Biotic Diversity in the Ocean

In this chapter, we shall consider patterns of biological diversity from the broader perspectives of evolution, extinction, and biogeography. The number of species in a region is controlled by short-term ecological processes, but in the long term the relative rates of speciation and extinction explain the number of species. We therefore need to consider the causes of speciation and extinction. Regional variation in geography and climate influences the origin of species, and also the degree of structuring of the world into subdivided biotas, or provinces. We must therefore also consider the conditions that enhance the presence of such geographic or climatic barriers to dispersal among provinces. Finally, there has been an ever-increasing recognition of the importance of conserving the earth's biodiversity,[1] and we will discuss in this chapter some of the important factors in understanding biodiversity conservation issues.

Patterns of Species Diversity

The Speciation–Extinction Balance

✳ Although local patterns of species diversity are often explained in terms of short-term dynamic interactions, regional patterns are probably as much explained by the balance of speciation and extinction.

In Chapter 3 we saw how a series of factors interacted to control the number of species in a community. In a simple case, according to the intermediate-predation hypothesis, diversity is the result of an interaction between short-term effects of competition and predation. Although this hypothesis may explain events on the short haul, we must take into account the processes of species origins and extinctions to explain variations in diversity on larger geographic and temporal scales. A predator may depress interspecific competitive exclusion and increase local diversity, but this process does not create species. Similarly, intense predation rarely drives species to extinction rapidly. Rather, extinction usually follows larger-scale regional changes, such as a deterioration of climate. Thus, an understanding of the factors that regulate the number of species on the long term leads to the need for an understanding of processes controlling speciation and the regional changes that cause extinction.

✳ Speciation requires some degree of isolation of populations, which results eventually in reproductive incompatibility between them.

It is generally believed that **geographic isolation** promotes speciation. This idea is known as the **allopatric model** of speciation. Isolation permits the separated

1. The student will often see the term *biodiversity* used in conservation studies. It refers to the number of species present in a defined area, and is equivalent to the term *species diversity*. In this text, both terms are used interchangeably with *diversity*. Many ecologists, however, consider diversity to be an amalgam of the total number of species in an area and the degree of dominance by the most common species.

populations to evolve in different directions and achieve incompatibility. It is possible that two populations might differentiate from each other even with some contact. The **parapatric model** of speciation emphasizes the possibility of the origin of differentiation despite contact, as long as there are different natural selection pressures in the semi-isolated populations, allowing divergence even in the face of some gene flow from other populations. In effect, according to this model, natural selection is sufficiently strong to balance the influx of genes from another population, and reproductive incompatibility eventually develops between the two semi-isolated populations.

Imagine a species divided by the rising of the Isthmus of Panama above sea level a few million years ago. Populations of the single species on either side of the isthmus became isolated at that time, and now a large number of recently derived pairs of species exist on either side of the land barrier. Natural selection, or evolutionary change involving a shift in genetic variants, may have been promoted by differing environmental conditions on either side of the isthmus. Such differences in selection on either side of the isthmus would enhance the differences among the species, and might even accelerate the degree of reproductive isolation, owing to genetic incompatibility. Random changes in populations might also eventually result in increased genetic differentiation between the two populations. Nancy Knowlton and colleagues[2] have demonstrated that snapping shrimp species pairs on either side of the isthmus have concomitantly evolved differences in mating preference and overall genetic difference, as measured by genetically controlled enzyme variation.

The sum total of such differentiation tends to increase the total number of species in the world. If the geographic barriers then break down and shift rapidly, then formerly isolated species will be combined, and the number of species in a given region will increase, unless interspecific competition results in the loss of some species.

✳ Extinction may be caused by habitat change or destruction, widespread diseases, biological interactions, or random fluctuations of population size.

Extinction, or the loss of species, may be caused by shifts in the environment, such as sudden changes of temperature. Destruction of major habitats may also cause extinction. For example, most coastal lagoons are geologically unstable habitats, and are destroyed after the passage of several thousand years. Any species that are restricted to the lagoons would be in similar danger of extinction, unless they had sufficient geographic range over a large number of lagoons, so that there would be a high probability that some would survive in the long run. Another such example of habitat destruction would be marginal seas, such as the Mediterranean, that have experienced massive anoxia, nearly complete evaporation, and other effects so major as occasionally to make them non-marine habitats.

Biological interactions may also be the cause of sudden extinctions. In Chapter 3, we discussed the rapid spread of disease in the ocean, and its potential of disease to destroy even a widespread dominant species. The immigration of competitors and predators may have a similar effect. The introduction by human beings of many species has resulted in major shifts of habitat use by formerly dominant species, although no extinctions of marine species seem to have been induced. Migrations into new areas can result in rapid expansions. For example, when the common Atlantic mud snail *Ilyanassa obsoleta* was introduced into San Francisco Bay, the local dominant was subsequently restricted to high intertidal sites. After the arrival of the periwinkle *Littorina littorea* from Europe to North America in the late 1800s, the snail spread south, and reduced the range of habitats used by the *I. obsoleta*.

The total number of species in a region, therefore, is the result of a net balance between the rate of species production and the rate of extinction. In unstable areas, where fluctuation between environmental extremes is the norm, newly isolated species are liable to become extinct, or are never established at all, owing to rapid shifts of climate and habitats. In such areas, the rate of extinction is likely to be high as well. Thus the speciation–extinction balance leans toward low standing diversity. In more stable habitats species when newly formed might have a higher probability of survival, thus increasing diversity.

Biogeographic Factors

✳ Geographic isolation and major geographic gradients in temperature and salinity combine to determine provinces of statistically distinct groupings of species.

The spatial arrangement of the continents and oceans, combined with the influence of the latitudinal gradi-

2. See Knowlton et al., 1993, in Further Reading.

ent of temperature, organizes the world oceans into a series of distinct areas, characterized by geography, local circulation patterns, and water properties. Owing to sea floor spreading and continental drift, most coastlines are oriented approximately north–south. Thus, the geographic ranges of many shallow-water species are limited by temperature, which varies greatly along the coast with changing latitude. Major differences in food regime usually limit a species' range of distance away from shore. Most inshore assemblages of both plankton and benthos are distinct from offshore assemblages. This leaves blocks of habitats that are distinct in their combined hydrographic and trophic characteristics.

