See also

Deep Submergence, Science of. Deep-sea Drilling Methodology. Manned Submersibles, Deep Water. Remotely Operated Vehicles (ROVs)

Further Reading

Bleil U and Thiede J (1988) *Geological History of the Polar Oceans; Arctic versus Antarctic*, NATO Series C, Mathematical and Physical Sciences, vol. 308. Dordrecht: Kluwer Academic.

Coffin MF and Eldholm O (1994) Large igneous provinces: crustal structure, dimensions, and external consequences. *Reviews of Geophysics* 32: 1–36.

Cullen V (1993/94) 25 years of Ocean Drilling. *Oceanus* 36(4).

Dickens GR, Paull CK, Wallace P and the Leg 164 Science party (1997) Direct measurement of *in situ* methane quantities in a large gas hydrate reservoir. *Nature* 385: 426–428.

Lomask M (1976) *Project Mohole and JOIDES, A Minor Miracle, An Informal History of the National Science Foundation*, National Science Foundation. Washington, DC: pp. 167–197.

Hsu KJ (1992) *Challenger at Sea, a Ship that Revolutionized Earth Science*. Princeton, NJ: Princeton University Press.

Kastner M, Elderfield H and Martin JB (1991) Fluids in convergent margins: what do we know about their composition, origin, role in diagenesis and importance of oceanic chemical fluxes? *Philosophical Transactions of the Royal Society* (*London*) 335: 275–288.

Kennett JP and Ingram BL (1995) A 20,000 year record of ocean circulation and climate change from Santa Barbara basin. *Nature* 377: 510–513.

Parkes RJ, Cragg SJ, Bale JM *et al.* (1994) Deep bacterial biosphere in Pacific Ocean sediments. *Nature* 371: 410–413.

Summerhayes CP, Prell WL and Emeis KC (1992) *Upwelling Systems: Evolution since the Early Miocene*, Geological Society Special Publication 64. London: Geological Society of London.

Summerhayes CP and Shackleton NJ (1986) *North Atlantic Paleoceanography*. Geological Society Special Publication 21. London: Blackwell Scientific.

Warme JE, Douglad RG and Winterer EL (1981) *The Deep Sea Drilling Project: a Decade of Progress*, Special Publication 32. Tulsa, OK: Society of Economic Paleontologists and Mineralogists.

DEEP-SEA FAUNA

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Overview

The deep sea covers more of the Earth's surface than any other habitat, but because of its remoteness and the difficulty in sampling such great depths, our sampling coverage and understanding of the environment have been limited. There has been a common misperception that the deep sea is species poor, and a commonly used 'desert' analogy is hardly surprising given that early sampling found few organisms, and the first deep-sea photographs revealed large plains of rolling hills covered in sediment with little obvious life (**Figure 1**). Indeed, all lines of evidence suggested that the deep sea is a very inhospitable environment. Temperatures are low (~4°C), ambient pressure is extremely high (hundreds of times greater than on land), light is completely absent, and food is generally in very low abundance. But within the last few decades, quantitative samples have revealed what primitive sampling gear and photographs could not – that sediments in the deep sea are teeming with a rich diversity of tiny invertebrates only a few millimeters in size or smaller. These benthic (bottom-dwelling) organisms may reside just above the bottom but closely associated with it (hyperbenthos), on the sediment surface (epifauna), or among the sediment grains (infauna).

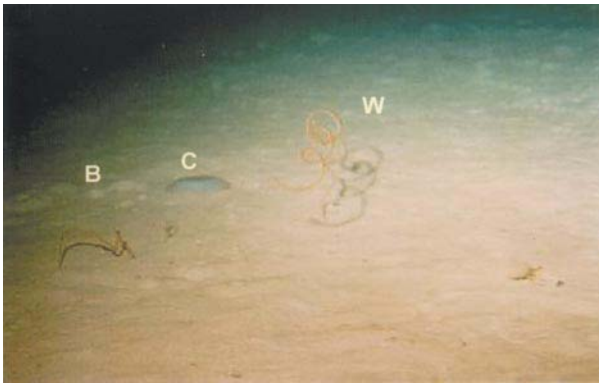

Figure 1 Photograph of a typical deep-sea landscape. This photo is from 750 m near St Croix, US Virgin Islands. Infaunal burrows (B), a sea cucumber (C) and a sea whip (W) are visible.

The change in perception regarding the species richness of the deep sea has continued to evolve; we now know that, on the basis of the combination of species richness per unit area and total size, the deep sea is the most species-rich habitat in the oceans and among the richest on earth. A similar change in perception has occurred with two other generalizations about the deep sea. First, the deep sea is generally thought of as a food-limited environment, where biomass of individuals and communities as a whole are extremely low. Although this generalization usually holds, the surprising discovery of hydrothermal vent communities in the late 1970s, with meter-long tube worms and biomass that rivaled even the most productive shallow-water areas, proved that clear exceptions exist. A second generalization is that the deep sea has been considered to be an extraordinarily stable habitat, where variables such as salinity, temperature, and food supply are constant, and light and photosynthesis are uniformly absent. Again, this generalization holds in some respects, in that temperature and salinity are often invariant and light is indeed absent. Studies in the last two decades, however, have indicated that small-scale patchiness is common, seasonal variation in phytoplankton production in surface waters can be directly reflected in the material that reaches deep-sea sediments, and some deep-sea areas are very dynamic in terms of currents and sediment movement.

The recent discoveries in the deep sea raise several interesting questions. First, how can a seemingly inhospitable and physically homogeneous habitat such as the deep sea support a rich diversity of organisms? Second, how can hydrothermal vents support such a high biomass of organisms relative to most deep-sea environments? We now have a firm understanding of the latter question and some definite ideas on the former.

