Ecology of the Deep-Sea Benthos

More detailed recent sampling has altered our concepts about the animals living on the deep-ocean floor.

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Marine benthic communities cover most of the earth's surface. At least 94 percent of the ocean bottom lies below the permanent thermocline, and, in its physical and chemical parameters, this region is remarkably stable and homogeneous. It is constantly dark, with bottom water of constant salinity, oxygen content, and low temperatures. Even the bottom sediments, largely derived from planktonic organisms, are unvarying for hundreds of square kilometers. Great pressures characterize the environment. Probably as a consequence of its separation both spatially and temporally from the primary organic production at the surface of the sea, there is a low rate of food supply to the deep-ocean floor.

There is little information about the kinds of animals living in this vast environment and about the relation of the high environmental stability to the ecology and physiology of the deep-sea fauna.

Because of the sparseness of animal life and the technical difficulties in sampling the deep-sea benthos, relatively few specimens were collected in the past century. Even nonquantitative trawls and dredges traversing appreciable distances on the deep-ocean floor have captured only a few animals. However, understanding of the deep-sea fauna requires that samples contain enough individuals to give statistical support to conclusions. We developed the large deep-sea *Anchor Dredge* (*1*) for quantitatively sampling the infauna (animals living in the bottom) and the *Epibenthic Sled* (*2*) to collect both epifauna (animals living on the bottom) and infauna in large quantities. From 1960 to 1966, we made a study of a transect of the ocean floor, between southern New England and Bermuda (the Gayhead-Bermuda transect, Fig. 1). Subsequently, we extended our study to the tropical Atlantic.

Faunal Composition

Initially, our sampling of the deep-sea benthos was done by the *Anchor Dredge*. These predominantly infaunal samples were dominated by Polychaeta, Crustacea, and Bivalvia. Polychaetes, comprising 40 to 80 percent of these samples by abundance and represented by numerous species, were the most abundant. Hartman (*3*) found from 65 to 77 polychaete species in each of the five quantitative samples which covered 0.5 to 1.0 square meter of bottom at upper slope depths. Crustaceans, the second most common group, formed 3 to almost 50 percent of the fauna and were represented by many isopod, amphipod, cumacean, and tanaid species. Other common faunal elements were glass sponges, sea anemones, pogonophores, sipunculids, echiurids, tunicates, priapulids, brittle stars, and starfish.

In the past most deep-sea collections were made with coarse-meshed trawls which collected predominately larger epifaunal organisms. To provide basic information on the neglected smaller epifaunal animals, as well as to obtain better samples of the total benthic macrofauna, we constructed the *Epibenthic Sled* (*2*). A door which closes the mouth of the net reduces the effect of winnowing of the sample as it is brought up through the long water column. A fine-meshed net in the sled and fine-meshed screens for processing the samples on board ship retain the abundant smaller animals which would otherwise be lost.

The effectiveness of the method is demonstrated by the following collection records.

Malletia abyssorum Verrill and Bush (bivalve); previous record, single specimen; sled samples, 3257 specimens from 19 samples.

Malletia polita Verrill and Bush (= *Malletia bermudiensis* Hass) (bivalve) both known from single empty valve; sled samples, 191 specimens from ten samples.

Tindaria callistiformis Verrill and Bush (bivalve); previous records, two specimens; sled samples, 1708 specimens from 11 samples.

Serolis vemae Menzies (isopod); previous record, two specimens from South Atlantic; sled samples, 255 specimens from seven samples on transect and in tropical Atlantic.

Desmosoma insigne Hansen (isopod); previous records, six individuals from Davis Strait; sled samples, 294 specimens from four samples.

In contrast to the pronounced abundance of polychaetes in the infaunal *Anchor Dredge* samples, dominance in the sled samples is shared about equally among the crustaceans, polychaetes, bivalves, and brittle stars. When these four groups are compared on the basis of diversity, crustaceans invariably have the largest number of species, followed by polychaetes and bivalves; ophiuroids are always represented by few species. If 1000 individuals of each group are counted for every species of brittle star there are 4.1 bivalve, 9.7 polychaete, and 16.5 crustacean species [see (*4*) for method of rarefaction].

Diversity

Our most unexpected finding was a high faunal diversity in individual samples. Such diversity is far in excess of anything obtained in the past, in contrast to the belief that the deep sea harbors a qualitatively restricted fauna (*5–7*). The results of the first five sled samples taken during the summer of 1964 are given in Table 1; subsequent samplings demonstrated similar diversity.

Only two previous samples from depths greater than 1000 meters have yielded more than 100 species of benthic invertebrates. They are *Challenger* station 320, at 1096 meters, with 124 species and 496 individuals (*8*), and *Galathea* station 716, at 3570 meters, with about 2100 specimens divided among 132 species (*9*).

