotted dolphins, *S. attenuata*, with days at liberty.

Recent length data from the fishery also support the concept of two races in the eastern Pacific. Several samples of animals taken in 1973 from within 30 km of the coast of Costa Rica were clearly from a different population than samples taken from more offshore waters throughout the range (Fig. 2). The coastal adult females (those with ovarian scars) were on the average about 22 cm longer than the offshore females.

The coastal adult males (those with testes weighing more than 200 g, the smallest size at which sperm has been found in the epididymis) were about 27 cm longer than the offshore males. Calculating from a length-weight relationship (unpublished data), this amounts to an average weight difference in adult males of about 35 kg (115 vs. 80 kg).

We have tagged 11 coastal and 1716 offshore

spotted dolphins (Fig. 3), and recovered 24 tagged offshore animals from known locations (Fig. 4). Time at liberty ranged from 1.7 h to 502 days, and the distance from release point to recapture point ranged from 13 to 2415 km. These results show a great deal of east-west and north-south movement, evidence for extensive mixing within the eastern half of the supposed range of the offshore race. The degree of continuity between the eastern and far-western portions of the range is still unknown because of insufficient tag returns.

The three forms clearly deserve subspecific status (Perrin 1972a). Assignment of trinomials to the offshore and Hawaiian forms will have to wait until the taxonomy of the genus at the species level has been unraveled. Many of the holotypes in *Stenella* are from unknown localities. Relationships among spotted dolphins in the Atlantic and Pacific need to be examined. The name *graffmani*, however, clearly applies to the coastal form, and I therefore provisionally call the coastal form *S. attenuata graffmani*.

Stenella longirostris — There are at least three races of spinner dolphin in the eastern Pacific (Fig. 5), differing modally in several characters (Table 3). One that occurs very near the coast of Central America, referred to below as the "Costa Rican" form, is relatively long, slender, and gray. A second race, called "eastern spinner," occurs along the coast of Mexico and seaward about 800 km and is relatively short, slender, and gray. A third, called "whitebelly spinner," occurs in far offshore waters west to about 145° W long. and is relatively short, robust, and white below.

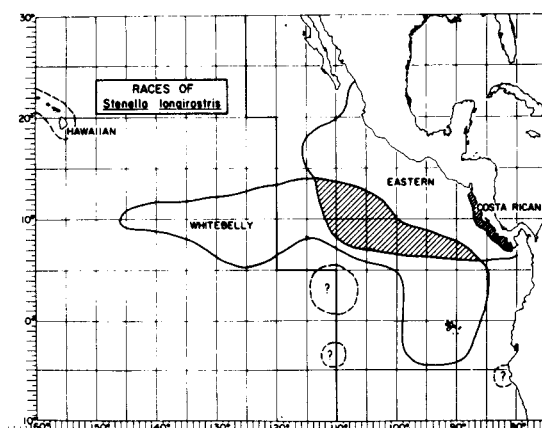


FIG. 5. Known ranges of races of *S. longirostris* in the eastern Pacific. Same data sources as Fig. 1. Boundaries are approximate only, and fluctuate seasonally and from year to year.

A fourth form occurs in Hawaiian waters and possibly to the south and west and is relatively long, robust, and white below. The ranges of the eastern and whitebelly forms overlap (Fig. 5). In the area of overlap, the two forms are occasionally captured together. A few apparent intergrades have also been collected.

The eastern and whitebelly forms are both involved in the tuna fishery (Table 1). Existence of eastern and whitebelly races was discovered through field observations of color patterns. The Costa Rican-eastern and whitebelly-Hawaiian dichotomies were discovered while examining skeletal specimens.

As with *S. attenuata*, most of the geographical variation in the skull is in features functional in feeding (Perrin 1972a). The Costa Rican spinner has a proportionately longer, more lightly built rostrum and mandible than does the eastern

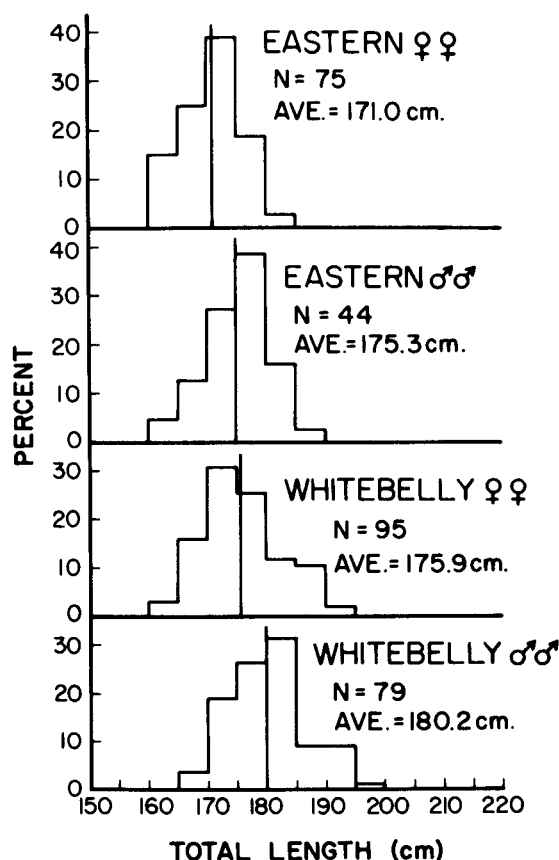


FIG. 6. Histograms of body lengths of spinner dolphins *S. longirostris*, of two races, collected aboard tuna seiners, 1968-73. Specimens identified to race on basis of locality of capture and color pattern.