Defining the Habitats

Some deep-sea biologists define deep-sea habitats somewhat arbitrarily as those greater than 1000 m in depth. For this review, the deep sea is defined as all benthic habitats beyond the edge of the continental shelf, including the continental slope, continental rise, abyssal plains, ocean ridges (including hydrothermal vents), and deep-ocean trenches. Thus, ocean bottom from ~ 200 to 10 000 m falls within this definition. Most of these regions share the features described above, including low temperature, dependence on organic production 1000s of meters above, high pressure and a sedimentary bottom, but each has unique characteristics as well (**Figure 2**). The continental slope, because it is adjacent to the

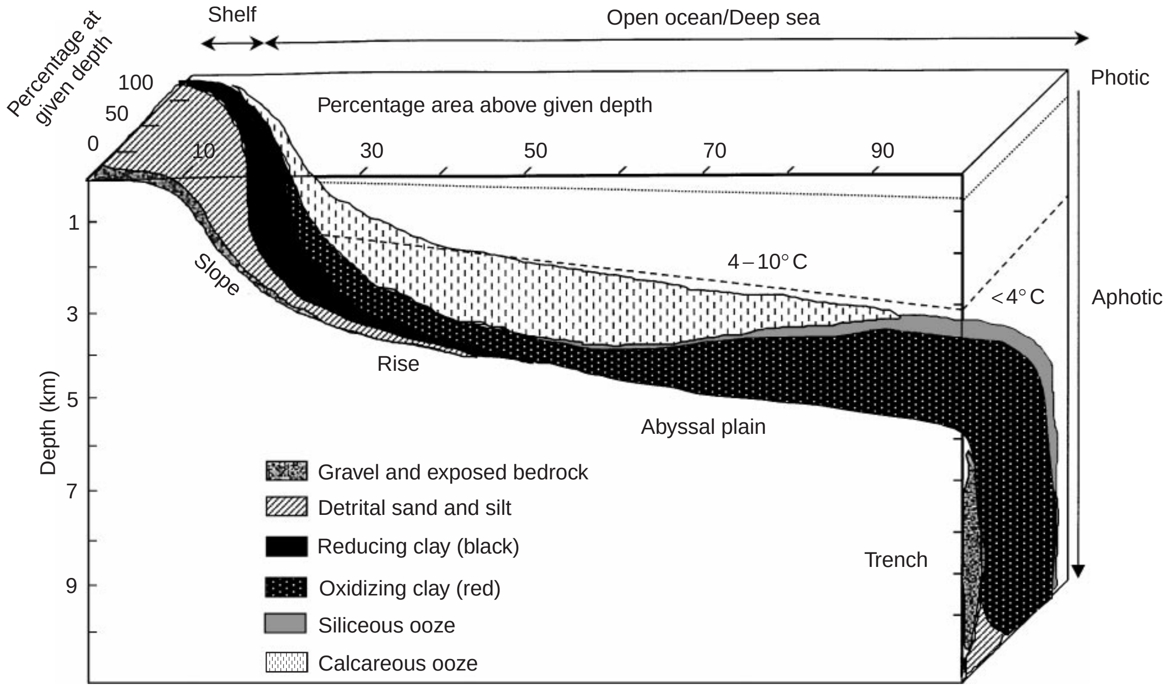

Figure 2 Schematic representation of the deep ocean environments and their sedimentary makeup. The horizontal axis has been greatly compressed, and the vertical axis is subsequently exaggerated. (Modified from Wright JE (ed.) (1977). *Introduction to the Oceans*. Milton Keynes, UK: The Open University.).

continental shelf, generally receives a higher level of organic input than abyssal areas and, with its ~3° slope, it is the steepest of the deep-sea environments other than trenches and seamounts and is subsequently subject to occasional sediment slides (called turbidity currents) that may move large volumes of sediment down the slope to the rise and abyssal plains. The continental slope is largely covered in sediments, which often derive from terrestrial and riverine runoff but may also come from marine biological production. The continental rise occurs at the base of the slope and can exhibit elevated organic matter relative to lower slope areas because material moving down the slope may accumulate at the rise. By far, the abyssal plains cover the largest portion of the deep sea (~40% of the Earth's surface), but they also represent the most benign of the deep-sea habitats. Because they are removed from land influence and very deep ($\gtrsim$4000 m), the amount of organic matter reaching the bottom is generally quite small, even in comparison with the slope and rise. The deepest ocean habitats are trenches, which form in subduction areas and are characterized by relatively steep sides, poor circulation, and occasional mud slumping. The poor circulation and slumping make trenches particularly inhospitable to most organisms.

The sedimentary environment is vertically structured in terms of geochemistry and living organisms. Sediments have limited permeability and oxygen normally penetrates only a few millimeters by diffusion alone. Greater oxygen penetration occurs when bottom currents mix sediments or when organisms move pore water and sediments around (bioturbation). Sediments with active bioturbation are usually oxygenated within the top few centimeters, although strong bioturbation can lead to deeper pockets of penetration. Because light is absent from the deep sea, most productivity is provided by phytoplankton detritus and fecal pellets sinking from surface waters above, or closer to coastal habitats, from organic material transported seaward (e.g. kelps, seagrass etc.). Most of the available organic matter is concentrated near the sediment surface, although some species are capable of 'caching' food deeper in the sediment for later use. The combination of limited food and oxygen penetration at depth in sediments results in the vast majority of organisms being confined to the upper few centimeters of sediment near the sediment–water interface. Smaller organisms that can tolerate anoxia and larger organisms that maintain a burrow or appendage to the surface can live deeper, but even then distributions are usually only a few centimeters deeper.

Historically, the deep sea was perceived to be aseasonal because temperature is largely invariant at deep-sea depths, the absence of any light negates any day-length signal, and the habitat is so far removed from surface waters that it was thought that any signal from surface production would be completely dampened. Evidence in the last two decades has indicated that seasonality is a factor in many deep-sea environments. Samples from a number of different areas around the world and at a full range of depths have shown that the organic content of sediment does change seasonally. The strength of the seasonal signal, not surprisingly, varies with latitude and location; areas with very strong spring blooms are more likely to result in pulses of phytodetritus that sink to the seafloor than areas with weak production cycles. Where pulses are strong, the benthic fauna has been shown to respond quickly to organic input in terms of activity and biomass. Experimental patches of organic enrichment also generate a response by colonizing species.

The deep-sea floor lacks the large-scale physical heterogeneity of habitats such as forests and coral reefs, but it is nonetheless far from uniform. Biologically generated features such as burrows and feeding mounds create small-scale heterogeneity that persists for longer periods of time than in shallow water because physical redistribution of sediments by waves does not occur in the deep sea. As organic matter such as phytodetritus sinks to the seafloor and is carried horizontally by currents, small-scale bottom topography creates spatial variation in how that material settles. Depressions on the sea floor, for example, trap phytodetritus. Sessile species such as sea whips, glass sponges and protozoans called xenophyophores co-occur with mobile groups such as sea spiders and sea cucumbers, whose movements across the sediment can create tracks and topography. All of this small-scale heterogeneity acts in concert to create a mosaic of microhabitats for different organisms.

Seamounts

Seamounts, like volcanic islands, are mountains that are formed above the ocean floor near spreading centers, and they subsequently break up the landscape of abyssal plains. Because they are generally steep-sided, much of the substrate is volcanic rock, but sedimentary environments occur where sides are not steeply sloped or if the top of the seamount is flattened to form a guyot. Because seamounts can extend large distances above the bottom (thousands of meters), the fauna is often different from that found on the surrounding abyssal plains. The hard substrate, of course, supports very different species from sedimentary environments, and the relatively high flows that can occur over seamounts can support a higher proportion of organisms that feed on suspended particles than most deep-sea environments. In some cases the seamount may extend through the oxygen minimum layer of the Pacific Ocean; these low oxygen conditions favor a very different set of species than areas where oxygen is not limited.

