

Marine Mammals

An Introduction

Mammals, like nearly all other tetrapods (or four-legged animals), evolved on land. Marine mammals are a diverse assemblage of at least seven distinct evolutionary lineages of mammals that independently returned to the sea and include whales, dolphins, and porpoises (**Cetartiodactylans**); seals, sea lions, and walruses (**Pinnipedia**); sea cows (**Sirenia**); extinct sea cow relatives (**Desmostylians**); polar bears; sea and marine otters; and extinct aquatic sloths. The secondary adaptation of mammals to life in water required various morphological specializations, including for some lineages dramatic changes in body size and shape compared to their terrestrial relatives. Marine mammals are relatively large, with streamlined bodies and reduced appendages (for example, small or no external ears) and thick fur or fat layers for insulation. Other modifications for swimming and diving include the transformation of limbs into flippers and/or use of the tail for propulsion in water.

The story of marine mammal diversity, evolution, and adaptation is intriguing. Where they originated and how they evolved provides a historical framework for understanding how marine mammals make a living today, guiding our future efforts in their conservation. Before telling this story, I need to introduce some basic information about the various groups of marine mammals.

MAJOR GROUPS OF MARINE MAMMALS

Marine mammals include approximately 125 **extant** (or currently living) species that are primarily ocean dwelling or dependent on the ocean for food. The polar bear, while not completely aquatic, is usually considered a marine mammal because it lives on sea ice most of the year. Fig. 1.1 shows the major groups of marine mammals and the numbers of living species. Marine mammals range in size from a sea otter, weighing as little as 1 kg (2.2 lb) at birth, to a female blue whale, the largest mammal to have ever lived, weighing over 100,000 kg (2,200 lb). Marine mammals live in diverse aquatic habitats around the world, including salt, brackish, and fresh water, occupying rivers, coastal shores, and the open ocean.

Apart from diversity in size and habitat, marine mammals are fascinating in a number of respects further explored in this book. Most are capable of prolonged and deep dives on a single breath of air. Such extreme diving requires a remarkable suite of anatomical and physiological specializations. Some whales undertake long annual migrations, among the longest known for any animal. Most feed on fish and various invertebrates, such as squid, mollusks, and crustaceans. Some whales filter water and prey through uniquely developed sieves, baleen plates, that hang down from their upper jaws. The remarkable ability to produce and receive high-frequency sounds among other whales has allowed them impressive navigation skills and the ability to precisely locate prey underwater. A few marine mammals, the sirenians, are herbivores, feeding on aquatic plants with their mobile lips and crushing teeth. Other marine mammals, such as the pinnipeds, display a variety of behaviors associated with mating, ranging from bloody dominance battles among males that compete for priority access to females to species stationed underwater engaging in complex vocal displays to attract females swimming past. Reproduction in marine mammals also differs; most give birth to a single offspring annually but in some species, including sirenians and nearly all whales, reproductive cycles are

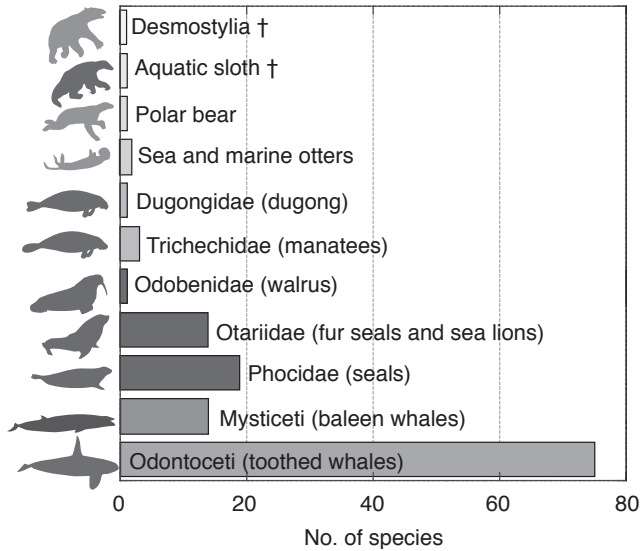


Figure 1.1. Diversity of marine mammals. Shading indicates major lineages.

separated by several years, an important factor to consider in their conservation and management strategies.

Many more marine mammal species existed in the past, some with no living counterparts. For example, extinct sloths and bizarre hippo-sized desmostylians, both herbivores, foraged in aquatic ecosystems. The number of species of marine mammals probably reached its maximum in the middle Miocene, 12–14 million years ago, and has been declining since then.