Because of the set of geographic and environmental barriers, the ocean can be divided into a series of **provinces**, or biogeographic regions with characteristic assemblages. Boundaries between provinces can be water-mass borders, major thermal discontinuities, points of land coinciding with thermal discontinuities, or boundaries between water bodies of differing salinity. Along the west coast of North America, for example, there is a series of provinces (Figure 17.1)

whose boundaries coincide with major thermal breaks. For example, Point Conception in southern California marks a major shift from southern warm water to northern cold water. Although most boundaries coincide with major environmental shifts, currents may isolate one region from another, which is true through the summer at Pt. Conception. Provinces are usually recognized statistically, and not by unique assemblages of species.

While provincial boundaries can be recognized by the ends of the geographic ranges of marine species, one would expect that broader-ranging species might still be isolated to some degree across the same boundaries. Therefore, one might expect some degree of genetic difference between populations of the same species on either side of the boundary. Figure 17.2 shows differences in frequencies of major variants in mitochondrial DNA length polymorphisms along the east and Gulf coasts of North America. The Atlantic coast of southern Florida is known to be an important provincial boundary. Species with ranges that transcend this boundary nevertheless are strongly differentiated genetically on either side of it.
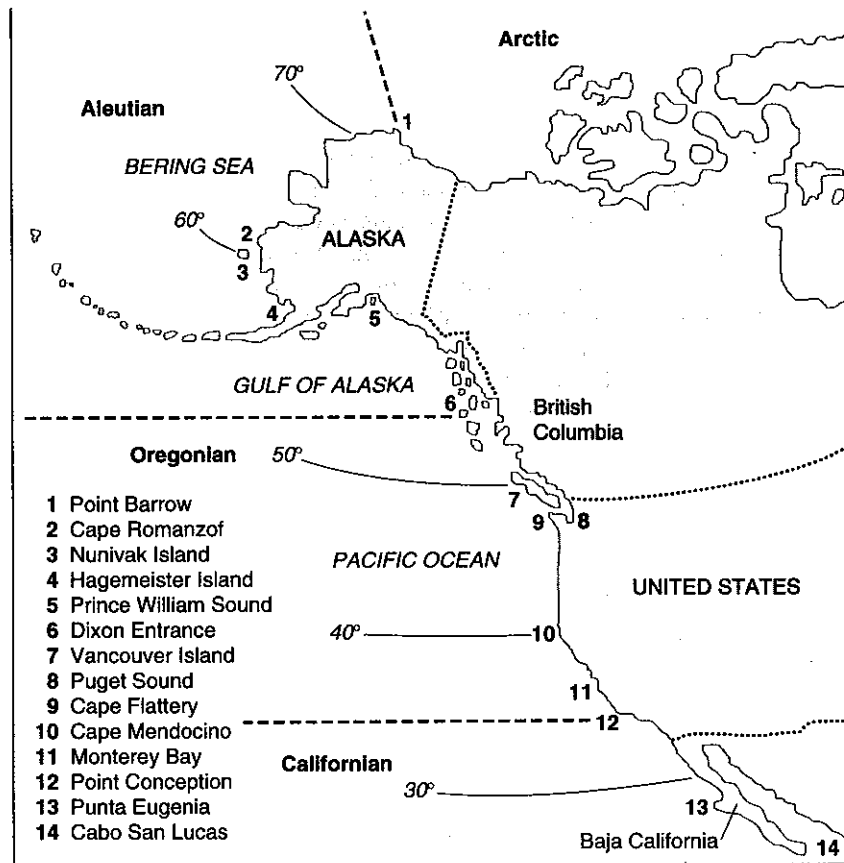

1 Point Barrow
2 Cape Romanzof
3 Nunivak Island
4 Hagemeister Island
5 Prince William Sound
6 Dixon Entrance
7 Vancouver Island
8 Puget Sound
9 Cape Flattery
10 Cape Mendocino
11 Monterey Bay
12 Point Conception
13 Punta Eugenia
14 Cabo San Lucas

Fig. 17.1 Biogeographic provinces defined by the continental-shelf mollusks of the northeastern Pacific. (After Valentine, 1966.)
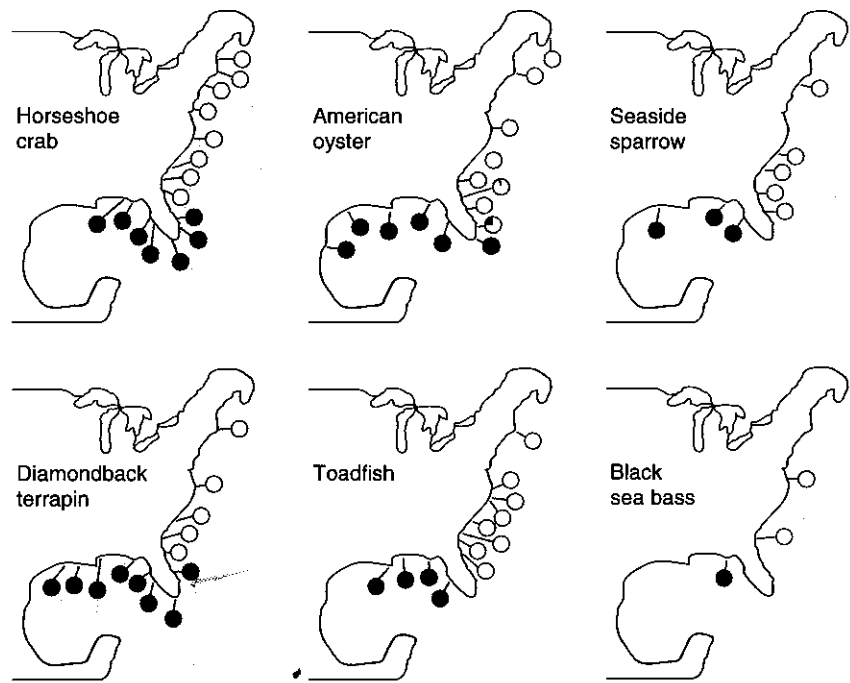
Fig. 17.2 Geographic distribution of mitochondrial DNA length variants in six coastal species. The pie diagram for a given species at each locality shows the relative frequencies of the two most common monophyletic groups of length variants (or groups of length variants with the same ancestor) for the given species. As can be seen, the south Florida region marks a major biogeographic discontinuity. (After Avise, 1992.)