Hydrothermal Vents

Hydrothermal vents represent a very specialized and unusual deep-sea environment, and prior to their discovery in 1977, the deep sea was thought to support very low densities of small invertebrates. There had been some debate until that time as to whether high pressure and low temperature constrain the size of benthic organisms, or whether deep-sea environments were simply food limited. The discovery of vents quickly answered that question, as researchers discovered dense concentrations of large organisms such as tube worms, clams, and crabs (**Figure 3**). Compared to the surrounding deep-sea environment, the vents supported extraordinary biomass of large organisms, and led to early analogies of 'oases in the desert'. From a biomass perspective this is an appropriate analogy, but from a species diversity perspective it is not.

Vents occur where tectonic spreading and subduction create fissures in the Earth's crust, allowing sea water to percolate through the crust and become heated by the mantle (**Figure 4**). When this water percolates out through the crust again, it is rich in minerals and reduced compounds such as hydrogen sulfide. Water temperature is extremely high (200–400°C), and is prevented from boiling by the extreme pressure. It cools quickly, however, as it mixes with the ambient sea water that is typically $\sim 4^\circ\text{C}$. The mixture of sedimentary and hard substrate habitats that are characteristic of vent fields often support a large biomass of a very specialized fauna.

The key to the high productivity of hydrothermal vents are chemoautotrophic bacteria that live freely or form symbioses within specialized tube worms, clams, and mussels. These bacteria utilize hydrogen sulfide to synthesize organic compounds, which in the latter case may be passed on to the symbiont hosts. Not surprisingly, the hosts are characterized by reduced guts and little or no feeding structures. For both members of the symbiotic partnership, there are clear advantages. The host provides a physically stable habitat in the immediate proximity of hydrogen sulfide and the bacteria provide a rich food supply to the host. But relatively few species can utilize this symbiotic relationship. The extreme temperature gradients and toxic concentrations of hydrogen sulfide create a habitat that few organisms can tolerate. Moreover, the transient nature of vent environments, which generally persist for time scales of only decades, means that organisms must be able to colonize, grow quickly, and reproduce before vent flow ceases.

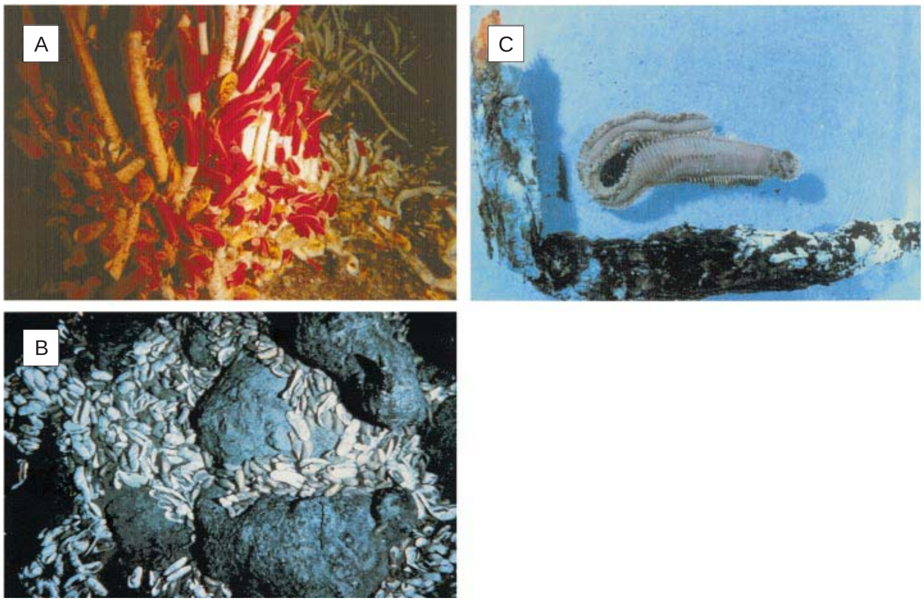

Figure 3 Photograph of tube worms (A), clams (B), and polychaete worms (C) from a hydrothermal vent.

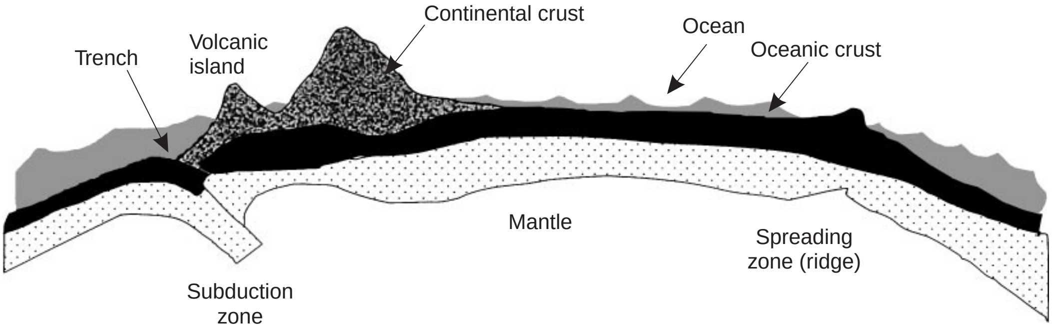

Figure 4 Hydrothermal vents occur where plate tectonic spreading and subduction occur. Water percolates through cracks that plate motion creates in the crust and is superheated in the mantle. The high temperatures cause chemical reactions, changing the chemistry of the sea water, and creating a fluid rich in hydrogen sulfide and various compounds.

