Biodiversity is the term used to describe the rich variety of life found on Earth. It was the subject of the UNCED conference in Rio in 1992, which resulted in the signing of the International Convention on Biodiversity and the adoption of Agenda 21, which lays down the guidelines under which the Convention will operate. However, biodiversity is used to express this variety over a great range of levels of organisation. It can be applied to different types of ecosystems, or to express the number of species found locally or globally, or even to the amount of genetic variation within individual species. This can lead to confused thinking, unless the term’s precise meaning is explicitly stated in each context. Our discussion concentrates on ecosystem diversity, and species richness and dominance within local and regional areas.

Diversity at these levels of organisation is the product of evolution. New species almost always evolve as a result of a subpopulation becoming isolated from its parent population for thousands of years, and being subjected to different selective pressures. Generally, the stock of species of the world has increased linearly over geological time (based on the fossil record), although several mass extinctions have interrupted this trend (Fig 15.1). The causes of these mass extinctions are still a subject of vigorous debate. However, since the beginning of the Mesozoic era the increase has been almost linear. If we are to understand the present patterns of biodiversity in our seas, we need to appreciate, first, how and why evolution has given the world such a rich compendium of species a second, how ecological processes continue to maintain this richness.

The Origins of Disparity

The earliest traces of life that have been found so far are imprints of single-celled micro-organisms in sedimentary rocks laid down in the proto-ocean about three and a half billion years ago. The first to appear were prokaryotic cells or bacteria which have no nucleus and are termed prokaryotes. Since they have the most ancient lineage of any thing so far, these apparently simple cells show remarkable variations in their physiology, chemistry, and genetics. As we learn more about them, there are proving to be greater differences.

![Figure 15.1 Diversity of marine families through the geological record since metazoan organisms first appeared. Note the steady increase until the end of the Ordovician (O, the lower scale), when the first of the mass extinctions occurred. Then the number of families remained roughly constant until the mass extinctions of the Triassic (T) and beginning of the fragmentation of the supercontinent Pangea (see Figure 15.4). Compare the steady increase in numbers of families since the Triassic with the patterns of continental drift shown in Figure 15.4. The one interruption was the mass extinction at the end of the Cretaceous (Cr), which more-or-less coincided with the split developing between Australasia and Antarctica, and resulted in the start of circum-polar circulation in the Southern Ocean (redrawn from Sepkoski11).](image-url)
natural mass (Figure 15.2) are still being added, since the fossil record has been affected by otherwise large events that have not yet been fully documented. Precisely how many species are given here is a matter of debate and, more fundamentally, how to distinguish species from one another.

... found so many more species in one small area, and the prototype is the Cambrian. The diversity of the protists, bacteria, and fungi is impressive, but the diversity of other organisms is even greater. Some of these organisms are so small that they can only be seen under a microscope. Other organisms are so large that they can be seen with the naked eye.

... within the prokaryotes than within all other living organisms. It took another two billion years before the first appearance of single-celled organisms with nuclei – the eukaryotes. Both the nucleus, which contains the genetic information, and other organelles within the cells – the mitochondria, in which the reactions that provide the cell with energy – are thought to have originated as a result of different prokaryotes forming symbiotic associations, which through time became a permanent and obligate relationship. It was almost another billion years before the first multicelled organisms made an appearance, just before the beginning of the Cambrian era some 670 million years ago, and it was yet another 155 million years before multicellular forms began to invade the land during the late Silurian.

... Considering its much greater geological age, it is hardly surprising that the fauna of the oceans is far more disparate than the terrestrial fauna, being made up of 26 phyla – the name given to the basic types of animals (Table 15.1), compared with just the 11 phyla represented in terrestrial faunas. However, is this greater disparity also repeated in a greater species richness in the oceans compared to the richness on land?

**Terrestrial Versus Marine Species Richness**

For pelagic faunas the answer appears to be no; terrestrial faunas appear to be far richer in species. For example, the most abundant and species-rich group of plankton are the copepods (Figure 15.2), of which there are just over 1900 species known from oceanic and brackish waters. Compare this with the most diverse inhabitants of terrestrial habitats – the insects (a group virtually absent from the oceans), in which just one order, the beetles, includes several hundreds of thousands of known species, and whose true global richness is estimated to be in excess of a million. Much the same applies to the plants; there are an estimated 250,000 species of terrestrial green plants, but merely 3500–4500 in the oceans (Figure 15.3). Why are there such major differences in species richness?