Major Gradients of Species Diversity

✳ We must distinguish between within-habitat and between-habitat comparisons of diversity.

In discussing geographic variation in species diversity, it becomes difficult to make comparisons between very different regions. An increase of species numbers, from one place to the next, may be explained simply in terms of an increase in the number of habitats. The shallow-water tropics, for example, have coral reefs that provide a large number of available microhabitats that are nonexistent in temperate-zone bottoms. The difference in diversity explained by multiplication of habitats is the **between-habitat component of species diversity.** Any changes in species diversity between regions in a single defined habitat comprises the **within-habitat component of species diversity.** For example, comparison of the number of species living in muddy-bottom shelf subtidal sediments in the Atlantic Ocean versus the Pacific Ocean is a within-habitat comparison of species diversity.

EFFECT OF LATITUDE

✳ Species diversity tends to increase with decreasing latitude.

The best-known diversity gradient is an increase of species diversity from high to low latitudes in conti-

nental shelf benthos, in the plankton in continental shelf regions, and in the open ocean. Figure 17.3 shows the latitudinal gradient for bivalve mollusks, but the trend applies to other shelf invertebrate groups and to planktonic groups such as copepods. There are some exceptions, and a couple of groups (e.g., nuculoid bivalve mollusks) even increase in diversity toward higher latitudes. The generalization of increased diversity with decreasing latitude also applies to higher taxonomic categories, such as genera and families. This generalization applies to species lists, but not necessarily to the number of species living within a small area of, say, a square meter. The regional species list for Costa Rica contains five times as many species as does the list for coastal Washington State, yet a square meter of typical tropical beach contains no more species than do typical temperate beach samples. The overall difference in species diversity seems to be due to the relative richness in Costa Rica of the low-shore cobble-beach habitat.

The present-day latitudinal species diversity gradients correlate with the strong climatic latitudinal gradient. One should keep in mind some of the conditions that are nearly unique to our time in geological history. At present, there is a strong latitudinal gradient in climate, owing to the recent (last few million years) cooling of world climate and glaciation from the poles. Also, sea-floor spreading and continental
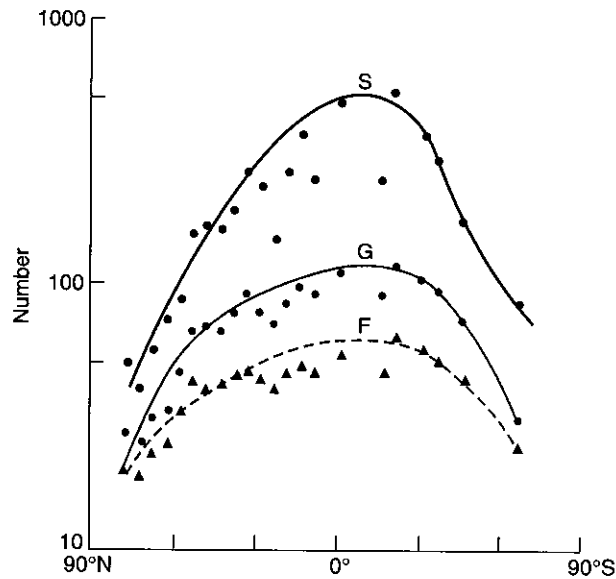
Fig. 17.3 The relationship of bivalve mollusk taxon diversity versus latitude. Points are average number of species, S, genera, G, and taxonomic families, F (After Stehli et al., 1967, courtesy of the Geological Society of America.)

has been becoming more obvious, however, that high-latitude deep-sea environments differ from low-latitude bottoms. This is especially apparent in terms of the fall of detritus from the plankton, which is greater in abundance and also more erratic in higher latitudes.

DIFFERENCES BETWEEN AND WITHIN OCEANS

* There are major differences in species diversity between ocean basins.

Even when latitude is held constant, the Pacific Ocean has far more species than the Atlantic. This fact has been documented for a wide variety of invertebrate groups and fishes, especially in coral reef habitats. The contrast is also obvious for many groups on the Atlantic and Pacific sides of North America (Table 17.1). In the northwest United States, one can find 19 species of shallow-shelf asteroid starfish, in contrast to only 6 species in the southern New England region. An interesting exception is the polychaete annelids, which are slightly more species-rich in the New England area.

* Within the Pacific Ocean, species diversity in coral reefs declines in all directions from an Indo–Pacific diversity maximum.

drift have produced extensive north–south-trending coastlines, which in turn places shallow water biotas along a lengthy climatic–geographic gradient.

In Chapter 16, the diversity gradient of benthos along a depth gradient from the continental shelf to the deep sea was discussed. It has been a recent surprise that there is a latitudinal diversity gradient in the deep sea of the North Atlantic Ocean. Formerly, marine biologists thought that there was no environmental latitudinal gradient in the deep sea at all. It

Although the latitudinal gradient is most prominent in all oceans, the Pacific has a prominent peak of diversity, especially in the species associated with coral-reef habitats. Diversity reaches a maximum in the southwest Pacific, in the region of the Philippines and Indonesia (Figure 17.4). From this center, diversity declines in all directions, although the latitudinal gradient is steeper than the longitudinal gradient.

Table 17.1 Species diversity of various invertebrate groups in the vicinity of Woods Hole, Massachusetts, and Friday Harbor, Washington.