Defining the Organisms

Deep-sea biologists, like other benthic researchers, divide organisms based on size groupings. These groupings are not absolute in that the larval or juvenile stages of one group may be similar in size to adults from a smaller group, but this division is necessary because the sampling logistics that are appropriate for large organisms are inappropriate for small ones. Organisms that can be readily identified in bottom photographs, such as seastars and crabs, are commonly called megafauna (**Figure 5A–C**). Included here are characteristic deep-sea fish such as grenadiers, which cruise around near the bottom feeding on any falling carcass or disturbing the sediment and creating feeding pits as they feed on bottom invertebrates. Some of these taxa migrate up into the water column, providing an additional means by which energy may be cycled between the water column and the benthos. Macrofauna are

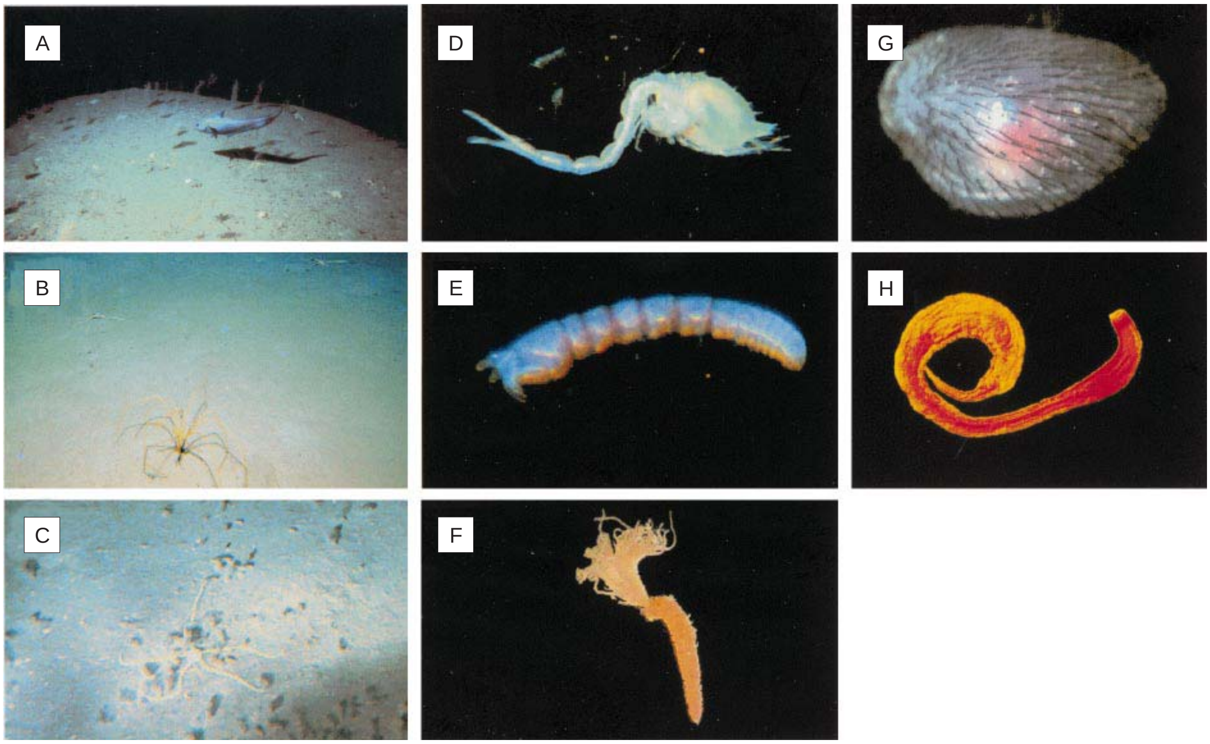

Figure 5 Deep-sea organisms, including megafauna (A, rattail fish; B, sea spider; C, brittle star), macrofauna (D, cumacean; E, tanaid; F, polychaete annelid) and meiofauna (G, ostracod; H, nematode). All taxa are from the northwest Atlantic except nematode from San Diego Trough (kindly provided by PJD Lambshead and D Thistle; G Hampson kindly provided photographs D, E and G).

organisms living on or in the sediments that are retained on a 300-μm sieve; this cutoff is in contrast to the coarser sieves used by shallow-water benthic researchers because the smaller size of deep-sea animals requires a finer sieve. This size grouping includes polychaete annelids, crustaceans, bivalves and many other phyla (**Figure 5D–F**). Meiofauna are organisms between 40 and 300 μm, and include nematodes, foraminiferans, tiny crustaceans, and many others (**Figure 5G–H**). Microorganisms pass through a 40-μm sieve and include bacteria and protists. Within any one of these groups, the taxonomic challenges are considerable in that few individuals are trained in taxonomy of deep-sea organisms and many species have yet to be described (see below). Not surprisingly, syntheses across groups are therefore rare in a single study.

Feeding modes in deep-sea sediments include omnivores, predators, scavengers and parasites. Most species are deposit feeders that ingest sediment grains and the organic particles and bacteria associated with them; through their feeding activity, these organisms are particularly important bioturbators. In some areas, suspension feeders filter particles out of the water column above the bottom, but because they rely on suspended particles they are most abundant in energetic environments such as seamounts.

As bottom depth increases, both biomass and densities of organisms decrease (**Figure 6**). Because food resources become scarcer and scarcer as distance from surface water and primary producers increases, this pattern is not unexpected. What is less intuitive, however, is that as food becomes more limiting and densities of organisms decrease, species diversity does not decline.

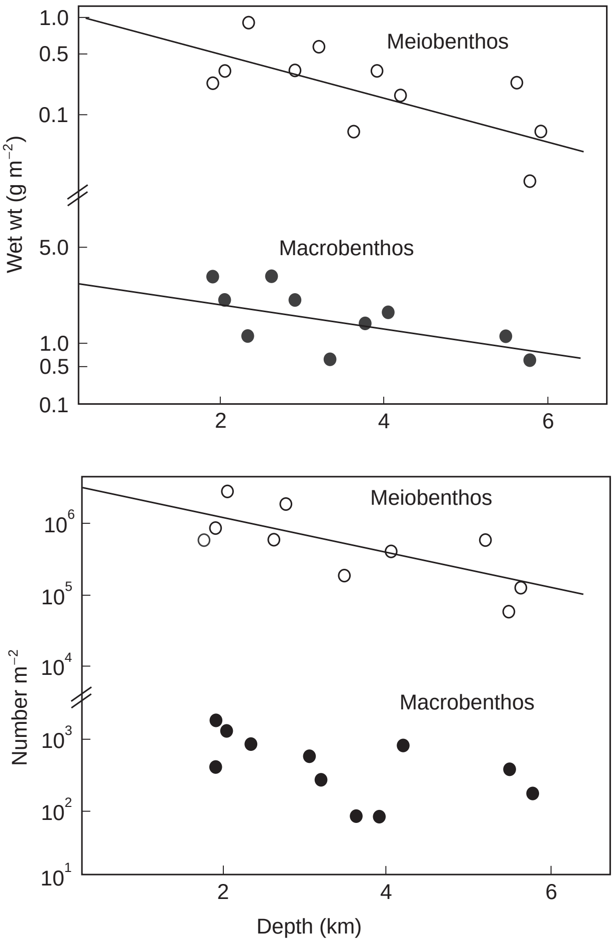

Figure 6 Based on Shirayama Y (1983) Size structure of deep-sea meio- and macrobenthos in the western Pacific. *International Revue der gesamten Hydrobiologie* 68: 799–810. Upper panel shows how densities of organisms decline with depth and lower panel shows a similar pattern for biomass.

