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Patterns of geographical variation in small cetaceans

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Morphological data that have become available in recent years show that small cetaceans vary sharply over sometimes relatively short distances. Species for which such data are reviewed include *Stenella attenuata, S. longirostris, Delphinus delphis*, and *Tursiops truncatus*. Two major patterns are variation between animals in enclosed vs. open seas and in offshore vs. inshore waters. An hypothesis of ecological character displacement is proposed to account for differentiation of races of *S. longirostris* in the central and eastern Pacific. Prevalence of pronounced geographical variation must reflect relatively high localization of populations and suggests that great care should be taken in the exploitation of small cetaceans to insure that the population unit has been adequately defined. Harvest quotas taken in limited areas but based on supposed existence of larger-scale populations could lead to local depletion if the population units are more circumscribed than thought.

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1. Introduction

Man exploits small cetaceans heavily. The estimated annual take exceeds 100 000 dolphins, porpoises and small whales (Perrin 1982). In recent years, considerable effort has been given to managing the impacted populations of small cetaceans on a scientific basis (Fox 1978, Scientific Committee, IWC 1976—1981). A major first step in this management is to define the populations involved. One tool for defining mammal populations is the analysis of geographical variation in morphology. Close study of adequate material, as in the case of the eastern Pacific (Perrin 1975a, 1975b, Perrin et al. 1979) and elsewhere, has revealed existence of sharply defined variation over relatively small distances in pelagic dolphins, and this has been reflected in scientific advice for management (Smith 1979). The purpose of this paper is to review apparent patterns in geographical variation and to briefly discuss implications for management and for taxonomy.

2. Patterns of variation

2.1. Enclosed seas vs. the open ocean

Dolphins in enclosed or semi-enclosed seas tend to be smaller than those of the same species in the open ocean. The most noted example of this "dwarfism" is in populations of the common dolphin, *Delphinus delphis*, and bottlenose dolphin, *Tursiops truncatus*, in the Black Sea, as described by Kleinenberg (1956). Common dolphins in the Black Sea are on the average 30—40 cm smaller than common dolphins in the eastern North Atlantic (Table 1). Although the samples are small, it appears that common dolphins in the Mediterranean, a larger but also enclosed sea, may be intermediate in size between those in the Black Sea and in the eastern North Atlantic.

Maximum-length data for the bottlenose dolphin from the three regions indicate that it follows the same pattern as the common dolphin, i.e., small animals in the Black Sea, large animals in the eastern North Atlantic, and animals of intermediate size in the Mediterranean (Table 2).

2.2. Inshore vs. offshore

This is the largest category of known cases of geographical variation. I will discuss examples of this type of variation in dolphins of the genera *Stenella, Delphinus* and *Tursiops*.

The pantropical spotted dolphin, *Stenella attenuata*, and the spinner dolphin, *S. longirostris*, each occur in several geographical races in the eastern and central tropical Pacific (Perrin 1975a, 1975b, Perrin et al. 1979, Smith 1979). There are two major forms of *S. attenuata* in the eastern Pacific, a relatively large, heavily spotted coastal form with massive jaw musculature and large teeth and a relatively small, less spotted offshore form with more lightly constructed skull and jaw musculature and smaller teeth. These two forms have been called *S. graffmani* (Lonnberg 1934) and *S. attenuata* (Gray 1846), respectively, in the past, but studies of large series of specimens have shown them to intergrade (Perrin 1975a).

Moving north in the eastern Pacific to temporate waters the common dolphin, *Delphinus delphis*, and bottlenose dolphin, *Tursiops truncatus*, exhibit inshore/offshore variation similar to that of the tropical *Stenella* spp. Banks & Brownell (1969) reviewed *Delphinus* in the eastern North Pacific. They referred a short-beaked form to *D. delphis* and a long-beaked form to *D. bairdii*. Evans (1975), however, found intergradation between the two forms and assigned them both to *D. delphis*. In subsequent assessment and management advice, these have been called the "Baja neritic common dolphin" and the "northern temperate common dolphin"

Table 1. Body-length data, in cm, for common dolphins, *Delphinus delphis*, from three different regions. (Sources summarized in W.F. Perrin & S.B. Reilly, MS). Sample sizes in parentheses.