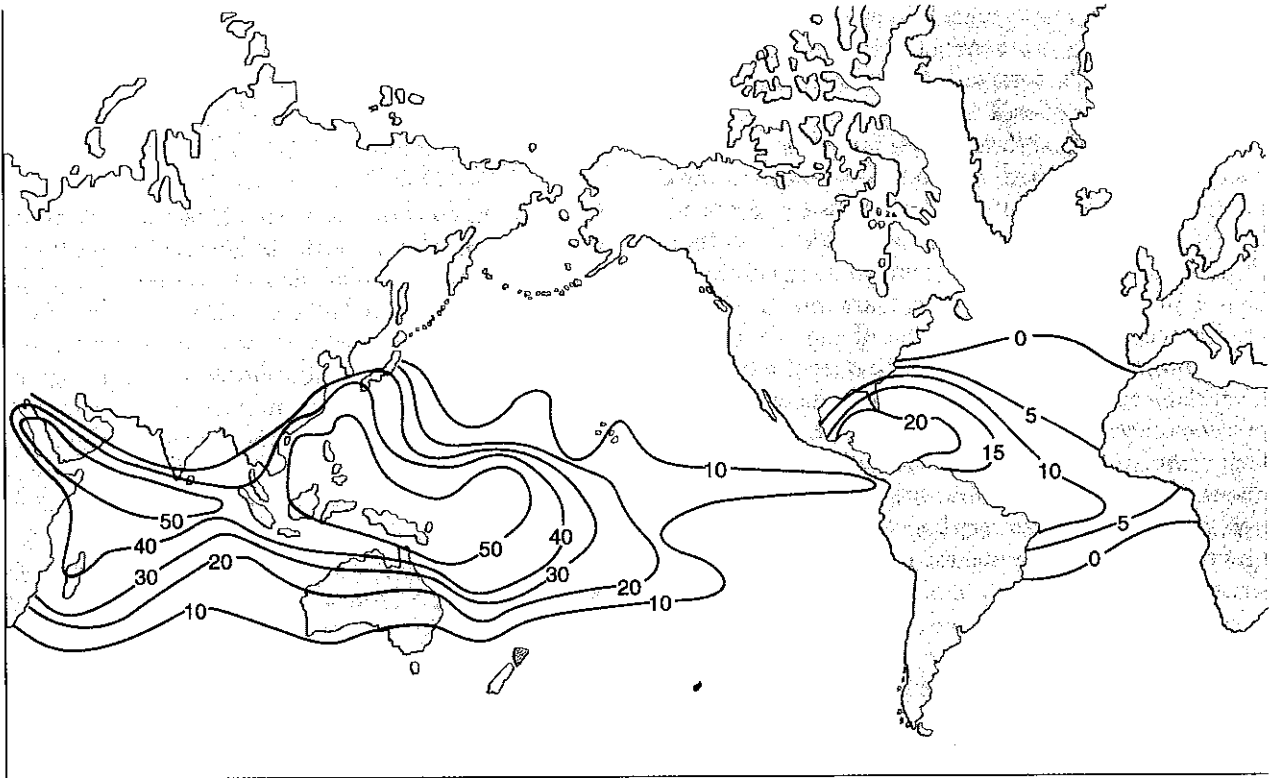| Taxonomic group	Number of species, Friday Harbor, Washington	Number of species, Woods Hole, Massachusetts
Shell-less opisthobranch gastropods	61	23
Shelled gastropods	88	51
Bivalve mollusks	114	55
Asteroid starfish	19	6
Polychaetes	174	218
Isopods	42	27
Amphipods	76	47

Fig. 17.4 Variation in numbers of genera of reef-building corals in the Indo–Pacific and Caribbean provinces. (After Stehli and Wells, 1971.)

LOWER DIVERSITY IN INSHORE AND ESTUARINE HABITATS

* Inshore and estuarine habitats are poorer in species than in comparable habitats in the open sea.

In both benthic and water-column assemblages, the open sea tends to have more species than do inshore habitats. Estuaries are the extreme cases, where one finds a small number of species, dominated by very few species with high abundance. By contrast, off-shore communities usually have more species, and the species abundances are more evenly divided. In the plankton, the increasing complexity offshore is cor-related with an increase in the number of trophic lev-els, as was discussed in Chapter 10.

In Chapter 16 the high diversity of the deep sea benthos was discussed. If one considers the muddy-bottom habitat alone, there is a regular change in ben-thic diversity from the coast to the abyssal plain. Spe-cies diversity of macroinvertebrates and fishes increases with depth, to a maximum just seaward of the continental rise, and then decreases with increas-ing distance toward the open abyssal plain. By con-trast, the species diversity of meiofaunal and micro-faunal groups seems to increase steadily toward the abyss.

Some Explanations of Regional Diversity Differences

Ecological Interactions

* Ecological interactions may determine regional dif-ferences in species diversity.

The processes of competition, predation, and distur-bance interact to determine species diversity in a local area. Predation and disturbance tend to reduce pop-ulation sizes of prey species, which relaxes competi-tion among species. This suggests that predation, for example, might allow more species to coexist. Dayton and Hessler (1972) have cited this as an explanation for high deep-sea diversity. In effect, a short-term eco-

logical process may control long-term species co-ocurrence. There is a problem with this hypothesis, because the life histories of deep-sea benthic species are characteristic of organisms that have suffered little predation. Species suffering high predation would be expected to have high reproductive output, rapid growth, and early reproductive maturity. Deep-sea benthic species seem generally to have the opposite of these traits. However, there seems to be no strong evidence of ecological differences among co-existing species that would be indicative of the influence of competition in the evolution of the deep-sea benthos. Disturbances are probably small in scale, which may preserve unpredictable combinations of species, with little extinction. Almost everything we might say about the deep-sea benthos with regard to competition and disturbance is very limited by a lack of direct observations or experimental studies of community structure.

Effects of Recent Events

* Complex recent historical events may explain current regional differences in species diversity.

As was mentioned above, some of the large-scale geographic difference in diversity can be ascribed to recent events. The gradients may not be due to a balance of extinction and speciation, as was postulated. For example, the present-day species pattern along the eastern U.S. coast is due primarily to a large scale extinction in the south, that was probably followed by the appearance of large numbers of new species. The diversity of the Caribbean has also been shaped by relatively recent events. The large-scale diversity gradient in the tropical American coral reef biota may be due in part to extinctions around the periphery of the province, as the earth's climate became cooler and the latitudinal oceanic temperature gradient steepened during the last few million years. The rise of the Isthmus of Panama a few million years ago was followed by an extinction of many Caribbean species that had close relatives in the Pacific. Despite this extinction, many new species were produced, so the total effect on diversity was not very great. Molluscan diversity apparently even increased after the rise of the isthmus.[3] The change in diversity in the last few million years, in sum, was very complex and probably consisted of a series of expansions and contractions of species richness.

Factors Causing High-Diversity Regions

* Areas of high diversity may be centers of origin of new species, or they may be regions where speciation is steady and extinction is low, resulting in geographically separate (vicariant) regions.