The greater diversity shown by our samples may be due to a more complete sampling of the total benthic fauna. Earlier samples contained few specimens, and the total number of species was therefore small. The restricted number of specimens in these samples made

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it impossible to determine the significance of apparently small taxonomic differences. When a specimen resembled a known species, it was usually included in that species. The resultant lumping helped to create the impression of relatively few, broadly distributed species. Our large samples allow us to conclude that most of the major taxa are characterized by numerous closely related species both at a specific locality and among spatially separated localities.

The data obtained from both the *Anchor Dredge* and *Epibenthic Sled* samples indicate that the deep-sea benthos is not impoverished but, instead, is represented by a remarkably diverse fauna. How, then, does the diversity in the deep sea compare with the diversities occurring in other regions of the world?

Table 1. The number of species and individuals collected in five *Epibenthic Sled* samples.

Station	Depth (m)	Individuals (No.)	Species (No.)
73	1400	25,242+	365
62	2496	13,425+	257
72	2864	5,897+	208
64	2891	12,083+	310
70	4680	3,737+	196

We answered this question by collecting benthic samples from boreal estuary, boreal shallow marine, tropical estuary, and tropical shallow marine environments. In all cases, the sediments were soft oozes and were therefore comparable in particle size. All samples were processed in a similar manner. The analysis is based on total fauna (*2*) and on the polychaete-bivalve fraction of the fauna (*4*). The polychaetes and bivalves comprise about 80 percent of the animals in most of the infaunal samples, and thus we can generalize from the results. Diversity in the deep sea, measured by a rarefaction method (*4*) which allows direct comparison of samples with differing numbers of specimens, is about the same as that in the physically stable, shallow, tropical marine environment and significantly greater than that of the other three environments (Fig. 2).

We believe that the constancy of physical conditions and the long past history of physical stability in the deep sea have permitted extensive biological interactions and accommodations among the benthic animals to yield the diverse fauna of this region. Such communities evolve wherever physical conditions remain constant and uniform for long periods. Other than the deep-sea, tropical shallow-water environments and tropical rain forests best approximate these conditions. Communities found in these environments are characterized by many species and can be termed biologically accommodated communities (*4*).

At the other end of the diversity spectrum are the physically unstable communities where physical conditions fluctuate widely and unpredictably, and thus the organisms are exposed to severe physiological stresses. Here the adaptations are primarily to the physical environment (*4*). Hypersaline bays and temporary ponds exemplify this state, and certain shallow boreal marine and estuarine environments approach such conditions. Physically unstable communities are characterized by a small number of species. A similar paucity of species is found in environments of recent past history, such as most freshwater lakes.

