DIVERSITY OF MARINE SPECIES

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Overview

The oceans comprise the largest habitat on Earth, both in area and in volume. Some 70.8% of the Earth's surface is covered by sea water, making marine benthos (bottom-living organisms) the most widespread collection of organisms on the planet. Pelagic organisms (organisms that live in the water column above the bottom) occupy the sea water that fills the ocean basins, which represent some 99.5% of occupied habitat on Earth. Within these benthic and pelagic environments, there is a wide variety of habitat types from tropical to polar latitudes, that ranges from the narrow band of rocky intertidal to open ocean surface waters to vast plains of muddy sediments on the deep-sea floor. Patterns of species composition and diversity vary considerably among habitats (**Figure 1**), although our understanding of these patterns is limited. Given the range and size of the habitats that occur in the oceans, this article will focus primarily on habitat and species diversity, while acknowledging the importance of genetic diversity.

Within the oceans, the major variables that delimit distributions of organisms include tidal exposure, temperature, salinity, oxygen, light availability, productivity, biotic interactions, and pressure. For benthic organisms, substrate composition (rock, gravel, sand, mud, etc.) also plays a key role. Not all of these variables play the same role in different environments but the sum total of their interactions determines biological pattern in the oceans.

Within the pelagic realm, organisms such as fish and whales are strong swimmers and can make significant headway against currents (nekton),

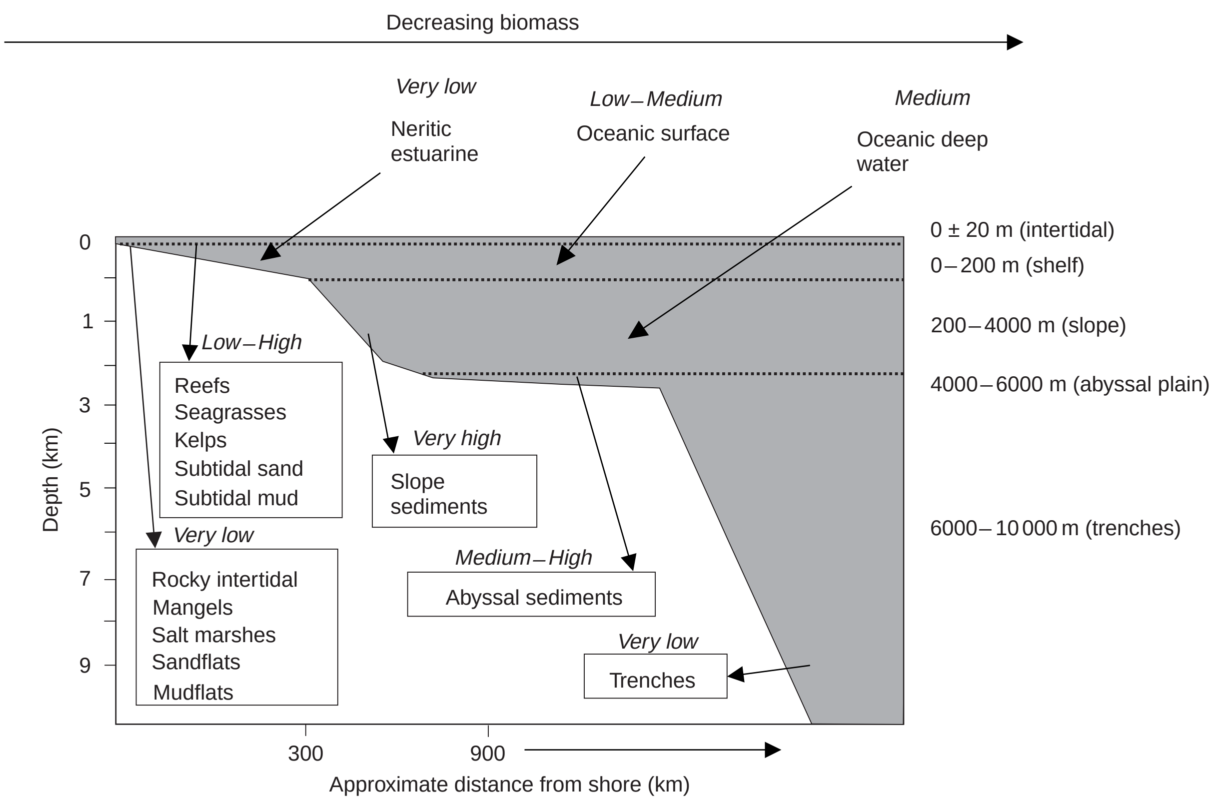

Figure 1 Diagram indicating different marine habitats. In relative terms, the horizontal axis is greatly compressed; it should also be noted that some continental margins are much narrower than the example shown. Bottom habitats are shown in the lower left boxes and water column habitats are shown in boxes near the top of the figure. Above each habitat name, a relative estimate of diversity within the different habitats is shown, but these comparisons are only generalities for which there are important exceptions. Coral reefs are almost always highly diverse.