There is still controversy as to why some regions are rich in species. This is particularly true of tropical species-rich regions, such as the southwest Pacific in the vicinity of Indonesia. There are two problems. First, why do more species seem to accumulate in species-rich regions? Second, are the species-rich regions sources of new species that migrate out to regions of lower diversity? Many favor the **center-of-origin** theory, which states that the tropical high-diversity regions are the source of species, which disperse to lower-diversity regions. For this to be true, either extinction must be lower in the tropical higher-diversity regions, or speciation rates must be higher. This hypothesis is difficult to test without reference to a fossil record. A study by Stehli and Wells[4] demonstrated that geologically younger reef coral genera are found most abundantly in the southwest Pacific, where diversity today is the greatest. This would seem to support the center-of-origin theory. A recent study of western Pacific sea grasses by Mukai has also supported the center-of-origin idea. Mukai hypothesized that species should be able to migrate most easily along major current systems. He then examined the number of species of sea grasses from the Indonesian southwest Pacific center of diversity along the Pacific Equatorial Current and several other current systems, and found that they decreased steadily downcurrent (Figure 17.5).

In contrast to the center-of-origin hypothesis, the **vicariance hypothesis** argues that species arise *in situ* on either side of a geographic barrier. Such a hypothesis requires that an ancestral species (or a group of species, all with the same geographic range) be widespread and be subsequently isolated into separate populations by a barrier such as an isthmus. This model may be appropriate for the division of the Atlantic and Pacific marine biotas. Before the Oligocene epoch, approximately 40 million years ago, a broad shallow sea, known as Tethys, connected the Atlantic and Pacific and there was greater homogeneity of the

3. See Jackson et al. 1993, in Further Reading.

4. See Stehli and Wells, 1971, in Further Reading.

marine faunas. Following the rise of land masses, the Tethyan sea disappeared and divergence soon followed. The barrier to dispersal not only allowed more local speciation in the two oceans, but also was accompanied by strong climatic differentiation, so that species also became adapted to the more variable Atlantic, for example, as opposed to the relatively more equable Pacific. The vicariance model also fits well with our understanding of the many species pairs on either side of the Isthmus of Panama. In a few other cases, the appearance of peninsulas appears to have caused separation and speciation on either side of these barriers.

* Species diversity increases with increasing habitat area.

It has long been known that there is a quantitative correlation between geographic area and the number of species that area contains (Figure 17.6). This is best described in the form of a simple equation:

$$S = CA^z$$

where S is the number of species, A is the area, z is an exponent used to fit the equation, and C is a constant that partly accommodates the use of different metrics for area (e.g., km^2 versus $miles^2$). The exponent z is usually less than 1, so a proportionate increase of area results in a smaller proportionate increase in species, that is, the curve is concave down. On a qualitative basis, this means that the differences in species numbers between the Atlantic and Pacific, for example, can be related to the fact that the Pacific Ocean has a larger area. Similarly, the Caribbean coral-reef province is far smaller in area than that of the Indo-Pacific, and the latter contains far more species of most invertebrate and vertebrate groups.

A simple theory may explain why larger numbers of species are associated with larger areas. Remember that the number of species in a large region is probably a result of a balance between speciation and extinction. In larger areas, the speciation per unit area may be greater, owing to the larger diversity of habitats associated with an increased area. Similarly, the rate of extinction may be lower, because more refuge habitats are available, and also because larger population sizes and geographic extent in the larger area may make species less prone to extinction. Areas that are richer in food might also support larger populations, which would retard the extinction rate and raise the equilibrium number of species. Thus, food-rich bodies of water might support more species than food-poor ones (Figure 17.6).
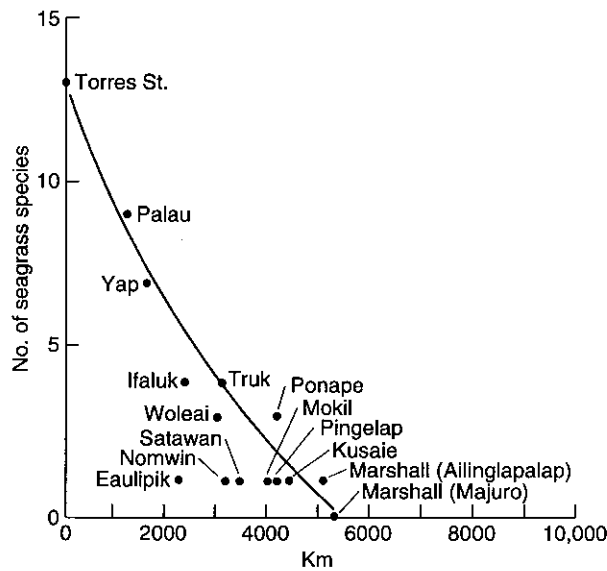

Fig. 17.5 Relationship between species richness of tropical sea grasses on various Indo–Pacific islands and distance from the Torres Strait (northern Australia), eastward along the Equatorial countercurrent. (After Mukai, 1993.)
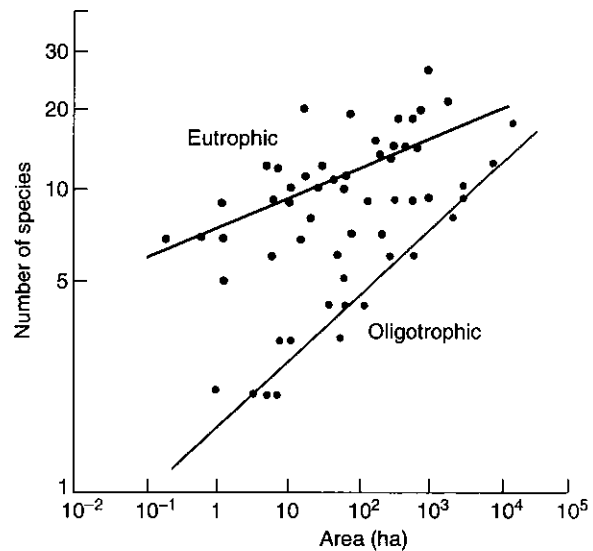

Fig. 17.6 The relationship between area and number of species of fresh-water snails in nutrient-rich (eutrophic) and nutrient-poor (oligotraphic) ponds in Denmark. (After Lassen, 1975.)