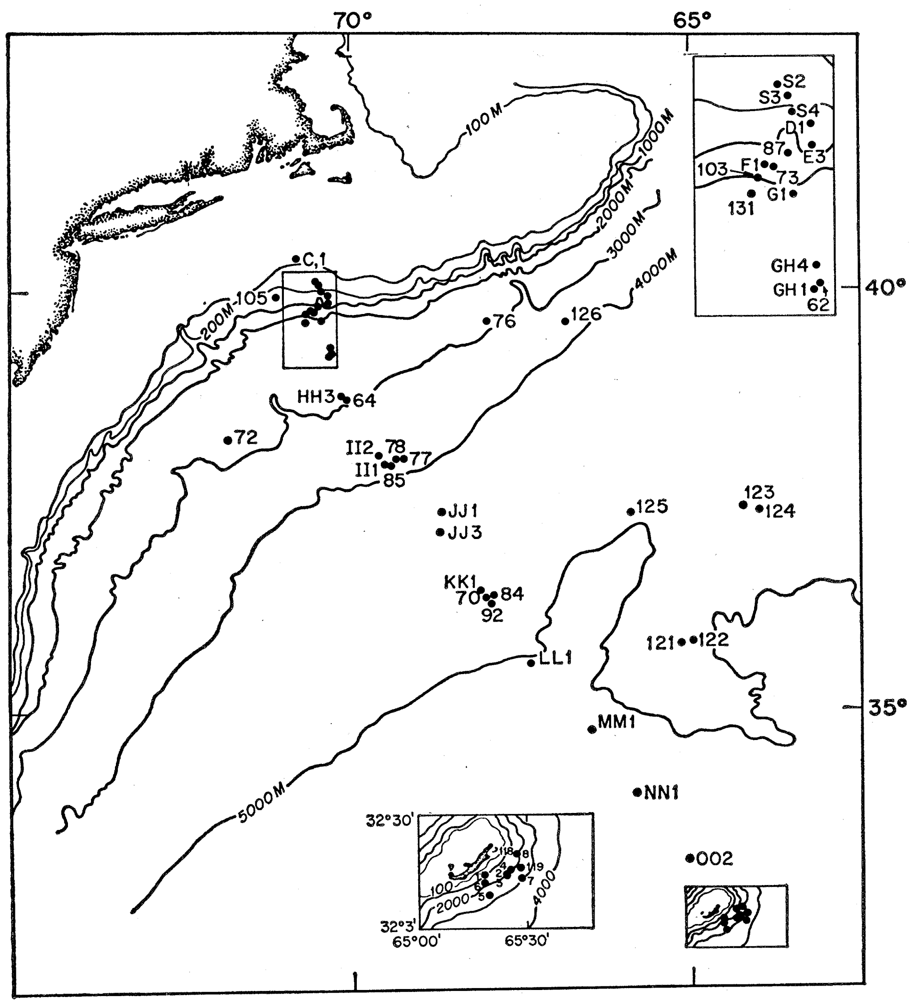

Fig. 1. Depth contours and locations of sampling stations of the Gayhead-Bermuda transect.

The term "diversity" as used above means "within-habitat" diversity, that is, the number of species in a specific habitat, and not "between-habitat" diversity or the total number of species for all habitats (*10*). (The habitat under study is that of soft, fine-grained sediments.) The pronounced homogeneity of the deep sea permits fewer habitats than do the shallow depths. Thus, although the animal diversity of the soft sediments in the deep sea is well above that of the equivalent inshore boreal habitat, the total between-habitat diversity may be lower.

Zonation and Zoogeography

How are the environmental stability and homogeneity on the deep-ocean floor reflected in faunal vertical zonation? Known abyssal and hadal records of vertical distribution for 1144 species of deep-sea benthic invertebrates, reviewed by Vinogradova (*11*), showed rapid decrease of species from 2000 to 6000 meters, with a much slower reduction at greater depths. (The bathyal region encompasses depths from 200 meters to 2000 or 3000 meters and includes the continental slope; the abyssal zone covers from 2000 or 3000 meters to 6000 meters; the hadal zone is at depths greater than 6000 meters and includes the deep-sea trenches.) At about 3000 and 4500 meters, important changes occur in the taxonomic composition of the benthic fauna. Numerous species and higher taxa, broadly distributed on the slope and even shallower, disappear and are replaced by new species, genera, and families found only at greater depths. For these reasons, Vinogradova concluded that 3000 meters represents the true upper limit of the abyssal zone.

We did not find such abrupt boundaries at bathyal and abyssal depths. Our analysis is not dependent on criteria of presence or absence; we measured the percentage of fauna shared by each possible pair of stations on the transect. The data for polychaetes, extracted from Hartman (*3*) and based on 264 species and almost 14,000 specimens, are given in Fig. 3.

The stations are arranged sequentially in a north to south direction traversing, in order, the outer continental shelf, the continental slope, the abyssal rise, the Sargasso abyss, and the Bermuda slope. The diagonal pattern running from the upper left to the lower right corner means that highest faunal indices are always with neighboring stations, that is, there is a gradual and continuous faunal change with depth and distance along the transect.

The very small faunal index values shared by stations C (97 meters) or SL-2 (200 meters) with other stations on the transect marks this portion of the transect as a region of pronounced faunal change. In fact, it is the sharpest zoogeographical boundary encountered. This discontinuity is also true for groups other than the polychaetes. Among the bivalves, the transition of faunal change at the shelf-slope break is even more pronounced. Within the isopods, the typically deep-water subtribe Paraselloidea is absent from station C and extensive samplings in shallower waters. The group makes its appearance on the upper slope at station SL-2 and is a major constituent in all deeper samples.

We believe that this faunal break is related to temperature. In 98 meters at station C, the seasonal temperature change is 10.5°C; in 300 meters at slope station 3, it is 5.1°C; and in 487 meters at station D, only 1.4°C. Therefore, the boreal continental shelf, with highly variable seasonal temperatures, supports a qualitatively impoverished eurytopic (broad physical tolerances) fauna, whereas the neighboring physically stable continental slope harbors a different stenotopic (narrow physical tolerances) benthic fauna of high diversity. Entirely analogous conditions are found in ancient Lake Baikal in Siberia, similarly dominated at shallow depths by a continental boreal climate (*12*). We conclude, on the basis of taxonomy, diversity, and environmental