Figure 15.3 Giant phytoplankton cells (1–2 mm in diameter) of the monad *Halosphaera viridis*. Apart from the large algae that grow in shallow coastal waters, virtually all life in the ocean is dependent on the photosynthetic production of the 3500–4500 species of phytoplankton. Which should receive the greatest priority for conservation, one of the few phytoplankton species or one of the quarter of a million terrestrial green plants? (© Heather Angel.)
Table 15.1 Distribution of phyla in major habitats.

<table>
<thead>
<tr>
<th>Phyla</th>
<th>Marine</th>
<th>Freshwater</th>
<th>Terrestrial</th>
<th>Symbiotic</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Benthic Pelagic</td>
<td>Benthic Pelagic</td>
<td>Moist Xeric</td>
<td>Ecto Endo</td>
</tr>
<tr>
<td>Porifera</td>
<td>+++</td>
<td>+</td>
<td></td>
<td>+</td>
</tr>
<tr>
<td>Placozoa</td>
<td>+</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Orthonecida</td>
<td></td>
<td></td>
<td>+</td>
<td></td>
</tr>
<tr>
<td>Dicyemida</td>
<td></td>
<td></td>
<td>+</td>
<td></td>
</tr>
<tr>
<td>Cnidaria</td>
<td>+++</td>
<td>++</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Ctenophora</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Platyhelminthes</td>
<td>+++</td>
<td>+</td>
<td>+++</td>
<td>+</td>
</tr>
<tr>
<td>Gnathostomulida</td>
<td>++</td>
<td></td>
<td></td>
<td>+++++</td>
</tr>
<tr>
<td>Nemertea</td>
<td>++</td>
<td></td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Nematoda</td>
<td>+++</td>
<td>+</td>
<td>+++</td>
<td>+++ +</td>
</tr>
<tr>
<td>Nematomorpha</td>
<td></td>
<td></td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Acanthocephala</td>
<td></td>
<td></td>
<td></td>
<td>++</td>
</tr>
<tr>
<td>Rotifera</td>
<td>+</td>
<td>+</td>
<td>++</td>
<td>+</td>
</tr>
<tr>
<td>Gastrotricha</td>
<td>++</td>
<td></td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Kinorhyncha</td>
<td>++</td>
<td></td>
<td></td>
<td>+</td>
</tr>
<tr>
<td>Loricifera</td>
<td>+</td>
<td></td>
<td></td>
<td>+</td>
</tr>
<tr>
<td>Tardigrada</td>
<td>+</td>
<td></td>
<td>++</td>
<td>+</td>
</tr>
<tr>
<td>Priapula</td>
<td>+</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mollusca</td>
<td>+++++</td>
<td>+</td>
<td>+++</td>
<td>+</td>
</tr>
<tr>
<td>Kamptozoa</td>
<td>+</td>
<td>+</td>
<td></td>
<td>+</td>
</tr>
<tr>
<td>Pogonophora</td>
<td>++</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sipuncula</td>
<td>++</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Echiura</td>
<td>++</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Annelida</td>
<td>+++++</td>
<td>+</td>
<td>++</td>
<td>+++</td>
</tr>
<tr>
<td>Onychophora</td>
<td></td>
<td></td>
<td></td>
<td>++</td>
</tr>
<tr>
<td>Arthropoda</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Crustacea</td>
<td>+++++</td>
<td>+++</td>
<td>+++</td>
<td>++</td>
</tr>
<tr>
<td>Chelicerata</td>
<td>++</td>
<td>+</td>
<td>++</td>
<td>+++ +</td>
</tr>
<tr>
<td>Uniramia</td>
<td>+</td>
<td>+++</td>
<td>+</td>
<td>+++ ++</td>
</tr>
<tr>
<td>Chaetognatha</td>
<td>+</td>
<td>+</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Phoronida</td>
<td>+</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Brachiopoda</td>
<td>++</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bryozoa</td>
<td>+++</td>
<td></td>
<td>+</td>
<td></td>
</tr>
<tr>
<td>Echinodermata</td>
<td>+++</td>
<td></td>
<td>+</td>
<td></td>
</tr>
<tr>
<td>Hemichordata</td>
<td>+</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Chordata</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Urochordata</td>
<td>+++</td>
<td>+</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cephalochordata</td>
<td>+</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Vertebrata</td>
<td>+++</td>
<td>+++</td>
<td>++</td>
<td>+++ +</td>
</tr>
</tbody>
</table>