There is a real problem with the area hypothesis when diversity in the deep sea is considered. It is true that deep-sea diversity is greater in the near-slope abyss. However, diversity increases with greater distance toward the mid-oceanic bottoms beneath the gyres. These bottoms are greater in areal extent, yet harbor fewer species than do the near-shelf abyssal bottoms. Clearly, reduced food supply has a major influence on diversity in these remote bottoms. Area cannot be the direct and only factor that lowers diversity.

* Increasing long-term habitat stability may tip the speciation–extinction balance toward higher species diversity.

Physically stable environments may accumulate more species than variable environments. H.L. Sanders and L.B. Slobodkin proposed that environmental stability influences the flexibility required of the resident species. By environmental stability, we mean the short-term range of environmental variation, for example, the degree of seasonality, seasonal changes in salinity, and frequency of storm events. If the environment varies often from state *a* to state *b*, then a species will become extinct unless it can survive and reproduce in both states. Given that resources may be limiting, the environment may be able to support only relatively few species of such broad adaptability. Unpredictably variable environments may have even more severe effects, because species must then have enough flexibility to deal with a wide range of environmental changes. J.W. Valentine suggested that fluctuations in primary production may be a major influence on the degree of specialization of consumers. Stable environments may also accumulate more species owing to reduced extinction rates. In stable environments, major habitat alterations may be less frequent and extinction may therefore be less important. This hypothesis also fits the recently discovered latitudinal gradient of benthic diversity in the deep sea of the North Atlantic. Very-high-latitude sites are characterized by greater deposition of detritus from the plankton, and the variation of this deposition is greater than at lower latitudes.

Several large-scale patterns of diversity might support the stability hypothesis. The Pacific coral reef province is demonstrably more constant in temperature variation than the Atlantic. The high diversity of the Pacific coast versus the Atlantic coast of the United States may be explained in the context of the more constant maritime climate of the Pacific as opposed to the continentally dominated climate of the North American Atlantic coast. The deep-sea increase in diversity may be explained by the extreme constancy of temperature and salinity, whereas the dropoff in diversity toward the open-sea abyssal plain may be due to severe food stress. In stressful environments, only a few species capable of evolving tolerance will come to dominate.

Sanders also suggested that ancient environments may accumulate more species than do young environments. This conclusion was based mainly on observations of the spectacular diversity of many of the rift-valley lakes in east Africa and of Lake Baikal in Siberia. All those lakes are millions of years old, unlike the majority of the world's lakes, which are only a few thousand years old at most. The concept is harder to apply to the ocean. The deep-sea biota does not seem to be more ancient on the whole than that of shallow water, despite the presence of a number of famous "living fossils" such as the stalked crinoids and the monoplacophoran *Neopolina*.
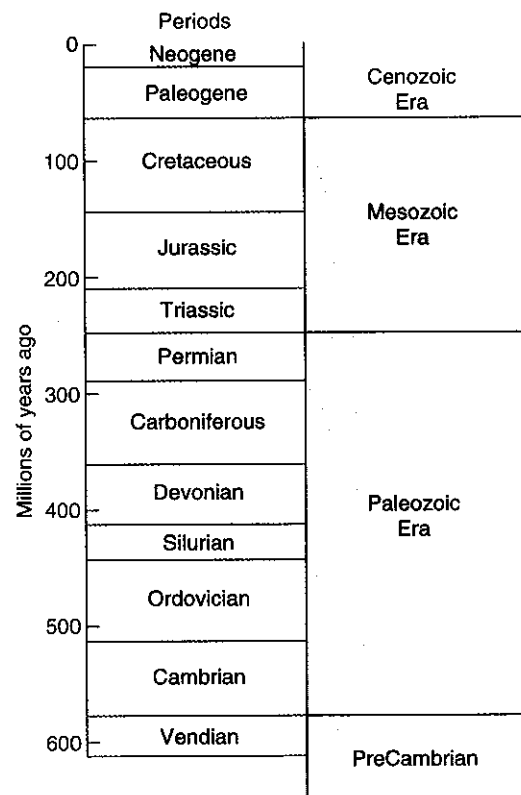

Fig. 17.7 The geological time scale, showing eras, periods, and epochs, and the absolute number of years, determined from radiometric dating.

Expansion and Extinction
in the Geological Past

❊ The fossil record allows us to distinguish periods of origin and extinction. During the Phanerozoic, there have been periods of rapid expansion and several episodes of major extinction.

Unfortunately, present-day species distributions provide only a kind of snapshot of the current situation, often offering little possibility of insight as to the historical events that may have led to current diversity conditions. Although the fossil record is known to be characterized by poor preservation and by marked gaps where there is no record at all, we nevertheless can get an idea of how diversity changed over longer periods of time, and of whether current conditions might be explained in terms of major changes in recent geological history. Only a brief sketch of some important patterns can be provided here, but such patterns demonstrate that many major changes have occurred, imbedded in a history of past climate change and lateral and vertical movements in the earth's crust, which have reoriented coasts and changed current systems.