In this chapter, I present a brief introduction to the naming and classifying of marine mammals, the process of forming new marine mammal species, and factors responsible for their distribution. Chapter 2 provides a geologic context for interpreting the life and evolutionary times of marine mammals. In chapters 3–5, the evolutionary history, diversification, and adaptations of the major lineages of marine mammals are described. The final chapter, chapter 6, reviews the ecology and conservation of marine mammals.

DISCOVERING, NAMING, AND
CLASSIFYING MARINE MAMMALS

The diversity of marine mammals makes their classification a challenge. The universal language of biology is **taxonomy**, which includes the identification, description, naming, and classification of organisms. Also, taxonomy plays an important role in conservation biology since before you can conserve organisms, you have to be able to identify what it is you intend to conserve. Although we often hear more about vanishing species, a number of new marine mammal species have also been discovered. For example, in the last decade two new species of baleen whales have been described: Omura's whale (*Balaenoptera omurai*) from the Indo-Pacific and a right whale (*Eubalaena japonica*) from the North Pacific. Among toothed whales, several new species of beaked whales (*Mesoplodon perrini* and *Mesoplodon peruvianus*), the Australian snub-fin dolphin (*Orcaella heinsobni*), and the narrow-ridged finless porpoise (*Neophocaena asiaorientalis*) have been described.

Common and Scientific Names

Marine mammals are given names and classified in much the same way as all organisms are named and classified. One problem in taxonomy is that the same common name is often applied to different animals. For example, the name "seal" has been applied to both sea lions and fur seals (or otariids) and seals (or phocids), which are two very different pinniped lineages. Another problem is that different common names can be applied to the same species. For example, the names "harbor porpoise" and "common porpoise" have been both applied to *Phocoena phocoena*. For these reasons, and since all species have a single, unique **scientific name**, it is more important to remember the scientific name than the common name. The scientific name of a species consists of the genus name and the species name and follows a set of rules of nomenclature developed by Carl von Linne, better known as Linnaeus, in the mid-1700s. In the previous example, following the Linnaean system of nomenclature, the

harbor porpoise has two names: the first indicating that it belongs to the genus *Phocoena* (Latin for “pig fish”) and the second, specific name, *phocoena*. Note that the first name is capitalized but that the second name is not.

DNA Bar Coding: Species Discovery and Conservation

Species-level differences between organisms encode genetic information (that is, changes in DNA). In much the same way as barcodes are used to uniquely identify commercial products in everyday life, **DNA bar coding** makes use of DNA sequences as unique identifiers of species (fig. 1.2). Given a reference database of sequences from validated specimens (identified by experts from diagnostic skeletal material or photographs), unknown specimens can be identified as belonging to a particular species. Application of DNA bar coding to the taxonomy of a poorly known family of beaked whales (Ziphiidae) resulted in the correct identification of previously misidentified specimens.

DNA bar coding also has important uses in conservation for the genetic identification of illegally imported animal or plant products. For example, DNA analysis of whale products (for example, meat and oil) found in retail market places in Japan, Korea, and the United States revealed the illegal trade of protected endangered species.

RECONSTRUCTING THE HIERARCHY
OF MARINE MAMMALS

The Linnaean system organizes groups of organisms (for example, species) into higher categories or ranks (that is, families, orders, classes, etc.). The species is the basic, smallest level of biological classification. For example, the species *Phoca vitulina* is grouped into a larger unit of related species, the genus *Phoca*, which is in turn grouped into even larger hierarchies, such as Phocidae (seals) and Pinnipedia (including Otariidae, Odobenidae, and Phocidae). Given the arbitrariness of all ranks above the species, however,

