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Stocks of Dolphins (*Stenella* spp. and *Delphinus delphis*) in the Eastern Tropical Pacific: A Phylogeographic Classification

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ABSTRACT

Current information is reviewed that provides clues to the intraspecific structure of dolphin species incidently killed in the yellowfin tuna purse-seine fishery of the eastern tropical Pacific (ETP). Current law requires that management efforts are focused on the intraspecific level, attempting to preserve local and presumably locally adapted populations. Four species are reviewed: pantropical spotted, *Stenella attenuata*; spinner, *S. longirostris*; striped, *S. coeruleoalba*; and common, *Delphinus delphis*, dolphins. For each species, distributional, demographic, phenotypic, and genotypic data are summarized, and the putative stocks are categorized based on four hierarchal phylogeographic criteria relative to their probability of being evolutionarily significant units.

For spotted dolphins, the morphological similarity of animals from the south and the west argues that stock designations (and boundaries) be changed from the current northern offshore and southern offshore to northeastern offshore and a combined western and southern offshore. For the striped dolphin, we find little reason to continue the present division into geographical stocks. For common dolphins, we reiterate an earlier recommendation that the long-beaked form (Baja neritic) and the northern short-beaked form be managed separately; recent morphological and genetic work provides evidence that they are probably separate species. Finally, we note that the stock structure of ETP spinner dolphins is complex, with the whitebelly form exhibiting characteristics of a hybrid swarm between the eastern and pantropical subspecies. There is little morphological basis at present for division of the whitebelly spinner dolphin into northern and southern stocks. However, we recommend continued separate management of the pooled whitebelly forms, despite their hybrid/intergrade status. Steps should be taken to ensure that management practices do not reduce the abundance of eastern relative to whitebelly spinner dolphins. To do so may lead to increased invasion of the eastern's stock range and possible replacement of the eastern spinner dolphin genome.

Introduction

Management of dolphins incidentally killed in the purse seines of the eastern tropical Pacific (ETP) yellowfin tuna fishery is directed at the stock or population level. Realistic stock delineations are necessary both for estimating the impact of the fishery on dolphin species and for ensuring conservation of locally adapted genetic variation. Incidental mortality has primarily affected four species of dolphins, listed in order of exploitation (DeMaster et al., 1992): the pantropical spotted dolphin, *Stenella attenuata*; the spinner dolphin, *S. longirostris*; the common dolphin, *Delphinus delphis*; and the striped dolphin, *S. coeruleoalba*. Over the years, two Status of Porpoise[1] Stocks (SOPS) workshops have been convened to review the status of the impacted stocks (Anon.[2]; Smith[3]). In 1983, for a planned third workshop,[4] Perrin et al. (1985) prepared a review of evi-

[1] Convention in the fishing community uses the term "porpoise" for dolphin.

[2] Anon. 1976. Report of the workshop on stock assessment of porpoises involved in the eastern Pacific yellowfin tuna fishery. Southwest Fisheries Center, National Marine Fisheries Service, NOAA, Admin. Rep. LJ-76-29, 53 p.

[3] Smith, T. D. 1979. Report of the status of porpoise stocks workshop (August 27–31, 1979, La Jolla, California). Southwest Fisheries Center, National Marine Fisheries Service, NOAA, Admin. Rep. LJ-79-41, 120 p.

[4] Although panels of experts were convened to review components of the assessment, including stock identity, the full work-

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dence regarding the geographic forms of ETP dolphins and recommended how intraspecific divisions should be made for status-of-stock assessments and management. Our present review includes new information collected since then and updates recommendations regarding stock boundaries.

Intraspecific structure of dolphin species is characterized by pronounced geographical variation probably reflecting local adaptation and mechanisms that limit gene flow between neighboring populations (Evans, 1982; Perrin, 1984; Perrin et al., 1991). Either relatively limited movement (perhaps hundreds of kilometers in spinner dolphins), socially mediated barriers, reproductive timing differences, or some combination of these allow genetic variation to accumulate, differentiating local populations. However, this abundance of variation can obscure rather than facilitate the interpretation of stock structure. Surveys are required that are large, in terms of sample size and area and time period sampled, and well designed, in terms of eliminating bias. Pronounced geographic variability also dictates that care be taken in circumscribing stocks so that local variation is preserved. Differential exploitation of local stocks coupled with a stock designation that is too broad could lead to destruction of locally adapted populations.

The intent of the Endangered Species Act of 1973 and the Marine Mammal Protection Act of 1972 is to manage exploitation of living marine resources so that locally adapted populations are not irreversibly reduced to the point where they no longer are functioning entities in the ecosystem. Although management-by-stock is a basic principle of the conservation acts, no meaningful attempts to define the term "stock" were made within the legislation, save to refer to the stock as a "distinct population" that "shares a common space" and that "interbreeds." Unfortunately, stock has no universally accepted definition among biologists because it is not immediately obvious how to define the extent of "sharing" or "interbreeding." Recently, Waples (1991, a and b) for Pacific salmon (*Oncorhynchus* spp.) and Dizon et al. (1992) for marine mammals have developed guidelines that, although not totally removing subjectivity in the process of stock designation, focus attention on important criteria. Both reviews considered that, for the purposes of management, a population will be considered distinct if it is an "evolutionarily significant unit" (ESU; Ryder, 1986). Waples suggested that for a population to be an ESU it must be "substantially reproductively isolated" and "represent an important component of the evolutionary legacy of the species." If reproductive isolation is sufficient, evolutionary differences can accrue within a population, increasing fitness within the local habitat. This increase in genetic variation then becomes an "important component in the evolutionary legacy of the species" (Waples, 1991, a and b).

Although the ESU concept is an improvement over that of "sharing a common space and interbreeding," which after all encompasses any arbitrary division of a panmictic population, it is still subjective in its use of "substantial" and "important." Existing measures of fitness, such as viability and growth rate (Leberg, 1990; Pastene et al., 1991), have little utility in defining specific fitness to a local environment in animals for which test breeding programs cannot be conducted. In practice, locally adapted populations are subjectively identified using a variety of proxy data. These data allow inferences to be made regarding isolation and genetic uniqueness and can be classified as distributional, populational (demographic) response, phenotypical, and genotypical. When differences between populations in one or more of the proxies are apparent, it is inferred that two separate biological populations, and potentially two ESU's, exist.

Dizon et al. (1992) argued that the degree to which a population is probably an ESU should be made part of the stock designation. In brief, their point for doing so was to ensure that the relative "worth" of a population in the management arena is made apparent and that due consideration is taken of the criteria of "significant isolation" and "important component of the evolutionary legacy." Dizon et al. (1992) proposed that a hierarchal classification scheme be applied to stock designations to create a matrix of Waples' (1991, a and b) criteria of isolation and genetic uniqueness.

Category I populations, having the highest probability of being ESU's, are characterized by a discontinuous genetic divergence pattern where a locally adapted and closely related population is geographically separated (i.e. allopatric or parapatric with physical barrier). Geographic separation increases the probability that habitat differences exist between the isolated populations, resulting in different selection pressures.

Category II is similarly characterized by significant genetic distances between assemblages but with weak geographic partitioning (i.e. partial sympatry or parapatry with no barrier).

Category III is the converse of II, having little genetic differentiation between assemblages that are clearly geographically separate (as in Category I) and probably reproductively isolated.

Category IV assemblages, having the lowest probability of being ESU's, are characterized by weak geographic partitioning (as in Category II) and no evidence of genetic uniqueness.

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shop was never held due to re-authorization of the Marine Mammal Protection Act, which permitted interim kill for five more years and required a five-year survey of trends in abundance.

They noted that under this scheme, a stock designation is always relative to some other reference population. In general, the reference population will be its nearest conspecific neighbor or neighbors, and it should be listed unless obvious.

In the categorizations, it is important to realize that geographic partitioning is used as a proxy for amount of gene flow. It is a statement regarding the probability of reproductive isolation. However, if fixed genetic differences exist between sympatric or parapatric populations, thus establishing that no gene flow occurs (Hey, 1991) and that the separation is presumably at the species level, it would be misleading to try to categorize the populations; the system is designed for intra- rather than interspecific classification. For instance, two sympatric populations that are totally isolated genetically would be classified mistakenly as Category II, that is, having a lower probability of being an ESU than a Category I population. In fact, rather than being two evolutionarily significant components of a single species, the populations in this example would represent two separate species. Long- and short-beaked common dolphins are probably an example of this situation and are discussed below.

In addition to phylogeographic designation, Dizon et al. (1992) proposed that the information used to classify be included by using the following single letter abbreviations: distributional (a), population response (b), phenotypic (c), and genotypic (d) information. To be included was both evidence for and against. For example in "Type IIbc/a," information to the left of the slash is evidence for "lumping," that to the right is evidence for "splitting"; missing letter abbreviations signify lack of reliable data.

When using this system to categorize populations, biological judgement is required to decide the significance of available data to determine which phylogeographic type is most appropriate. In the following, we attempt to apply this approach to categorize stocks of the impacted dolphin species. We use the Perrin et al. (1985) review as a starting point and consider what new information is available. Each of the four species is considered separately, and the treatment is organized by the four data types: distribution, population response, phenotype, and genotype. At the end of each species section, we offer our classifications of the geographic stocks of the tropical dolphins in the ETP. Note that each stock is classified relative to some other population.

