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DEEP-SEA SPECIES RICHNESS: REGIONAL AND LOCAL DIVERSITY ESTIMATES FROM QUANTITATIVE BOTTOM SAMPLES

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Abstract.—The deep-sea communities of the continental slope and rise off the eastern coast of the United States have a remarkably high diversity—measured regionally or locally either as species richness or as the evenness of relative abundance among species. In a 1,500–2,500-m depth range off New Jersey and Delaware, 233 30 × 30-cm samples contained 798 species in 171 families and 14 phyla. Addition of stations from sites to the north and south approximately doubled the number of samples and doubled the number of species to 1,597. Species-area curves do not level off within stations or when stations are added together. Moreover, the proportion of species represented by single individuals is high at all scales of sampling, which indicates that much more sampling is needed to adequately represent the species richness either locally or regionally. Diversity changes very little through time at a single site or with distance along a 180-km transect at a depth of 2,100 m. Diversity is maintained by a combination of biogenic microhabitat heterogeneity in a system with few barriers to dispersal, disturbance created by feeding activities of larger animals, and food resources divided into patches of a few square meters to square centimeters initiated by specific temporally separated events.

Our results, from the first extensive quantitative sampling of deep-sea communities, indicate a much greater diversity of species in the deep sea than previously thought. Thousands of species of small invertebrates living on or in the sediments of the deep-sea floor coexist in a shifting mosaic of microhabitats. Several space and time scales need to be considered in studying deep-sea communities; however, small-scale processes appear to be particularly important in this ecosystem. Deep-sea microhabitats tend to persist longer, be smaller in spatial extent, and be separated by longer distances between patches in comparison with the most closely studied shallow-water marine communities.

Community ecologists have long been interested in explaining patterns of species diversity of marine and terrestrial ecosystems, especially the large number of species that coexist in tropical regions (Wallace 1878; Hutchinson 1959; Fischer 1960; MacArthur 1965; Pianka 1966). Hessler and Sanders (1967) discovered an unexpectedly high species richness in the deep sea, which led to extensive speculation on the reasons for the observed patterns of species richness in marine habitats (Sanders 1968; Dayton and Hessler 1972; Grassle 1972, 1989; MacArthur 1972; Grassle and Sanders 1973; Rex 1973, 1976; Jumars 1976; Menge and Sutherland 1976; Van Valen 1976; Osman and Whitlatch 1978; Abele and Walters 1979;

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Thistle 1979; Smith 1986; Grassle and Morse-Porteous 1987). The potential for tremendous loss of species in the tropics has led to increased interest and concern about species diversity and associated ecosystem functions, in both marine and terrestrial environments (E. O. Wilson 1985, 1988; May 1988; National Science Board 1989; di Castri and Younes 1990). Further development of theory relevant to the processes that control species diversity requires better measurements of regional species richness and investigation of the interaction of this species pool with a more local scale of direct contact among species (e.g., predation, competition, symbiosis; Ricklefs 1987; May 1988; Petraitis et al. 1989; Menge and Olson 1990).

Until the late 1960s, deep-sea species richness was thought to be lower than species richness in shallower environments (Ekman 1953). The earliest recognition of relatively high species richness in the deep sea was based on five qualitative epibenthic sled samples from the northwest Atlantic (Hessler and Sanders 1967). The largest number of species in one of these samples, 365, was obtained from an epibenthic sled that was pulled over the bottom at 1,400-m depth for an indeterminate distance of more than 1 km. Numerous taxonomic studies based on these and other similar trawl samples support the initial reports of high diversity for portions of the fauna such as polychaetes (Hartman 1965; Hartman and Fauchald 1971; Maciolek 1981, 1985, 1987), isopods (Hessler 1967, 1968, 1970*a*, 1970*b*; Wilson and Hessler 1974, 1980, 1981; Thistle and Hessler 1976, 1977; G. D. Wilson 1976, 1980*a*, 1980*b*, 1981; Siebenaller and Hessler 1977, 1981; Thistle 1980; Kensley 1982), and bivalves (Allen and Sanders 1966, 1969, 1973; Sanders and Allen 1973, 1977; Allen and Turner 1974; Allen and Morgan 1981). Prior to the present study, quantitative data on deep-sea species diversity have been limited to analyses of only a few (<10) box-core samples (0.25 m^2) from any one geographic area. The paucity of quantitative data on deep-sea species diversity led Nybakken (1982, p. 147) to argue that "the idea of a highly diverse deep-sea fauna must remain speculative."