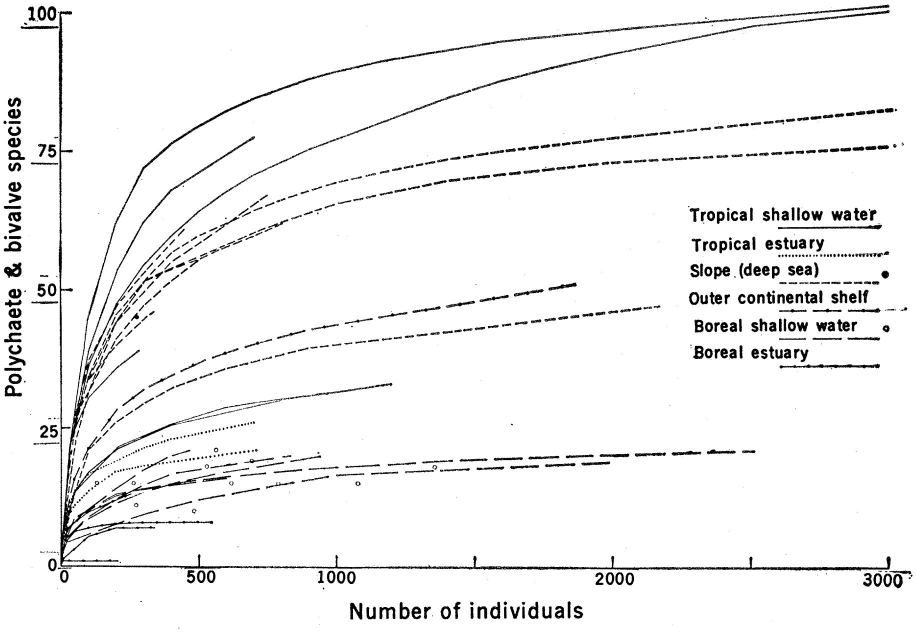

Fig. 2. Diversity values for different benthic environments by the rarefaction method. The lines represent the interpolated curves. The larger circles represent actual samples that have not been rarefied.

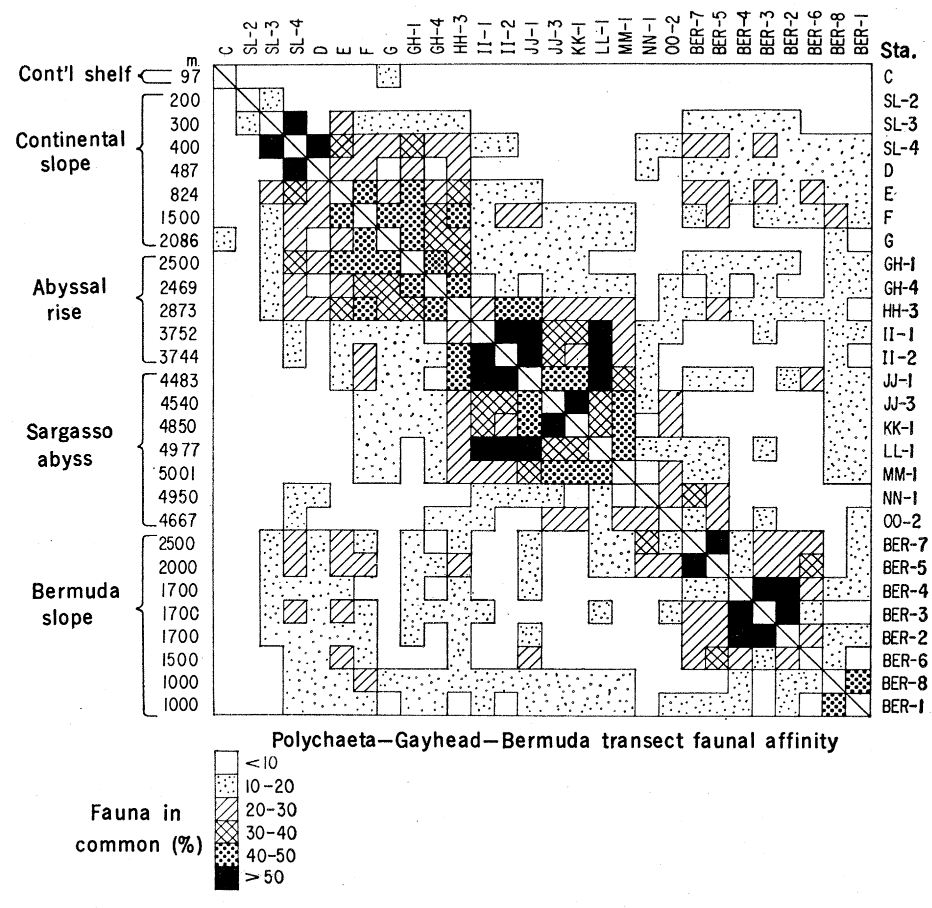

Fig. 3. Degree of polychaete faunal similarity among the stations (*Sta.*) of the Gayhead-Bermuda transect.

Table 2. Degree of bivalve faunal similarity and percentage of bivalve species shared per 500 specimens with station 64 on the Gayhead-Bermuda transect.