whereas planktonic organisms, such as single celled and chain-forming algae (phytoplankton) and gelatinous forms (jellyfish, comb jellies, salps) drift passively with the predominant currents. Distributions of organisms are regulated by water mass characteristics such as salinity and temperature, water depth, and productivity; productivity varies with geography and depth in the water column. Life in the benthic environment is very different. Many benthic organisms have either limited mobility or are completely sessile. Much of their dispersal process occurs at the larval stage, which is planktonic for many species. The nature of the ocean bottom is a critical factor in determining the species that reside upon it. Species that attach to rocky substrate rarely occur in sediments, and species that occur in sands are usually relatively rare in mud. Shallow areas of the near-shore may be densely vegetated whereas deep-sea bottoms completely lack plant structure or photosynthetic primary producers of any sort.

The Organisms

The number of described plant species in the oceans is relatively modest. Vascular plants, such as those found in seagrass beds, mangrove forests (mangels) and salt marshes, are few in number (~45 described species of seagrasses, for example), and the numbers of these species that co-occur at a given site are few. Described species of phytoplankton (~3500–4500) are considerably higher than for marine vascular plants, but by comparison with terrestrial plants (~250 000) the numbers are also modest. There has been some suggestion that phytoplankton taxonomists have tended to lump species, and that the number of described species in some groups is significantly less than the actual number of species, but this possibility has not yet been resolved.

Defining species is even more problematic in marine microbes, a group for which it is believed that we have not yet even begun to describe their species numbers. In the past, species were defined based on characteristics of populations grown in culture. Recent advances in molecular biology have indicated that there are vast numbers of species that are completely missed with this approach, and that a small volume of sea water or sediment may contain tremendous microbial diversity.

Invertebrates comprise most of the described diversity in the oceans. Some field researchers studying invertebrate communities subdivide the fauna into size groupings, rather than along strict taxonomic lines. Benthic ecologists define megafauna as animals that can be identified from bottom photographs; macrofauna are those that are retained on a 300 μm sieve; meiofauna are those that are retained on a 44 μm sieve; and microbes are organisms that pass through a 44 μm sieve. Similar size groupings are used by plankton biologists. Examples of megafauna are fish and crabs, whereas macrofauna include polychaete worms, amphipod crustaceans, and small clams. Meiofauna include nematodes, small crustaceans, and foraminifera. Microbes include bacteria and protistans. In the past, larger organisms such as vertebrates have generated the greatest interest in terms of marine biodiversity and conservation, but in recent years the concern for smaller invertebrate and single-celled organisms has increased with the recognition that they form the bulk of the global species pool.

Sampling Biodiversity

Organisms are subdivided on size out of practical necessity, in that the sampling approach and sample size that are appropriate for one group are often inappropriate for another. For megafauna living in the bottom or in the water column, trawls and nets of various sorts are used. In some cases, photographic identification is also used, but if a high degree of taxonomic resolution is desired then this approach is only useful for larger organisms. Similarly, acoustic devices use sound waves to estimate abundances of megafauna over comparatively large swaths of the ocean (hundreds of square kilometers can be covered in a day), but the taxonomic resolution is again poor and the approach has only limited utility for benthic habitats. For macrofaunal and meiofaunal groups, net samplers or pumps are used in the water column, and various types of grabs or corers are used to sample marine sediments. For microbial groups, a single cubic centimeter of sediment may typically contain 10^6 bacteria and it is clear that different sampling approaches are needed for different groups of organisms; typically, small water samples are collected for pelagic microbes whereas subsamples of bottom cores are typically taken for benthic microbes. The disparity in appropriate techniques for different size groups of organisms has contributed greatly to the paucity of studies on more than one taxonomic size grouping at a given locale.

Unfortunately, where conflicting conclusions have been drawn about patterns in different groups of organisms, it is rarely possible to know whether the patterns truly vary among groups or merely reflect differences in sampling efforts.

Coastal Environments

The shallowest marine environments are those forming the transition between land and sea, and include intertidal habitats that are regularly exposed to air, full sunlight, rapid changes in salinity and temperature and, at higher latitudes, ice abrasion. The best studied of these environments are rocky intertidal habitats, but sand- and mudflats, salt marshes, and mangels (mangrove communities) are other intertidal environments that occur at the land–sea interface and are alternately flooded with sea water, and then exposed to high temperatures, desiccation, and potentially hypersaline conditions. Intertidal habitats, because they are physically harsh environments that require specialized adaptation, are relatively low in diversity, although the modest numbers of species that are present are often represented by many individuals.