Our results are based on analysis of macrofauna from quantitative samples from 10 stations along 176 km of the 2,100-m depth contour off New Jersey and Delaware and four additional stations at 1,500-m and 2,500-m depth (fig. 1). These samples were taken to describe the deep-sea communities as part of a monitoring program to evaluate the impacts of oil and gas exploration activities. Exploratory drilling took place near one of the 2,100-m stations (Maciolek et al. 1987*a*), and most of the stations were at this depth on the lower continental slope. There is no ecological significance to the choice of bottom depths. Additional samples from the slope and rise off North and South Carolina (Blake et al. 1987) and off New England (Maciolek et al. 1987*b*) were used to show the number of species from a larger area of the western Atlantic. This large number of quantitative samples enabled us to address the issue of regional versus local diversity and to answer some basic questions concerning species diversity in the deep sea: Does diversity differ between stations in an apparently homogeneous region? Does diversity vary seasonally? Does the number of new species decrease as the number of samples increases? What is the species richness at any given site? Can the

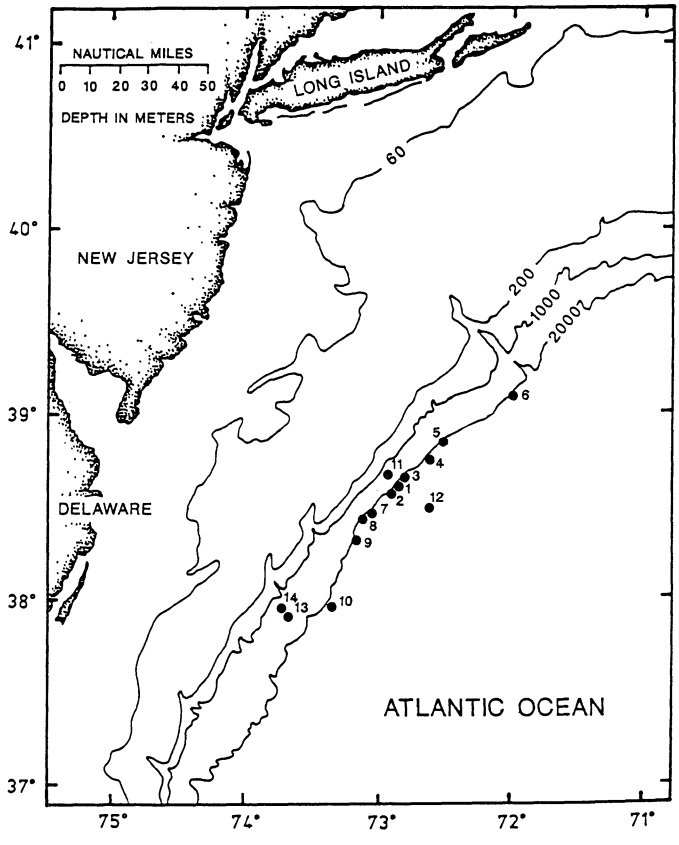

FIG. 1.—Location of deep-sea box-coring stations on the continental slope off New Jersey and Delaware.

number of western Atlantic continental rise species be estimated? The answers to these questions are needed to understand the processes controlling species diversity in the deep sea.

Species diversity depends on the number of species, the relative abundance of those species, and the number of individuals sampled (Pielou 1966). Where possible, we have used graphic methods to emphasize the relationship of species richness to the sampling pattern, and we illustrate our results with plots of actual data, avoiding measures of diversity derived from assumptions about the distribution of individuals among species. Relationships between numbers of species and sampling area, between species and individuals in samples of differing size, relative abundances in different areas, and expected numbers of species shared between areas are used to provide an overview. Estimates of species present in a single area and how this varies spatially allow us to make a conservative estimate of how many macrofaunal species may be present in the deep sea.

TABLE 1

STATION LOCATIONS AND DEPTH IN METERS

Station Number*	Reference Depth (m)	Depth Range (m)	No. of Samples	Latitude N	Longitude W
M6	2,090	2,045–2,091	17	38°05.54′	72°02.97′
M5	2,065	2,055–2,090	18	38°50.49′	72°33.01′
M4	2,100	2,091–2,124	18	38°44.47′	72°33.01′
M11	1,515	1,502–1,540	17	38°40.17′	72°56.37′
M3	2,055	2,045–2,064	18	38°36.84′	72°51.35′
M1	2,195	2,165–2,209	18	38°35.98′	72°52.97′
M2	2,020	2,005–2,024	18	38°35.78′	72°53.65′
M12	2,505	2,495–2,509	18	38°29.30′	72°42.15′
M7	2,100	2,085–2,110	17	38°27.36′	73°03.44′
M8	2,150	2,148–2,159	8	38°27.31′	73°04.87′
M9	2,105	2,100–2,114	18	38°17.28′	73°14.51′
M14	1,500	1,409–1,515	12	37°53.91′	73°44.62′
M13	1,613	1,605–1,619	18	37°53.33′	73°45.09′
M10	2,095	2,093–2,114	18	37°51.80′	73°19.84′

*Ordered from north to south.