Pantropical Spotted Dolphin
Stenella attenuata

Current U.S. Management Situation

In the eastern and central Pacific Ocean, four stocks are recognized: coastal, *Stenella attenuata graffmani*; northern offshore, southern offshore, and Hawaiian. Quotas have been established for the U.S. fleet for northern and southern offshore as well as coastal spotted dolphins (Anon., 1986). These divisions were recommended by the SOPS meetings in 1983 and are shown in Figure 1. Procedures for assigning spotted dolphins in the ETP to stock type were based on either geographic location, morphology, or both. The coastal and northern offshore forms cannot be discriminated solely on the basis of coastal location, because occasionally the offshore form is found inshore. The coastal type, formerly known as *Stenella graffmani*, can be distinguished by its relatively larger body and heavier spotting. In contrast, the northern and southern offshore forms have to be discriminated strictly on a geographical location, the division being near the Equator, although modal morphological differences exist. The Hawaiian form is discriminated based on its proximity to the Hawaiian Islands and will not be discussed further.

Evidence of Stock Divisions

Distribution

Range — Pantropical spotted dolphins are distributed globally in tropical waters and in some warmer temperate waters. In the Atlantic, they range off the coasts of England and New Jersey southward, including the Caribbean and Gulf of Mexico, through the tropical South Atlantic. In the Indian Ocean, they are found from the Red Sea and the Seychelles offshore to the southern

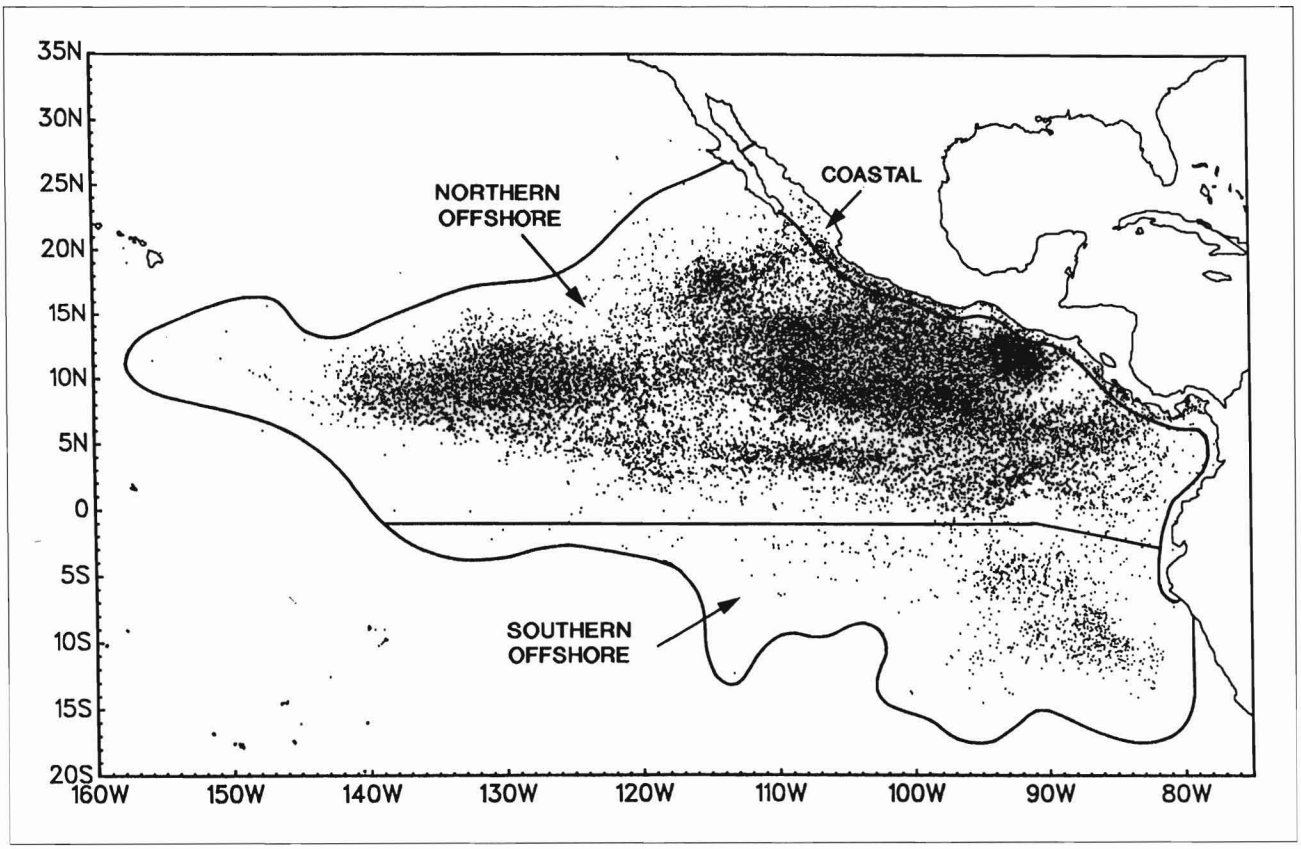

Figure 1
Distribution of the pantropical spotted dolphin, *Stenella attenuata*, stocks in the eastern tropical Pacific Ocean based on sighting data collected between 1971 and 1991 by observers on tuna purse-seining vessels and research vessels. Stock boundaries are from Perrin et al. (1985).

coast of Australia. In the Pacific, they range north off the coast of Japan, east to the South China Sea, and south to New Zealand (Gilpatrick et al., 1987; Perrin and Hohn, in press).

Details of the distribution of the pantropical spotted dolphin are best known for the eastern and central Pacific. A near hiatus in distribution exists at about 2°S (Perrin et al., 1983) reflecting a preference for tropical surface water (Au and Perryman, 1985; Reilly, 1990; Reilly and Fiedler[5]). The hiatus, together with demographic and morphological criteria, justified segregating the offshore form into northern and southern stocks with a boundary first set at 1°S. The equatorial front, dividing the ETP into northern and southern habitats (Pak and Zaneveld, 1974), may be instrumental in the development of the two populations (Reilly and Fiedler[5]). To better reflect actual distribution of the animals, the SOPS 1979 workshop modified the one-degree north-south boundary by slanting it southeasterly at 90°W to intersect the coastline of South America at 3°S (Fig. 1; Smith[3]).

The northern offshore form occurs from near the coast of southern Mexico at 25°N, off Central and South America, to 1°S and west to 145°W. The coastal form occurs within about 200 km of the coastline and off coastal islands from northern Mexico to Ecuador. The offshore and coastal forms are sympatric throughout much of the coastal form's range, but the two forms are not known to school together.

Spotted dolphins also occur in the waters surrounding the Hawaiian Islands and are considered a separate stock. There is an apparent hiatus in distribution of about 800 km between the westernmost range of the northern offshore form (about 157°W) and the Hawaiian area (Perrin, 1975; Perrin et al., 1983).

Movements — Between 1969 and 1976, almost 3000 northern offshore spotted dolphins were tagged with spaghetti tags, and by the beginning of 1977, 97 tags had been returned (Perrin et al., 1979a). Tagging effort extended to just north of the Galapagos Islands, and none of the 97 recaptures occurred south of the Equator. Minimum distance traveled (defined as the distance between release point and recapture point) ranged from 12.8 to 1,071 km; time at liberty ranged from less than 1 day to 1,478 days. Average short-term movement was 55–92 km/day with a circular distribution 400–600 km in diameter. No evidence of movement across the 1°S boundary is consistent with some degree of isolation of the northern and southern stocks. Rather than north-south movements, the authors suggested that onshore migrations in the fall and offshore migrations in the spring may occur.

Tagging, tag sightings without recoveries, and recoveries continued after 1977, and 642 more spotted dolphins were tagged during a single cruise in 1978 (Hedgepeth[6]). Perrin et al. (1985) reported that the total of 206 tag recoveries or sightings made by the time the manuscript was written allowed greater confidence to be placed in the east-west movement of the northern offshore form. One individual, tagged and released at about 10°N, was reportedly sighted by a fisherman (but not recovered) at 10°37'S after 4 or 5 months. This unconfirmed record is the only indication of movement across the stock boundary at the Equator.

Population Response

Reproduction — The attempt to use life history parameters to ascertain stock differences in the spotted dolphin of the ETP is confounded by differences in the history of exploitation and potential differences in carrying capacity over the course of the time series. Barlow (1985) compared reproductive parameters of the putative northern and southern offshore populations, which have been subjected to very different levels of fishing-related mortality. Because the northern offshore stock has been so heavily exploited, one would expect density-dependent increases in reproductive rates for the northern offshore population relative to the southern one. He found the proportion of females mature, the proportion pregnant, and the proportion simultaneously pregnant and lactating higher in the less exploited southern offshore population—the reverse of what was expected.

Chivers and DeMaster (in press) found the proportion of pregnant females significantly higher in the southern offshore population compared with the northern, and the proportion of lactating ones significantly lower, also opposite to that expected under a density-compensatory model. Similar differences were found when northern offshore samples were compared with coastal samples; however, the magnitude of the difference was greater.

Perrin et al. (1976) noted seasonality of breeding in northern offshore spotted dolphins, with two or more peak periods annually. Barlow (1984) and Hohn and Hammond (1985) found geographic differences in patterns of seasonality. Although births were found all year, the northern offshore form exhibited distinct

[5] Reilly, S. B., and P. C. Fiedler. 1991. Interannual variability in dolphin habitats in the eastern tropical Pacific, 1986–1990. Southwest Fisheries Science Center, National Marine Fisheries Service, NOAA, Admin. Rep. LJ-91-42, 41 p.