'Pluses' indicate approximate abundance of living described species:

- $+ = 1-10^2$
- $++ = 10^2-10^3$
- $+++ = 10^3-10^4$
- $++++ = 10^4-10^5$
Factors Leading to Speciation

New species tend to evolve when populations are split and isolated. Isolation in both marine and terrestrial environments can arise from tectonic events, resulting from the drift of the continents altering the shape and morphology of ocean basins, and forming new islands and mountain ridges. Over the past 175 million years, plate tectonic movements have resulted in major redistributions of the land masses (see Chapter 20). Since the pattern of large-scale thermohaline circulation of ocean currents is determined by the interaction between the shape of the oceans and wind patterns (Chapter 2), ocean circulations during the geological past can be reconstructed with confidence. In the modern ocean, the distributions of major pelagic ecosystems match the patterns of the major ocean current gyres, and are likely to have done so in the past (Figure 15.4). Analyses of the present-day distributions of some of the more ancient families and genera of pelagic organisms reveal persistent echoes of these ancient circulations.

In addition to these major changes to ocean-basin morphology, other events have had major impacts on the distribution patterns of species. During the Miocene, for example, the Straits of Gibraltar repeatedly closed and opened. Each time the straits closed the sea dried out, leaving behind vast deposits of salt that today still underlie a drape of pelagic sediments beneath the Mediterranean Sea. When the Straits re-opened the sea catastrophically reflooded, lowering sea levels globally by tens of metres within relatively few years, maybe centuries. Such catastrophic lowering of sea level caused the deaths of many shallow-living species, and probably led to many extinctions. Another such event was the opening of the Isthmus of Panama about ten million years ago, which allowed the exchange of shallow-living faunas between the Pacific and Atlantic Oceans. As a result, many shallow-living tropical families, genera, and even species have circumequatorial distributions.

Throughout the Quaternary sea levels fluctuated by around 100 m as a result of the alternating glacial and interglacial stages, which appear to have been a response in the Earth’s climate to
eccentricities in its orbit around the Sun, the so-called Milankovitch cycles. Around the East Indies, in particular, fluctuating sea levels resulted in connections between the islands appearing and disappearing, so that the deep basins between the islands were isolated and then reconnected. Consequently, populations both on land and in the coastal seas were divided and then recombined.

This led to a series of biogeographical divisions between the islands’ faunas and floras, such as the Wallace’s, Weber’s, and Lydekker’s Lines, which are reflected, to some extent, in the marine faunas as well. Similarly, in the Mediterranean there are glacial relict species which entered the sea during the most recent glaciation and are now not only totally isolated from their parent stock in the North Atlantic, but are also living in very different conditions.

During the past 22,000 years, since the height of the latest glaciation (note that recent calibrations of $^{14}$C dating methods have resulted in this time interval being increased from 18,000 years), it is probable that at least some of these relicts have diverged sufficiently to become genetically incompatible. Thus, the isolation between populations in the ocean, that in time results in their diverging and evolving into new species, tends to be related to large-scale and persistent events.

Figure 15.5 Changes in the numbers of pelagic species sampled across the shelf, shelf-break, and continental slope off Florida in the Gulf of Mexico: A, copepod; B, mid-water fish; C, decapod crustaceans; and D, euphausiids. For these four pelagic taxa the numbers of species increase offshore and often peak at or close to the shelf-break (modified from Hopkins et al.).

**Fine-Scale Habitat Variability**

Such large-scale events play an equally important role in speciation on land, but in addition there are much finer-scale processes at work. These result from terrestrial ecosystems being more finely structured, with much greater development of microclimates, and dispersal between the different patches being much more restricted. The physical structure and aspect of the landscape, the types of soils, and the availability of water and nutrients all contribute to the creation of fine-scale habitat mosaics in terrestrial ecosystems. These patches are dynamic; for example, forest clearings are created by trees dying or being razed to the ground by violent storms.

Animals and plants vary in their abilities to disperse, so populations of a given species may become isolated as the patches become too far apart for individuals to move between them, or a phenomenon such as a landslide or lava flow creates an impassable barrier. So, even within a mosaic of habitats, similar patches may be supporting slightly different assemblages of plant and animal species.

