Deep-Sea Benthic Biodiversity

The ocean bottom supports communities that may be as diverse as those of any habitat on Earth

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The life that inhabits ocean depths beyond the continental shelves is unfamiliar, even to most biologists. Samples of deep-ocean sediments typically contain representatives of a dozen phyla, but most deep-sea animals are small and live below the sediment surface.

Collection of biological samples on the ocean floor is extremely difficult because the depths, of half a mile or greater, are well beyond those at which divers can work. Until the recent use of manned submersibles, samples were collected blindly at the end of a wire from surface ships. Even with submersibles, the process of manually removing animals from deep-sea sediments is long and tedious. It is difficult to keep animals from dying during collection and processing, so few deep-sea species have been observed or photographed alive. Once collected, specimens are hard to identify, because few biologists are trained in taxonomy of deep-sea species.

Until the 1960s, the deep sea was thought to have relatively few species. Graphs showed reductions in numbers of species with increasing depth (Abele 1982, Eckman 1953, Murray 1895, Vinogradova 1979a). However, these figures were not standardized according to the number of individuals or samples collected at each depth, so they represented primarily the decline in density and biomass of animals with increasing depth. These declines, combined with images from the popular imagination, may be responsible for the misconceptions that still appear in textbooks (e.g., Davis 1987, Ingmanson and Wallace 1989).

Species at the bottom
The richness of deep-sea life was discovered by Woods Hole Oceanographic Institution scientists more than two decades ago (Hessler and Sanders 1967, Sanders and Hessler 1969). To collect their samples, Hessler and Sanders used an epibenthic sled, a metal frame with a fine-mesh bag that was dragged along the bottom to collect sediment. Doors that could be closed prevented the sample from washing out during the long haul back to the surface. A single epibenthic sled sample often contained many times the number of animals captured from deep-sea depths during entire expeditions with the trawls then in common use (Sanders 1977).

The new sampling method revealed that, for similar efforts, the numbers of deep-sea species collected were much greater than the numbers of...
species collected in shallow temperate communities and of the same order as in collections from shallow tropical communities (Hessler and Sanders 1967, Sanders 1968). By enumerating species from many epibenthic sled samples, scientists further demonstrated the existence of large numbers of species in the deep sea (Sanders 1977), but the data were not quantitative and the idea of a highly diverse deep-sea fauna was not universally accepted (Nybakkken 1982, 1988).

Adding up the species

Samples taken to monitor the potential effect of deep-water oil and gas exploration provided quantitative data for new estimates of the richness of deep-sea communities (Blake et al. 1987, Grassle and Maciolek in press, Maciolek et al. 1987a,b). Before these studies, deep-sea biologists had only been able to process a few quantitative samples from each of half a dozen sites. Even for a team of experienced specialists, identifications are extremely time-consuming and often require consultations with the one or two world authorities on each taxon. The most intensive effort has been the Eastern United States Continental Slope and Rise Study, for which a large team of systematists was assembled in 1982 by Nancy Maciolek and James Blake at Battelle Ocean Sciences in Duxbury, Massachusetts, (see Acknowledgments) and my laboratory at the Woods Hole Oceanographic Institution. Most of the team had already worked together to answer questions that required study of the whole fauna from the better-described, species-rich Georges Bank continental shelf.

Three areas along the eastern coast of the United States have been well-studied: a northern area on the continental slope south of Georges Bank, a central area off New Jersey and Delaware (Figure 1), and a southern area off North and South Carolina. Both the northern and southern regions were found to be heterogeneous. The northern area was characterized by several kinds of communities because of sediment and bottom-current differences among the many canyons and gullies on the southern margin of Georges Bank. The continental slope and rise region off the Carolinas was also heterogeneous in sediment composition and community structure because of strong bottom currents at many of the sites sampled.

To estimate species richness from a relatively homogenous deep-sea region, Grassle and Maciolek (in press) focused on the slope environment off New Jersey and Delaware, where community structure, sediments, bottom currents, and topographic relief did not vary greatly among sites. In this region, we sampled 233 areas, each 0.09 m$^2$ in surface area (total area of 21 m$^2$) from ten 2100-meters, three 1500-meters, and one 2500-meter depth stations. The effort yielded 798 species, 171 families, and 14 phyla (excluding planktonic forms and fauna attached to rocks or shells; Table 1).

Samples from a single station (three replicates, three times a year for two years) combine to make a species-area curve that shows some diminution in the rate of species accumulation with increasing area (Figure 2). Samples from all stations at a single depth (2100 m) within a region combine to make a similar curve (Figure 3). If samples from all depths and all three geographic areas are combined, the number of species continues to increase to 1397 species from 556 samples (total surface area of 50 m$^2$ from all three study areas; Figure 4).

To see whether our samples were sufficient to estimate the total number

![Figure 1. Location of 14 deep-sea box-coring stations on the continental slope off New Jersey and Delaware.](image_url)
of deep-sea species, we calculated the proportion of species represented by single individuals. We found that this proportion does not decline with increasing area sampled (Figure 4). Therefore, the entire collection of species is a serious underrepresentation of the total number of species in the deep sea, and many more species remain to be discovered at each of the scales of sampling.