[6] Hedgepeth, J. B. 1985. Database for dolphin tagging operations in the eastern tropical Pacific, 1969–1978, with discussion of 1978 tagging results. Southwest Fisheries Center, National Marine Fisheries Service, NOAA, Admin. Rep. LJ-85-03, 40 p.

modes in spring and autumn, whereas the southern offshore form had a much more strongly pulsed reproductive period occurring only in the spring.

Spermatozoa scores elevate in the northern offshore form during the predicted breeding season in May and September (Barlow, 1984; Hohn et al., 1985), but testes weight peaks halfway between the calving periods (Hohn et al., 1985). In the southern offshore form, seasonal change in testes weight and development is the same, yet only one calving season (January) has been identified. An unidentified second season may occur six months later.

Marked seasonal difference in reproduction times between the northern and southern offshore populations may indicate reproductive isolation. However, the transition from the diffuse bimodal pattern in the north to the strongly unimodal pattern in the south may not be abrupt. Dolphins in the area from 0° to 5°N show a single peak reproductive mode that is synchronized with animals to the south but also show a diffuse pattern of seasonality similar to that in the northern offshore form. This could be a region of overlap in the seasonal distributions of the northern and southern populations or could be a clinal change.

Age and growth — Perrin et al. (1976) estimated, by linear regression of fetal and neonatal length, an average length at birth of 82.5 cm in the northern offshore population. Hohn and Hammond (1985) claimed that this figure was biased because animals were sampled mainly from small-kill sets (≤40 individuals killed per set) in which calves are over represented, causing an underestimation of length-at-birth. They eliminated small-kill sets, used a logistic model fitted to the fraction postnatal at various lengths, and used a 50% criterion to produce an estimate of 85.4 cm. If not stratified to kill-per-set, their value was 82.0 cm. They estimated the southern offshore form to be 83.2 cm at birth but used only unstratified data in this case. Recently, Bright and Chivers[7] reestimated length at birth for females from both the southern and northern offshore populations (northern sampled west of 120°W). Their result of 83.1 cm for the northern samples was similar to that of Perrin et al. (1976). For the southern samples, length at birth was 86.4 cm, somewhat larger than Hohn and Hammond's (1985) value of 82.9 cm. The difference between the northern and southern length-at-birth values was significant at the 0.05 level.

Length-at-birth measurements establish the origin of the growth curve, although work by Bright and Chivers[7] demonstrates that the Laird-Gompertz growth model was not particularly sensitive to a wide range of initial length-at-birth values. No significant differences between the northern and southern offshore samples were observed in predicted length at age one.

Average length at attainment of sexual maturity (LSM) in the female northern offshore form increased from 176 cm in 1974 to 181 cm in 1983 (Barlow, 1985), although the adoption of a different method for measuring animals in the interim period may be responsible for the trend. From pooled data (1974–83) for the southern offshore form, the estimated LSM was 175 cm.

Myrick et al. (1985) estimated average age of attainment of sexual maturity (ASM) in the northern offshore females to be from 10.7 to 12.2 years (mean=11.4). They also found a correlation between color phase and state of sexual maturity. In a blind study (samples aged without knowledge of stock origins) of 546 northern and 319 southern offshore animals sampled between 1974 and 1988, Chivers and Myrick (1993) demonstrated significant differences in ASM between the northern and southern populations (11.12 years versus 9.78 years, respectively; $P<0.001$). No definitive conclusions regarding stock differences between the northern and southern offshore forms can be drawn from their age and growth data. Several reasons plague all such comparisons: (1) the confounding problems of bias (Chivers and Myrick, 1993), (2) possible changes in carrying capacity due to environmental changes (Chivers and Myrick, 1993), (3) niche replacement in the north versus the south (Chivers and Myrick, 1993), or (4) potential stress effects (Myrick, 1988).

Phenotype

Coastal spotted dolphins are the largest of the four forms in the ETP: males average 223.2 cm; females, 206.5 cm (Perrin et al., 1985). Offshore animals are generally smaller and more slender and have lighter skulls and smaller teeth than the more massive coastal spotted form. This general impression was quantified in a multivariate study of total body length and 36 measures of skull morphology (Schnell et al.[8]). These differences include portions of the skull associated with feeding (Perrin, 1975); the coastal form appears to be adapted to feeding on larger and more substantial prey than does the offshore form.

The southern offshore form is shorter than the northern: males, 186.6 cm versus 200.1 cm (east of 120°W); females, 185.3 cm versus 187.8 cm (east of 120°W; Perrin et al., 1985). Schnell et al. (1986) and Perrin et al.

[7] Bright, A. M., and S. J. Chivers. 1991. Post-natal growth rates: comparison of northern and southern stocks of the offshore spotted dolphin. Southwest Fisheries Science Center, National Marine Fisheries Service, NOAA, Admin. Rep. LJ-91-30, 24 p.

[8] Schnell, G. D., M. E. Douglas, and D. J. Hough. 1982. Geographic variation in morphology of spotted and spinner dolphins (*Stenella attenuata* and *S. longirostris*) from the eastern tropical Pacific. Southwest Fisheries Center, National Marine Fisheries Service, NOAA, Admin. Rep. LJ-82-15C, 213 p.

(1994) found that skulls, excluding the temporal fossa, of the southern offshore form were relatively more robust than those of the northern. Therefore, the southern animals are smaller but have relatively larger heads. The temporal fossa of the southern offshore group was most like that in the Hawaiian stock, which is also separable on the basis of skull measurements (Perrin, 1975). Samples from westerly locations differed substantially from samples from the northern and more easterly locations, which were studied in the multivariate analyses, but were similar to those from the south.

Coloration differs markedly among the various groups as well. Overall coloration in spotted dolphins follows a predictable pattern of development: no spots at birth, then dark spots first appear on the ventrum, followed by light spots on the dorsum at maturity. The ventral spots enlarge and merge until the adult is uniform gray below (Perrin, 1975). In offshore animals, those from the east are the most heavily spotted; those from the far west, the Hawaiian form, are the least—nearly unspotted as adults. An east-west or concentric cline in color patterns, and skull characteristics, may exist because the coloration of southern animals is similar to that of Hawaiian animals (Perrin, 1975). The southern offshore form has lighter spotting than the northern offshore one; it also has a distinctly contrasted dark cape and a white lateral field pattern. This pattern is similar to that in Hawaiian spotted dolphins and the far-offshore populations at the western end of the ETP distribution.

Recent work based on more extensive sampling reinforces the earlier tentative conclusions; the earlier simple notion of a north-south division of the offshore population now has been discarded (Perrin et al., 1994). Variation in skulls was examined using 26 morphometric measures and 4 tooth counts from 611 specimens. As in previous studies (Schnell et al., 1986), northern offshore spotted dolphins from the eastern portion of their range were distinct from southern animals, while animals from the northwestern portion of the range (including Hawaii) were more similar to animals from the southern portion. Specific morphotypes were significantly correlated with specific environmental parameters, which also argues for ecological segregating mechanisms. The authors suggested a concentric pattern of variation, similar to that found in the spinner dolphin (Douglas et al., 1992). Based on this analysis, they recommended altered stock boundaries to divide the offshore populations into a northeastern unit and a combined western-southern management unit, with boundaries at 120°W longitude and 5°N latitude.

Genotype

Although karyotype (Worthen[9]), isozyme (Sharp, 1975; Shimura and Numachi, 1987; Savin, 1988), and mitochondrial DNA (mtDNA; Dizon et al., 1991) studies have been done on a few spotted dolphins, they were not useful for discriminating northern and southern stocks. In general, comparative isozyme studies on cetaceans have revealed low genetic divergence for a given taxonomic level when compared to other highly mobile animals (Shimura and Numachi, 1987). The potential for effective use of karotyping and isozyme information to separate the two populations is low because there is probably some gene flow between the populations. Perhaps the application of other techniques, such as sequencing of mtDNA or nuclear DNA, which have the ability to resolve low levels of genetic variation between closely related populations, would be more likely to demonstrate differences.

Classification

The spotted dolphin is the most heavily exploited of all target species of dolphins (DeMaster et al., 1992). Quotas for the U.S. fleet have been established for all three ETP stocks. The recommendations of Perrin et al. (1985) and current management practice are fairly concordant: they emphasize that a decision regarding school identification of coastal or, the then referred to, northern offshore forms should not be based solely on geographic location. Fortunately, the coastal and northeastern stocks are reasonably easy to discriminate because of strong morphological differences. Although the stock pairs are partially sympatric, some isolating mechanism must operate to reduce gene flow between the groups. Because of the strong morphological differentiation (a proxy for presumably adaptive genetic variation), we classify the population division as IIa/c (Table 1). We use Category II because the populations are partially sympatric and use a/c because of the lack of significant geographic separation, which argues for potential gene flow, and because of morphological differences, which argues for genetic uniqueness. We use the same reasons to categorize the comparison between the coastal and western-southern offshore stocks.