	Average length of adults		Maximum length	
	Males	Females	Males	Females
Eastern North Atlantic	218 cm (17)	203 (26)	258 (168)	230 (169)
Black Sea	—	171 (198)	219 (> 20000)	200 (> 20000)
Mediterranean	—	—	222 (35)	222 (35)

Table 2. Maximum body length of bottlenose dolphins, *Tursiops truncatus*, from three different regions. Sample sizes in parentheses (Sources summarized in W.F. Perrin & S.B. Reilly, MS).

Region	Males	Females
Eastern N. Atlantic	381 (67)	350 (47)
Black Sea	310 (> 500)	< 310 (> 500)
Mediterranean	330 (14)	320 (6)

(Smith 1979). The inshore Baja neritic form differs from the more offshore northern temperate form in several features. As well as having a proportionately longer rostrum, it is longer overall, ranging in males to over 240 cm and in females to over 220 cm (Hui 1977) as opposed to 200 cm and 190 cm (Evans 1975). The two forms also differ modally in coloration; the overall pattern is much less sharply defined, and the thoracic patch (terminology of Mitchell 1970) is noticeably less yellowish in the inshore form. In addition, the anterior end of the flipper stripe (terminology of Perrin 1969) abuts on the gape mark considerably more posteriorly than in the offshore form. The skull also differs in size and shape in the two forms (Evans 1975).

Similar inshore/offshore variation may exist in *Delphinus* elsewhere. The extremely long-beaked common dolphins that occur in the Indian Ocean and in the South China Sea and which have been referred to the nominal species *D. tropicalis* (van Bree 1971, Zhou et al. 1980) may be inshore animals; the body lengths reported (to 229 cm, Blanford 1881) lie above the ranges of lengths reported for other, larger samples of common dolphins from similar latitudes in the western Indo-Pacific (Tomilin 1957, Ogawa 1936).

Inshore and offshore populations of *Tursiops* in the eastern North Pacific also differ modally, in skull size and shape, tooth size, and possibly in adult body length (Walker 1981). The inshore form has the larger teeth, as in *S. attenuata*. These bottlenose dolphins have been referred to varying permutations of *T. truncatus*, *T. gilli* and *T. nuuanu*. Most workers today favor a single species, *T. truncatus*. Another example of inshore/offshore variation in *Tursiops* exists along the southeast coast of South Africa; in this case the inshore from (referred to *T. aduncus*) is the smaller and the offshore form (referred to *T. truncatus*) is the larger (Ross 1979). A similar situation may exist along the western North Atlantic, although the large offshore animal has not yet been well studied because of the scarcity of material (pers. comm. James G. Mead, U.S. National Mus. Nat. Hist., Washington, D.C.).

The morphological difference between inshore and offshore races of the various dolphins, especially in the number and size of teeth and in the robustness of jaw musculature, may be related to feeding ecology, perhaps to differing size and toughness of major prey species (Perrin 1975a, Ross 1979).

2.3. Other patterns

Modal differences in body shape and coloration between spinner dolphins, *Stenella longirostris*, in the far eastern Pacific and those in the Central Pacific and around the world in tropical waters are extreme (Perrin 1972, 1975a, 1975b). The spinner dolphins in the far eastern Pacific (the "Costa Rican" and "eastern" forms; see Smith 1979 for ranges) are unique in being nearly uniformly dark gray (as opposed to having a three-part dark-gray, light-gray and white pattern as do spinner dolphins to the west and in other parts of the world) and, in large males, in having the dorsal fin canted forward to varying degree (with correlated development of a ventral post anal "hump" of connective tissue). Spinner dolphins from the regions between the Central Pacific and the far eastern Pacific are intermediate, strong grounds for including all the forms in the single species *S. longirostris*, but the interesting question remains of why the spinners in the far eastern Pacific are so different. I put forward here an hypothesis of *ecological character displacement*. The relevant information concerns morphology, ecology, behavior (Table 2) and oceanography. The hypothesis is suggested by two facts: 1) while both spinner and spotted dophins outside the eastern tropical Pacific are limited in distribution to waters near continents and islands, where they school separately and feed on similar prey, the spinner dolphin is unusual in that it migrates diurnally between offshore feeding grounds and relatively protected bays, where it spends most of day in a quiescent resting state, presumably relying on the shallow bottom and the shoreline for protection from predators (Norris & Dohl 1980), and 2) the far-eastern Pacific is peculiar in having a relatively thin warm mixed layer (< 50 m thick) below which are a stable steep thermocline and a thick oxygen-minimum layer, establishing an effective shallow habitat much like the nearshore habitat in other tropical waters (Perrin et al. 1976).