Sampling the Fauna

Early efforts to sample the deep ocean floor used crude trawls towed from surface ships that were ineffective, and undoubtedly contributed to the idea that the environment is species poor. Modern trawls are now used in deep-sea fisheries, and some of these are effective for sampling megafauna living above the sediment or on bedrock. For smaller organisms, Howard Sanders and Robert Hessler, in their important work in the 1960s, used a semiquantitative device called an epibenthic sled comprising a metal frame surrounding a mesh bag. The sled is lowered to the bottom and towed behind a ship, where it skims off the surface sediment and associated fauna (**Figure 7C**). For hyperbenthos, this is still an instrument of choice, but for infauna it is only semiquantitative and has been replaced by quantitative samplers.

In the late 1960s, biologists began using a large metal device called a spade or box corer that is commonly used today to sample macrofaunal organisms. Box corers range in size but typically sample $\sim 0.25\,\mathrm{m} \times 0.25\,\mathrm{m}$ of ocean bottom. A metal frame surrounds a metal box that is lowered into the sediment from a surface ship (**Figure 7A**). After the box, which is often subdivided by a grid of metal subcores, enters the sediment, the spade swings down and slices beneath the box, locks in place, and seals the sediment within the corer for the return trip to the surface ship. Although the box corer is effective for sampling macrofauna, it must be handled carefully to avoid a bow wave as it approaches the sediment. For meiofauna and microbes living right at the sediment surface, even

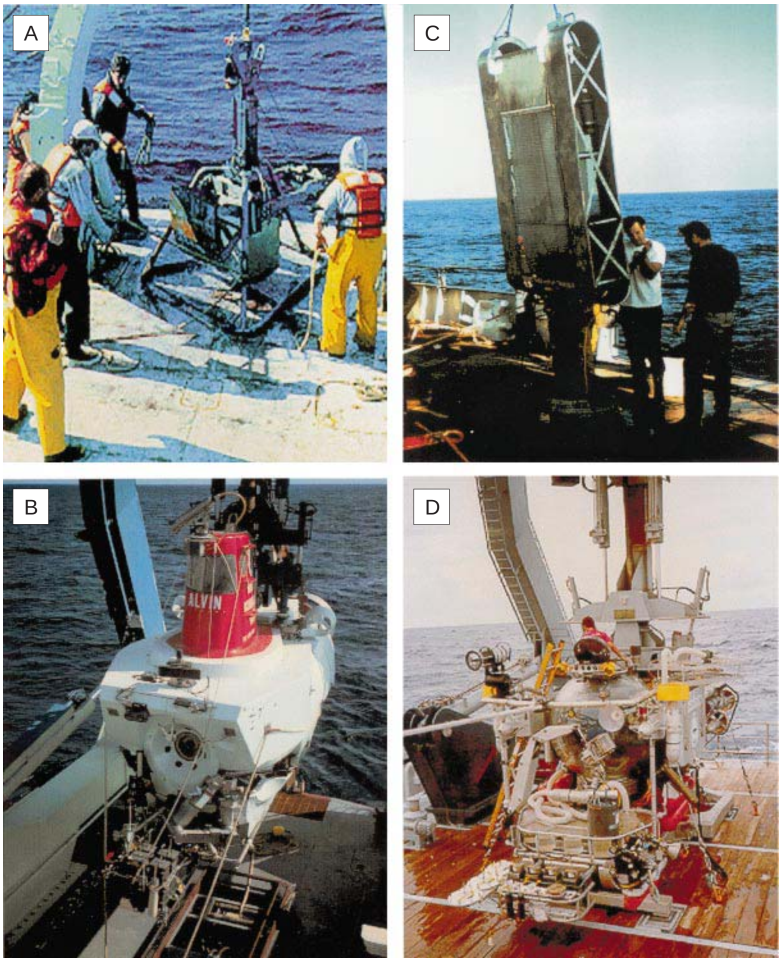

Figure 7 (A) The box corer is one of the basic sampling tools for deep-sea sediments. The corer is lowered from a surface vessel on a wire, and when the box penetrates into the sediment, the spade swings down and slices through the sediment, sealing the sample in the box. Fred Grassle is shown directing the deployment of the corer. (B) ALVIN was one of the first submersibles to be used for deep-sea research and played a vital role in the early characterization of hydrothermal vents. (C) An epibenthic sled, developed for deep-sea sampling in the 1960s, is towed so that it skims along the seafloor and samples sediments and near-bottom fauna. (D) The Johnson Sealink is a submersible that allows scientists to descend, with a pilot, to the deep-sea floor. ALVIN corers and colonization trays, seen on the front of the submersible, were to be deployed on this dive along with other gear.

a slight bow wave is a problem because it can blow away the lightest sediments and organisms at the sediment–water interface. To circumvent this problem, a device called a multicorer was developed by the Scottish Marine Biological Association (now the Scottish Association of Marine Sciences). With this sampler, a frame is gently lowered onto the seafloor from a surface ship and individual acrylic cores slowly enter the sediment. Individual cores are typically ~ 6 cm in diameter and a corer can have 4–12 individual cores or more.

Sampling gear that is deployed from surface ships has a distinct disadvantage; although the samples are quantitative, they are largely collected blindly, meaning that there is no frame of reference for the area where the sample was collected. Thus, the corer could land on or near some anomalous feature on the seafloor, and the investigating scientist could have trouble interpreting why the fauna was unusual. The development of research submersibles, such as ALVIN (**Figure 7B**) or the Johnson Sealink (**Figure 7D**) allows scientists to actually visit deep-sea environments and watch as their samples are collected at precisely the locations they request. To achieve this, a device called an ALVIN box corer, which is effectively a miniaturized box corer, has been developed. The manipulator arm of the submersible pushes the corer (typically 15 cm × 15 cm) into the sediment and then trips the doors that seal-in the sample, much as the spade does for the larger box corer. On board ship, individual subcores are processed over a sieve and then preserved in buffered 4% formaldehyde. Samples are kept in formaldehyde for at least 48 hours and then transferred to 70% ethanol.

Hard substrate environments present a different challenge in terms of quantitative sampling. Quantitative removal of hard substrate fauna is near impossible except where the substratum itself may be removed (e.g. manganese nodules). For these environments, visually based surveys, achieved through submersibles, remotely operated vehicles (ROVs), or towed cameras provide the most common means of evaluating fauna. These same approaches are also used for some megafaunal studies in sedimentary environments.