The currently designated northern and southern offshore stocks have been the subject of a greater degree of controversy. Although the populations are clearly morphologically distinct based on modal differences (see Schnell et al., 1986; Perrin et al., 1994), distinguishing the two forms at sea is difficult, and schools are currently designated as northern or southern based on geographic position, i.e. either north or south of 1°S. Some disagreement has occurred because the evi-

[9] Worthen, G. L. 1981. Preliminary analysis of the potential for stock assessment of Pacific Ocean delphinids by G and C chromosome banding. Southwest Fisheries Center, National Marine Fisheries Service, NOAA, Admin. Rep. LJ-81-02C, 99 p.

dence of hiatus in distibution is based on lowered densities rather than the absence of sightings, giving the appearance of a lack of a firm boundary. However, the small amount of tagging data still suggests no movement across boundaries. The morphological evidence is compelling, and the life history data are supportive, although suspect because of problems such as sampling bias. For these reasons, we categorize this stock division as IIa/abc and strongly recommend that present management practices be retained with altered stock boundaries (Table 1, Fig. 2). The morphological similarity of animals from far south to those from far west north of the Equator argues that spotted dolphins from west of 120°W should not be grouped with those to the east but rather with those in the south. In addition, the present north-south boundary should be moved from 1°S to 5°N to better reflect the distributional hiatus and distribution of morphotypes. Current morphological data do not warrant managing southern and western offshore populations separately, but because there is some evidence of restricted movements between population centers (based on life history data), we recommend that the pooled management unit be considered provisional.

Table 1

Recommended stock structure and stock classification of pantropical spotted dolphins, *Stenella attenuata*, in the eastern tropical Pacific Ocean. Proxy data to the left of the slash argue against the existence of a population division; data to the right argue for the existence of two stocks (a = distribution, b = population response, c = phenotype, and d = genotype).

Stock	Classification of division between stocks	Stock
Coastal	IIa/c	Northeastern Offshore
Coastal	IIa/c	Western-Southern Offshore
Northeastern Offshore	IIa/abc	Western-Southern Offshore

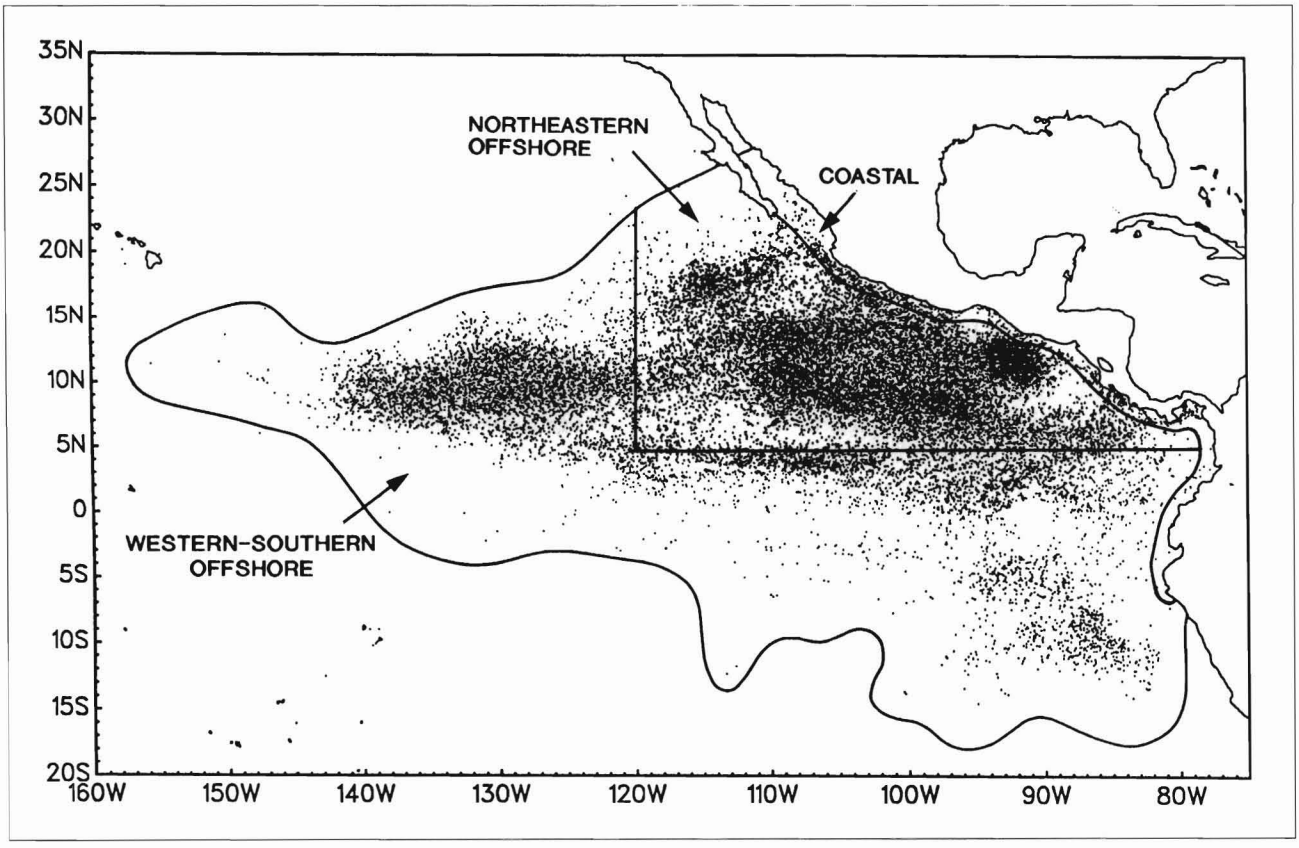

Figure 2

Recommended stock division boundaries for the pantropical spotted dolphin, *Stenella attenuata*. Note that the coastal and the northeastern offshore stocks exist in sympatry within the northern range (above 5°N) of the former, and the coastal and the western-southern offshore stocks, within the southern range (below 5°N) of the former.

Spinner Dolphin
Stenella longirostris

Current U.S. Management Situation

In the eastern and central Pacific Ocean, five stocks are recognized: Central American (also known as Costa Rican, *S. l. centroamericanus*; Perrin, 1990), eastern (*S. l. orientalis*; Perrin, 1990), northern whitebelly, southern whitebelly, and Hawaiian (also known as pantropical, *S. l. longirostris*; Perrin, 1990). Take is allowed by U.S. fishermen for northern and southern whitebelly spinner and eastern spinner dolphins (Anon., 1986). The stock division boundaries recommended for the SOPS workshop in 1983 (Perrin et al., 1985) are shown in Figure 3. It was recommended that the spinner dolphins in the ETP be assigned to stock type as follows: (1) Animals encountered south of 16°N, north of 7°N, and within 92 km (50 nmi) of the coast should be assigned to Central American or eastern stocks based on relative body length and rostral length. (2) Identification of eastern versus whitebelly forms should be based on modal color pattern and dorsal-fin shape in adult males. (3) Identification of northern and southern whitebelly forms should be based on geographic location of sightings.

Evidence of Stock Divisions

Distribution

Range — Spinner dolphins occur throughout the tropics and subtropics (Perrin and Gilpatrick, in press). They are considered pelagic, although in some areas

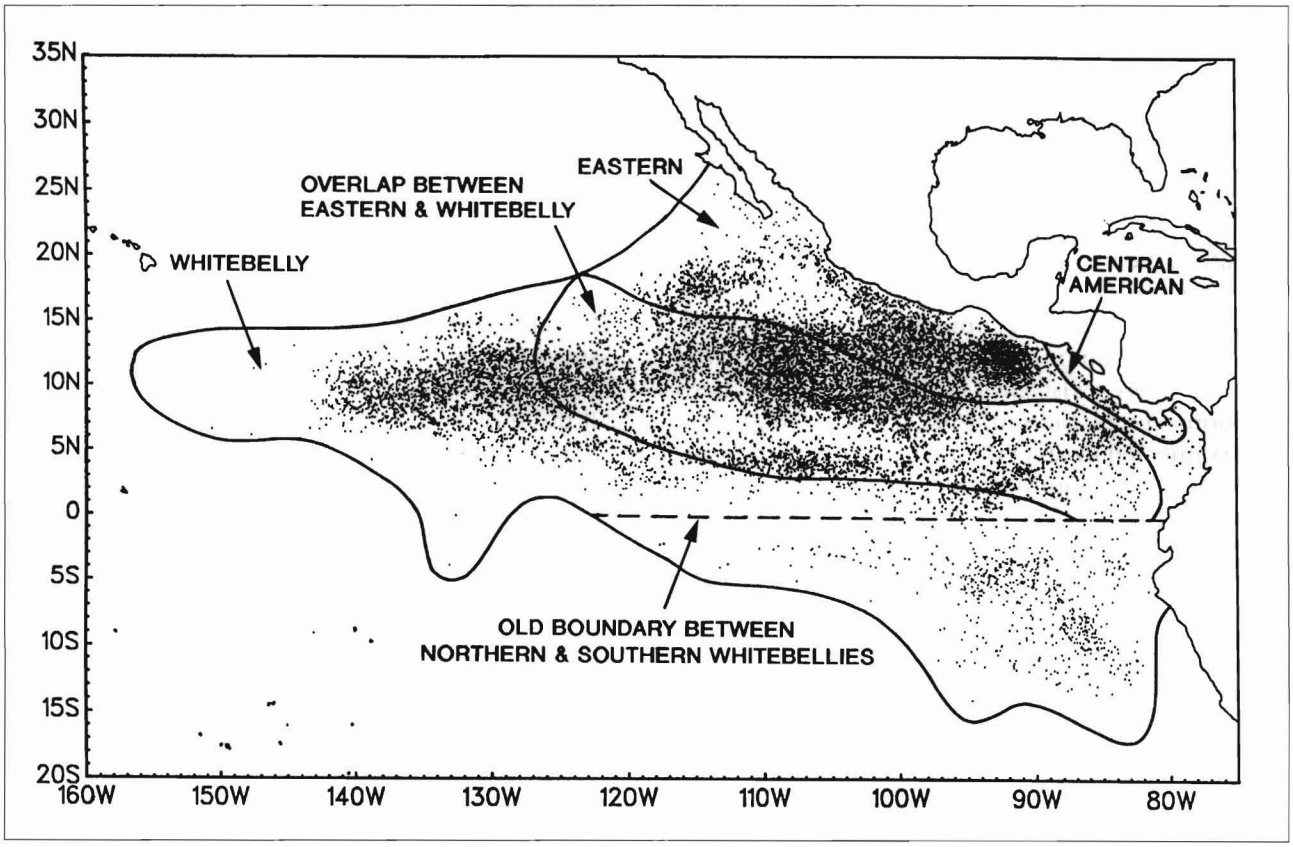

Figure 3
Distribution of the spinner dolphin, *Stenella longirostris*, in the eastern tropical Pacific Ocean based on sightings data collected between 1971 and 1991 by observers on tuna purse-seining vessels and research vessels. No boundary in the northern Gulf of California has been established. Stock boundaries are from Perrin et al. (1985), except that our current recommendation is to drop the northern and southern whitebelly stock division (dotted line) in favor of a single whitebelly spinner designation.