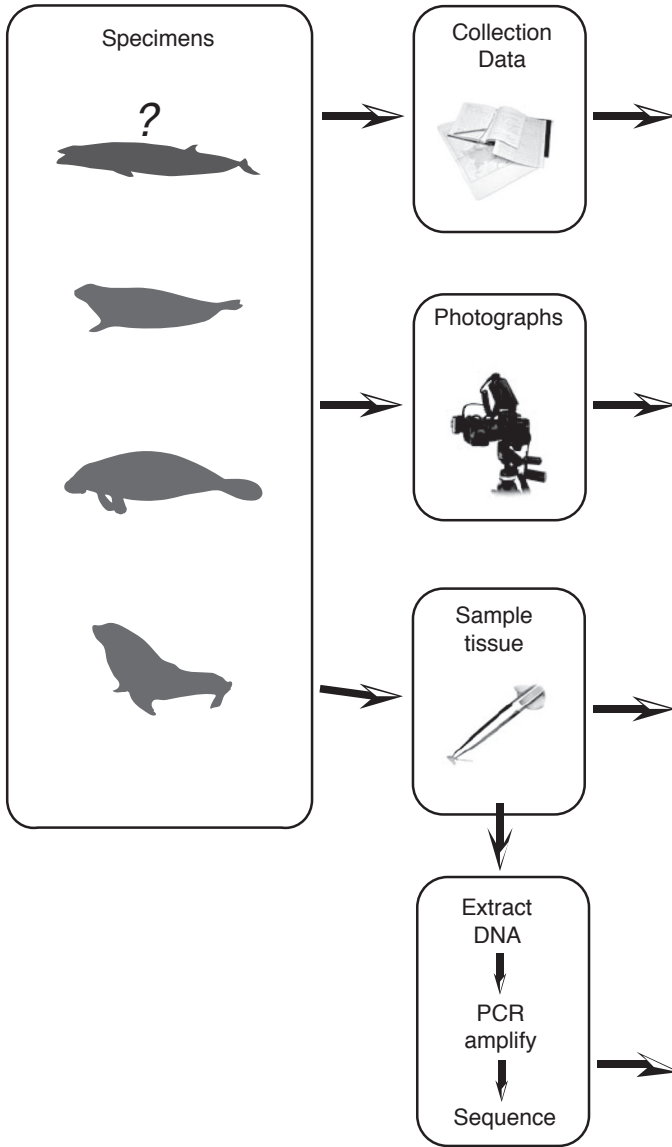


Figure 1.2. Steps involved in DNA barcoding: specimens, laboratory analysis, and database.

Web-accessible Data and DNA Barcode

Sample # _____ Date _____
Location _____ Collector _____

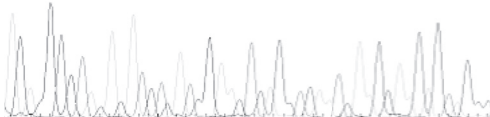


Confirm identification
as *Megaptera novaeangliae*



Compare to DNA Library

ATAGGTGCAGAGACTCGACGGAAGCTATTCTAACGAATGAATATCATT



some biologists have offered compelling arguments for the elimination of ranks above the species level altogether. However, regardless of whether ranks are employed, organisms can be organized into nested hierarchies based on the distribution of their shared features or characters. The reason for this underlying pattern of nested hierarchy was recognized by Charles Darwin in his 1859 masterpiece *The Origin of Species*, and attributed to common descent with modification—that is, **evolution**. The hierarchical nature of life reflects the tree-like nature of the history of life.

Characters are diverse, heritable attributes of organisms that include DNA sequences, anatomical features, and behavioral traits. Any characters that are shared by two or more species that have been inherited from a common ancestor are said to be **homologous**. For example, think of a bird wing and a seal flipper. They display similarities and differences. Although the forelimbs of a bird and a seal have different functions—one is employed in flying and the other is used for swimming—it is their similarities (that is, basic limb structure and bone relationships) that we are most interested in. We refer to this as a homologous similarity. Because homologous characters show evidence of inheritance, they are useful to determine evolutionary relationships among organisms. In this case, a bird wing and seal flipper are similar because they inherited this similarity from a common tetrapod ancestor. Homologous characters are also known as **synapomorphies**. Synapomorphies are **derived** characters shared among organisms. A derived character is one that is different from the ancestral character. For example, all tetrapods share four limbs; however, pinnipeds, a more inclusive group of tetrapods, share a more recent common ancestry and they can be distinguished from other tetrapods by possession of the derived character of limbs modified into flippers. Not all characters are evidence of relatedness. Similar traits in organisms can develop for other reasons, such as ecology. For example, the flipper of a seal and the flipper of a whale are not homologous because they evolved independently from the forelimbs of different ancestors—that is, the flipper of a sea lion is derived from carnivorans (for example, otters, bears, and weasels) whereas the flipper of a whale evolved from artiodactyls

TABLE 1.1
Summary of the distribution of a few pinniped characters.

Taxon	Lacrimal Absent	Flippers	Orbital Maxilla	Reduced Claws	Tusks
Arctoids (outgroup)	0	0	0	0	0
<i>Enaliarctos</i>	?	√	?	0	0
Seal	√	√	√	0	0
Walrus	√	√	√	√	√
Sea lion	√	√	√	√	0

(even-toed ungulates like cows, pigs, and hippopotamuses). This is known as an **analogous** similarity; two characters are analogous if they have separate evolutionary origins. This is known as **convergent evolution**.