TABLE 3. Races of *S. longirostris* in eastern Pacific and Hawaiian waters. Length data previously unpublished; other data from Perrin 1972a. Sample sizes in parentheses.

Race	Adult length (cm)			Shape of adult males		Color pattern (terminology of Perrin 1972b)	Skull	
	Males	Females		Dorsal fin	Ventral hump		Condylbasal length (mm)	Zygomatic width (mm)
Costa Rican	181-216 (2)	193-203 (3)		Canted to triangular	—	Poorly known, but like that of eastern.	416-437 (4)	149-152 (4)
Eastern	161-186 (44)	160-181 (75)		Canted to triangular	Medium to extreme	Dark dorsal field obscures cape and extends ventrad, leaving light areas in genital and axillary regions. Monotone effect.	351-407 (26)	139-153 (29)
Whitebelly	170-196 (79)	161-194 (95)		Triangular to falcate	Medium to slight	Dorsal field extends ventrad only to level of eye laterally and has irregular margin. Cape faintly visible through dorsal field. Bipartite effect.	365-419 (13)	145-158 (14)
Hawaiian	185 (1)	183-201 (2)		Falcate	Slight	Light dorsal field to level of eye, with smooth margin. Cape very obvious. Tripartite effect.	431-464 (10)	159-171 (10)

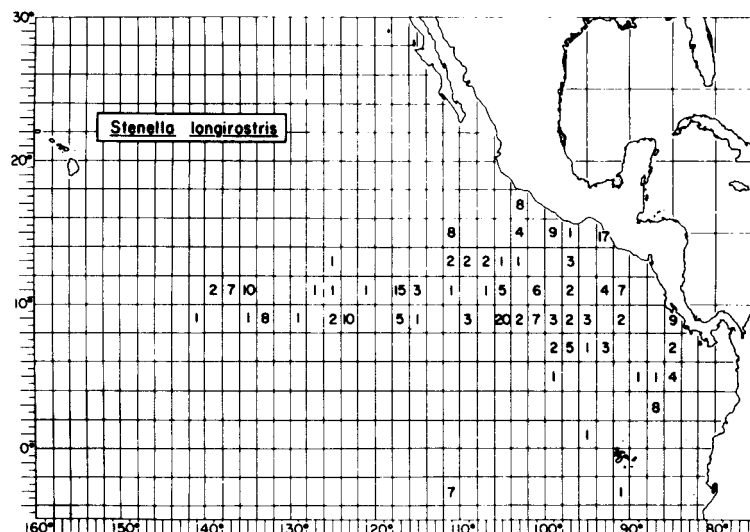


FIG. 7. Numbers of spinner dolphins, *S. longirostris*, tagged, 1969–74, by 2-degree square.

spinner, the reverse of the trend in *S. attenuata*. The skulls of the eastern and whitebelly spinners do not differ in proportion, but the whitebelly skull is on the average slightly larger. The skull of the Hawaiian spinner is longer and broader than those of the other three forms. The four series of specimens can easily be separated statistically (Perrin 1972a).

We know little about the external appearance of the Costa Rican spinner, other than it is very long and slim (a 216-cm male weighed only 57 kg) and has a color pattern very much like that of the eastern spinner. The obviously disparate color patterns of the eastern, whitebelly, and Hawaiian forms can be compared in terms of differential development of a dorsal dark field (Perrin 1972b). The dorsal field is darkest and most extensive in the eastern form and lightest and least extensive in the Hawaiian form. In the Hawaiian form, an underlying dark cape shows strongly through the light dorsal field. The result is to make the coloration of the eastern, whitebelly and Hawaiian spinners effectively uniform, bipartite, and tripartite, respectively. In some apparent intergrades from the area of overlap of the eastern and whitebelly ranges, the dark cape shows faintly through the dorsal field, but the ventral margin of the field is lower and more irregular than in the typical whitebelly spinner.

The dorsal fin of the adult male differs among the three races. In the eastern spinner the tip is forward of midlength of the fin base, giving the fin a reversed appearance. The forward cant is

much more developed in some males than in others (Perrin 1972a). In the whitebelly form, the adult male fin is never "reversed" but usually triangular. In the Hawaiian form, it is always at least slightly falcate. Development of a ventral, postanal keel, of unknown function, is correlated with degree of forward cant of the dorsal fin. It is largest in eastern males and nearly absent in Hawaiian males.