Regional species diversity

Most studies of species diversity do not consider the magnitude of the entire species pool from a region. How does local or within-habitat diversity (considering areas of less than 100 m²) compare with regional diversity (areas of hundreds of square meters; Osman and Dean 1987, Ricklefs 1987)?

Summaries of all the recorded species from a region can be used to approximate regional species richness. Two areas in the United States with long traditions of coastal research provide examples. The checklist of the biota of Lower Chesapeake Bay notes 115 recorded species of polychaete worms and 99 species of peracarid crustacea (Wass et al. 1972). The Woods Hole checklist (Smith 1964) has 226 polychaetes and 104 species of peracarids (although Smith notes that the peracarid number is too low).

Regional studies of the systematics of whole taxa provide further data on regional species richness. For example, a study of the known shallow-water polychaetes from British Columbia and Washington (Hobson and Banse 1981) includes 273 species.

In comparison with these shallow-water studies, the Eastern US Slope and Rise Study obtained more species in each taxon examined, although it employed a much lower level of sampling effort. The 356 deep-sea box-core samples (an area of sediment 30 cm on a side and 10 cm deep) from the entire study contained 707 species of polychaetes and 426 species of peracarid crustacea (Grassle and Macek in press). These species were collected during only six sampling periods, and the surface area sampled was only approximately 50 m²—a minuscule sampling effort in comparison with the years of collecting from many areas in the shallow-water studies. The large number of species from this limited sampling effort further underscores the inadequacy of knowledge of deep-sea fauna.

Accounting for deep-sea diversity

No single theory can account for the high diversity in the deep sea. Several major features of the deep sea contribute to its relatively high diversity.

Absence of widespread disruption of habitat. The lack of widespread mortality from environmental extremes, such as high or low temperature, high or low salinity, or low oxygen, led Sanders (1968) to suggest that the relative constancy of deep-sea conditions leads to high diversity. This hypothesis can be improved by consideration of potential microhabitats. X-rays of deep-sea sediments indicate a complex pattern of sediment heterogeneity and burrows of many shapes and sizes developed from the activities of animals during long periods (Figure 5). In most shallow-water environments, the sediments are resuspended during storms, so that these complex burrow structures do not have a chance to develop and persist (Grassle and Morse-Porteous 1987). The absence of events in at least part of the system that cause widespread mortality allows some species to live a long time—a century or more (Turekian et al. 1975). Therefore, a species can survive even if its members produce low numbers of offspring each time they reproduce (Grassle and Sanders 1973). In addition to creating burrow structures, long-lived species themselves provide habitat for parasites, attached or internal symbionts, and especially external symbionts. Parasites are common in the deep sea. The incidence of mutually beneficial relationships is in need of investigation.

Patchy food resources. In the deep sea, food resources (phytoplankton and plant and animal tissues settling from the surface) are divided into patches of small spatial extent (square centimeters to square meters). Pieces of wood (Turner 1973, 1977, Wolff and Hesler 1979) and the remains of nektonic animals (Isaacs 1969, Smith et al.
1986, Stockton and DeLaca 1982) that fall to the bottom are the best-known sources of these patches. But unequal distribution of smaller organic-rich particles, especially phytoplancton, are likely to be more important in maintaining high species richness.

Surface phytoplankton blooms result in phytodetritus patches on the deep-sea floor (Billett et al. 1983, Gooday and Turley 1990, Lampitt 1985). The phytodetritus and other types of organic material, such as salps (gelatinous zooplankton), may be redistributed by bottom currents and accumulate in burrows and other depressions on the sea floor (Aller and Aller 1986, Grassle and Morse-Porteous 1987). These patterns of organic matter are analogous to the relatively nutrient-rich gaps that form as a result of tree falls in the rainforest (Grubb 1977).

Disturbance. The movements and feeding activities of large animals such as fish, snails, and sea urchins may disturb the sediment, generating gaps for subsequent occupancy by early colonists. Biogenic structures altering near-bottom flow, such as sediment mounds produced by individual animals, are especially important in allowing many species to coexist in the deep sea (Jumars 1976, Smith et al. 1986). The effects of disturbance-producing structures may be similar to disturbance caused by episodic influxes of organic-rich particles, but these processes may be usefully separated.

A major question is how animals that project above the sediment surface into the bottom boundary layer, such as the mudball cirratulid polychaete Tharyx luticostellus (Jumars 1976, Thistle and Eckman 1988, 1990) or xenophyophore protozoans (Levin et al. 1986), influence the deep-sea community. Do they enhance the accumulation of organic particles, thereby increasing the ability of organisms to obtain this food, act as refuges from predation, or simply provide additional space for colonization? Experiments have not thus far distinguished among these possibilities.