Since the dominant terrestrial plants are larger and longer-lived than their marine counterparts, many have co-evolved with invertebrates, especially with insects; for example, in Britain the oak tree alone has about 600 insect associates. Moreover, terrestrial plants by their physical presences, as well as their physiological activity, modify the habitats they inhabit; the environment inside a wood is very different from that immediately outside.

There is some similar modification of habitats by the biota in the sea (for example, around coral reefs, in kelp forests, and over mussel beds), but the creation of such three-dimensional habitat structures by the organisms themselves is almost entirely limited to shallow coastal waters. The hermatypic corals, which create much of the structure of coral reefs, are limited to depths where their symbiotic algae can obtain enough light to photosynthesise.

In shallow seas, even where there is no biological structuring of the environment, the complex interactions between tides, waves, and the coastal morphology and geology create much finer-scaled mosaics of different habitats than occur in open-ocean habitats, particularly pelagic ones (see Chapter 16). A sampling transect across a continental-shelf sea and into the open ocean reveals rel-
pelagic species and continental species; A, copepods; B, salps; C, mesozooplankton; D, fish larvae; E, the numbers of species are at a given location over the shelf and a sharp increase in the number of species just beyond the shelf-break (Figure 15.5). However, if the sampling is extended to become regional in its coverage, the number of species caught inshore soon begins to exceed those caught in the open ocean; oceanic habitats are large-scale, whereas inshore and coastal habitats (which range from muddy estuaries to sandy shores and rocky beaches) are much finer in scale.

Another feature of coastal habitats is that they are geographically linear, so any break caused by a large estuary, a strait, or even a major piece of coastal engineering can act as a barrier to the dispersal of some taxa. Most (but not all) of the species which live between the tides or in association with the sea bed have dispersal phases as planktonic larvae, which may last from a few days to several months. Those with short planktonic phases, or none at all, may not be able to cross these barriers because of the prevailing currents. As a result, taxa which inhabit coastal waters are much more restricted in their distributions and are globally more diverse than similar taxa inhabiting the open ocean. This trend is illustrated below.

Recently, some human activities have begun to break down some of these barriers to distribution, with serious implications for the maintenance of marine biodiversity. For example, the building of the Suez Canal has led to increasingly large numbers of species entering the Red Sea and the Mediterranean. More recently, evidence has emerged that the transoceanic transportation of coastal species in the ballast waters of fast cargo vessels is disturbing local faunas.

**Gradients and Ecotones in the Oceanic Water Column**

In the water column of the deep ocean, there are important vertical gradients in many chemical and physical properties, including temperature, salinity, nutrient and oxygen concentrations, light, and hydrostatic pressure. The primary production on which all life depends is almost entirely restricted to the surface 100 m or so, where there is sufficient sunlight for photosynthesis (the chemosynthesis which occurs in the immediate vicinity of hydrothermal vents is the main exception, see Chapter 10). Only about 1–3% of the organic matter produced by photosynthesis at the surface reaches the sea bed at depths of 4000 m. So, the general availability of food declines exponentially and depth profiles of biomass show that the pelagic biomass at a depth of 1000 m is a tenth that at the surface, and declines by another tenth at 4000 m (Figure 15.6). The only place that these vertical gradients combine to be steep enough to act as a barrier to the dispersal of a few species is across the seasonal thermocline. But even there some of the vertically migrating species are uninhibited in their movements, as they commute daily from the safety of day-time depths of 500 m or more, to spend the night feeding in the surface waters. During these migrations they may experience greater changes in temperature than occur throughout the year in the surface waters.

Horizontal gradients are almost always weaker, even at boundaries between different water masses, such as at the Antarctic Convergence. The one possible exception is in upwelling areas, where boluses of cold subthermocline water that have upwelled to the surface can create very sharp sea-surface temperature discontinuities. However, such fronts are far too ephemeral to have a long-term influence on diversity. Otherwise, the continual stirring of the water by currents and eddies blurs all such boundaries. As a result, there are almost no clearly defined ecosystems in pelagic environments; the assemblages of animals which merge almost seamlessly across the gradients are described as ecotones. Locally, patchiness and variability is high,

![Figure 15.6](image-url)
but this is not translated into large-scale variability.