Mangroves comprise globally only ~ 50 species, and within a given area only one or two mangrove species may be present, but mangels contribute to local diversity patterns by creating habitat for marine and terrestrial species. Mangroves are limited to tropical waters, and in temperature and boreal latitudes a similar niche is filled by salt marshes. Marshes and mangroves are also extremely productive habitats, and although some of the detritus resulting from breakdown of the plant materials is exported to, and diluted in, the adjacent shelf system, decomposition of large amounts of this detrital organic matter can occur in bottom sediments within the marsh or mangel. As a general rule, near-shore environments that are highly productive are often relatively low in diversity. This is true of primary producers, which are often dominated by only a few species as occurs in marshes and mangroves, but also in near-shore areas where phytoplankton thrive under high nutrient conditions. The benthic communities in these environments are often low in diversity because a few species are able to take advantage of the abundance of food and are tolerant of the hypoxic conditions that are often associated with high organic input.

All of these harsh environmental variables require specific adaptations for survival, and the relatively few species that are able to live under these conditions often occur in very high densities. This diversity is, nonetheless, important. The relative simplicity of intertidal habitats in terms of the numbers of species present and their accessibility has made them particularly conducive to experimental manipulation, and our understanding of biodiversity regulation in intertidal environments is probably greater than in any other marine habitat. Indeed, intertidal systems provide a useful model community that has generated many of the major paradigms for marine ecosystems. Limited data from sedimentary communities suggest that paradigms developed in the rocky intertidal are not necessarily transferable to sedimentary habitats, but they do provide a useful framework of ideas for other environments.

Intertidal habitats are important not only for the ecosystem services they provide (summarized below) but also because they represent a key ecotone (a transition zone between different communities) between land and ocean. The plants in mangels and salt marshes, for example, support a terrestrial fauna in their upper branches but a marine fauna in the sediments at their roots. These faunas may also interact with one another, and with other groups of organisms such as migratory birds that pass through the environment and feed while in transit.

Estuaries represent another group of specialized coastal habitats, where fresh water and sea water meet and mix to form a gradient in salinity. Estuaries can encompass the intertidal habitats described above but they also contain a subtidal habitat and their influence may be felt well beyond the land–sea interface. Typically, estuaries are relatively low in diversity because the salinity is too high or variable for freshwater species or too dilute for most marine species. Thus, most estuarine species have physiological adaptations to cope with the salinity problem. Depending on the hydrography of the estuary, salinity can also vary considerably on a seasonal or even a tidal basis, and variation can be even more limiting to species diversity than mean salinity.

Although some estuarine bottoms are rocky, most are at least partially covered by sediments transported from land by rivers and runoff. As is the case with most sedimentary bottoms, the majority of species and individuals live among the sediment grains, concentrated in the upper few centimeters below the sediment–water interface where oxygen is available. Further down in the sediment, oxygen is typically reduced or absent, so that organisms living deeper in the sediment (to tens of centimeters) must be able to tolerate low oxygen or use a long siphon or burrow to maintain oxygen exchange with the surface. Thus, diversity at depth is usually reduced relative to that near the sediment–water interface. Many estuaries are very productive, in part because they are often relatively nutrient rich as a result of the freshwater inflow and terrestrial runoff. As a result, these estuaries often support a very high biomass of a relatively species-poor community.

Some coastal habitats are vegetated with photosynthetic plants. Seagrasses are true grasses with roots that occur in shallow subtidal areas, and are usually most abundant in estuaries. Globally, there are only 45 species, but seagrasses provide habitat for other species; these species may include epibionts that live on the seagrass blades, or a variety of fish and sedimentary invertebrates that live below or between the grass blades. Seagrass beds are more diverse, for example, than adjacent sandy bottoms, likely because they provide a predator refuge that a sand bottom cannot.

Another common form of vegetation along the seashore is seaweeds. Seaweeds, like seagrasses, require light for photosynthesis and are typically attached to a shallow hard bottom; they are therefore confined to nearshore environments. Some seaweeds are intertidal, showing strong zonation patterns with tidal exposure. Species that are tolerant to prolonged exposure have adaptations that allow them to tolerate the harsh conditions, but again the harsh conditions mean that species numbers in a given intertidal area are relatively few.

Kelps make up another dense vegetation habitat that occurs subtidally in cold, clear, nutrient-rich water less than ~ 30m depth. The kelps are attached to the hard bottom, but in some cases sediments may accumulate in areas around the holdfast that attaches the kelp to the substrate. As is the case with seagrasses, a kelp bed is typically dominated by one or two kelp species, but provides critical habitat for many other species. Another feature common to kelps and seagrasses is that they are extremely productive habitats and often support a high biomass of primary and secondary producers.