Figure 17.7 shows the geological time scale, which is broken up into eras, periods, and epochs. Although absolute time boundaries have been determined by the use of various radioactive isotopes, most of the time scale comes originally from the rock record and the location of fossils in relative positions (older fossils are lower down in the rock record, generally). Figure 17.8 shows that there was an explosive appearance of new phyla near the beginning of the Paleozoic Era, but that there were two more explosive periods, which led to our current high level of diversity. The general increase, however, was punctuated by so-called mass extinctions. The most dramatic occurred at the end of the Paleozoic Era, and paleontologist David Raup has estimated that over 95% of marine species became extinct at that time. More famous is the somewhat less dramatic extinction at the end of the Cretaceous Period, when many marine species and, of course, the dinosaurs became extinct. There is still no general theory that satisfactorily and conclusively explains these mass extinctions, but the end-Cretaceous event coincided with a rather large asteroid fall, for which there is evidence in the form of an extraordinary iridium anomaly and a large crater-like structure in Yucatan (Mexico), which suggests a major impact in the Caribbean basin. In the rocks at the end of the Cretaceous there also are in some places minerals indicative of high pressure (i.e., an impact). It is still possible, however, that some of the major extinctions were caused by major climate change or even changes in sea level. The Permian mass extinc-
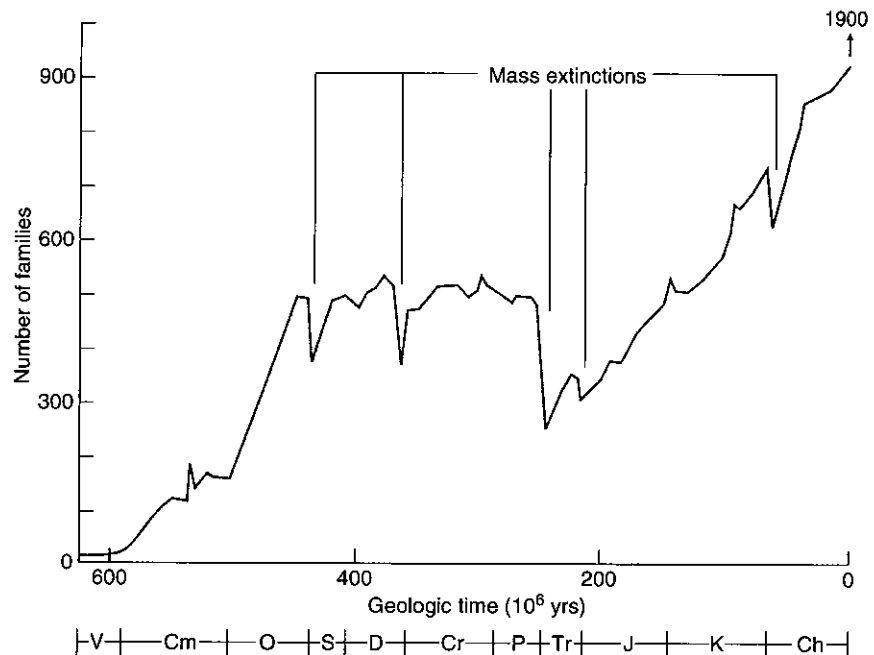

Fig. 17.8 Changes in the numbers of readily fossilizable marine fossil families throughout the Phanerozoic Era. Major episodes of mass extinction are indicated by downward arrows. V = Vendian; Cm = Cambrian; O = Ordovician; S = Silurian; D = Devonian; Cr = Carboniferous; P = Permian; Tr = Triassic; J = Jurassic; K = Cretaceous; Cn = Cenozoic. (After Sepkosk, 1984.)

tion coincided with what was probably the greatest fall in sea level in geological history. On the other hand, the large-scale Pleistocene changes in sea level, which occurred because of expansion and contraction of glacial ice, appear to have had little impact on extinctions.

The fossil record also allows examination of the origin of major evolutionary novelties. The Cambrian explosion has been discussed in Chapter 11, but throughout the fossil record we can see the rise of new morphologies, which often are identified by the rise of new higher taxa (e.g., orders). Recent evidence compiled by David Jablonski suggests that the tropics are a major source of new evolutionary novelties in the marine biota. The reason for this is not entirely clear, but it may relate to the presence of tropical reefs, which are complex habitats that could allow for more morphological evolution as adaptation to a larger number of habitats. More new taxonomic groups also seem to arise near shore, relative to offshore habitats. This may be related to the greater degree of environmental change near shore, which may cause more directional selection and evolution of new adaptive types.

Conserving Marine Biodiversity

Estimating Diversity

✻ A great deal of the total diversity of marine life is as yet unknown.

Although many important conservation efforts are underway, most ecologists and systematists agree that there is not yet an adequate understanding of the biodiversity of many habitats, particularly in the diverse tropics and in the deep sea. Coral reefs, for example, have hundreds of known species of epibenthic invertebrates, but many species remain undescribed, and probably many more remain undiscovered. Seaweeds are in particular very poorly understood. Application of molecular techniques, such as sequencing of DNA and evaluation of length polymorphisms of mitochondrial DNA may provide us some important tools for distinguishing unambiguously among marine species that are otherwise very difficult to identify.

Value of Biodiversity

✻ Diversity may increase the potential for change in an ecosystem and also may have the value of providing more sources of drugs and other products.

There of course is an aesthetic and ethical issue behind the notion that biodiversity should be conserved. We cannot deny our biological heritage and we benefit in many aesthetic and even emotional ways by conserving the diversity of life. Most of us would agree that a world with only mussels and blue-green algae would be very dull. Some would even argue that it is immoral to allow the destruction of species. A new awareness of the continuity of all of life with humankind has led to a new concern for our fellow species.

There are also practical reasons to be concerned about the loss of diversity. Much of our knowledge of community ecology suggests that many species play crucial roles in elemental cycling and in regulating the distribution and abundance of marine organisms. Some of these important species are particularly vulnerable to human destruction. Top carnivores in food webs, for example, are likely to be lowest in population size and any negative effects of the environment may drive them to extinction. While being most vulnerable, they also may play an important regulatory role in keeping prey populations down. Accidental effects of environmental degradation could eliminate species, such as sea grasses and reef-building corals, that create structural habitats for large numbers of other species, many of which are commercially important (e.g., scallops depend upon sea grasses in eastern U.S. coastal habitats). Marine biodiversity may also be a source of innumerable drugs and other marine products. Unfortunately, it is not predictable where the next important drug will emerge.

Reduction of Biodiversity

✻ Marine biodiversity may be reduced by habitat destruction, habitat fragmentation, and habitat degradation.

Biodiversity within a given habitat type can be reduced by three human activities. **Habitat destruction,** such as filling of marshes, human-induced erosion, and destruction of shorelines by the building of bulwarks is one of the major sources of biodiversity reduction, because it removes the habitats upon which species depend. A more subtle, but equally important, source of reduction is **habitat fragmentation,** in which a previously continuous marine habitat is broken up into smaller isolated parcels. Shoreline development in the tropics, for example, tends to have a negative effect coastal coral reefs, which are broken up into smaller tracts. As a large habitat, such as a sea grass bed, is broken into fragments, ready colonization of

planktonic larvae becomes more difficult. Also, larger predators and other foragers will no longer have a continuous range of habitat over which to feed. A habitat fragment may still contain members of a species, but the population size may be too small to sustain the species over long periods. On the other hand, habitat fragments may have a greater length of edge habitats, which may create new habitats for some species. Finally, **habitat degradation** is probably the most important potential source of loss of biodiversity (See Chapter 19). Nutrient input into estuaries of North America has caused increased phytoplankton density, which in turn has choked off light from sea grasses. Because many fishes and invertebrate species depend upon the sea grass as a structural habitat, many species are lost when sea grasses disappear. Toxic substances tend to eliminate sensitive species and leave a hardy residue of fewer species. Degraded marine environments are typically species-poor environments.

