Why are there so many kinds of whales and dolphins?

Although the cetaceans are a small group, compared with, say, beetles (thought to have millions of species) or even with some other mammalian orders, such as the rodents (with 1700 species), they include 75–80 species and are extremely diverse morphologically. They range from the generalized dolphins, such as the bottlenose dolphin, *Tursiops truncatus*, to highly derived forms such as the right whale dolphin, *Lissodelphis borealis*, which has no dorsal fin; from river dolphins weighing 20 or 30 kg to leviathans such as the sperm whale, *Physeter macrocephalus*, weighing more than 100,000 kg.

Even 75 species seems to be a lot for such mobile animals. After all, the oceans are continuous. Some dolphins have been recorded as traveling as much as 50–100 km per day. And we know that many whales and dolphins, like other large marine animals such as tunas and sharks, are almost worldwide in distribution. Some of these species are closely related to each other. How did they arise?

One model of speciation in isolation has to do with past climate fluctuations during which cold water may have pinched off the tropical Atlantic one or more times. At present, warm-temperate water flows around the Cape of Good Hope from east to west during the austral summer. This flow provides communication between the tropical Indo-Pacific and the tropical Atlantic. During the austral winter, water around the cape is too cold for tropical cetaceans, as it probably was during the Pleistocene or earlier cold periods. The Cape of Good Hope was probably embedded in very cold water year round. This cold water isolated the tropical Atlantic from the Indo-Pacific and may account for the relatively high degree of endemism in dolphins in the tropical Atlantic. For example, there are two species of spotted dolphin (*Stenella*) in the tropical Atlantic, but only one occurs in other tropical oceans.

In another example, there is one dolphin in the monotypic genus *Sousa* in the subfamily Steninae that ranges from China into the Indian Ocean and up the western coast of Africa. A second, closely related dolphin in another monotypic genus, *Sotalia,* inhabits the coast of northeastern South America and the Amazon and Orinoco rivers. A third dolphin species, still another monotypic genus, *Steno*, lives on the high seas.

The pair of strictly coastal and riverine species is adapted to warm, shallow, murky waters. There is a wide gap in such habitats across the tropical Atlantic, and an even wider expanse of oceanic waters between the Indo-Pacific and the western coasts of the New World.

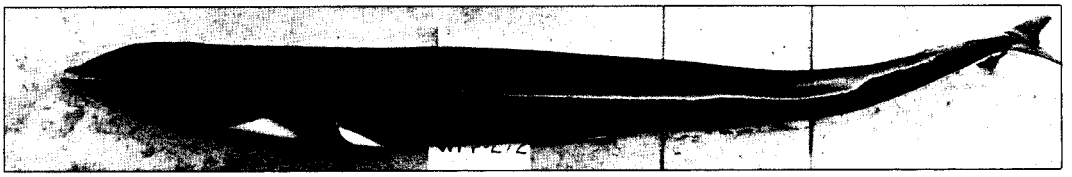
There are at least two hypotheses for the origin of the two coastal species. In the first, *Sousa* stragglers made it across the Atlantic at least once, long enough ago to result in species-level divergence. In the second hypothesis, the two coastal species arose independently by coastal colonization from the oceanic species. There are other possible permutations of events, but these seem to be the most likely ones.

There are other models of isolation and speciation in the Cetacea, including, for example, antitropical isolation (cold water distributions in the Northern and Southern hemispheres separated by warm tropical waters) during warm geological periods. Although marine habitats for mammals are indeed generally more continuous than terrestrial habitats, there has been enough structure and partitioning in the oceans to allow easily for the evolution of the species diversity through allopatric speciation (speciation through isolation).

Another level of diversity in the cetaceans is that below the species level. Wherever we have enough data, we have found pronounced geographical variation within a species. There are some patterns in this: variation between populations in open and enclosed seas, in coastal versus offshore habitats, and in different pelagic habitats in the open sea.

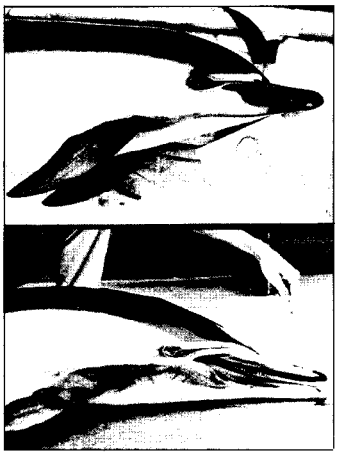
Dolphins tend to be larger in open waters than in closed seas. For example, in the common dolphin (*Delphinus*) in the contiguous waters of the North Atlantic, in the Mediterranean, and in the Black Sea, maximal size is greatest in the North Atlantic, least in the Black Sea, and intermediate in the Mediterranean. The bottlenose dolphin (*Tursiops*) shows the same pattern; again, the animals in the open Atlantic are the largest and those in the Black Sea the smallest.

Another common pattern is larger size in inshore coastal



The extremely attenuated northern right whale dolphin, *Lissodelphis borealis*, lacks a dorsal fin and is sometimes called "snake porpoise" by fishermen.

The dwarf sperm whale, *Kogia simus*, has many of the highly derived features of the sperm whale, *Physeter macrocephalus*, but it is only 2–3 meters long.



Two forms of the common dolphin, *Delphinus delphis*, inhabit the coast of California. The pelagic form (top) is smaller and has a proportionately shorter beak than the neritic form (bottom). They also have different color patterns; note the width and position of the stripe running forward from the flipper.

populations than in more offshore populations. Two forms of the common dolphin, *Delphinus delphis*, inhabit the coastal waters of California. One is neritic and the other pelagic. The more inshore form is larger and has a larger skull than the more offshore one.

In a last example, spinner dolphins (*Stenella longirostris*) in the far eastern oceanic tropical Pacific are sharply different from those in other tropical oceans around the world. The spinner dolphins in the eastern tropical Pacific are all gray, and in the adult male the dorsal fin is canted forward. This unusual dorsal fin is correlated with a large ventral hump behind the anus. These spinners are found in areas of the eastern Pacific where the thermocline is steep and the mixed layer shallow, approximately 50–60 meters. The spinner dolphins in other tropical waters, for example around Hawaii, have a sharply defined three-part color pattern, a slightly falcate dorsal fin, and no ventral hump; this type is found in areas of deeper thermocline.

These two different forms used to be called separate species, but we now recognize them as subspecies. There is a broad zone of intergradation between them. The form endemic to the eastern Pacific is called the eastern spinner dolphin. The range of morphological variation here is much greater than is usually found in wild mammal species.

The major point about morphology in cetaceans is that diversity is as great or greater than in most terrestrial mammal groups. One just about has to go to the human species, or to domesticated animals, to find the degree of combined variation in size, coloration, and shape that exists in the spinner dolphin, for example.

We can safely say that the extensive geographical variation in cetaceans probably indicates that regional populations have been subjected to strong and diverse regional selection pressures, implying high habitat diversity within the major marine habitat types. The seas most definitely are not continuous in these terms. There is more diversity in the oceans than has been generally assumed, and therefore there are more kinds of animals, at and below the species level, that qualify as evolutionarily significant units that we should work to save.

WILLIAM F. PERRIN
National Marine Fisheries Service
Southwest Fisheries Science Center
La Jolla, CA 92038