MATERIALS AND METHODS

Study Sites and Sampling Methods

The 176-km transect extended from 37.9° to 39.1°N and 72.1° to 73.8°W. Three replicate samples were taken at each of 14 stations (table 1) three times per year for 2 yr (March/April/May, August, and November/December in 1984; May, August, and November in 1985). Careful attention to navigational position using Loran C ensured that samples were generally within 200 m of the station location regardless of sampling date.

The samples were taken using a modified Ocean Instruments Mark III 0.25-m^2 box corer (Hessler and Jumars 1974). The box corer was partitioned into 25 subcores, each with a surface area of 0.01 m^2. A block of nine contiguous central subcores was designated for infaunal analysis, with the remaining undisturbed subcores reserved for sediment chemistry and grain-size analyses (data in Maciolek et al. 1987*a*). Subcores for infaunal analysis were sieved on board using 0.3-mm-mesh screens and fixed in 10% buffered Formalin.

Laboratory Methods

In the laboratory, each sample was resieved on a 0.3-mm-mesh screen and transferred from Formalin to 80% ethanol. Samples were stained with Rose Bengal at least 4 h prior to sorting under a dissecting microscope. The single most critical, difficult, and time-consuming part of this work was the taxonomic identification of each specimen. We were very fortunate to have assembled a team of experts, most of whom had many years of experience with deep-sea taxa (see Acknowledgments). Individuals of uncertain species identity (because they were very young juveniles or were missing morphological features needed for identification) were not included in the statistical analyses. Samples were gently handled

during processing so that only 2.8% (including unidentifiable juveniles) of the total number of individuals collected were not identified to species. Animals attached to hard surfaces such as rocks and shells and parasitic or planktonic species were also excluded from the analyses. Meiofaunal taxa such as nematodes, harpacticoid copepods, ostracods, foraminifera, and mites were not included because they were inadequately sampled by the 0.3-mm-mesh screens and were therefore not considered part of the macrofauna.

Results were based on 233 box-core samples from 14 stations; however, particular emphasis was placed on the 160 samples from the nine 2,100-m depth stations (for comparison of combined samples within stations, station 8 was left out because it was sampled only three rather than six times). Only the total number of species and individuals from an additional 323 box cores from off the Carolinas and New England were used. Data entry was replicated and cross-checked, and the tabulated data were returned to the taxonomic specialists who eliminated any redundant entries or similar errors. In the analysis involving random combinations of all samples from 2,100-m depth, samples from the stations at either end of the along-contour transect (6 and 10) were also dropped because of the limited capacity of the VAX 11/780 used in the calculations.

Hurlbert's (1971) modification of the rarefaction method (Sanders 1968) was used to generate species-individuals curves. The points on each curve are the number of species calculated to occur in computer-generated subsamples of m individuals from single or combined samples (Smith and Grassle 1977). The rarefaction curves were estimated from the total fauna and also on separate faunal groups: polychaetes, mollusks, and peracarid crustaceans. Shannon-Wiener diversity indexes (H') were calculated for individual samples (Pielou 1966). Faunal similarities were measured using the normalized expected species shared in samples of m individuals (NESS; Grassle and Smith 1976; Smith et al. 1979). In this article, NESS is expressed as the percentage of species shared.

Plots of species versus area (number of samples) were computed using the methods of Gaufin et al. (1956) to calculate the average number of new species contributed by random combinations of 1, 2, 3, . . . , n replicate samples. Species-accumulation curves were also calculated by adding samples in sequences ordered according to time or station. Fit to the lognormal distribution was estimated using the Gauss-fit program described by Gauch and Chase (1974).

RESULTS

Diversity and Abundance of Higher Taxa

A total of 798 species representing 171 families and 14 phyla were identified from 90,677 individuals in 233 box cores that had a combined surface area of 21 m^2 (table 2). An additional 64 macrofaunal species were present in the samples but were planktonic or lived on hard surfaces and therefore were omitted from the analyses (see Maciolek et al. 1987 for a complete list of species). Annelids accounted for 48%, peracarid arthropods (amphipods, isopods, tanaids, and cumaceans) 23%, and mollusks 13% of the macrofaunal individuals.