The instruments described above are the bases for evaluating faunal abundance, but studies of deep-sea fauna do not always focus on species composition. Physiologists have developed special respiration chambers to study metabolic processes, and ecologists have developed baited traps, colonization trays, and settlement tiles to study species response to resource availability. Most of these instruments are most effectively deployed by submersibles but other approaches have also been used, including free vehicles that are dropped to the bottom from surface ships, and later float to the surface when a release mechanism is triggered.

Patterns of Diversity

Although a few scientists before the turn of the century recognized that the deep sea was indeed a species-rich environment, general recognition of this fact did not occur until a series of papers were published by Howard Sanders and Robert Hessler. They collected a series of samples using an epibenthic sled; although this sampling approach is now known to significantly undersample, it represented a marked improvement over previous gear. Comparison of the data with data from other environments (**Figure 8**) indicated that the deep sea was among the most diverse of marine sedimentary habitats. From data collected along a transect running from Martha's Vineyard, Massachusetts to Bermuda, they demonstrated that diversity in deep-sea sediments exceeded that in most shallow areas and rivaled that observed in shallow tropical areas. At the time, this finding represented a startling contrast to current thinking, and even now the desert analogy still persists in some textbooks. More recent work using a box corer (**Figure 7A**), has shown that the deep sea is not only species rich, but it may also rival tropical rain forests in terms of total species present.

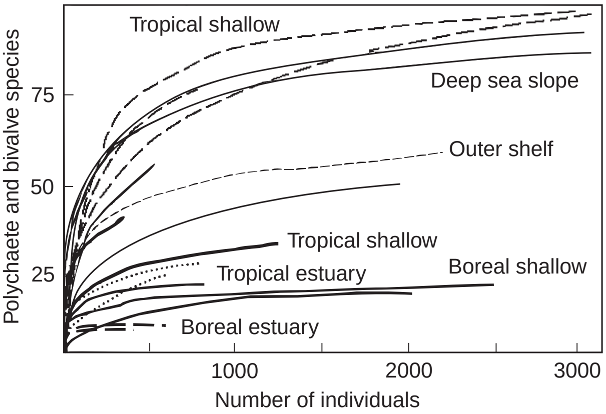

Figure 8 Comparison of deep-sea communities to other marine sedimentary communities based on plotting numbers of species versus numbers of individuals. (From Sanders HL (1969) Marine benthic diversity and the stability-time hypothesis. *Brookhaven Symposium on Biology* 22: 71–80.)

Several studies have looked at broad scale pattern in the deep sea, and found that diversity is not uniform with depth, location, or latitude. Michael Rex analyzed patterns with depth in gastropods and other taxa, and found a parabolic pattern, with a peak in diversity between 2000 and 3000 m on the continental slope. Diversity in shallow-water sedimentary habitats, such as in estuaries and tidal flats, is relatively low, then increases somewhat on the continental shelf, peaks along the mid to lower slope and then declines to abyssal plains. A similar pattern has been noted by other researchers, although the slope depth of the diversity peak varies among studies. There have been exceptions noted to this pattern. The abyssal Pacific, for example, has higher diversity than shallower areas, and work in Australia suggests that some coastal environments are extremely diverse, perhaps even exceeding that observed in the deep sea.

Studies have examined latitudinal patterns and suggest that diversity in the deep sea may decrease with latitude, at least in the North Atlantic. This work has focused on North Atlantic macrofauna, but other studies on meiofaunal nematodes in the Atlantic and isopod crustaceans from the South Pacific do not support such a trend.

How Many Species Are There?

At higher taxonomic levels, the marine environment is inarguably more diverse than any other habitat on Earth, and most of the phyla and classes of organisms that are unique to the marine environment occur in sedimentary environments. Some 90% of all animal families and 28 of 29 nonsymbiont animal phyla occur in marine environments, and of these 29, 13 occur only in marine habitats. Only one animal phylum, the Onychophora, has no living representatives in marine habitats, but even then there are marine fossil forms now known.

A number of estimates have been made regarding the possible number of species in the oceans (**Figure 9**) and considerable debate has arisen from these estimates; much of this controversy arises from the general acceptance that the deep sea has many undescribed species but disagreement over how many. Of particular uncertainty is the validity of assumptions that have gone into various estimates. One approach has been to survey taxonomic specialists who work on different groups, and determine what proportion of their taxon remains undescribed (left panel in **Figure 9**). The famous tropical rainforest estimate by Terry Erwin (central panel in **Figure 9**) of 10 million insect species was generated by looking at numbers of beetle species associated with a given species of rainforest tree, estimating what portion of insects comprises beetles, and then multiplying by estimated numbers of tropical tree species. Based on the rate at which species were added with increased area sampled along a 176-km long depth contour off the eastern United States, Grassle and Maciolek extrapolated to the total area of the deep sea and estimated that there are 10 million deep-sea macrofaunal species. Robert May suggested that because about half of Grassle and Maciolek's species were previously undescribed, one could extrapolate from the presently described 250 000 marine species to arrive at a projection of ~ 500 000 total species. Data from the Pacific suggests that only 1 in 20 species has been described; using this estimate, May's approach would yield ~ 5 million species. John Lambshead, a nematode ecologist, has noted that meiofaunal nematodes are more abundant and species rich in individual core samples than macrofauna, and his estimate for total nematodes in the deep sea is 100 million species. At present we know little about how widely distributed nematode species may be, making extrapolation even more tenuous than for macrofauna.

Species richness comparisons across different environments are complex. Within any given environment, estimating the total numbers of species present is difficult because it is impossible to fully sample the environment. The deep sea is particularly problematic. It has been estimated that of the $\sim 3.25 \times 10^8\,\mathrm{km}^2$ of seafloor that is part of the deep sea, only about $2\,\mathrm{km}^2$ has been sampled for macrofauna and $5\,\mathrm{m}^2$ has been sampled for meiofauna. Sampling coverage for microbes is poorer still. In addition to the huge area involved, ship time and sample processing are expensive, and relatively few taxonomic specialists know the deep-sea fauna. Thus, current conclusions on pattern and numbers are based on very limited spatial coverage.