✳ The species–area effect might be used to predict the loss of species, but an understanding of habitat and biogeographic effects is crucial as well.

Earlier in this chapter the species–area effect was introduced, whereby the total number of species in a region can be predicted approximately through a knowledge of habitat area. Robert H. MacArthur and Edward O. Wilson[5] suggested that the number of species on an island (this can generalized to larger areas of land or ocean) is a dynamic balance between arrival of species and extinction. Larger areas receive more species per unit time and have lower extinction rates; they therefore maintain more species than do smaller islands. The arrival of species may stem from colonization, or "arrival" may mean speciation within the area.

To some degree, therefore, the degree of habitat destruction might be used to predict the loss of species. Destruction of coral reefs, for example, might be used to predict loss of coral-dependent species, if one knew the degree of loss of total reef areal extent. Such an approach, however, would have to be modulated by knowledge of effects on habitat loss. Species might not be lost in proportion to area, for example, if some species can be supported on very small habitat fragments. Alternatively, larger top carnivorous fishes— which require large foraging areas and are more sensitive to extinction owing to smaller population size— might be lost even faster than the general species–area relationship would predict. Biogeographic provincial structure may also have an important influence on loss of species. In marine habitats where there are many biogeographic zones, loss of habitat may have far stronger effects than it does in habitat types where there are provinces of greater geographic extent.

✳ Introductions of ecologically potent species may cause local extinctions and a homogenization of the world marine biota.

Increasingly, marine commerce is delivering exotic species over great distances, which is causing major changes in marine communities around the world. The few excellent colonists have the potential of homogenizing the between habitat diversity of our coastal environments. In Chapter 14, the tremendous colonization potential of species of the marsh grass *Spartina* was discussed, as was the disruption of a great many coastal habitats. The recent arrival of the ctenophore *Mnemiopsis leidyi* in the Black Sea resulted in the loss of a number of zooplankton and fish species. Owing to these trans-oceanic movements, the world's coastal biota is losing its individual differences. For example, all of the dominant hard-bottom intertidal species of San Francisco Bay are now exotics; local species have become extinct.

Conservation Genetics

✳ Genetic approaches can be used to identify species and to identify genetically distinct populations within species.

We have come to appreciate that many marine species have been overlooked completely, partially because morphological similarities often mask complete reproductive separation and independent evolutionary histories. In recent years a number of molecular techniques have greatly improved our ability to discriminate among species. DNA sequencing is now becoming the routine means of identifying new species.

It is also important to be able to identify genetically distinct populations that belong to the same species. Consider baleen whales, whose geographic range is often worldwide. If a humpback whale is hunted in Australia, will that affect the New Zealand population? If summering whales in one part of Antarctica are killed, will that affect the population of whales throughout the world, or just a section of the population that migrates to a specific place? For example, eastern Pacific humpback whales appear to have a population that migrates between Hawaii and Alaska, and another population that migrates between Mexico and California. DNA differences demonstrate that

5. See MacArthur and Wilson, 1967, in Further Reading.

Table 17.2 Some major programs and legislation now being used to conserve marine biodiversity.

Program or legislation	Major objectives
National Marine Sanctuaries Program	Identifies and provides management programs to protect important and potentially endangered marine habitats (e.g., Channel Islands off California, Flower Garden Banks in the Gulf of Mexico)
National Estuarine Research Reserve System	Identifies estuarine sites important in long-term ecological research (e.g., Hudson River estuarine reserve)
National Wildlife Refuge System	Identifies areas where wildlife is especially valuable, especially those in which species or migratory-bird sites are threatened by extinction
Endangered Species Act	Identifies species that are in danger of extinction (marine species identification is not well developed as yet)
Marine Mammal Protection Act	Is intended to halt the decline of marine mammal species and to restore populations to healthy levels
Fisheries Conservation and Management Act	Is intended to prevent decline of fisheries within 200 miles of U.S. coast, especially with regard to foreign fisheries (and did not work; See Chapter 18)

these two populations are, in fact, genetically distinct. The populations must therefore be managed separately.

Genetic markers also have been very useful in proving that the hunting of loggerhead turtles in the western Mediterranean was the cause of decline of the nesting population in the southeastern United States. It is now possible to trace hunting to its effects on populations in distant places. This is quite useful for cetaceans and turtles, both of which have species with long-distance migration. Management of the individual populations for the purposes of conservation can thus be based on a detailed knowledge of interchange of individuals among separately migrating populations. A United Nations convention has given the nation where a species nests or spawns the right to file complaints against those who hunt such species in places removed from the territorial waters of the reproductive site.

Protective Legislation

✳ Laws are now being used to protect both biodiversity and habitats.

In recent decades, a new concern for conservation has led to a variety of legislative acts that attempt to conserve biodiversity itself and to protect the habitats upon which marine species depend. Table 17.2 provides a list of major programs or legislation.

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Review Questions

1. What major factors enhance speciation in the sea?

2. What has caused groups of coastal marine species to have rather similar biogeographic ranges?

3. Describe four consistent gradients or regional differences in species diversity.

4. How might long-term historical factors and shorter-term ecological interactions combine to determine species diversity in a given area?

5. How might environmental stability have contributed to high species diversity?

6. Describe the difference between the centers-of-origin theory of diversity differences and the vicariance hypothesis of the development of diversity. Is it possible to test between these two?

7. Why might regions of greater areal extent tend to harbor greater numbers of species?

8. What does the fossil record reveal about the extent of extinction over long periods of geological time?

9. What are the major processes that contribute to human influences on the loss of biodiversity?

10. How might the species area relationship allow us to predict the reduction in biodiversity, by means of estimates of the extent of habitat destruction? Why might such estimates be inaccurate?