The most spectacular marine habitat in terms of diversity of organisms is the coral reef. Coral reefs are formed by hard corals, which are limited to areas with average surface temperatures above $\sim 20°C$. Reefs offer a wide variety of three-dimensional habitat that is utilized by a variety of other species, resulting in the most diverse marine habitat in terms of number of species per unit area. Many of the most productive marine environments are low in diversity, but reefs are an interesting exception. They are very productive (tight nutrient cycling) as a result of photosynthesizing dinoflagellates called zooxanthellae that are symbionts with reef-building corals. Thus, coral reefs support a high biomass of organisms from corals to fishes.

Beyond the immediate near-shore environment lies the continental shelf, which is largely sediment-covered and extends to approximately 200 m depth. The continental shelf varies in width from tens of kilometers to ~ 200 km. Depending on the current and wave regime, sediments may be sandy or muddy, and the sediment composition will influence species composition. Most of the primary production in the shelf environment is provided by phytoplankton in near-surface waters, and light penetration is typically reduced relative to the open ocean because of increased turbidity and phytoplankton abundance. Benthic vegetation is lacking, but benthic algal diatom mats can sometimes be important where light penetration is sufficient to support them. These mats provide a potential food source for benthic organisms, but contribute little in the form of structural habitat. Epifaunal organisms (those living upon rather than within the seafloor) can provide a habitat that can be important for some species. The productivity of shelf environments is extremely variable geographically, but most of the world's most-productive fisheries occur on the shelf, particularly where nutrient-rich deep waters are upwelled to the surface. Relative to the near-shore, shelf habitats are usually more diverse, but the level of diversity on shelf environments can vary considerably with geography.

For groups as varied as shallow-water molluscs, hard substrate fauna, and deep-sea macrofauna, it has been suggested that species number generally declines from the tropics to the poles. This gradient is much more obvious in the northern hemisphere, where relatively recent glaciation-related extinctions contribute greatly to the pattern. The latitudinal gradient has also been described in the southern hemisphere, though the pattern is less striking. Not surprisingly, given their relative ages, the older Antarctic benthos is more diverse than its Arctic counterpart. But a simple latitudinal gradient is not evident in all taxa. Some groups, such as macroalgae, appear to be most diverse at temperate latitudes, and emerging evidence suggests that shallow-water and deep-sea nematodes may also peak in diversity at temperate latitudes.

The Open Ocean

Beyond the continental shelf lies the open ocean, or the pelagic environment. Pelagic communities are delineated primarily by water masses, so that assemblages are often broadly distributed over ranges that may be characterized by differences in temperature, salinity, and nutrient values. Thus, surface circulation and wind effects can interact with thermohaline circulation patterns to create distinct water masses with distinct faunas. Interesting processes occur where these water masses meet, creating complex spatial patterns at the boundaries. Clearly these environmental variables play a major role in regulating pattern, but the geological history of a habitat can also play a role by determining the regional species pool. Major geological events such as the elevation of the Panama Isthmus, the opening of the Drake Passage, and Pleistocene glaciation all had profound effects on circulation, which in turn had major effects on marine distribution patterns that are reflected in modern communities. Unlike shelf and coastal environments, the influence of benthic communities on water column processes in the open ocean is minimal and indirect.

Vertically migrating species play a significant role in oceanic pelagic communities and provide a conduit between surface and deep waters. Some species migrate many hundreds of meters on a daily basis, thus complicating efforts to evaluate biodiversity in a given water mass. These migrating species provide a means of energy transfer between waters at different depths and also provide a mechanism by which regulation of diversity pattern in surface waters could be related to diversity patterns in deeper waters or the benthos. Many benthic species also produce larval stages that may contribute to the biodiversity of surface waters, often on a seasonal basis. Surface waters may also have a major impact on benthic communities in the deep sea because the deep sea depends largely on surface primary production.

Photosynthesis is limited to the upper portion of the water column (~ 200 m) where there is sufficient light penetration. Beneath these waters are the continental slope (200–3000 m), the continental rise (3000–4000 m), the abyssal plains (4000–6500 m), and trenches (6500–10 000 m) of the deep ocean, which will be grouped here as 'deep-sea' habitats. Like the shelf environment, most of the deep-sea bottom is covered in sediments, some of which are geologically derived and others that have formed from sinking skeletons of pelagic organisms.