Derived characters are distributed hierarchically among a select group of organisms. Consider the example of flippers possessed by pinnipeds. Since all pinnipeds have both foreflippers and hind flippers, it follows that if one wanted to tell a pinniped from a nonpinniped (any other animal), one would need only observe that the pinniped is the one with four flippers. On the other hand, the character possession of foreflippers and hind flippers is not useful for distinguishing a seal from a sea lion—both have four flippers. To distinguish a seal from a sea lion, characters other than the presence of flippers must be used to identify subsets within the group that includes all pinnipeds.

We commonly use a branching diagram known as a **cladogram** or **phylogenetic tree** to visualize the hierarchies of derived characters within a group of organisms. The lines of a tree of life are known as **lineages** and represent the sequence of descent from parents to offspring over many generations. To illustrate how a tree is constructed, let's consider four pinnipeds: seal (phocid), walrus (odobenid), sea lion (otariid), and the fossil (*Enaliarctos*). For simplicity, I have selected traits that are either present (√) or absent (0) (table 1.1, fig. 1.3).

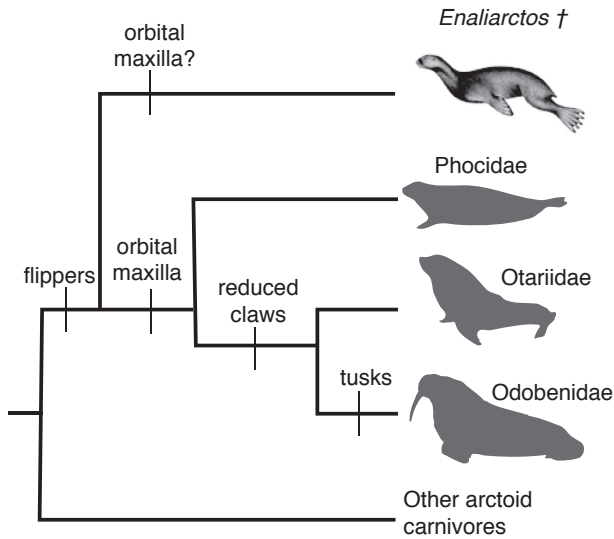


Figure 1.3. Distribution of character states among pinnipeds (restoration of stem pinniped by Mary Parrish).

A group of terrestrial carnivores, the arctoid carnivores (bears, weasels, and raccoons and their kin), are thought to have separated from the lineage leading to pinnipeds before the evolution of flippers. Therefore, arctoids are chosen as the **outgroup**—that is, outside the group of interest—for our analysis. As we will see in chapter 3, the extinct pinniped *Enaliarctos* is thought to have separated from the lineage leading to all other pinnipeds. Extant pinnipeds (and possibly *Enaliarctos*) differ from terrestrial arctoids in having the maxilla (upper jaw bone) form part of the lateral (side) and anterior (front) walls of the eye orbit. Walruses and otariids share a derived trait: the presence of reduced claws. We infer that reduced claws evolved in the common ancestor of walruses and otariids after that lineage separated from phocids. Walruses have one unique character in our list: the presence of tusks.

Any group of species that consists of all the descendants of a common ancestor is called a **monophyletic** group or a **clade**. In this example, walruses, phocids, and otariids are separate monophyletic clades that are

united in a larger, more inclusive monophyletic, Pinnipedia. Two species or taxa that are each other's closest relatives are called **sister species** or sister clades. In this example, walruses and otariids are sister clades.

A group of species that does not include the common ancestor or all the descendants of a common ancestor is called a **nonmonophyletic** group. An example of a nonmonophyletic group is that of **river dolphins**. They differ from oceanic dolphins in inhabiting freshwater rivers and estuaries. Recent molecular data supports river dolphins as a nonmonophyletic group. Ganges river dolphins do not share the same common ancestor as other river dolphins (see also chapter 4). Most taxonomists agree that it is not appropriate to recognize nonmonophyletic groups as taxonomic units because they misrepresent evolutionary history.