The hypothetical scenario of ecological character displacement is as follows: habitat in most of the world for the spinner dolphin is defined by availability of shoreline near suitable food supplies (within range of diurnal migration and not too deep), but habitat for the spotted dolphin is determined only by availability of food within efficient diving range (near continents and islands). In the far-eastern Pacific, because of its peculiar vertical structure that creates a shallow mixed-layer habitat with sharply-defined floor, both animals can "make a living" far from land on the high seas. The spinner dolphins, however, must have a surrogate "shoreline" for shelter during their daytime quiescent period. They use schools of spotted dolphins for this, staying with them even when not feeding (first suggested by Norris & Dohl 1980). In the course of the move into the far-offshore habitat and evolution of the mixed-species association, direct competition for prey by the two species has been minimized by specializations in feeding habits that are reflected in morphological divergence in morphology, the spinner dolphin becoming more adapted to smaller, deep-living prey (hence the more

Table 3. Comparison of morphology (Perrin 1972, 1975a, 1975b), ecology and behavior (Perrin et al. 1973) of *Stenella longirostris* and *S. attenuata* in the Central Pacific with those in the far-eastern Pacific.

	Central Pacific	Far-eastern Pacific
Morphology		
Coloration	Similar (countershaded)	Different (unifrom vs. countershaded)
Body size	Similar (~ 200 cm)	Different (~ 170 vs. ~ 200 cm)
Body shape	Similar	Different (dorsal-fin cant & ventral hump)
Skull size	Similar	Different
Temporal fossa	Similar size & shape	Different
Ecology & behavior		
Feeding habits	Similar (mostly mesopelagic spp.), but few data	Different (mostly smaller, mesopelagic spp. vs. larger, epipelagic spp).
Schooling	School separately	School together
Diurnal migration	Different (inshore migration vs. none)	Same (none)

lightly built feeding apparatus and the loss of counter shading) and the spotted dolphin becoming more adapted to larger, surface-living prey.

Other hypotheses to explain the morphological variation are possible, but this exercise does demonstrate the complexity of factors possibly affecting population structure and points up the importance of considering the full range of oceanographic information (beyond merely single variables, e.g., surface temperature) when attempting to define the habitats and ranges of breeding populations.

3. Conclusions

The findings on geographical variation have had an effect on the taxonomy of the small cetaceans. We have relegated many species to junior synonymy in recent years. This is continuing. For example, Ross (1979) has recently found intergradation between the currently recognized species of humpbacked dolphins, *Sousa chinensis* and *S. teuszii*, in South Africa. As more material accumulates, we may find similar intergradation between nominal species of *Delphinus, Tursiops, Lagenorhynchus, Cephalorhynchus, Mesoplodon* and perhaps other genera.

It would seem that pronounced geographical variation (and the inferred reproductive isolation) is found to exist in small cetaceans in each instance of study of adequate samples of specimens. The import of this for exploitation and management of small detaceans is clear. It cannot be assumed that animals inhabiting adjacent seas, oceans, or even parts of oceans belong to a single population. Definition of management units should be based on knowledge of geographical variation in morphology and autecology and, beyond that, should take into consideration the likely populational divisions predicted by our knowledge of patterns of geographical variation and by knowledge of definable marine habitats and systems.

In summary, then, in the future there will likely be fewer recognized species of small cetaceans, but there will be many more recognized breeding populations that may require assessment and management as separate units.

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