they are found in a neritic (Leatherwood and Reeves, 1983) or coral reef habitat (Perrin et al., 1989). Their distribution is well described only for the eastern and central Pacific (Perrin et al., 1983 and 1985), although records are slowly accumulating for the western Pacific (west of 160°W) and Indian Oceans (as well as the Red and Arabian Seas). In the western Pacific Ocean, they range north to about 35°N and south to about 20°S; in the Indian Ocean, to about 35°S along the western coast of Africa (Gilpatrick et al., 1987). In the Atlantic, spinner dolphins are distributed between 35°N and 20°S in the west and 20°N and the Equator in the east. There they are sympatric with the closely related clymene dolphin, *S. clymene* (Perrin et al., 1981).

Central American spinner and eastern spinner dolphins are likely parapatric or partially sympatric within 92 km (50 nmi) of the coastline between the Gulf of Tehuantepec and Panama. There are no confirmed records of eastern spinner dolphin much more inshore of 92 km and no records of Central American spinner dolphins much farther offshore (Perrin et al., 1985).

The known ranges of spinner dolphins in the ETP are illustrated in Figure 3. A weak distributional hiatus exists that could be used to divide the whitebelly spinner dolphins into northern and southern hemisphere stocks. The hiatus is thought to represent the preference of spinner dolphins for warm, low-saline tropical waters with intermediate-to-shallow thermocline structure, which are centered off southern Mexico and extend westward along 10°N. This type of water appears seasonally in the tropical waters south of the Galapagos Islands (Au and Perryman, 1985; Reilly, 1990). In the eastern portion of the ETP, upwelling-modified waters, favored by the common dolphins, are interposed. However, while there exist clear northern and southern population centers, the southeast centers of high density are connected by areas of low, but not zero, density. Perhaps of greater significance for separation of spinner stocks is the equatorial front that exists from 2° to 5°N and divides the ETP into two clearly defined ecosystems (Pak and Zaneveld, 1974; Reilly and Fiedler[5]).

From the hiatus in distribution, but relying more on demographic and morphological evidence, Perrin et al. (1985) divided the whitebelly spinner dolphins provisionally into northern and southern stocks. The results of recent more extensive morphological studies have reversed this, leading to a recommendation that the two putative populations be pooled into a single stock (Perrin et al., 1991). A similar distributional hiatus separates Hawaiian spinner dolphins from those in the ETP; again, this and morphological criteria led to the separation of the Hawaiian stock (Perrin et al., 1985). Subsequent work linked the Hawaiian form with a more generalized, pantropical type that is found in all of the tropical and subtropical oceans except where it is replaced in the ETP by the eastern and Central American subspecies (Perrin, 1990).

Presumed preferences for a particular habitat may also argue for separate stock status of whitebelly and eastern spinner dolphin populations. Whitebelly spinner dolphins that co-school with spotted dolphins can statistically be placed in habitats with a deeper thermocline compared to eastern spinner dolphins that also co-school with spotted dolphins (Reilly and Fiedler[5]).

Movements — Little information is available from tag returns to assess movement across the north-south stock boundary. Perrin et al. (1979a) conducted tagging experiments between 1969 and 1976: 324 spinner dolphins were tagged but only 7 were recovered by the time of the report. Minimum distances traveled ranged 22–506 km; days at liberty, from less than one day to 776 days. Hedgepeth[6] described a 1978 Rototag experiment that mostly focused on spotted dolphins, but during the experiment 16 spinner dolphins were tagged. Only one spinner dolphin was resighted (not recovered). Little can be concluded from such limited data save that spinner dolphins, compared with spotted dolphins, may disperse less. Studies of morphological variation reinforce the notion of more limited home ranges in the spinner dolphin compared with the spotted dolphin (Perrin et al., 1991; Douglas et al., 1992).

Population Response

Reproduction — Sex ratio in the eastern form was the same as in the northern and southern whitebelly forms (Perrin and Henderson, 1984; Henderson et al.[10]). In all three cases, the fraction of females was not significantly different from 0.5. However, there was a smaller proportion of reproductively active females in the eastern form (0.43) compared to the northern whitebelly form (0.53, Table 2).

Using an extensive data set that spanned 1974 to 1990, Chivers and DeMaster (in press) found that the proportion of females mature varied among the eastern, northern whitebelly, and southern whitebelly populations: 0.455, 0.556, and 0.681, respectively. However, these data are likely biased and probably not useful as a proxy for stock difference.

Initial analyses indicated that eastern spinner dolphins had lower ovulation/pregnancy rates than northern whitebelly spinner dolphins (Perrin and Henderson,

[10] Henderson, J. R., W. F. Perrin, and R. B. Miller. 1980. Rate of gross annual production in dolphin populations (*Stenella* spp. and *Delphinus delphis*) in the eastern tropical Pacific, 1973–1978. Southwest Fisheries Center, National Marine Fisheries Service, NOAA, Admin. Rep. LJ-80-02, 51 p.

Table 2
Summary of parameters for two populations of spinner dolphins, *Stenella longirostris* (from table 5 in Perrin and Henderson, 1984).

Parameters	Eastern	Northern whitebelly
Fraction ♀	0.510	0.509
Annual pregnancy rate	0.339	0.356
Fraction ♀ mature	0.432	0.533
Gross annual reproductive rate	0.075	0.094
Length-at-birth	77 cm	76 cm
Length-at-one year	132.5 cm, ♀	137.2 cm, ♀ ♂
LSM[1]	164.1 cm, ♀	175.6 cm, ♀
ASM[2]	~5 years, ♀	~6 years, ♀

[1] LSM = Length at attainment of sexual maturity.
[2] ASM = Average age of attainment of sexual maturity.

1984). Using the larger data set, Chivers and DeMaster (in press) observed that the proportion of females pregnant and lactating was higher in the eastern form, while the proportion of females resting was higher in the northern whitebelly form.

Perrin et al. (1977) reported that eastern spinner dolphins tend toward a single mode in the timing of breeding. Barlow (1984) reported that whitebelly spinner dolphins have two modes separated by about six months. However, he found regional differences in timing of breeding for the eastern form, with an earlier calving season for the more offshore animals. Gross annual reproductive rates were estimated at 0.075 for the eastern (Perrin and Henderson, 1984), 0.094 for the northern whitebelly (Perrin and Henderson, 1984), and 0.067 for the southern whitebelly (Henderson et al.[10]) forms.

Age and growth — Average length at birth was similar in both the eastern form and northern whitebelly form (Table 2); northern whitebelly calves grew somewhat faster. Although ageing and determining absolute ASM is subject to some disagreements, comparisons between stocks using these measures can be useful as long as the same methodologies were used. For instance, the ASM of eastern spinner females was about 5 years; the LSM was about 164 cm; ASM was about one year earlier than in the female northern whitebelly form, which matures at 167 cm (males at 165–170 cm) (Perrin et al., 1977; Perrin and Henderson, 1984). Chivers and DeMaster (in press), using data from 1974 to 1990, found the same LSM differences, albeit smaller in magnitude than found in the previous studies. The difference in LSM's in the two populations may reflect a density-dependent response in a recovering population versus a stable one.

Northern whitebelly males and eastern males differ markedly in morphological indices of maturity (Perrin and Henderson, 1984); whitebelly spinner dolphins have larger testes than eastern spinner dolphins. Four alternative explanations were proposed by the authors: (1) seasonal fluctuations occur, and the differences reflect seasonal bias; (2) inherent genetic differences in populations result in different reproductive morphogenesis; (3) age-specific sampling biases exist; and (4) testis size and possibly male fertility is depressed in the eastern population, conceivably because of more intense exploitation. Perrin and Henderson (1984) favored the last explanation but could not unequivocally rule out genetic differences or sampling biases. Seasonal fluctuations were eliminated as an explanation.

Phenotype

Eastern males have an average length of 176.1 cm; females, 171.3 cm (Perrin et al., 1977). Northern whitebelly males have an average length of 179.8 cm; females, 175.6 cm (Perrin et al, 1985).