Important concepts when defining members of a clade are stem and crown groups. A **crown group** is the smallest monophyletic group, or clade, to contain the last common ancestor of all extant members, and all of that ancestor's descendants. Extinct organisms can still be part of a crown group: for instance, the extinct northern fur seal (*Callorhinus gilmorei*) is still descended from the last common ancestor of all living otariids, so it falls within the otariid crown group. Some organisms fall close to but outside a particular crown group. A good example is *Enaliarctos*, which, although clearly pinniped-like, is not descended from the last common ancestor of all living pinnipeds. Such organisms can be classified within the **stem group** of a clade. In fig. 1.3, *Enaliarctos* is a stem group pinniped. All organisms more closely related to crown group pinnipeds than to any other living group are referable to the stem group. As living pinnipeds are by definition in the crown group, it follows that all members of the stem group of a clade are extinct; thus, stem groups only have fossil members.

ADAPTATIONS AND EXAPTATIONS

Adaptations are features that are common in a population because they provide improved function. For example, the ability of toothed whales

to hear high-frequency sounds or echolocate is an adaptation for navigation and foraging. **Exaptations** are features that provide a function that is different from its original function. For example, it is hypothesized that the lower jaw of toothed whales may have arisen originally to transmit low-frequency sounds (as in some other mammals such as the mole rat, which hears ground vibrations) and later became specialized for transmitting high-frequency sounds. In this way, the lower jaw of toothed whales may be viewed as an exaptation for hearing high-frequency sounds, having initially functioned in low-frequency hearing.

WHAT IS A SPECIES AND HOW DO NEW SPECIES FORM?

One common but sometimes difficult question is how best to decide which particular species an organism belongs to. Another challenge is deciding when to recognize a new species. This is a question for the biologist, who discovers organisms that appear to be different from those that belong to already described species. Thus there are disagreements regarding what constitutes a species (that is, species concepts) as well as what are the best criteria for identifying species. Since species are often granted a greater degree of protection than populations, failure to recognize species may lead to inaccurate assessments of biodiversity.

For example, there is current debate over the species status of the killer whale. Traditionally, a single species of killer whale, *Orcinus orca*, found in all the world's oceans, has been recognized. There is now good evidence that several different species of killer whales exist in the northeast Pacific and Antarctic, based on differences in coloration, prey selection, habitat, and genetic data (fig. 1.4). Establishing appropriate taxonomic designations for killer whales is critical for understanding the ecologic impacts and conservation needs of these top marine predators.

Speciation is the process by which new species form from a common ancestor. In fig. 1.3, the branching of the tree denotes speciation

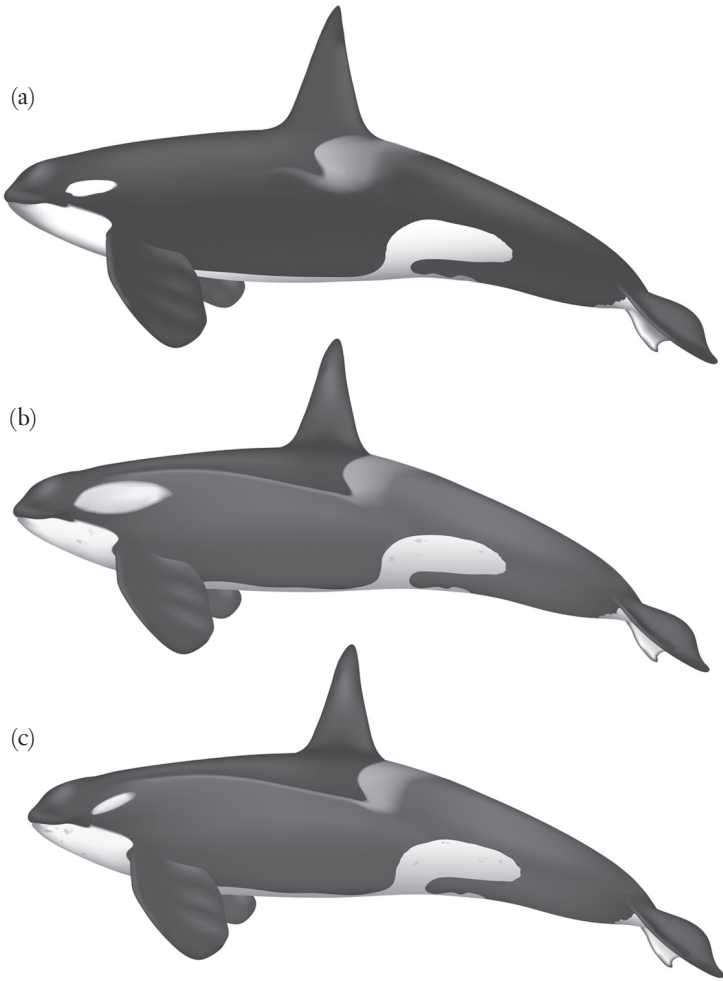


Figure 1.4. Antarctic killer whales, a and b, have been proposed as new species, with c proposed as a new subspecies (courtesy U. Gorter).