Station	Depth (m)	Species shared* (%)	Fauna shared† (%)	Depth deviations‡ (m)
105b	530	7.77	2.61	−2361
87	1102	25.79	4.80	−1789
73	1400	24.47	5.90	−1491
103	2022	22.87	5.80	− 869
131	2178	30.68	6.81	− 713
62	2496	46.41	28.71	− 395
72	2864	60.19	77.74	− 27
64	2891	100.00	100.00	0
126	3806	53.05	9.02	+ 915
85	3834	35.42	6.34	+ 943
70	4680	10.64	1.45	+1789
92	4694	11.65	1.36	+1803
84	4747	16.70	2.68	+1856
121	4800	7.57	1.03	+1909
125	4825	5.75	0.93	+1934
122	4833	13.98	1.38	+1942
123	4853	3.88	0.83	+1962
124	4862	3.88	0.83	+1971

* There are 25.75 species per 500 individuals at station 64. † With station 64. ‡ Minus (—) values mean that the station is the given number of meters shallower than station 64; plus (+) values mean that the station is that number of meters deeper than station 64. Station 64 is at a depth of 2891 meters.

factors, that the self-slope break within the depth range of 100 to 300 meters represents the true upper boundary of the deep-sea benthos in this part of the ocean.

Changes in species composition with depth also can be demonstrated by the use of a modification of the rarefaction method (Table 2). The criterion is the number of species shared between a given station and each of the other stations along the transect when equal-sized samples are compared. The results of such an analysis for the bivalves (excluding the taxonomically difficult family Thyasiridae) are presented in Table 2 for station 64 (2891 meters). The stations are arranged in sequential order by depth from the upper continental slope to the abyssal plain in the Sargasso Sea; the depths, the percentage of species per 500 individuals (by rarefaction), the percentage of the fauna that each station shares with station 64, and the deviation of each station in depth from station 64 are given.

In percentages of species and of fauna shared, there is a continuous decrease in similarity with departure in depth from station 64. The only small alterations in this pattern occur with stations that are widely separated in depth from station 64 (stations 103, 73, 87, and 122). The gradient of change is steeper, with percentage of fauna than with percentage of species shared. This difference in the steepness of the two gradients means that species that are numerically dominant at station 64 are relatively less important or even rare faunal constituents at stations separated from station 64 by more than 800 meters. Station 126 is a case in point. With 53 percent of the species in common, it shares many species with station 64. Yet with only 9 percent of the fauna common to both stations, species that are numerically dominant at one station are not numerically dominant at the other.

The horizontal and vertical components of zonation can also be measured. Station 73 at 1400 meters on the Gayhead-Bermuda transect shares 47.9 percent of its bivalves with station 142 at 1700 meters off the coast of West Africa (10°30.0′N; 17°51.5′W). If we follow the contours of 1000 to 2000 meters in depth along northern North America, Greenland, Iceland, Europe, and Africa, these two stations are separated by about 16,500 kilometers. Yet, if the depth is altered as little as 800 meters either shallower or deeper from station 73 on the transect (a distance of 10 kilometers landward or 12 kilometers seaward), the number of species shared with station 73 falls below 48 percent. Thus a change of only 800 meters in a vertical direction on the transect is at least equivalent to a 16,500-kilometer change horizontally. The implication, at least for bivalves, is that faunal composition is far more sensitive to change in depth than to the effects of distance.

To assess the patchiness of the fauna, we took three samples (stations 72, 64, and 76) within the depth range of 2862 to 2891 meters over a horizontal distance of 366 kilometers. Another series of five samples (121, 122, 123, 124, and 125) was taken within the depth range of 4800 to 4862 meters, at three widely separated localities (Fig. 1). In both series, the faunal index of each pair of stations was very high and, with two minor exceptions, higher than with any station outside the series. These high faunal values imply that many components of the deep-sea benthic fauna at any given depth are uniformly and homogeneously distributed over extensive distances of the ocean floor.

Breeding Patterns

On land and in the shallow boreal and arctic marine regions, reproduction is usually coupled with some cyclical and often seasonal phenomenon such as day length, temperature, or rainfall. This synchrony allows the adult portion of the population to be ready for reproduction at the same time, and the resulting young or larvae are usually present when feeding conditions are best.

The monotonously constant conditions of the deep sea provide no such obvious cyclical environmental phenomena. Even seasonal pulses of primary production in the surface waters are probably dampened and dissipated long before the slow rain of these minute particles reaches abyssal depths.

George and Menzies (*13*) suggest that cyclic reproduction may be present among deep-sea isopods. Their data, derived from studies of the genus *Storthyngura,* are based on only six ovigerous specimens of three species taken at widely differing localities and depths. The statistical inadequacy of these data make their conclusion conjectural.

Schoener (*14*) studied the state of reproduction in two species of brittle stars, *Ophiura ljungmani* and *Ophiomusium lymani,* collected from the continental slope, and abyssal rise on the Gayhead-Bermuda transect. Her analysis of a large number of specimens obtained at different times of the year provides convincing evidence for reproductive periodicity for these deep-sea species.