Schnell et al.[8], Perrin et al. (1985 and 1991), and Douglas et al. (1992) reported significant external and internal morphological differentiation between Central American, eastern, whitebelly, and Hawaiian populations. Perrin et al. (1979b) reported modal differences in color pattern, body size, and skull measurements between geographically widely separated samples of the southern (called southwestern) form and the northern whitebelly form. In all characteristics, the values for these southern animals fell between those for the northern whitebelly form and the Hawaiian form. Akin (1988) reported significant differentiation between northern and southern forms (as well as between the eastern and whitebelly forms) in tooth morphology, which included length of tooth and other dimensions, as well as internal layering characteristics. In later work that assumed no a priori stock or subspecies stratifications, Douglas et al. (1992), besides finding that skull measurements discriminated subspecies, found that many of the characteristics of the Hawaiian, or pantropical, form were more similar to those of the extreme southern samples than to those samples from adjacent regions to the east. This supported the Perrin et al. (1991) observation of a radial pattern of variation, in which animals from the far west, southwest, and south differed markedly from those to the northeast. Variation in color pattern, dorsal-fin shape, and total body length were graded steeply in the north-south direction at about 10°N and 125°W (Perrin et al., 1991). Outside this boundary, complex and geographically

discordant variation as well as higher standard deviations of body length existed. This discordant variation, suggestive of contact and partial interbreeding, and the radial nature of the variation within the ETP, has prompted the suggestion that the whitebelly stock is, in reality, a hybrid swarm bridging the eastern and Hawaiian, or pantropical, subspecies (Perrin, 1990; Perrin et al., 1991) and that the management of this form as southern and northern populations is not justified on morphological grounds alone (Perrin et al., 1991).

Genotype

Allozyme studies on eastern and whitebelly populations did not detect population differences (Sharp, 1981; Landino, 1987). Dizon et al. (1991), employing a restriction fragment (RFLP) analysis using six different restriction enzymes, found a unique mtDNA haplotype in the Timor Sea off northern Australia, distinguishing the specimens there from ETP spinner dolphins. However, the two morphologically distinct ETP spinner dolphins (whitebelly and eastern) were not genetically distinct at the level of resolution of the analysis (Dizon et al., 1991). The mtDNA homogeneity of whitebelly and eastern samples suggests a degree of genetic exchange or mtDNA introgression and supports the hypothesis of Perrin et al. (1991) that the whitebelly spinner is a hybrid/intergrade.

Classification

Quotas have been established based on the existence of more-or-less discrete stocks separated into latitudinal bands (Anon., 1986). Current management practice and the recommendations of Perrin et al. (1985) are reasonably concordant.

Perrin (1990) has proposed the Central American, eastern, and pantropical forms for separate subspecies status, and there has been general agreement that these populations be considered separate for assessment and management. We categorize the parapatric Central American versus eastern or whitebelly division as IIa/c (Table 3). Category II is chosen because of the strong reliance we place on morphological data as a proxy for adaptive genetic divergence. For the Central American versus pantropical division, allopatry elevates the classification to Category I.

The whitebelly and eastern stock division is problematic. Recent work by Perrin et al. (1991) argues that the whitebelly form is a hybrid swarm between the eastern form and the pantropical subspecies. In that case, stock divisions between the whitebelly and eastern forms or the whitebelly and pantropical forms are somewhat artificial; a more meaningful division would be between the eastern and pantropical forms. Hybridization probably occurs between virtually all intraspecific parapatric populations. The pantropical-whitebelly-eastern situation represents an extreme because of the large number of hybrid individuals and the broad zone of hybridization. Under the hybrid swarm hypothesis, we categorized the eastern-pantropical division as I/abc (Table 3). We judged the population division to be Category I because of the relative distance between the two groups, although the whitebelly hybrids may provide an avenue for gene flow.

Given the problematic status of the whitebelly form, it makes little sense to attempt to divide the group into two forms. Morphological studies show a lack of geographically concordant variation within the group, although some demographic indices differ. The lack of clear geographic concordance, absence of mtDNA difference, weak evidence of a distributional hiatus, and presence of demographic evidence (albeit potentially biased) would lead us to categorize the stock division as IVacd/ab. We see little reason to manage the northern and southern areas as separate units, and hence the division is absent from Table 3. We also recommend management of the pooled whitebelly forms as a separate stock, despite their hybrid/intergrade status. There is a danger that heavier exploitation of the eastern form may potentiate unsymmetrical gene flow from the numerically vast pantropical populations to the west via the whitebelly populations, perhaps swamping out the eastern genotype. Perrin et al. (1991) proposed a conservation zone for the eastern spinner that would facilitate management and protection of the subspecies.

Table 3

Recommended stock structure and stock classification of spinner dolphins, *Stenella longirostris*, in the eastern tropical Pacific Ocean. Proxy data to the left of the slash argue against the existence of a population division; data to the right argue for the existence of two stocks (a = distribution, b = population response, c = phenotype, and d = genotype).

Stock	Classification of division between stocks	Stock
Central American	IIa/c	Eastern
Central American	IIa/c	Whitebelly
Central American	I/ac	Pantropical
Eastern	see text	Whitebelly
Eastern	I/abc	Pantropical

Common Dolphin
Delphinus delphis

Current U.S. Management Situation

Despite the recommendations of Perrin et al. (1985), current management practice uses five units in the eastern and central Pacific Ocean: northern temperate, northern tropical, central tropical, southern tropical, and southern temperate. U.S. quotas are established for the tropical units (Anon., 1986). The Baja neritic or long-beaked form, a morphologically distinct coastal population, is managed with the northern tropical population, despite the recommendations of the SOPS meetings in 1983 (Perrin et al., 1985). At that meeting, it was recommended that common dolphins in the ETP be assigned to stocks as follows (Fig. 4; see also Holt and Powers, 1982; Smith, 1983): (1) Within 184 km (100 nmi) of the Pacific coast of southern California and Baja California, as well as in the Gulf of California, long-beaked and northern forms should be distinguished based on modal length, coloration, and relative rostral length. (2) The temperate units should be combined with the adjacent tropical ones, and these new units (northern, central, and southern) distinguished based on distribution.

Evidence of Stock Divisions

Distribution

Range — Common dolphins are distributed worldwide in temperate, tropical, and subtropical waters in both coastal and offshore areas (Evans, 1982). In the eastern Pacific, they range from 36°N, including the Gulf of California (Evans, 1982), to at least 13°S (Fig. 4). Both the northern and the long-beaked forms are sympatric from the coast to perhaps 184 km (100 nmi) offshore

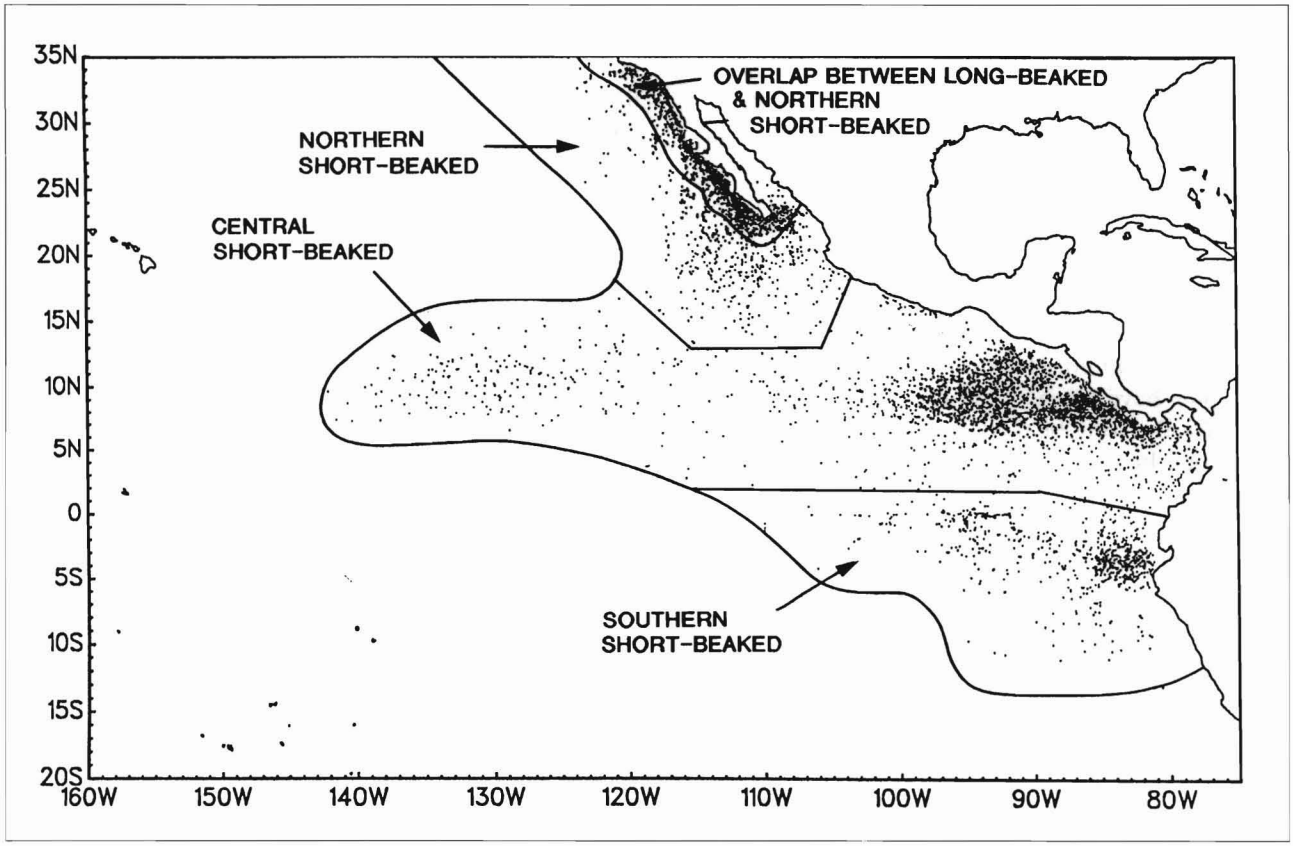

Figure 4
Distribution and boundaries of the stocks of the common dolphin, *Delphinus delphis*, in the eastern tropical Pacific Ocean based on sightings data collected between 1971 and 1991 by observers on tuna purse-seining vessels and research vessels. Stock boundaries are from Perrin et al. (1985).