Over the time-scales that are important to the creation of biodiversity, ocean waters mix rapidly; in the Atlantic and the Indian Oceans the waters exchange every 250 years and in the Pacific about every 500 years (see Chapter 3), times which are extremely short for evolutionary changes. So, perhaps a pertinent question is ‘Are all pelagic taxa in the open ocean completely cosmopolitan?’ It should be no surprise to find that they are, indeed, far more cosmopolitan than their benthic or coastal counterparts.

Specialists Versus Generalists

Another factor that may help to keep the numbers of pelagic species low is the lack of opportunity to specialise, to become adapted to a narrow range of environmental factors or a specific source of food (for example, many insect species are associated with a single food plant in terrestrial habitats). Palaeontologists have observed in the fossil record that specialist genera have much higher rates of turnover (extinction and speciation) than do generalist genera. In the pelagic realm, habitat variability is considerable over all spatial scales, being dominated by the changing conditions induced by oceanic turbulence and meso-scale eddies (see Chapter 4); this seems to have maintained a strong selective pressure for pelagic species to remain tolerant of these changes and hence remain as generalists.

Similarly, species inhabiting latitudes where the production cycle is more seasonal have less opportunity to specialise than do those inhabiting environments where the supply of food is more uniform and continuous. As always, there are some exceptions to every generalisation (Figure 15.7 illustrates one). In addition, in the oceans food-web relationships appear to be very differently structured, tending to be based more on size of ‘particle’ than on quality. Thus, an individual may occupy very different niches throughout its life cycle, changing not only what it feeds on, but also the depth at which it lives. Terrestrial species tend to be much more conservative in the role they play in food-webs and the space they occupy.

The contrast in species richness between oceanic and freshwater communities is indicative. Freshwater environments are more fragmented and over geological time-scales, ephemeral. But freshwater microhabitats are distinct and favour specialisation; in the great lakes of Africa some of the fish are believed to have speciated within the past 50 years. Freshwater biomes contain a tiny fraction of the Earth’s water and occupy a minute area of the land surface, and yet global species-richness of freshwater taxa is much greater than that of marine taxa. Moreover, given long-enough geological continuity, local species-richness can be exceptionally high. For example, in the catchment of the River Zaire there are over 690 species of fish, of which 84% are endemic, not so very many fewer than are known from the world’s deep oceans. These freshwater fish are often highly specialised in their ecological requirements and have been reported to speciate within a few hundreds of years.

In oceanic fish, the main adaptations appear to be related to predator avoidance and finding enough food within specific depth zones; in an environment where hydrostatic pressure increases, the light environment changes systematically (Chapter 14), and availability of food decreases with increasing depth. In the tropics, water temperature may change more in 1 km vertically than in 2000–3000 km horizontally. So, as depth increases, there are systematic changes in both pelagic and benthic species composition, and in their physiological and morphological adaptations. If horizontal
gradients in the ocean were as strong as those in the vertical, then diversity in the ocean might be expected to rival that of the land.

Where is Species Diversity Highest in Marine Communities?

This is not a straightforward question to answer, partly because very few surveys attempt to identify all the taxa present, even within the limited size range of organisms collected by a single sampler. Moreover, for certain size ranges known to be highly speciose, such as benthic macrofauna and meiofauna, the systematics of most of the component taxonomic groups are far too sketchy for inter-regional comparisons to be meaningful. Another problem which militates against making sensible inter-regional comparisons is the lack of standardisation of sampling methods and protocols of analysis. With the added problems created by the absence of any international databases incorporating taxonomic information, it is well-nigh impossible to compile all the relevant data; the true difficulty of making even rough attempts at answering this very basic question is all too apparent. For limited areas in which standardised sampling and analytical procedures have been used, and for those groups for which the numbers of species appears to be well-known and for which the systematics have remained quite stable, comparisons are possible.
coastal, or inshore waters, or are associated with the sea bed. There are a few open-ocean pelagic mysid species, which, as might be expected, are far more cosmopolitan than their shallow-water relatives. The total of euphausiid species described up to 1994 is 86, and this is likely to be close to the actual total number in the world ocean. In contrast, the number of known mysids species (983) has continued to increase steadily as more coastal faunas around the world are studied, and the list must still be far from complete. This, of course, assumes that the presence of numerous cryptic species (those which cannot be separated using traditional morphological characters, but which are distinguished using molecular biological techniques) will not be revealed when the genetics of euphausiid species are investigated.