We are now gradually accumulating information on other deep-sea groups. An August sample from the lower continental slope (station 73, 1400 meters) contained 71 females of an unidentified species of isopod belonging to the genus *Ilyarchna.* Twenty-four percent of the females had well-developed marsupial plates and were therefore in the brooding condition. (As with all peracarid crustaceans, the embryos of isopods are carried in a marsupium.) A December sample (station 131, 2178 meters) yielded 59 females of the same species, with 27 percent bearing well-developed marsupial plates.

Sections were made on 25 adult specimens of the bivalve *Nucula cancellata*, 2.4 to 2.8 millimeters in size, from each of three samples, station 103 (May, 2022 meters), station 73 (August, 1400 meters), and station 131 (December, 2178 meters) (*15*). The findings for each of the stations were essentially identical. At least part of the gonad contained ripe sexual products in almost every individual examined.

These results for *Ilyarchna* sp. and *Nucula cancellata* indicate that reproduction is constant and continuous in the two forms. Schoener's evidence of reproductive periodicity for the two brittle star species suggests that no pattern need be universal. Analysis of numerous additional species will indicate whether there is a characteristic pattern of reproduction in the deep sea.

Table 3. A comparison of the range in amount of benthic faunal density to the range of the amount of organic carbon in the sediment and the annual primary productivity in surface waters.

Area of study	Bathyal-abyssal bottoms		Annual productivity in surface water (cg/m^2)
	Density (No./m^2)	Organic carbon* (%)	
Gayhead-Bermuda transect	21,263–33(*1*)	1.0–0.1(*1*) 2.5–0.8(*20*)	180–72(*25*)
Oregon	2,200–14(*20*)	3.5–0.1(*39*)	152–60(*40*)

* Excluding sand bottoms

Animal Abundance and Food

Deep-sea benthos show a decrease in animal life with increasing depth of water and distance from land (*5, 6, 8, 16–20*). Although certain departures from this pattern occur in the shallower water of the sublittoral and upper bathyal zones (*1, 21*), the lower bathyal and abyssal zones invariably support a smaller biomass or density than shallower depths. Island arc trenches are ideal traps for organic material, and, therefore, the high concentration of life occasionally reported from these hadal depths (*22*) are special cases.

In our series of *Anchor Dredge* samples taken along the transect, numerical density of animals increased from near shore (approximately 6000 per square meter) to the edge of the shelf (13,000 to 23,000 per square meter) (*1*). From this depth to the bottom of the continental slope, density dropped precipitously to approximately 500 animals per square meter, with a more gradual decrease on the continental rise, and then a leveling off on the abyssal plain under the Sargasso Sea (25 to 100 animals per square meter). Thus, from the edge of the continental shelf to the abyssal plain, there was a reduction in density by a factor of several hundreds.

The biomass of our samples has never been analyzed; the material was biologically too valuable for mechanical abuse. However, density is an adequate index of biomass in our samples, because the size of animals and the relative proportions of major animal groups do not change between localities.

The abundance of food is generally assumed to control density and biomass in the deep sea (*5, 17, 19, 23, 24*). Oxygen concentration, sediment type, and temperature either do not show correlated changes or never reach levels regarded as limiting. Hydrostatic pressure is depth-dependent, but although pressure could limit the kinds of species present, there is no apparent way in which it can regulate biomass.

Sources of food fall into two broad categories: either it is produced in the euphotic zone (the relatively narrow, lighted, upper water layer) and conveyed into the deep sea, or it is generated *in situ* in the deep-sea environment. The theory that food is of euphotic origin has until recently dominated our thinking (*6, 23*) because the distribution of biomass in the deep sea correlates with primary production. The highest productivity is in shallow coastal waters (*25*). This concentration of food is enhanced by the outwash from terrestrial sources: the farther from inshore waters of highest production, the lower the benthic biomass. Biomass also decreases with increasing depth, because during its transport the amount of food is progressively diminished by autolysis, bacterial decay, and scavengers.

The rapid decline in animal density on the continental slope, the region of greatest rate of depth change on the transect, labels depth as having more importance than distance from land in determining the amount of available food (*26*). Density decreases 25 times from 200 to 2500 meters of depth. Yet, these localities are so close (61 kilometers) that primary production at the surface barely changes. Stations at 4500 to 5000 meters have densities 50 to 390 times less than at 200 meters, and productivity in surface waters is only half as great (*25*) (Table 3).