As described earlier, pelagic communities are delineated primarily by water masses, and a number of biogeographic provinces have been described for the world's oceans. Shelf and offshore communities are markedly different in composition and abundance. Local shelf communities are less species rich than offshore communities, but greater spatial heterogeneity in near-shore environments typically results in greater total species richness in neritic environments. One major variable that affects diversity is productivity; species richness tends to be depressed in areas where productivity is high and seasonally variable. This pattern may explain the general pattern of decreasing species number with increased latitude. Characteristics of the regional circulation can offset this general pattern, particularly in coastal environments where productivity does not show as clear a relationship with latitude. Variation in diversity has also been observed with depth in the water column, which is also consistent with primary productivity being restricted to the lighted surface layer of the ocean. The shallowest areas of the oligotrophic North Pacific are more productive in terms of phytoplankton than deeper waters, and phytoplankton diversity is higher in deeper waters than near the surface. Zooplankton, by contrast, show a slightly different pattern where species numbers are higher in surface waters. Studies from the North Atlantic suggest that species richness increases and then peaks at approximately 1000 m. One critical variable that may contribute to these differences in pattern is the pulsed nature of organic input in some systems; highly variable organic flux may represent a strong disturbance, and therefore depress diversity.

Because water depth is so great, much of the water column and benthic environment is devoid of light, and the food source is the material sinking from surface waters and advected from the adjacent shelf habitat. The great depths also result in ambient pressures far in excess of those in shallow water, and water temperatures are relatively low ($<4°C$) and are seasonally and spatially much less variant than in shallow-water systems. The seeming inhospitable nature of the deep-sea environment led some earlier investigators to speculate that it was azoic, or devoid of life. Work by Hessler and Sanders in the 1960s and more recent work by Grassle and Maciolek in the 1980s has dramatically changed this view. Although the densities of organisms that live in deep-sea sediments are very low and individuals tend to be very small, the numbers of species present is usually very high. Thus, a given sample will contain few individuals, but many of them will represent different species. This generalization is true for most deep-sea habitats, but areas such as trenches, upwelling areas, areas with intense currents, and high latitudes can be low in diversity. Low diversity in these areas results from some overwhelming environmental variable, such as low oxygen, resulting in the exclusion of many species.

Depth-related patterns have also been described in benthic communities. A peak in biodiversity has been described at continental slope depths, with lower diversity at shelf and abyssal plain depths. This pattern depends on how diversity is defined. In terms of total numbers of species per unit area, shallow water habitats sometimes have higher values because they support much higher densities of individuals. Shallow-water habitats are also patchier over spatial scales of tens to hundreds of kilometers in terms of sediment type, and other habitat variables that change species composition.

Thus, pooling of samples from coastal environments can sometimes produce greater total species numbers than pooling over similar distances in deep-sea sediments. For most areas that have been sampled, there is another key difference between deep-sea and shallow-water samples. An individual deep-sea sample is typically characterized by low dominance and greater dissimilarity between proximate samples than would be found in shallow-water samples. One other key difference is total area; although densities of organisms in the deep sea are much lower than in shallow water, the tremendous area of the deep sea alone is enough to support very large numbers of species. But some recent evidence from Australian shelf samples suggests that some shallow-water communities may rival deep-sea communities even at the sample scale. Thus, poorly sampled areas such as tropical shorelines and the southern hemisphere need to be better understood before definitive 'rules' on biodiversity patterns can be established.

The one major exception to the generality of low productivity in the deep sea is hydrothermal vents, which were first discovered in 1977. Their discovery came as a great surprise to deep-sea scientists because they supported high abundances of novel megafaunal species. The size and numbers of vent organisms is in sharp contrast to most deep-sea habitats, and is possible only because of the chemosynthetic bacteria that form mats or live symbiotically with several vent species. These bacteria are dependent on hydrogen sulfide and other reduced compounds emitted at vents. Since the discovery of vents over 20 new families, 100 new genera, and 200 new species have been described from these communities, but diversity is very low as a result of the toxic hydrogen sulfide. Vent habitats have extremely high levels of endemism resulting from the evolution of forms that are able to thrive in the toxic conditions and take advantage of the high levels of bacterial chemosynthetic production that drives the food chain at vents. Moreover, the fauna at vents is very distinct from other habitats, sometimes at the family level or higher.

Among deep-sea habitats, there are other low-diversity communities. Low diversity is also observed beneath upwelling regions, where high levels of organic matter sinking from surface water to bottom sediments may create hypoxic conditions that eliminate many species. Deep-sea trenches are subject to slumping events that contribute to relatively low numbers of species. Deep-sea areas in the Arctic are also still rebounding from loss of much of the fauna during glaciation and anoxic periods that were associated with that time period.

Regulation of Pattern and Linkages Between Organisms and Habitats

One pattern common to marine communities and terrestrial communities alike is that habitats characterized by high levels of disturbance, or conditions that are extremely challenging from a physiological perspective, often support relatively few species.