There is also an interesting contrast between the pattern of distribution of the mysids and that of the euphausiids. Figure 15.11 shows one way of dividing up the world’s seas into biogeographical regions, together with the numbers of mysid species known from each. There is a suggestion in the southern hemisphere of there being a poleward latitudinal decrease in the numbers of species present. However, this may result either from the relative undersampling of the Southern Ocean regions, or because there are fewer and less varied coastal areas around the Southern Ocean than at similar latitudes in the northern hemisphere. Similarly, the high numbers of species around Japan and the South China Sea may, indeed, be a true reflection of the richness of the mysid fauna in this region relative to all the others — a richness that could be a result of either the Pleistocene oscillations of sea level or the rich variety of coastal environments in the island archipelagos of the region. However, it may also be an artefact resulting from the particular fascination the group has had for Japanese taxonomists. Figure 15.12 shows the numbers of species of both mysids and euphausiids inhabiting one or more of the regions shown in Figure 15.11. It is the pelagic, open-ocean species that are trans- and inter-oceanic in their distributions and so occur in several of the zones, whereas most of the coastal, inshore, and littoral species are restricted to a single region. In the euphausiids, only 11 of the 86 species are neritic (10 of these 11 are restricted to a single region), whereas the vast majority of the 75 oceanic species occur in more than one region. Compare this with the 720 species (73%) of mysids which inhabit coastal inshore waters and occur in just one region.
**Seasonality**

The latitudinal limits at 40° for the regions in Figure 15.11 represent a significant change in the ecology of the oceans. This is the approximate poleward limit of oceanic waters in which the near-surface 100 m remain thermally stratified throughout the year. During winter at higher latitudes, the surface layers are cooled sufficiently for deep mixing to break-up the stratification and to renew supplies of nutrients in the surface waters. As a result, at temperate and subpolar latitudes not only is there a marked seasonal cycle in the primary production, but also the mean annual primary production is higher. At temperate latitudes, the production cycle is marked by a sharp increase in production in the spring, which occurs as the seasonal thermocline begins to be re-established. In most years there is often another smaller peak in production in the autumn, after the equinoctial storms have started to erode the thermocline but not destroyed it.

These increases in production may or may not be accompanied by a sharp increase in the standing crop of phytoplankton, i.e., a bloom (Chapter 6). Such blooms can be readily detected in cloud-free conditions by colour scanners in satellites (Chapter 5). Using satellites to record the timing of the blooms has shown that towards subpolar and polar latitudes, the spring and autumn blooms converge to form a single summer peak. Following close after these peaks in production are peaks in sedimentary fluxes, which transmit the products of seasonal events in the surface waters to the benthic communities (Chapter 7). Generally, on the equatorial side of the 40° latitude line, production is not only far less variable seasonally, but is lower, except in upwelling regions where the physical conditions result in deep nutrient-rich water being mixed or upwelled toward the surface.

The annual amount of secondary production (i.e., how much animal growth occurs) is related to the amount of primary production, although the ecological efficiency with which material and energy is transferred from plants to herbivores and on to carnivores and the consumers of detritus varies between different ecosystems. Likewise, the standing crop of biomass also shows some relationship to primary productivity, but tends to be higher where the production cycle is markedly seasonal.
These shifts in the annual levels and seasonality of production must play some role in the maintenance of diversity in the communities.

**Latitudinal Trends in Species Richness**

Species lists often indicate that tropical and subtropical faunas are richer in species than are temperate and boreal faunas. However, the crude distributional data for the euphausiids and the mysids presented in Figure 15.11 give little indication of how these environmental changes may affect their diversity.

More detailed data are available for planktonic ostracods (Figure 15.13) which, while having the advantage of being sampled using the same technique and also analysed with the same protocols, are limited to the North Atlantic. Plots of the numbers of ostracod species caught in the top 2000 m within contiguous depth strata (100 m in the top 1000 m and coarser between 1000–2000 m) at stations between 10°–60°N along 20°W (Figure 15.14) show that relatively few species are caught near the surface, and the numbers increase with depth to reach a maximum at around 1000 m. This is quite different to the trend for biomass (Figure 15.6).

When these profiles of species number are superimposed a clear latitudinal trend emerges. At all the depths sampled, the ostracod communities are richer in species at latitudes <40°N, and are appreciably poorer at higher latitudes.