Large area. The potential importance of a large surface area with few barriers to dispersal was recognized by Osman and Whitlatch (1978). The area of the deep sea having depths greater than 1000 m is approximately $3 \times 10^8$ km² world-wide. The observed species-area relationships (Figure 3) suggest linear rates of accumulation of species from the same depth of one species per square kilometer. Extrapolation to the total surface area of deep-sea sediments, with a correction for low-density abyssal areas, leads to estimates of the total species pool on the order of $10^7$, but even this large number may be conservative.

The rate of addition of new species is much more rapid with changing depth than with changes in sediment composition or habitat. Therefore, the rate of increase in number of species with increasing area is much greater if samples from a variety of depths are added.

Accurate estimation for large areas of ocean floor would require enormous sampling efforts to answer the question of whether the rare species described in our previous samples have narrow or broad distributions. (If the rare species have narrow distributions, estimates based on relatively few samples might be adequate.) Vinogradova (1979b) estimated that approximately 85% of deep-sea fauna occur in only one ocean. Molecular techniques for the study of genetic relatedness need to be used to determine which, if any, deep-sea species occur in all oceans or whether, despite the apparent openness of the system, populations isolated by distance are separate species.

### What determines community structure?

The deep sea is an ideal place to study the relative importance of temporally and spatially varying processes in determining community structure, because disturbance in most of these environments (see Grassle 1989 for discussion of deep-sea areas subject to large-scale disturbance) is on a scale of less than a few meters and occurs as discrete events not compounded by larger-scale physical perturbations. Biological interactions such as predation and competition may also be important in enhancing the development of high local species diversities, but such within-system properties cannot provide complete explana-

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**Figure 4.** Relationship between number of species and number of individuals in successively larger combinations of samples. The open symbols show the relationship between the number of individuals collected and the number of rare species (i.e., species represented by a single individual). The closed symbols show the relationship between the number of individuals and the total number of species. These data demonstrate that the number of species continues to increase logarithmically, and the proportion of rare species does not diminish, with increased area of sampling. ▼, ▲: mean of all individual samples; ◻, ■: mean of combined 2100-meter depth samples (groups of 3) within each sampling date; △, ▽: mean of combined 2100-meter depth samples (groups of 18) within each station; ◆, ○: combined 2100-meter samples (group of 125) for all stations; and ○, ●: combined samples (group of 556) from all three regions and all depths. (Figure from Grassle and Maciolek in press.)

**Table 1.** Number of species and number of families in each phylum from 233 0.99-square-meter samples taken between 1500-meter and 2500-meter depths on the continental slope off New Jersey (Grassle et al. 1990).

<table>
<thead>
<tr>
<th>Phylum</th>
<th>Number of species</th>
<th>Number of families</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cnidaria</td>
<td>19</td>
<td>10</td>
</tr>
<tr>
<td>Nemertea</td>
<td>22</td>
<td>1</td>
</tr>
<tr>
<td>Priapulida</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td>Amelida</td>
<td>385</td>
<td>49</td>
</tr>
<tr>
<td>Echiurida</td>
<td>4</td>
<td>2</td>
</tr>
<tr>
<td>Spinulida</td>
<td>15</td>
<td>3</td>
</tr>
<tr>
<td>Pogonophora</td>
<td>13</td>
<td>5</td>
</tr>
<tr>
<td>Mollusca</td>
<td>106</td>
<td>43</td>
</tr>
<tr>
<td>Arthropoda</td>
<td>185</td>
<td>40</td>
</tr>
<tr>
<td>Bryozoa</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Brachiopoda</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td>Echinodermata</td>
<td>39</td>
<td>13</td>
</tr>
<tr>
<td>Hemichordata</td>
<td>4</td>
<td>1</td>
</tr>
<tr>
<td>Chordata</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Total</td>
<td>798</td>
<td>171</td>
</tr>
</tbody>
</table>
tions without reference to a physical or external property of the system.

In concentrated patches of food, for example, predators may prevent single species from monopolizing food resources and hasten the successional sequence of species that contributes to the mosaic of species distributions. But the low average densities of life are believed to be a consequence of an external property—low food inputs. Such low densities suggest less competition among species as a result of few instances of direct interference. However, because species that forage more widely are favored in low-food environments (Jumars and Fauchald 1977), the low food input may explain only the low density of the sessile portion of the fauna.

The threat of humanity

The vastness and remoteness of the deep-sea floor makes it seem safe from the anthropogenic perturbations that threaten highly diverse terrestrial and shallow-water environments. However, these very factors make it appear attractive as a waste disposal area. A serious cause for concern is the potential effect of toxic compounds that have been found to accumulate in deep-sea sediments (Farrington and Tripp 1977, Harvey and Steinhauer 1976, Knap et al. 1986).

Almost nothing is known about the tolerances of deep-sea organisms to the gradual build-up of anthropogenic chemicals, and there is a potential for changes to be widespread if they do occur. Measurement of pollutants, descriptions of deep-sea communities from many parts of the ocean, and in situ toxicity studies are urgently needed. The establishment of long-term stations to better understand the interactions of deep-sea organisms with their natural environment and to monitor the potential effects of pollution are necessary to provide the information required for wise management of ocean resources.

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References cited