The whitebelly form is on the average about 5 cm longer than the eastern form (Fig. 6) and is more robust, having a greater average girth at the axilla (Perrin 1972a). Few measurements are available for the Hawaiian spinner, but it ap-

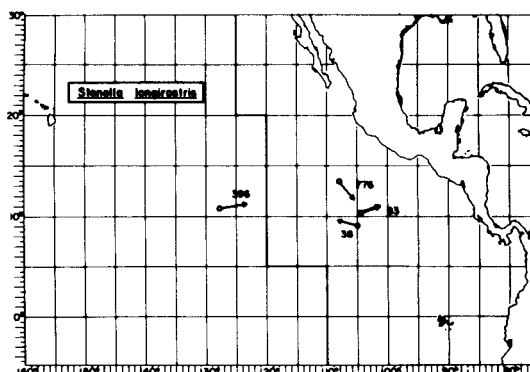


FIG. 8. Net movements of recovered tagged spinner dolphins, *S. longirostris*, with days at liberty.

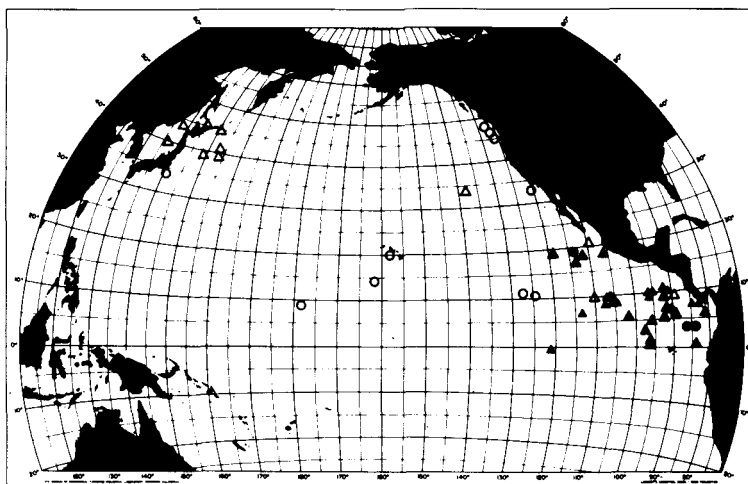


FIG. 9. *Stenella coeruleoalba* in the Pacific. Circles are specimen localities; triangles are sighting localities. Shaded symbols are new records. Open symbols are previously published records (Hubbs et al. 1973).

parently is, on the average, longer than the whitebelly spinner.

We have tagged 242 spinner dolphins (Fig. 7) and recovered five (Fig. 8). Time at liberty ranged from 38 to 776 days, and net distance traveled from 333 to 733 km. Two animals tagged together were recaptured together 83 days later. The limited results show less net movement than for *S. attenuata* and agree with the hypothesis of offshore (eastern) and far offshore (whitebelly) populations.

The four races of spinners deserve subspecific status, but, as is the case for the spotted dolphins, assignment of trinomials must wait until the question of how many species of spinner dolphin exist in the world's oceans has been settled. For the time being, they are best considered as unnamed subspecies of *S. longirostris* Gray.²

Stenella coeruleoalba — The striped dolphin was not known from the eastern tropical Pacific

until 1970 (Hubbs et al. 1973). In addition to the published locality records (Hubbs et al. 1973) we now have 36 more records, including three for which specimens were collected (Fig. 9). The known range has been extended south to below the equator and east to the Panama Bight. There may be a break in the distribution between about 10° and 17° N lat. This would make the distribution similar to that of *Delphinus* in the eastern tropical Pacific (W. E. Evans personal communication) and may indicate that there is more than one stock. Enough specimens have now been collected from the tropical Pacific (26) so that morphological comparisons can begin to be made between this population or populations and those in the western Pacific and Japan.

Discussion

Geographical races exist for each species of small delphinid that has been closely looked at in the eastern tropical Pacific. It seems reasonable to assume that the eastern Pacific (and world) populations of the other, less well-known delphinids, e.g. *S. coeruleoalba*, *Tursiops*, and *Globicephala*, are similarly subdivided. This points out the need for emphasis on research and management at the stock level.

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²Note: There is room for speculation about the identity of Gray's holotype (Perrin 1972a). The spinner skull that Schlegel in 1846 figured and re-described as the holotype may not have been the specimen examined by Gray. Gray described his specimen as having a strongly carinated palate, a feature present in *Delphinus* but not in *Stenella*. If Schlegel was indeed mistaken about the origin of the specimen he examined, *longirostris* may be preoccupied by *Delphinus* and unavailable for *Stenella*. However, in the interest of stability of nomenclature and in the light of other known inconsistencies in Gray's work, it seems best to ignore this uncertainty now and retain the long-used *longirostris* for the spinners.

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