Aside from habitats that are strongly influenced by overriding environmental variables that depress diversity, regulation of diversity in marine ecosystems is not fully understood. As a general rule in ecology, high habitat complexity is thought to support the highest diversity because of the many available habitats and niches. Certainly the high level of habitat complexity observed in reefs contributes to their diversity, but pelagic habitats and deep-sea sediments would appear at first glance to be among the least spatially complex habitats in nature. But in these environments, complexity may occur at small temporal and spatial scales. In the pelagic realm, microstructure of nutrients is thought to be an important aspect of species coexistence. Thus, where nutrient levels are relatively low and patchy, primary producers are most diverse. Patchiness is also thought to be important in maintaining diversity in coral reefs and deep-sea communities, the two most speciose community types in the oceans. In both cases, it is thought that intermediate levels of disturbance may be important in preventing the strongest competitors from taking over and eliminating the weaker competitors. In reef habitats, periodic small-scale disturbance in the form of storms keeps any one species from taking over. In the deep sea, it is thought that small-scale disturbances in the form of food patches, biological structures, and sediment topography, can all create microhabitats that allow species to coexist. Determining the factors that regulate biodiversity in marine systems is, nonetheless, an ongoing research question.

Estimates of Total Species Numbers

Because such a large portion of the ocean is poorly sampled, estimates of total species numbers vary considerably depending on the specific assumptions used to extrapolate from those areas that have been well sampled. The number of described species from the oceans is approximately 300 000. For some areas of the ocean, such as coastal environments of the North Atlantic, most faunal groups are reasonably well described. However, major gaps in our knowledge exist for some taxonomic groups and some marine habitats. In terms of taxonomic groups, microbes are very poorly known but new evidence based on molecular approaches suggests that the pelagic and sedimentary realms may both support numbers of bacterial species that would add greatly to the approximately 1.75 million species of nonmicrobial species presently described globally. Protistan diversity is also poorly known. Surprisingly, even for relatively well-sampled areas of the oceans, diversity in some groups of organisms, such as the nematodes, remains poorly known. The specific habitats that are very poorly known include tropical sediments, coral reefs, and deep-sea sediments. Reaka-Kudla has estimated that up to 9 million species may inhabit coral reefs, and Grassle and Maciolek estimated that there may be 10 million macrofaunal species in the deep sea. Others have extrapolated from the ratio of known to unknown species in specific areas to generate estimates of 500 000 to 5 million macrofaunal species in deep-sea sediments alone. Based on the typical ratio of nematode species to macrofaunal species, Lambshead hypothesized that there may be as many as 100 million nematode species in the deep sea. The problem with these estimates is that they are based on a relatively small area, so that the error in extrapolating to the whole of the deep sea, or all oceans, is quite large. For example, it has been estimated that deep-sea sediments (defined here as shelf edge and greater depths) cover approximately 65% of the Earth's surface yet globally only $\sim 2\,km^2$ of ocean floor has been sampled for macrofauna, and $\sim 5\,m^2$ has been sampled for meiofauna.

Threats

Different habitats presently face different levels of threat as a result of human activity. Open ocean habitats, both pelagic and benthic, have been least impacted by human activity. The greater distance from human populations and their influences, and the shear size of the habitats themselves, make them much less vulnerable than the shoreline and shelf habitat where most marine habitat destruction and local species loss is occurring.

Most of the world's fisheries are concentrated in shelf or near-shore environments, although the capacity to fish deeper waters is increasing all the time. It is estimated that $>65\%$ of global fisheries are either fully or overexploited. There are a variety of mechanisms by which this fishing activity may affect biodiversity of marine systems. One of the greatest concerns in terms of benthic habitats is the habitat destruction caused by fishing gear that is dragged across the sea floor, damaging organisms that live in and upon the seabed, homogenizing bottom habitats, and disrupting the sediment fabric and its geochemistry and microhabitats. Recent estimates suggest that some major fishing grounds, such as Georges Bank, have experienced trawl coverage that exceeds 200–400% annually. Habitat damage is not an issue for the fluid pelagic habitat, but the removal of nontarget species as by-catch remains a problem in bottom and pelagic fisheries. Organisms ranging from sea birds to marine mammals to fish to invertebrates are all known to suffer high by-catch mortality; by-catch levels can often rival or even exceed the biomass of the target species removed from an ecosystem. Another major concern with fisheries is that they are often very effective at removing large numbers of individuals of the target species, which is often a top predator within the ecosystem. The potential for alteration of food chains is great, both for pelagic and benthic species. Evidence is accumulating that the trophic structure of many heavily fished ecosystems is changing, with upper trophic levels sometimes being eliminated and the transfer of energy through remaining species altered substantially. One final aspect of fishing activity that is of particular concern for pelagic habitats is lost fishing gear and debris that may continue to 'ghost fish' and capture target and nontarget organisms for years after the gear has been lost.

One chronic problem with studies of fisheries impacts is that we lack good 'control' sites where fishing impacts are minimal. Advances in fishing technology have made most habitats accessible to fishing gear, and the few areas that remain inaccessible are typically poor 'control' sites because they are fundamentally different in physical topography and species composition than the areas that are fished.