Analysis of the total numbers of species caught in three other pelagic groups in the same set of samples shows a similar latitudinal trend (Figure 15.15), although from these data it is impossible to determine whether the decrease across 40°N is smooth or stepped. This latitudinal trend in species richness runs counter to the trends in total annual productivity and integrated pelagic biomass along this transect. The maximum in numbers of species occurred near 18°N. At the time of the sampling, the boundary between the South and North Atlantic central waters was very close to this locality, and the communities included a mixture of both southern and northern faunal elements. Since this boundary moves latitudinally by 1° or so, it seems likely that this maximum in species richness will move with it.

**Figure 15.14** Profiles of the numbers of planktonic ostracod species throughout the surface 2000 m along 20°W in the northeast Atlantic, showing how at latitudes <40°N there are more species at all depths than at higher latitudes. The change in average species richness appears to occur at the southern boundary of seasonal turnover in the near-surface waters, and in the regions where there is a spring peak in phytoplankton production.
Species Richness in Benthic Communities

The depth profiles of species numbers for four taxonomic groups of benthic megafauna from the Porcupine Seabight region off southwest Eire (Figure 15.16) show much the same trends as for the pelagic ostracods, with peaks in species richness at around 1000 m in three of the groups. However, the data for decapod crustaceans appear to be somewhat anomalous because the most species-rich group, the brachyuran crabs, is almost entirely limited to shelf and upper-slope depths.

Earlier data from the eastern seaboard of the US for four groups of macrobenthos (i.e., animals passing through 4 mm but retained by 1 mm sieves) — polychaetes, gastropods, proetobranchs, and cumaceans — implied (on the basis of a statistical method for comparing the numbers of species in samples of different sizes) that the maximum occurred in these groups rather deeper, at about 1-2 km depth (IOSDL database).
2000–3000 m (Figure 15.17). As for pelagic communities, both benthic biomass and the density of organisms decrease almost exponentially with depth (Figure 15.18), with a 10% reduction in biomass between 200 m and 2000 m; so, once again, the link between productivity and diversity is not straightforward, since the peak in species richness occurs where the biomass of the benthic community has fallen to nearly a tenth of that at the shelf-break.

Some recent evidence suggests that the species richness of benthic assemblages may match the rich disparity and may even be on a par with that of tropical rain forests. An intensive programme of sampling the benthic communities living on the sea bed at depths of 2000 m off the east coast of the US, involving the analysis of over 200 grab samples, revealed the presence of nearly 800 different species, of which over 50% were new to science. When the sampling was extended both northward and southward along the slope, an extra species was added for each extra square kilometre that the sampling programme covered. If that rate is maintained throughout the global ocean, then the numbers of benthic species would be approximately equivalent to the area in square kilometres of the ocean floor – over 300 million. Moreover, this study did not include the meio-benthos, which contains the two most speciose groups in the oceans – the nematodes and foraminifers. Over 100 species of each of these groups were found in a cubic centimetre of mud scraped off the surface of the sea bed at a depth of just over 1000 m off the southwest of Ireland.

No one really knows how to extrapolate from the results of a few very localised samples to give a credible estimate of how many species occur on Earth, or even if this is possible. Many benthic species appear to have very extensive geographical distributions, so estimates that they exceed a million might seem excessive, but are they? It is worth noting that the huge estimates of the numbers of species inhabiting tropical rain forests are based on similar extrapolations from data obtained by misting just six trees with insecticides, and so are equally lacking in credibility! But perhaps, in this case, the extrapolations are not so wildly excessive given the very large numbers of plants, especially trees, that occur in rain forests and the strong ecological links between the plants and specialist insects.
Effects of the Seasonality on Benthic Diversity

Are changes in the production cycle reflected in changes in benthic diversity? We know that at temperate latitudes, where the production cycle is highly seasonally pulsed, the amounts of detrital material reaching the sea bed vary seasonally (Chapter 7). So, once again, we expect there to be substantial change in the benthic communities at latitudes of around 40°. Each year the deep-sea bed to the west of Britain, at depths of 4000 m, becomes carpeted with detrital material 6–8 weeks after the onset of the spring bloom. This provides a food bonanza for the bottom-living animals, some of whom appear to specialise in exploiting this detritus. No such bonanza is seen further south, either at 30°N on the Madeiran Abyssal Plain or at 20°N on the Cape Verde Rise. The animals which specifically feed on these detrital falls are missing at these latitudes, and there appears to be insufficient food available to support some of the larger animals.