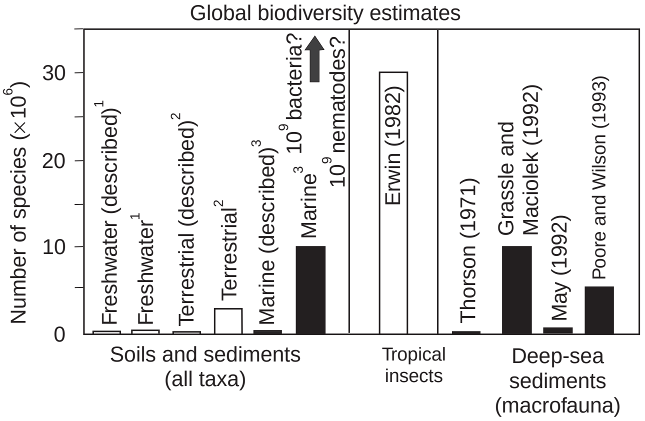

Figure 9 Various estimates of total species richness in marine sediments in comparison with estimates for other environments. Numbered sources in the left panel are: [1]Palmer MA, Covich AP, Finlay BJ *et al.* (1997) Biodiversity and ecosystem processes in freshwater sediments. *Ambio* 26: 571–577; [2]Brussaard L, Behan-Pelletier VM, Bignell DE *et al.* (1997) Biodiversity and ecosystem functioning in soil. *Ambio* 26: 563–570; [3]Snelgrove PVR, Blackburn TH, Hutchings PA *et al.* (1997). The importance of marine sedimentary biodiversity in ecosystem processes. *Ambio* 26: 578–583. For each of these sources, the numbers of described and projected species are given. The arrow in Snelgrove *et al.* indicates estimates if bacteria (10^{12}?) or nematodes (10^9?) are included; data on which estimates for these groups are based are very limited. Values in other panels are projected numbers of species. Numbers for marine systems are solid bars. Freshwater and terrestrial refer to species number for all global components of those environments pooled, although estimates for bacteria are not included in these numbers. Additional data sources are Thorson G (1971). *Life in the Sea.* New York; McGraw-Hill and Erwin TL (1982) Tropical forests: their richness in Coleoptera and other Arthropod species. *Coleopterists' Bulletin* 36: 74–75.

Most of the data on species number and pattern has been based on data from the North Atlantic. Clearly the variability in patterns described above suggests that a wider database is needed to effectively test the generality of these concepts. Areas such as the southern oceans that have been poorly sampled in the past offer key pieces to the puzzle of deep-sea pattern. Another shortcoming with large-scale comparisons is that most focus on just one of the size groupings of organisms. Thus, between-group differences in pattern are difficult to attribute to differences in areas sampled or to real differences between the groups. In short, we need deep-sea studies that are broader in geographic coverage and taxonomic coverage before these questions can be resolved definitively.

Low Diversity Environments

Not all deep-sea communities are species rich. As described earlier, the hydrogen sulfide and heavy metals emitted at vents are toxic to most species, and species diversity is quite low. Moreover, the short life span of most individual vents makes them among the most unpredictable environments in the deep sea. Like the hard substrate environment around vents, the sediments that occur in hydrothermal vent areas are inhospitable because of high concentrations of metals, sulfide, and hydrocarbons. There are, nonetheless, often mats of bacteria over these sediments that utilize the hydrogen sulfide as an energy source. Not surprisingly, an increase in hydrothermal flux can quickly 'cook' the bacteria, whereas a decrease in flux can starve them to death.

A number of other specialized deep-sea environments are species depauperate. Deep-sea trenches are subject to mud slumping and poor circulation as a result of the steep trench sides, and species diversity is very low. Sediments beneath upwelling regions and other highly productive areas, such as the upper slope off Cape Hatteras, are also generally low in diversity because large amounts of organic matter accumulate on the ocean floor and decompose, resulting in hypoxic (low oxygen) conditions that few organisms can tolerate. A few deep-sea areas, such as the 'HEBBLE' site on the continental slope off Nova Scotia, are subject to intensive 'storms', where currents become intense and sediment resuspension occurs. Evidence suggests that macrofaunal diversity is depressed in such areas, but surprisingly meiofaunal diversity is not. Presumably, the meiofauna are able to cope with the disturbance more effectively than the macrofauna.

Although ecological processes are undoubtedly important in the deep sea, evolutionary time scales and processes are also important. Defaunation of some deep-sea areas such as the Norwegian Sea over recent geological time scales is thought to have contributed to low diversity. Glaciation defaunated the area by blocking sunlight and reducing circulation, and the shallow sills that surround the basin have likely resulted in very slow reestablishment of deep-sea communities from adjacent basins.

Theories

One of the driving questions in deep-sea ecology since the 1960s is how an environment that appears so physically homogeneous is able to support a species-rich fauna. When Sanders documented the high diversity of deep-sea systems in the late 1960s, he proposed the stability–time hypothesis, in which the high level of stability afforded by the deep sea over evolutionary time has resulted in greater specialization and niche diversification in deep-sea fauna. Certainly the relative stability of deep-sea environments has contributed to the numbers of species present, but if stability were the lone explanation then it is inconsistent with observations of lower diversity on abyssal plains than on adjacent slope habitats. An additional problem is that most species are thought to be relatively nonselective deposit feeders, which is inconsistent with niche specialization.

In the early 1970s, several alternative theories were proposed. Predators could prevent competitive equilibria from being attained by infauna by cropping back individuals. But most deep-sea predators appear to be nonselective, and infauna are characterized by slow growth, late reproductive maturity and dominance by older age classes; none of these characteristics would be expected in a predator-controlled system. Evidence from shallow-water sediments suggests that at small scales at least, predators decrease sedimentary diversity, but the role that predators may play in maintaining deep-sea diversity remains largely unanswered at this point.

The increasing evidence for small-scale spatial and temporal heterogeneity in deep-sea systems has led to speculation that small-scale patches may be important. The patch mosaic model proposes that small patches create disequilibria habitats that promote different species and thus promote coexistence. Studies have tested the patch mosaic model by sampling natural patches or creating experimental patches; both types of study have found that species that occur in most patch types are usually rare or absent from nonpatch sediments. This pattern is consistent with the patch mosaic model, but experiments so far have demonstrated that patches promote only a modest number of species and the overall species richness in a given patch tends to be lower than in nonpatch areas. It is unclear whether we need to sample more patch types or invoke an altogether different explanation for high diversity.

Island biogeography has shown that larger areas tend to support more species, and it has been argued that the large area of the deep sea may be the primary reason for its species richness. To some extent this areal relationship must be a contributing factor, but if area were the only issue then abyssal plains would consistently exceed all other habitats in diversity. Moreover, the deep sea does not appear to add habitat heterogeneity with area as most habitats do; vast areas of sedimentary bottom may sometimes exhibit changes in sediment composition, but even compared to shallow areas the habitat heterogeneity is quite small.

Intermediate disturbance has been touted in a number of ecological systems as being important for high diversity. High levels of disturbance can eliminate sensitive species and invariant habitats may allow superior competitors to outcompete weaker species; both scenarios result in reduced diversity. Intermediate disturbance prevents competitive dominants from taking over but is not severe enough to eliminate sensitive species, resulting in high diversity. The strongest evidence for this hypothesis in the deep sea is the mid-slope peak in diversity described earlier, and the reduced diversity observed in disturbed deep-sea habitats such as hydrothermal vents, low oxygen areas, environments with benthic storms, and slumping areas.