among various lineages of pinnipeds. There are three primary ways that new species form: (1) allopatric, (2) parapatric, and (3) sympatric speciation. In the most common type of speciation, **allopatric speciation**, new species arise from geographically isolated populations (fig. 1.5). In this type of speciation, a physical barrier prevents two or more groups

EVOLUTIONARY HYPOTHESES AND THE USES OF PHYLOGENIES

An important aspect of science is providing testable hypotheses to explain a set of data. Cladograms, or phylogenetic trees, are hypotheses of evolutionary relationship among a group of organisms. The phylogeny of extant pinnipeds is based on a small sample of characters. Typically, biologists construct phylogenetic trees using hundreds or thousands of characters. Large data sets require the use of computer programs to sort through millions or even billions of trees, searching for the best tree. One method of distinguishing among different hypotheses of relationship uses the principle of **parsimony**, which states that the preferred explanation of the observed data is the simplest explanation—that is, one that requires the fewest additional ad hoc assumptions.

Once a phylogenetic tree is reconstructed, it can be used to address wider evolutionary, ecological, and behavioral questions. For example, consider the evolution of locomotion in whales. If we map the various modes of locomotion onto whale phylogeny, we can hypothesize that the tail-based propulsion of extant whales in water evolved from initial use of fore and hindlimbs on land. This was followed by a pelvic phase that involved paddling with their feet (for example, *Ambulocetus*), a caudal undulation phase in which the tail and back were used (for example, *Kutchicetus*), and the final adoption of tail-based propulsion (dorudontines and crown cetaceans).

Phylogenies can help us determine conservation priorities. For example, the Ganges river dolphin lineage, formerly a diverse clade, is made up of only one extant member (*Platanista gangetica*). Among toothed whales, this species is an early diverging lineage and preserves ancestral character states of toothed whales, such as their origin in marine waters prior to invading present-day freshwater habitats. For this reason, on the basis of their evolutionary distinctiveness as well as other factors, including human activities, this lineage of river dolphins is critically endangered and is a high priority for conservation.

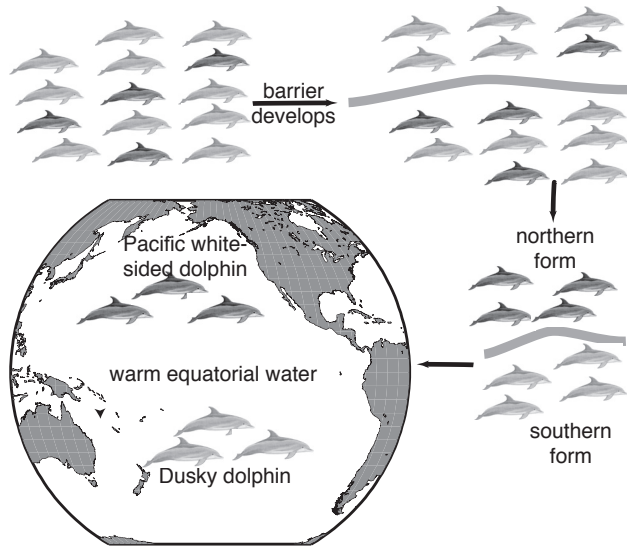


Figure 1.5. Allopatric speciation in dolphins.

from mating with each other regularly, so the lineage divides over time. In the case of marine mammals, isolation might occur because a barrier, such as warm equatorial water, divided a broadly distributed ancestral population inhabiting cool temperate water. An allopatric origin has been suggested for Pacific white-sided dolphins (*Lagenorhynchus obliquidens*), which inhabit the Northern Hemisphere, and their sister species, the dusky dolphin (*L. obscurus*), which lives in the Southern Hemisphere. The two species are separated by warm equatorial water.

A special version of allopatric speciation is **peripatric speciation**. It occurs when a small population becomes isolated at the edge of a larger, ancestral population (fig. 1.6). The small population is referred to as the **founder population**. Elephant seals are an example of peripatric speciation. During the late 1800s, entire herds of northern elephant seals (*Mirounga angustirostris*) in California were slaughtered for the high oil content of their blubber. The Mexican government protected them on the Isla Guadalupe off the coast of Mexico. This small, isolated founder