The mode of transport of food in the deep sea has long been regarded as a rain of dead plants and animals from the euphotic zone (*6, 23, 27*). This mechanism has often been criticized because settling velocities are so slow and intermediate attrition is so efficient that little of nutritive value would reach the bottom. Inefficiency alone is not a valid reason for rejecting this mechanism. The deep-sea biomass is so much smaller than that of surface waters that an inefficient food supply can account for it. Downward movement by means of diurnal migration would increase the efficiency of food transport (*28*). However, the chain of migrating animals postulated by Vinogradov might be less efficient than passive settling since it entails large energy losses in every change of trophic level.

Turbidity currents provide another possible means of rapid downward movements of organics (*29*). Yet, the infrequency and destructiveness of such phenomena suggest that they are of no more than minor importance in food transport. The presence of layers of carbon associated with turbidity current deposits (*30*) indicates that while organics have been moved, they were never made available to organisms.

Organic aggregates, with considerable surface activity, adsorb dissolved organics and convert them into particulate compounds. Thus, they may serve as an *in situ* source of nutrition for intermediate bacteria (*31*) or directly for metazoans in deep water. However, the concentration of dissolved organics and the amount of carbon bound up in organic aggregates are relatively constant in deep water (*32*) and therefore correlate poorly with the marked decrease in benthic biomass with depth. There is no quantitative data on deep-sea heterotrophic algae (*33, 34*); therefore this food source cannot be evaluated.

Extensive degradation of organics during the slow transport from the surface waters to the deep-sea benthos permits only the most refractory substances to reach the bottom. Here benthic microorganisms (bacteria and, possibly, fungi) are probably a critical intermediate in the food cycle (*6, 7*). The abundance of bacteria has been reported (*35*), and some metazoans show adaptations to utilize an intestinal flora (*36*). The true importance of bacteria and fungi must still be determined.

The amount of organic carbon in deep-sea sediments follows a variety of patterns with relation to depth and distance from land (*1, 20, 28, 29, 37, 38, 39*). Yet, the absolute range of variation is usually less than an order of magnitude, far less than the corresponding variation in animal density (Table 3). Therefore, organic carbon in the sediment is not a good index of available food. If bacteria are nutritional intermediates of major importance, then the ratio of bacterial biomass to metazoan biomass or density should remain constant from place to place, and changes in bacterial biomass would not be correlated with changes in organic carbon content in the sediment. Such a pattern, if true, would suggest that in deep water much of the deposited organic material is not readily available to bacteria.

Feeding Types

According to the principle of competitive exclusion, ecological niches of species living together must have areas of nonoverlap. The uniformity of the deep sea and the limited amount of food indicate that niche separation is especially critical with respect to feeding.

Our knowledge of feeding types in this environment is fragmentary, but interpretation of morphology, analogy with shallow-water relatives, and gut-content analyses show that deposit feeders dominate in our samples. At station 64 (2891 meters), for example, the most diverse groups contain the following percentage of detritus feeders: Polychaeta, 60 percent; Tanaidacea, greater than 90 percent; Isopoda, 90 percent (*23*); Amphipoda, greater than 50 percent (*41*); and Pelecypoda, 45 percent; totaling 47 percent of the species in the whole sample. Many species of other, less diverse groups (Holothuroidea, Sipunculida, Oligochaeta, and others) also eat detritus, and thus this feeding type includes well over half of the fauna.

The high diversity in the deep sea implies a degree of niche fractionation far greater than in equivalent shallow boreal communities. Yet, studies of zonation indicate that appreciable flexibility must exist in intraspecific interactions, for each species has a zone depth preference whose limits vary with the species. Therefore, each species must be associated with a continuously altering assemblage of animals within its depth range.

Intraspecific flexibility, in conjunction with the low density of the benthic fauna, may explain high faunal diversity coupled with environmental homogeneity. Since density is low, only a fraction of the total number of species lives in any one area, for example in a single square meter. An individual organism, because of its small size and presumably restricted mobility, will interact with a relatively small suite of competing species. This hypothesis permits high faunal diversity with an increased, but not necessarily extraordinary, degree of specialization.

Summary

The benthos of the deep sea in a region between southern New England and Bermuda can be characterized by low density but high within-habitat diversity. The low density is probably determined by the amount of food present and is correlated with depth and distance from land. Depth is the more critical variable. The high diversity, about the same order as that found in shallow tropical seas, can be related to the seasonal and geological stability of the deep-sea environment. An unexpectedly large number of deposit-feeding species are found in individual samples. The composition of the benthic fauna gradually and continuously changes with depth throughout the bathyal and abyssal regions, but an abrupt faunal discontinuity is found at the shelf-slope break in from 100 to 300 meters of water. In this region of our study, the fauna shallower than the zone of discontinuity is eurytopic, of low diversity, and taxonomically distinct from the stenotopic, highly diverse populations living below the discontinuity. In comparing faunal composition, a vertical change of a few hundred meters is equivalent to a change of thousands of kilometers horizontally. The few data on reproduction reveal that some elements of the deep-sea fauna breed continuously, whereas others are restricted to a limited period of the year.