In summary, we still lack a definitive explanation for which factors are most important in promoting diversity in deep-sea ecosystems. In all likelihood, no single explanation is correct and multiple factors will prove to be important. Efforts are currently underway to try to clarify this question using experimental approaches such as predator exclusion experiments and creation of artificial food patches, along with analytical approaches that analyze pattern with respect to environmental variables. As the available data increase, many of the questions about pattern and cause may become clearer, but there is considerable work to be done.

Threats and Benefits

The deep-sea environment has attributes that render it vulnerable to human disturbance, but impacts have nonetheless been modest compared to most marine habitats because of the distance from land, large size, and great depth. Pollutants and nutrients that have created severe problems in coastal areas via land runoff, river runoff or aerosol transport, are usually sufficiently diluted by the time they reach the open ocean that impacts are modest. There is biochemical evidence, however, that pollutants may occur in deep-sea organisms at low concentrations. Fishing, and the habitat destruction it causes, is less widespread in the deep sea than in shallow water because it is expensive and time consuming to fish at great depths. Moreover, the densities of organisms that are present are often insufficient to support commercial fishing. Having said that, there are a number of deep-sea fisheries, many of which utilize trawls and dredges that damage the integrity of the benthic habitat, injure organisms, and remove many nontarget species as by-catch. The vulnerability of deep-sea species to human activities is well exemplified by fisheries such as that for the Australian orange roughy. Like many deep-sea fisheries, fishing effort has outpaced the capacity of the population to recover, raising the distinct possibility that a sustainable deep-sea fishery may represent an oxymoron. This same vulnerability presumably applies to nontarget species that are removed as by-catch or injured by fishing gear.

A third human impact is through waste disposal. Materials ranging from sewage sludge to radioactive waste have been dumped in the deep ocean, largely justified on the basis that the currents are weak so containment is more likely, food chains are far removed from most human harvesting activities, and the large area of the deep sea reduces the likelihood of a major impact. There is also a feeling among some that even if an impact occurs, the organisms that would be affected have little or no obvious economic value to humans. A final potential threat to deep-sea communities is deep-sea mining. There has been some interest in the mining of manganese nodules, small softball-sized nodules that are rich in manganese, nickel and other metals. These nodules occur on the seabed in abyssal plain areas of the oceans, but because of the depths involved, deep-sea mining is not commercially viable at present. Metals such as manganese are, however, of great strategic importance because many countries presently rely on foreign suppliers. Thus, there is a very real chance that deep-sea mining may someday occur. Different mining strategies will, of course, have different types of impact but habitat destruction is likely to be the greatest problem.

Because many deep-sea organisms grow very slowly, reproduce at an older age than their shallow-water counterparts, and produce very few offspring per individual, they are thought to be extremely vulnerable to disturbance and habitat damage. In the past it has been assumed, however, that many deep-sea species are broadly distributed because there are few barriers to dispersal and little obvious habitat heterogeneity. If this assumption holds, then their vulnerability to extinction might be reduced. At present, our understanding of how quickly species turn over spatially is very limited, particularly for some of the groups like nematodes that have been least studied. With emerging molecular approaches, it is also becoming clear that species that have been treated as cosmopolitan may, in some instances, be species complexes.

Given that many deep-sea environments support species that are either of no commercial fishing interest or are not sustainable, is there any reason to exercise caution in how humans impact the deep sea? There are, in fact, several compelling reasons to be concerned. First, the deep sea represents one of the few remaining pristine habitats on Earth. We can say, with only a few exceptions, that deep-sea communities have not been compromised by human development. This attribute makes them one of the last natural laboratories on Earth where the 'chemicals' have not been tainted. Because it is so very diverse, the deep sea can provide a natural and uncompromised laboratory in which to test ideas on regulation of biodiversity. A second reason to exercise caution is that the deep sea may represent one of the largest species pools on Earth. From an ethical and esthetic perspective, it could be argued that this characteristic alone is sufficient motivation to limit human disturbance. But from an economic perspective, there is great interest among pharmaceutical companies in organisms with unusual physiologies; the thermophilic bacteria that live at hydrothermal vents, for example, have generated tremendous interest for their bioactive compounds. A third concern is with respect to remediation. Although material dumped in the deep sea may be out of sight and mind, any decision at a later time to remediate (e.g. leaking radioactive waste) would be prohibitively expensive, if it was possible at all.

In summary, the deep sea is a vast and relatively undisturbed habitat that may be very vulnerable to human disturbances. Our current understanding of the deep sea and its immense diversity is very limited, but is nonetheless advancing steadily. A precautionary approach will ensure that the unusual attributes of the deep sea, including its rich biodiversity, will not be inadvertently destroyed by ignorance.

See also

Benthic Boundary Layer Effects. Benthic Foraminifera. Benthic Organisms Overview. Demersal Fishes. Macrobenthos. Meiobenthos. Ocean Margin Sediments. Pelagic Biogeography.

Further Reading

Gage JD and Tyler PA (1991) *Deep-Sea Biology. A Natural History of Organisms at the Deep-Sea Floor*. Cambridge: Cambridge University Press.

Grassle JF and Maciolek NJ (1992) Deep-sea species richness: regional and local diversity estimates from quantitative bottom samples. *American Naturalist* 139: 313–341.

Gray J, Poore G, Ugland K *et al.* (1997) Coastal and deep-sea benthic diversities compared. *Marine Ecology Progress Series* 159: 97–103.

Lambshead PJD (1993) Recent developments in marine benthic biodiversity research. *Oceanis* 19: 5–24.

May R (1992) Bottoms up for the oceans. *Nature* 357: 278–279.

Merrett NR and Haedrich RL (1997) *Deep-sea demersal fish and fisheries*. London: Chapman & Hall.

Poore GBC and Wilson GDF (1993) Marine species richness. *Nature* 361: 597–598.

Rex MA (1983) Geographic patterns of species diversity in the deep-sea benthos. In: Rowe GT (ed.) *The Sea*, vol. 8: *Deep-Sea Biology*, pp. 453–472. New York: John Wiley.

Rex MA, Stuart CT, Hessler RR *et al.* (1993) Global-scale latitudinal patterns of species diversity in the deep-sea benthos. *Nature* 365: 636–639.

Sanders HL and Hessler RR (1969) Ecology of the deep-sea benthos. *Science* 163: 1419–1424.

DEEP-SEA FISHES

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Introduction

For the purpose of this article a deep-sea fish is one that lives, at least for most of its life, at depths greater than 400 m. The fishes of the continental