
19 Are Deep-Sea Communities Resilient?

J. FREDERICK GRASSLE, NANCY J. MACIOLEK, AND JAMES A. BLAKE

Editor's Note: The bottom of the deep sea is dark and cold and a very old habitat by most terrestrial standards. Dr. Grassle and his colleagues have shown that the benthos contains an extraordinary diversity of life with different life histories and adaptations to habitat. A combined sample from 1,500 m to 2,500 m off New Jersey that covered merely 241 m² yielded 798 species, a diversity that approaches the upper limits of what can be found on land anywhere. Another sampling off the East Coast of North America yielded nearly 600 species. Most deep-sea species are rare, and species once recognized as “cosmopolitan” are now seen as groups of species with restricted distributions. Experience in study of this extraordinary diversity remains minuscule in proportion to the area, and estimates of the total number of species in the oceans now exceed by many orders of magnitude the earlier estimate of 160,000. The experience is similar to that in tropical forests where access to the crowns of trees has recently revealed not only new populations of birds, but thousands of new insect populations. The knowledge has caused estimates of the total number of species on earth to soar to 10 million or more. Experience with the benthos may push this number higher still.

Chronic disturbance of either the benthos or the water column increases the abundance of a few species. In such sites one species may comprise more than 30 percent of the fauna and a few species will make up more than half of the total fauna. Factors that cause such a shift are many, including such minor or local changes as the entry of a fish carcass to the benthic region, or general disturbance such as a sudden change in temperature or contamination with sewage or other human wastes.

Not surprisingly, in view of the difficulty of working on the bottom of the oceanic abyss, two to three miles below the surface, the communities and their responses are imperfectly known. Patterns seem consistent with extensive experience on land where improved information reveals the extent to which species contain ecotypes specific to locales and where chronic disturbance reduces diversity both within and among species and favors groups of a few hardy species recognized as resistant to a wide variety of disturbances. The small glimpses we have of the benthos, one of the oldest and most extensive habitats on earth, offer still another view of evolution in process, including the responses to disturbance that seem, again not surprisingly, to be well established in all ecosystems.

Introduction

The prevalent view of the nature of deep-sea ecosystems has changed twice in the last two decades. The sea floor is not the impoverished desert that was
envisioned by most biologists (e.g., Ekman 1953; Williams 1964) until publication of the first deep-sea studies using fine-mesh trawls that skimmed the animals from the surface layers of sediment (Hessler and Sanders 1967). Nor is it the uniform, aseasonal, “chemostatic” environment that was proposed to explain the rich diversity of deep-sea species (Sanders 1968). Although deep-sea environments are relatively uniform in temperature and seawater chemistry, the supply of food is seasonal and erratic and results in spatial patchiness. Large aggregates of organic matter from terrestrial, near-shore, and surface-dwelling plants and animals generate spatial and temporal heterogeneity. The activities of living animals on the bottom add to the mosaic of differing resources by altering the sediments or introducing biogenic structures. The relatively organic-rich surface layer of sediment that provides food for bottom-dwellers is resuspended by occasional intense current flows generated by events analogous to storms.

By using submersibles it has been possible to gain a close-up view of deep-sea life and to conduct in situ experiments. The information from the portholes and cameras of submarines has greatly altered our image of the deep sea but even these views are inadequate. Experiments on the sea floor, and more nearly complete analysis of a greater number of quantitative samples, in addition to improved first-hand observations have brought a revolution in thinking about the deep sea in the last decade. The ecological processes operating in the deep sea are more like those operating in other species-rich ecosystems than has been previously supposed. For example, the effects of small-scale disturbance are similar to the effects of gaps in rain-forest canopy produced by falling trees. Despite these similarities to dynamic processes operating in other environments, vast areas of sea floor are at one extreme of the known patterns of environmental change. In comparison to shallow water, most of the deep sea has modest levels of sediment deposition and resuspension and minimal changes in temperature and salinity. Biological activities outside the system supply organic materials that are a particularly important source of spatial and temporal heterogeneity. Deep-sea species have evolved a broad range of life histories and habitat specializations in response to differing aspects of this heterogeneity.