Coral reef fisheries have their own unique problems. Dynamite, cyanide, and bleach fishing are all used to get around the problem of fishing a topographically complex habitat, but they are also methods that destroy many nontarget species including the corals that make up the habitat itself. One of the discouraging facts about reef systems is that in most instances, reefs were considerably altered by removal of large and potentially important species by early settlers, and we have little idea of what the pristine systems looked like in terms of species relationships.

Aquaculture represents a special case in terms of fishing activity, in that impacts are typically more localized and easily seen. The issue of ownership is also less contentious, stocks are more easily managed, and in some cases it is also easier to assign accountability for environmental damage. But aquaculture can be extremely destructive, in that some activities such as shrimp farming are often achieved by destroying other coastal habitats such as mangroves. Aquaculture also often involves moving organisms around as brood stock, potentially allowing invasion of nonnative habitat by the species being cultured, or parasites and diseases that the organism may carry into the new environment. Even for those organisms that have been deliberately moved, there are potential consequences in terms of alteration of local genetic structure of natural populations.

Many coastal environments are also threatened by pollution resulting from the dumping of various toxic wastes such as heavy metals, organic compounds (e.g., polychlorinated biphenyls or PCBs), metals, and eutrophication resulting from increased input of macronutrients from sewage and agricultural runoff. These excess nutrients result in blooms of a low diversity phytoplankton community (sometimes favoring toxic species) that sink to the bottom and undergo microbial decomposition. In some instances, microbial respiration will deplete bottom waters of oxygen, and benthic communities may subsequently be wiped out. Whether the cause is eutrophication or toxic chemicals, both forms of pollution depress diversity and favor a few weedy species. On coral reefs, increased nutrients will typically lead to macroalgal blooms and the loss of corals. In this instance, the entire habitat may be destroyed.

The effect of fisheries operations on habitat alteration has already been mentioned, but marine habitats may also be altered for other activities. The demand for coastal real estate, both for industrial and residential use, has eliminated large areas of salt marsh and mangrove. Expansion of coastal waterways by dredging and replenishing of eroded beaches by mining subtidal sands are two mechanisms by which habitats may be altered. Invariably, the loss of habitat means the loss of species, at least on a local scale. Unfortunately, the amount of habitat being lost is becoming so extensive that the number of habitat refugia remaining are becoming fewer and fewer and more widely separated.

There has been great concern over the introduction of non-native ('exotic') species into marine habitats in recent years, a phenomenon that has been ongoing for some time. Indeed, it has been estimated that between the years 1500 and 1800, more than 1000 intertidal and subtidal species worldwide may have been transported and introduced into nonnative habitats. As many as 3000 species may be in transit in the ballast water of ships on a given day. In some instances it has been documented that invasive species have greatly altered the species composition and ecological processes in the areas they have invaded. San Francisco Bay, for example, now harbors hundreds of exotic species, including Asian clams that have become so abundant that they have altered the seasonal phytoplankton production cycle within the bay. The problem of invasive species is thought to be most severe in coastal and estuarine regions, where open ocean waters have historically provided a barrier to dispersal. Ballast water is not, however, the only culprit in facilitating the movement of invasive species. Fouling organisms on the hulls of ships provide another mechanism, and aquaculture and scientific study are additional transport vectors.

One other threat to marine biodiversity is global climate change. The effects of climate change are difficult to know given the different trajectories predicted by different models, but several general categories of effect may be expected. First, as air temperatures increase, so will ocean surface temperatures, presumably shifting faunas toward the poles. Such an effect has already been documented in California intertidal and pelagic communities. What is less obvious is that some species will be unable to simply shift poleward because other habitat requirements, such as the presence of a shallow bank, may not be met at another latitude. Coral reefs provide an excellent example of this phenomenon. Recently, large areas of coral reefs have experienced increased occurrences of bleaching, a phenomenon where corals expel their symbiotic dinoflagellates and die. Bleaching has been linked to the increased frequency of El Niño events, higher water temperature, and elevated ultraviolet radiation; in this case, corals cannot simply colonize an adjacent habitat because it is typically too deep and warming trends are much faster than potential colonization rates. A second category of effect is rising sea level. In some instances it may be possible that intertidal organisms may simply shift upward in response to rising waters, but in areas where human populations have developed areas in the landward direction, mangroves, salt marshes, and intertidal habitats may be prevented from advancing by seawalls or other physical barriers. Perhaps the most difficult aspect of global change to predict is the effect that alteration of temperature and rainfall pattern will have on ocean circulation. Some global warming models have suggested that even relatively modest temperature increases may alter ocean circulation patterns. Because ocean circulation is a critical variable in terms of surface productivity and transport of reproductive propagules, any change to ocean circulation could potentially affect every marine community from shallow surface waters to the deepest areas of the ocean.