So each region is inhabited by a different assortment of animals, with much fewer large species at the more southerly sites. For example, sea cucumbers – the holothurians – which are animals that feed on the enriched surficial sediment layer, become rare where the sedimentary flux is too low. So their species richness runs counter to the expected latitudinal trend seen, to some extent, in other groups (Figure 15.19). Fish abundances are also sharply reduced at the lower latitudes, but the specimens there belong to an unexpectedly rich assortment of species. The numbers of species taken in the limited sampling that has been done are lower than those taken at temperate latitudes. However, a comparison of the species counts in samples of a standard size indicate that sample diversity is as high as, if not higher than, those at temperate latitudes.

The difficulties of drawing generalisations are further illustrated by recent results comparing macrobenthic communities from undisturbed soft muddy sediments at depths of 30–80 m off Spitzbergen (78°N), in the North Sea (55°N), and off Java (7°N), all sampled and analysed using exactly the same methods.7 The results show that the diversity profiles at all three sites were indistinguishable, and gave no indication of a latitudinal trend (Figure 15.20). Is this observation merely a quirk of history? In other words, were the investigators unfortunate in choosing sites where, by chance, evolutionary history had resulted in the diversity being identical. This solution seems far-fetched, but is testable by repeating the comparison elsewhere. An alternative explanation might be that the processes that maintain the diversity at these three locations are not influenced by latitudinal forcing. For example, in such muddy environments, is there always an unlimited amount of organic matter around, irrespective of the production cycle?

Diversity and Productivity

There is an apparent paradox in the trends in pelagic diversity with depth and geographically, which run counter to the trends in productivity and biomass (standing crop) of animals, certainly in the water column and maybe on the sea floor. Populations in low-productivity regions seem to be characterised by being rich in species-richness without any one or two species being overwhelmingly dominant. In contrast, where productivity is high (and often more variable seasonally) far fewer species occur and one or two species tend to be numerically dominant. Does this explain why, when we fertilise the seas with our sewage and with the agricultural run-off of dissolved nitrates and phosphates in our rivers, the local productivity goes up, but the numbers of species goes down (a process called eutrophication)?
Figure 15.19 Numbers of three macrobenthic taxa expected to be caught in samples of 5 specimens from deep-ocean basins in the Atlantic Ocean: (a) isopoda, (b) gastropoda, and (c) bivalva (modified from Rex et al.53).

Figure 22.3 shows the effects of several decades of dumping sewage sludge off Garrock Head in the Clyde on the biomass, number of species, and number of specimens of benthic animals across the dump site, with the central position showing a massive increase in specimens, a smaller increase in biomass, and a sharp reduction in numbers of species. Is such an impact the consequence of ecological disturbance regardless of its nature? It warns us that if we concentrate all our efforts on conserving those regions richest in species, then we will run the danger of allowing degradation to go unchecked in those regions where ecological processes are most important in keeping the Earth habitable.

Postscript – Genetic Diversity
One important type of diversity, genetic diversity, has received no mention in this chapter. Populations living in stable environments are expected to have low genetic diversity, in that they show relatively little variation in their DNA and hence in the structure of their proteins and enzymes. When observations were first made on oceanic species the results were expected to reveal very low levels of genetic heterogeneity, but the outcome has been quite the opposite. The genetic variability within pelagic oceanic species is proving to be among the highest. There are numerous hypotheses to explain this high variability, but little in the way of proof. For example, are the mesoscale eddies so prevalent in the ocean persistent enough to select different genetic strains, but not to
keep them isolated? Is this why pelagic species, despite having wide geographical ranges, do not show a greater tendency to split into races and subspecies? Or should the species concept be modified in some way to account for how oceanic populations diverge and recombine?

On land, within time-scales of millenia, geographical localities are fixed, but in the ocean ‘place’ is dynamic and so has much less significance, even for the many benthiic species which have a dispersive phase to their life history. Genetic studies have hardly begun to scratch the surface of these problems. The removal of barriers to dispersion through human introduction, either purposeful for mariculture or by accident in the ballast waters of large bulk-carrying vessels, may well have a far greater impact at this level of organisation than we are prepared for, but will it matter? There is still so much to understand before we can evaluate whether maintenance of biodiversity in the oceans is a cause for real concern or a red herring.

**General References**


**References**