**Species Diversity of Deep-Sea Benthos**

Quantitative sampling on the continental slope off New Jersey indicates that deep-sea diversity has been underestimated (Grassle and Maciolek in preparation). A box corer was used to collect 233 samples, each with a surface area of 900 cm², from a 176 km transect along the depth contours between 1,500 m and 2,500 m depth. Thus, the combined surface area of
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Table 19.1. Number of species and number of families in each phylum from 233 0.09-m² samples taken between 1,500-m and 2,500-m depth on the continental slope off New Jersey

<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>Annelida</td>
<td>385</td>
<td>49</td>
</tr>
<tr>
<td>Echiurida</td>
<td>4</td>
<td>2</td>
</tr>
<tr>
<td>Sipuncula</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><strong>Total</strong></td>
<td><strong>798</strong></td>
<td><strong>171</strong></td>
</tr>
</tbody>
</table>

The number of species in these samples is about 21 m². The number of species in these samples is 798 (Table 19.1). From 32° to 41° N latitude and several depths down to 3,000 m on the continental slope and rise off the eastern coast of the United States 554 samples (including the 233 samples from off New Jersey) contained nearly 1,600 species (Blake et al. 1987; Maciolek et al. 1987a, b). Since most deep-sea species are very rare, the sampling effort required to describe the limits of species distributions would be enormous. As more powerful techniques for distinguishing species are used, "cosmopolitan species" are being shown to be groups of related species with relatively restricted distributions. Since the surface area of the deep-sea floor below 1,000 m is on the order of $3 \times 10^6$ km², extrapolations from these data show an earlier estimate of 160,000 species in the oceans at all depths (Thorson 1971) to be orders of magnitude too low.

How Is Deep-Sea Diversity Maintained?

Spatial and temporal heterogeneity are maintained by biogenic structures, a patchy supply of food, and small-scale disturbance (Grassle and Morse-Porteous 1987). Burrows, mounds, shells, and other structures provide refuges and may enhance larval settlement or food supply by influencing the
near-bottom flow regime. Irregularities in the surface of the bottom created by the activities of animals result in uneven distribution of organic material settling from the surface. Large organic aggregates such as pieces of wood, seaweed, grasses, and the bodies of surface dwellers such as salps or fish constitute a small-scale disturbance at the sites where they land and become patchy and ephemeral resources for recruiting populations.

Three broad-scale features of the deep sea have been cited as correlates of the high diversity: large surface area (Osman and Whitlatch 1978; Abele and Walters 1979), low food supply (Van Valen 1976), and relative constancy of the physical environment (Sanders 1968). The large surface area and the potential for wide dispersal of populations has allowed species to specialize on very rare ephemeral resources. The low food supply to large areas of the deep sea results in a low background concentration of organic matter in sediments. This low background enhances development of a mosaic of sharply contrasting food resources as material collects in response to currents and the uneven topography. The feeding activities of large epifaunal animals also add to this shifting pattern of disturbance on the spatial scale of individual organisms. The large-scale disruptions observed during storm events on continental shelves (Maciolek and Grassle 1987) homogenize and obliterate sediment structure. Such intense storm events occur at very few sites in the deep sea; therefore, the resource mosaic, produced by small patches of disturbance and organic input, survives long enough to provide the habitats for a diverse assemblage of species.

What Are the Consequences of Large-Scale Disturbances in Deep-Sea Ecosystems?

Some deep-sea areas are subjected to disruption of the entire community by large-scale disturbance, such as intense currents, mudslides, hydrothermal activity, upwelling, or low oxygen. Fewer species are found in regions subjected to these events. The reduction in species may be the result of widespread mortality or disruption of the habitat structures colonized by species in areas of greater sediment stability.

The best-studied region of intense currents is a lower continental rise site south of Halifax, Nova Scotia, with current velocities up to 73 cm/sec, suspended sediment concentrations up to 12 g/m^3, and ripple marks on the bottom (Hollister and McCave 1984). Meiofaunal diversity appears to be unaffected by these disturbances (Thistle 1983; Thistle and Sherman 1985). The polychaetes (the main macrofaunal group identified to species) have a relatively low diversity. The most common species contributes 34–39 percent of the individuals (Thistle, Yingst, and Fauchald 1985; Russell
The most common species in less-disturbed deep-sea environments is 6–7 percent of the total number of macrofaunal individuals (Grassle and Morse-Porteous 1987; Grassle and Maciolek, in preparation).

In deep-sea trenches, mud slumps from the walls of the trench smother the deep-sea fauna. The occasional burial of the bottom fauna has been the explanation for low diversity in these environments (Jumars and Hessler 1976). Upwellings at upper continental slope depths off Walvis Bay on the West African coast result in increased surface productivity and reduced oxygen in sediments. The fauna is dominated by a filter-feeding epifaunal species and a few species relatively tolerant of low-oxygen conditions (Sanders 1969). Occasional periods of low oxygen in the overlying water have been used to explain the relatively low deep-sea diversity in Santa Catalina Basin off southern California (Jumars 1976).