References and Notes

1. H. L. Sanders, R. R. Hessler, G. R. Hampson, *Deep-Sea Res.* **12**, 845 (1965).
2. R. R. Hessler and H. L. Sanders, *ibid.* **14**, 65 (1967).
3. O. Hartman, "Deep-Water benthic polychaetous annelids off New England to Bermuda and other Atlantic areas," *Allen Hancock Found. Publ. Occas. Pap. No. 28* (1965), p. 1.
4. H. L. Sanders, *Amer. Natur.* **102**, 243 (1968).
5. S. Ekman, *Zoogeography of the Sea* (Sidgwick and Jackson, London, 1953).
6. N. B. Marshall, *Aspects of Deep Sea Biology* (Hutchinson, London, 1954).
7. A. F. Bruun, *Geol. Soc. Amer. Mem. No. 67* (1957), vol. 1, p. 641.
8. J. Murray, *Challenger Rep.* **1895**, 1608 (1895).
9. T. Wolff, *Galathea Rep.* **5**, 129 (1961).
10. R. H. Whittaker, *Science* **147**, 250 (1965).
11. N. G. Vinogradova, *Deep-Sea Res.* **8**, 245 (1962).
12. M. Kohzov, *Monogr. Biol.* **11**, 352 (1963).
13. R Y. George and R. J. Menzies, *Nature* **215**, 878 (1967).
14. A. Schoener, *Ecology* **49**, 81 (1968).
15. R. Scheltema sectioned, stained, and interpreted the bivalve material.
16. R. J. Menzies, *Oceanogr. Mar. Biol. Annu. Rev.* **3**, 195 (1965).
17. L. A. Zenkevitch and J. A. Birstein, *Deep-Sea Res.* **4**, 54 (1956).
18. R. L. Wigley and A. D. McIntyre, *Limnol. Oceanogr.* **9**, 485 (1964).
19. N. G. Vinogradova, *J. Oceanogr. Soc. Japan* **20**, 724 (1962).
20. A. G. Carey Jr., *Trans. Joint Conf. Exhibit Ocean Sci. Ocean Eng.* **1**, 100 (1965).
21. A. P. Kuznetsov, *Benthic Invertebrate Fauna of the Kamchatka Waters of the Pacific Ocean and the Northern Kurile Islands* (Moscow, 1963).
22. G. M. Belyaev, *Bottom fauna of the Ultra-abyssal depths of the World Ocean* (Academy Nauk USSR Inst. Okeanol., Moscow, 1966).
23. R. J. Menzies, *Int. Rev. Ges. Hydrobiol.* **47**, 339 (1962).
24. L. B. Slobodkin, F. E. Smith, N. G. Hairston, *Amer. Natur.* **101**, 109 (1967).
25. J. H. Ryther, in *Geographic Variations in Productivity, the Sea*, M. N. Hill, Ed. [Interscience (Wiley), New York, 1963], vol. 2, chap. 17, p. 347.
26. This is in contrast to the findings of G. M. Belyaev [*Trudy Inst. Okeanologii* **34**, 85 (1960)].
27. A. Agassiz, *Bull. Mus. Comp. Zool.* **14**, 1 (1888).
28. M. Vinogradov, *Rapp. Process-Verbaux Reunions Cons. Perma. Int. Explor. Mer.* **153**, 114 (1962).
29. R. C. Heezen, M. W. Ewing, R. J. Menzies, *Oikos* **6**, 170 (1955).
30. D. B. Ericson, M. Ewing, G. Wollin, R. C. Heezen, *Bull. Geol. Soc. Amer.* **72**, 193 (1961).
31. G. A. Riley, D. Van Hemert, P. J. Wangersky, *Limnol. Oceanogr.* **10**, 354 (1965).
32. D. Menzel, *Deep-Sea Res.* **14**, 229 (1967).
33. R. V. Fournier, *Science* **153**, 1250 (1966).
34. J. F. Kimball, E. F. Corcoran, E. J. F. Wood, *Bull. Mar. Sci.* **13**, 574 (1963).
35. C. E. ZoBell and R. Y. Morita, *Galathea Rep.* **1**, 139 (1959).
36. J. A. Allen and H. L. Sanders, *Deep-Sea Res.* **13**, 1175 (1966).
37. D. Ye. Garshanovich, *Okeanology* **5**, 85 (in English translation) (1965).
38. F. A. Richards and A. C. Redfield, *Deep-Sea Res.* **1**, 279 (1954).
39. M. G. Gross, *Int. J. Oceanogr. Limnol.* **1**, 46 (1967).
40. G. C. Anderson, *Limnol. Oceanogr.* **9**, 284 (1964).
41. E. L. Mills, personal communication.
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