(Perrin et al., 1985). Because of this, an "offshore" appellation is inappropriate, and Heyning and Perrin (in press) suggested that "short-beaked" be used for all of the offshore stocks (northern, central, and southern) and, for consistency, that "long-beaked" instead of "Baja neritic" be used for the inshore form.

The long-beaked common dolphin occurs within 184 km (100 nmi) of the Pacific coast of Baja California and southern California and in the Gulf of California (Perrin et al., 1985). As mentioned above, there is no geographic separation between the long-beaked and northern forms. The range of the former is completely contained within that of the latter, so these populations must be distinguished based on morphology and not on the basis of distance from shore alone. The hiatus at 13–20°N and another at about 3°N is used to divide the offshore populations into northern, central, and southern stocks (Fig. 4). The central form occurs at 3–18°N (Evans, 1982; Perrin et al., 1985). Based on lowered density at 105–120°W, it was proposed that this stock be divided into two, an eastern and western one (Au et al.[11]). This proposal was never accepted for lack of adequate data (Perrin et al., 1985; Smith[3]). The southern common dolphin is found from 3°N to at least 13°S. Based on 1986–90 research vessel cruises, a region of low density separates the central and southern populations. However, some sightings have shown animals in the area of low density (Perrin et al., 1983), and there are no clearly definable habitat differences isolating the population center areas (Reilly and Fiedler[5]).

Morphologically distinct common dolphins may be found off southern Mexico at about 15°N (Evans, 1982), the so-called Guerrero stock. Perrin et al. (1985) considered them "marginally justified" as a separate stock based on their larger sizes but recommended that more specimens be examined. However, since then no additional samples have been obtained. It is conceivable that these are the long-beaked form, which would extend the range beyond the Baja California coast. It is also possible that this form inhabits all coastal waters in the eastern Pacific from California to Peru.

Movements — During tagging studies conducted from 1969 to 1976, 193 common dolphins were tagged, probably all of the northern form, but none were recovered or resighted. However, information from radiotelemetry studies indicates that common dolphins are quite mobile (Evans, 1971, 1974, and 1982; Perrin et al., 1979a). Net movements of 1.4–5.84 km/hr (0.77–3.20 nmi/hr) were recorded. Although no evidence is available for common dolphins crossing the putative stock boundaries, the potential vagility of this species suggests that the development and maintenance of population differences involves more than simple isolation by distance. Evans' studies (1971, 1974, and 1982) showed that the movements of common dolphins in the ETP were correlated with stable physiographic features (e.g. banks and seamounts) suggesting a knowledge by the dolphins of a home range. He suggested that this, coupled with his observation of subtle morphological differences between schools, argued for a degree of site fidelity and lack of long-range movements; this view is not generally accepted by other workers.

Population Response

Reproduction — Evans (1975) found differences in the timing of reproduction between northern and central stock areas but did not have sufficient data to define patterns in either area. The proportion of females that were neither pregnant nor lactating was higher in the central population. Recently, Perryman and Lynn (1993) used aerial photogrammetry techniques to measure body lengths of calves in herds of common dolphins. Assuming linear growth in the first year, back calculating from current body length gives approximate birth dates. Preliminary results showed monthly birthrates to be bimodal, peaking in spring and early summer, for both the northern and southern forms; while for the central form births seem to be fairly evenly distributed throughout the year.

Chivers and DeMaster (in press) examined life history parameters estimated from data collected between 1974 and 1980. No significant differences in the proportion of mature females in various reproductive states (i.e. pregnant, lactating, resting, and simultaneously pregnant and lactating) were found between the three short-beaked and one long-beaked populations. However, there were significant differences among the stocks in proportion mature. They also noted a predictable difference (under a density-compensatory model) in temporal trends of reproductive parameters in the pooled short-beaked populations and the long-beaked population.

Other — Walker and Cowan[12] studied parasites as indicators of population groups in common dolphins in the ETP and found the nematode *Crassicauda* sp. in 34.9% of the central specimens but none in the long-

[11] Au, D. W. K., W. L. Perryman, and W. F. Perrin. 1979. Dolphin distribution and the relationship to environmental features in the eastern tropical Pacific. Southwest Fisheries Center, National Marine Fisheries Service, NOAA, Admin. Rep. LJ-79-43, 59 p.

[12] Walker, W., and D. F. Cowan. 1981. Air sinus parasitism and pathology in free-ranging common dolphins (*Delphinus delphis*) in the eastern tropical Pacific. Southwest Fisheries Center, National Marine Fisheries Service, NOAA, Admin. Rep. LJ-81-23C, 19 p.

beaked or northern ones. The opposite pattern was found for *Nasitrema* sp. infections.

Phenotype

Based on morphological evidence from examination of small series of specimens, over two dozen nominal species have been put forth for the genus world-wide, although, in general, authorities recognize one or two species (Heyning and Perrin, in press). Banks and Brownell (1969) examined a fairly lengthy series and concluded that two sympatric species existed in the northeast Pacific: the long-beaked common dolphin, *Delphinus bairdii*, and the short-beaked nominate, *D. delphis*. They found no indication of overlap in the two forms in the ratio of zygomatic width to rostrum length. After examining 70 specimens from widely divergent locations, van Bree and Purves (1972) disagreed, claiming intergrades existed in specimens collected outside of the study area of Banks and Brownell (1969). They suggested that interschool variation was responsible for the clear separation demonstrated previously. Current work seems to have resolved the argument, in so far as concerns the animals in the northeastern Pacific. Heyning and Perrin (in press) have obtained results consistent with a hypothesis of separate species. Reexamination of 318 specimens, for which complete information on sex and age existed, allowed examination of variation between and within the forms stratified by sex and age class. In adults, color pattern, total length, and all measures of rostral length separated the two forms. The species-level taxonomic question must await morphological studies of series from other areas.

In addition to distributional hiatuses and evidence of differential breeding seasons, the northern, central, and southern populations can be discriminated on the basis of total length of adult animals. Evans (1982) separated the northern into two stocks, one off southern California (the so-called northern temperate stock) and one off Baja (the northern tropical stock) based on total length and various cranial features; this stock division corresponded to his finding of a hiatus in distribution. However, this division was abandoned after further work (Perrin et al., 1985). Evans (1982) also found a size difference between adults of northern populations and those further south, which he called the "southern short-beaked form." That difference has been supported by further study (Perrin et al., 1985; Perryman and Lynn, 1993). The form, now called the central form, is significantly larger than the northern one (Perrin et al., 1985; females, 194.3 versus 178.5 cm, respectively; males, 206.8 versus 189.3 cm, respectively). The differences obtained by Perrin et al. (1985) were confirmed using measurements from aerial photographic images (Perryman and Lynn, 1993).

Less is known about differentiation of the central and southern populations. Perrin et al. (1985) reported the sizes of six adult southern females that constituted the entire sample set through 1983. Including data through the present only adds individuals from one additional school, which were collected from about the same location as the Perrin et al. (1985) samples. The averages of the data sets are 190.4 cm (sd=5.3, n=16) for females and 192.8 cm (sd=6.6, n=5) for males. These averages can be contrasted with an aerial photographic average of 184.3 cm (sd=6.8, n=20) for southern females with calves (Perryman and Lynn, 1993) and the Perrin et al. (1985) average of 194.3 cm for central and 178.5 cm for northern females.

Although it is tempting to use size differences to establish the existence of two, three, or four separate stocks in the central and southern areas, caution is necessary because data from the far-west region of the central population and the southern populations are based mostly on information from single schools. Evans (1982) asserted that schools within only 73.6 km (40 nmi) of each other differed in color patterns and skull measurements.

Genotype

Evans (1975) suggested that local subpopulations represent single, limited gene pools because certain elements of the color pattern, such as white blazing in the dorsal fin, serve as a herd identification character and possibly an isolating mechanism. Amos (1988) used DNA fingerprinting to examine its potential to differentiate stocks. He found high variability between two common dolphins whose stock origins, however, were not specified.

Recently Rosel (1992) sequenced the PCR-amplified control loop region (D-loop) and the cytochrome b gene of mtDNA in an attempt to differentiate samples of short-beaked and long-beaked common dolphins. The northern and long-beaked samples came from some of the same specimens employed by Heyning and Perrin (in press). In approximately 750 bp sequenced, fixed and significant frequency differences segregated the long-beaked samples from the offshore ones. Of particular significance was the discovery of differences in the cytochrome b gene that resulted in an amino acid substitution in the protein. Because the cytochrome b gene evolves more slowly than the control region, these differences are evidence of a long genetic separation consistent with the status of separate, albeit closely related, species.