Along the Mid-Ocean Ridges at depths of 2,000–4,000 m, fluids from hydrothermal vents result in increased microbial productivity. Dense populations of a considerably reduced number of species inhabit both hard-surface and soft-sediment environments in the vicinity of these vents (Grassle et al. 1985). The several reasons for the reduced diversity apply to a greater or lesser extent depending on proximity to the undiluted hydrothermal fluid. Fluctuating amounts of oxygen and toxic chemicals such as sulfide may prevent many deep-sea species from living at vents. The supply of hydrothermal fluid and hence the food supply fluctuates drastically so that species must be either highly mobile or continually colonizing to take advantage of the increased productivity.

In each of the instances of large-scale disturbance, the change in community structure is obvious from the disproportionate abundance of a few species. In relatively undisturbed parts of the deep sea the most common species generally forms less than 10 percent of the total fauna (Grassle and Maciolek, in preparation), whereas in highly disturbed areas there is usually a single species that comprises more than 30 percent of the fauna, and the top few species make up more than half the total number of individuals (Grassle and Morse-Porteous 1987). Deep-sea waste disposal and mining are likely to reduce diversity by increasing a few relatively tolerant species and reducing or eliminating many of the rare species. The relative susceptibilities of deep-sea species to human-made disturbances have yet to be investigated. Even though parts of the ocean are increasingly being used for waste disposal, effects of these activities on the highly diverse communities of the deep sea are not being studied. Small-scale recolonization experiments suggest that recovery will be slow in instances where the disturbance is large enough so that recolonization by planktonic dispersal stages predominates, rather than movements of adults through sediments (Grassle and Morse-
The most diverse deep-sea ecosystems are likely to be less resilient than most shallow-water ecosystems.

Are Deep-Sea Ecosystems Changing?

The longest series of quantitative estimates of population fluctuations are sets of three samples taken three times each year for two years at a number of stations on the slope off the eastern United States (Blake et al. 1987; Maciolek et al. 1987a, 1987b). A time series of qualitative samples from the Rockall Trough off the west coast of Scotland has been extremely valuable in determining growth and reproduction of a number of larger, common deep-sea species (Gage 1986; Tyler 1986). Some of the species can be aged by following cohorts of individuals in these samples. For example, by this method, the sea urchin *Echinus affinis* has been inferred to live up to 28 years. Direct experiments indicate the shortest time to maturity in sediment-dwelling species is one year in polychaetes and tunicates and two years in bivalves (Grassle and Morse-Porteous 1987). Some species of bivalves in sediments may live as long as a hundred years based on a single estimate using a radiometric technique to age the shells (Turekian et al. 1975). The resilience of deep-sea ecosystems cannot be predicted without studies of the population dynamics of a wide spectrum of deep-sea species.

Research Priorities

Organisms in, on, and immediately above deep-sea sediments are important in determining chemical transformations, flux, and burial of materials. These processes cannot be understood from bulk metabolic, biomass, or chemical measurements. Studies of the microhabitats of individual species, their feeding behavior, metabolism, and population dynamics are needed. Deep-sea ecosystems are the product of evolution, and although coevolution may be important, the unit that survives and replicates is the species. Single species or a small functional group of species may dominate a particular process. These species may be large or small, common or rare; and, without better descriptions of deep-sea systems, we will not know which they are.

Another reason for emphasizing studies at the species level is that there is a high variance associated with bulk measures that integrate processes operating at the species level. Oxygen uptake of sediments varies by a factor of two in adjacent measurements (Smith and Hinga 1983) and biomass may vary by an order of magnitude. By comparison, the abundances of the most common species in the deep sea show little variance between replicates or
seasons (Blake et al. 1987; Maciolek et al. 1987a, 1987b) and can be a relatively sensitive measure of change when it occurs.

Severe pollution in coastal areas is resulting in increasing pressures to use the deep sea for waste disposal. Even shallow-water discharge of wastes can have consequences for the deep ocean. Radioactive wastes discharged at a single point into the Irish Sea have been traced in surface currents to the sites of deep-water formation in the Arctic Ocean. Currents containing traces of these wastes flow over deep-water communities of the western Atlantic (Livingston, Swift, and Østland 1985; Aarkrog et al. 1987). Other studies have shown increased levels of organic pollutants in deep-sea sediments and bottom-dwelling organisms (e.g., Harvey and Steinhauer 1976; Farrington and Tripp 1977; Knap, Binkley, and Deuser 1986). In these circumstances it is prudent to describe quantitatively deep-sea communities over periods of years. Existing descriptions are inadequate for detecting change over intervals of decades.

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