The Importance of Marine Biodiversity

Marine organisms contribute to many critical processes that have direct and indirect effects on the health of the oceans and humans. In the majority of instances there are few data to demonstrate that total numbers of species are important, but data on this question are only starting to be assembled. What is obvious is that there are specific species and functional groups that play very critical roles in important ecosystem processes, and the loss of these species may have significant repercussions for the whole ecosystem.

Primary and secondary production are critical mechanisms by which marine communities contribute to global processes. It has been estimated that approximately half the primary production on Earth is attributable to marine organisms. It has also been estimated that approximately 20% of animal protein consumed by humans is from the oceans. Perhaps more importantly, this consumption is much higher in some countries than in others, making it a critical staple of many diets. Marine organisms are also harvested for extractable products, including medicines and various industrial products.

The global cycling of nutrients and even carbon depend on marine communities. Without primary producers in surface waters, the oceans would quickly run out of food, but without planktonic and benthic organisms to facilitate nutrient cycling, the primary producers would quickly become nutrient limited.

Benthic marine organisms can contribute to sediment and shoreline stability. Mangroves, salt marsh plants, and seagrasses all bind sediments together and thereby reduce shoreline erosion. Sedimentary organisms can either stabilize or destabilize sediments, thus affecting coastal sediment budgets. One direct ramification of these activities is that sediment bound pollutants will be greatly affected by binding and destabilization of sediments, creating a situation where sedimentary bacteria, diatoms, and invertebrates can influence whether pollutants are buried or resuspended. Some bacteria and invertebrates are also able to metabolize certain pollutants and reduce or eliminate their toxicity.

In coastal environments, salt marshes, mangroves, and seagrasses can help trap sediments and absorb nutrients from sewage and agricultural sources, thereby filtering coastal runoff and helping to maintain relatively non-turbid, non-eutrophied coastal waters. In a related manner, benthic organisms may be important filter feeders, removing particles that would reduce water clarity. In addition to allowing light penetration to greater depths, this filtering activity can contribute to coastal aesthetics and clear water. Other aesthetic services are provided by coastal wetlands and coral reefs, both of which generate tremendous tourist interest.

Concluding Remarks

Although documented extinctions are relatively few, there are good reasons for improving our understanding of biodiversity pattern and regulation, and the role that biodiversity plays in key ecosystem processes. One problem is that biodiversity in the oceans is poorly described, and the handful of seabirds, marine mammals, and marine snails that have become extinct may represent the visible few of a much larger number of organisms that have been lost without our knowing it. It has been estimated, for example, that 50 000 undescribed species may have already been eliminated from coral reefs. A second concern is that some of the species we have treated as cosmopolitan may, in fact, represent a sibling species group, and when we eliminate a species from an area, it may be a different species than occurs elsewhere. A third concern is that even if the elimination of species from a given area does not represent a global extinction, it may represent a unique genotype that cannot be replaced from a surviving population elsewhere.

Although several general patterns of biodiversity have been described in the oceans, and our understanding of how biodiversity is regulated and maintained is still limited, several paradigms point to the importance of disturbance and habitat heterogeneity. Because vast areas of the oceans remain unsampled, our estimates of species numbers are crude and based on a very small portion of the marine habitat, but they do suggest that the oceans contain a significant portion of the global species pool. Unfortunately, we know little about how biodiversity contributes to the many critical ecosystem services that marine communities provide. In many instances, it is possible to generate very clear examples of a single species having a major impact on its ecosystem, and based on this observation it is safe to say that loss of biodiversity may have very negative effects on marine ecosystems if the species lost is one of these key players. But we have little idea of whether numbers of species matter, or which species are most important in maintaining a properly functioning ecosystem. An improved understanding of biodiversity and regulation will give us better tools to predict where biodiversity changes are likely to occur and why, how these changes will affect other components of marine biodiversity, and the best strategy to mitigate such changes.

See also

Benthic Boundary Layer Effects. Benthic Foraminifera. Benthic Organisms Overview. Deep-Sea Fauna. Demersal Fishes. Macrobenthos. Meiobenthos. Ocean Margin Sediments.

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DOLPHINS

See **MARINE MAMMAL OVERVIEW**

DOUBLE-DIFFUSIVE CONVECTION

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Introduction

The density of sea water is determined by both its temperature and its salt content or salinity. Whereas added heat makes water lighter, added salt makes it denser, so both must be considered when evaluating the gravitational stability of the water column. That is, a given column of water will 'convect' or overturn if dense waters overlie lighter waters. In many parts of the world ocean, the distributions of temperature and salinity are opposed in their effects on density. This arises because of the tendency of warm water to evaporate easily in low latitudes, the predominance of rainfall in cold, high latitude regions,