Mitochondrial DNA sequence analysis failed to discriminate northern and central forms, although only six central specimens were sequenced and available for

analysis. Clear differences, however, were apparent between the Pacific short-beaked forms and four dolphins from the Black Sea. Interestingly, the genetic distance between the Pacific short-beaked forms and the Black Sea form was smaller than the genetic distance between the Pacific short-beaked forms and the sympatric long-beaked form.

Classification

Although the common dolphin is not as heavily exploited as spotted and spinner dolphins, U.S. mortality quotas have been set for the three offshore stocks. Over the years, management has pooled the northern and long-beaked forms. Clearly this is a problem, because stock status is hardly in question. Obviously the two forms should be assessed and managed separately because they show species-level separation in the eastern Pacific. No categorization is given in Table 4; the classification scheme notation is inappropriate for species-level comparisons because proxy information is unnecessary when one assumes no meaningful gene flow and significant genetic distinctiveness. In addition, the possibly morphologically distinct common dolphin, the Guerrero stock found off southern Mexico at about 15°N, which Perrin et al. (1985) recommended be provisionally considered a separate stock, must still be considered provisional because of lack of data.

The northern-central-southern divisions are conceptually straightforward. Because common dolphins prefer waters modified by upwelling, the hiatus between the northern and central stocks is fairly clear. Allopatric distribution coupled with significant size and breeding seasonality differences, supported by differences in proportion of mature females, suggest categorization of the northern-central division as IIId/abc (Table 4). Genetic information is available, albeit based on a small sample of central forms.

Table 4
Recommended stock structure and stock classification of short-beaked comon dolphins, *Delphinus delphis*, in the eastern tropical Pacific Ocean. Proxy data to the left of the slash argue against the existence of a population division; data to the right argue for the existence of two stocks (a = distribution, b = population response, c = phenotype, and d = genotype).

Stock	Classification of division between stocks	Stock
Northern	IIId/abc	Central
Central	IIIac/abc	Southern

The southern-central division is clouded by the paucity of samples and some concern over the existence of an "inshore corridor" allowing the exchange of individuals between the two regions. In addition, there is the equivocal evidence from size measurements of animals sampled near the Galapagos. Their size range places them in an intermediate position between the far offshore southern animals measured by Perryman and Lynn (1993) in an aerial photographic study. We categorized the division as IIIac/abc.

Striped Dolphin
Stenella coeruleoalba

Current U.S. Management Situation

In the eastern and central Pacific ocean, current U.S. management units include northern temperate, northern tropical, central tropical, southern tropical, and southern temperate stocks. U.S. quotas have been established for the three tropical populations (Anon., 1986). This management scheme is in conflict with that recommended by Perrin et al. (1985), who recommended that striped dolphins in the eastern Pacific be assigned to either the northern or southern stock, depending on geographic location (Fig. 5).

Evidence of Stock Divisions

Distribution

Range — The striped dolphin is widely distributed in tropical, subtropical, and temperate oceans of the world. It occurs in the Atlantic, Pacific, and Indian Oceans and in the Mediterranean and Red Seas (Perrin et al., in press). Because the hiatus in distribution between 10°N and 15°N may inhibit direct interchange between the north and south, Perrin et al. (1985) suggested a single provisional division into northern and southern stocks, pending the examination of existing osteological material.

Movements — No tagging-recapture studies have been conducted on striped dolphins, and nothing is known about their movements in the ETP. However, this species is known to be highly migratory in the western Pacific (Miyazaki et al., 1974).

Population Response

Chivers and DeMaster (in press) estimated life history parameters from data collected between 1974 and 1979

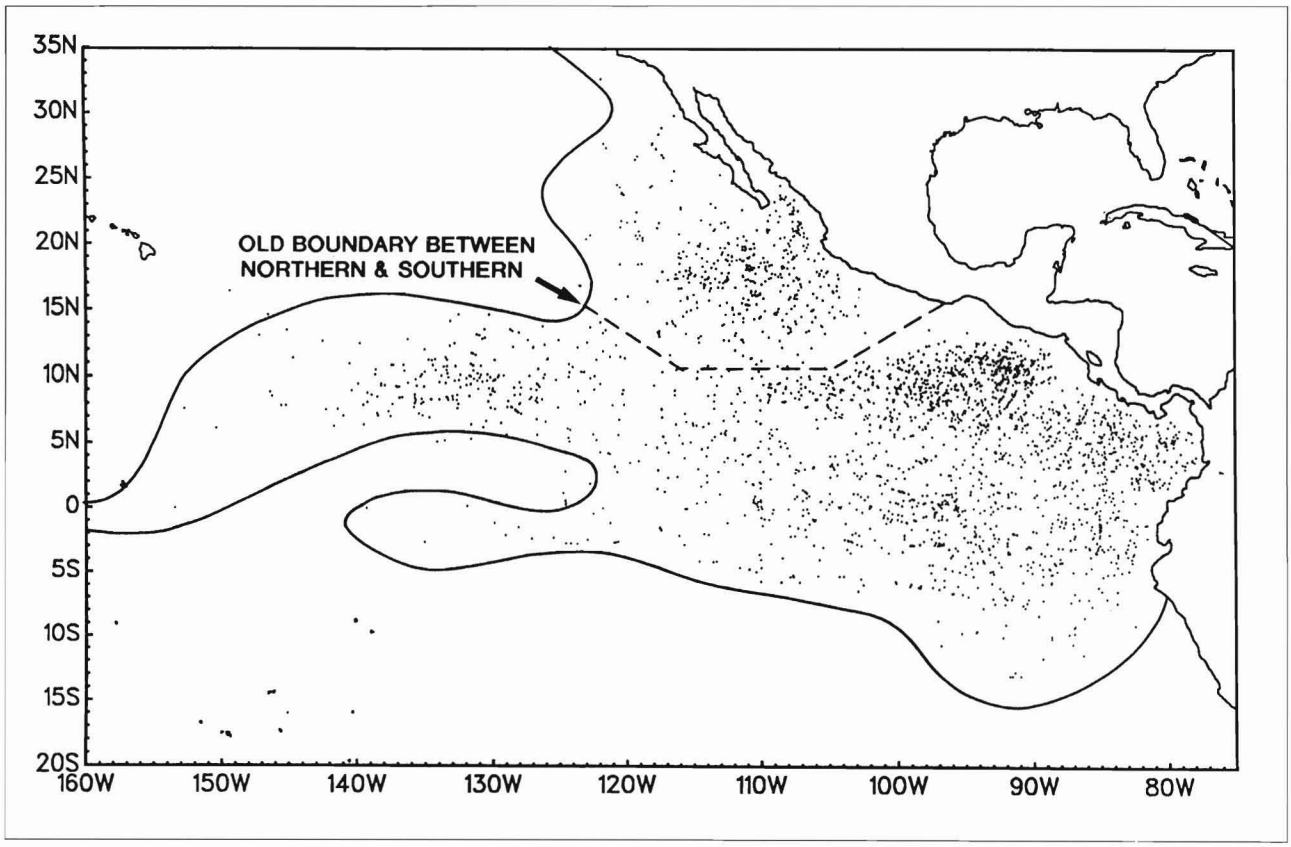

Figure 5
Distribution and stock boundaries of the striped dolphin, *Stenella coeruleoalba*, in the eastern tropical Pacific Ocean—sightings data collected between 1971 and 1991 by observers on tuna purse-seining vessels and research vessels. No boundary in the northern Gulf of California has been established. We recommend that the northern and southern division (dotted line) be dropped in favor of a single stock.

and detected no significant differences between north and south in mean proportions of mature females in various reproductive conditions. However, the comparison was based on only 21 mature females from the northern stock and 25 from the southern stock and must be viewed with caution.

Phenotype

Gurevich and Stewart[13] estimated maximum body length at 220 cm in females and 225 cm in males from a sample of 70 pooled from both the northern and southern populations. Perrin et al. (1985) reported mean lengths from 9 northern and 10 central males and 21 northern and 22 central females; the means were not significantly different between regions. More data are currently being made available from aerial photographs. Using the Perrin et al. (1985) stock boundaries (Fig. 5), no significant differences in average size of individuals (n=197, northern; n=608, southern) or in average size of females with calves (n=19, northern; n=66, southern) were found (Perryman and Lynn, 1994). Additional studies of the morphology of the skull and postcranial skeleton are underway (Archer[14]).

Genotype

Electrophoretic heterozygosity at specific loci was tested in Japanese striped dolphins by Wada (1983), who found less genetic variability (average heterozygosity = 0.021 at 15 loci tested) than for 48 other mammalian species. He attributed this to either population subdivision or inbreeding over long periods of time. The first genetic work on striped dolphin in the eastern Pacific is underway (Archer[14]).

Classification

The most recent distribution data show several apparent foci of abundance and little discontinuity (Fig. 5). Because the length-frequency data comparing northern and southern samples show no difference, because the distributional gap separating the northern and southern population centers is very small, and because the species is known to be highly migratory in other regions, we classify the division as Category IVac/a and recommend that all striped dolphins in the eastern Pacific be provisionally managed as a single unit. The results of ongoing studies of geographic variation in morphology and mtDNA may require reconsideration of this classification. Because the demographic data were based on very small samples of specimens, we have chosen to exclude the data as evidence for lumping the two populations, so a "b" does not appear to the left of the slash.

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