TABLE 2

TAXONOMIC COMPOSITION OF SOFT-SEDIMENT BENTHOS FROM U.S. MID-ATLANTIC CONTINENTAL SLOPE SAMPLES

Species and Family	No. of Species	No. of Families
Cnidaria	19	10
Hydrozoa	6	3
Anthozoa	12	6
Scyphozoa	1	1
Nemertea	22	1
Priapulida	2	1
Annelida	385	49
Polychaeta	367	47
Oligochaeta	18	2
Echiurida	4	2
Sipuncula	15	3
Pogonophora	13	5
Mollusca	106	43
Bivalvia	45	18
Gastropoda	28	18
Scaphopoda	9	4
Aplacophora	24	3
Arthropoda:	185	40
Cumacea	25	4
Tanaidacea	45	8
Isopoda	59	11
Amphipoda	55	16
Pycnogonida	1	1
Bryozoa	1	1
Brachiopoda	2	1
Echinodermata	39	13
Echinoidea	9	2
Ophiuroidea	16	6
Asteroidea	3	3
Holothuroidea	11	2
Hemichordata	4	1
Chordata	1	1
Total	798	171

Of all species, 58% (460) are new to science. Among the peracarid crustacea and polychaetes, 69% (127 species) and 64% (236 species), respectively, are undescribed. Within several polychaete families, such as the Dorvilleidae, Cirratulidae, Spionidae, Flabelligeridae, and Terebellidae, 75%–93% are new. The mollusks are somewhat better known, however, and 37% (42 species) are undescribed.

Community Homogeneity

The relative abundances of species at the nine 2,100-m stations sampled over the entire 2-yr period were similar from station to station (fig. 2). The relative proportions of these 10 species abundances within these stations did not change radically when samples were combined according to sampling date, station, or entire region (table 3). When the samples were combined, only 10 species had an average abundance greater than 2%. The single most common species (the

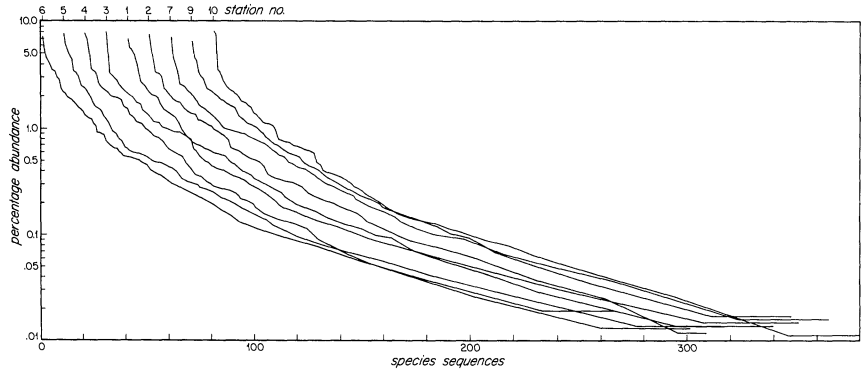

FIG. 2.—Percentage abundance of species ranked from the most common to the least common (species sequences) at each of nine stations ordered by position on a NE-to-SW transect along the 2,100-m depth contour. The intervals of 10 on the baseline are numbers of species (offset by 10 species for each station). Each station has a similar distribution of individuals among species.

TABLE 3

PERCENTAGE CONTRIBUTION OF THE 10 MOST ABUNDANT SPECIES AT 2,100-M DEPTH

Species Ordered by Rank	All Samples Combined	Replicates and Times Combined, Averaged across Stations (%)	Replicates Combined, Averaged across Stations and Times (%)	Averaged across Stations, Times, and Replicates (%)
Aurospio dibranchiata (P)	7.1	7.2 (9.5)	7.7 (16.6)	8.3 (26.9)
Pholoe anoculata (P)	4.6	5.6 (17.4)	5.8 (19.2)	6.2 (21.9)
Spathoderma clenchi (A)	3.9	4.2 (19.5)	4.6 (18.8)	4.9 (18.1)
Tharyx sp. 1 (P)	3.8	3.6 (15.4)	3.9 (17.8)	4.2 (17.0)
Prionospio sp. 2 (P)	3.1	3.4 (17.6)	3.4 (15.4)	3.8 (15.9)
Tubificoides aculeatus (O)	3.0	3.1 (13.1)	3.2 (14.9)	3.4 (14.9)
Prochaetoderma yongei (A)	2.8	2.8 (12.3)	2.9 (14.1)	3.2 (14.9)
Aricidea tetrabranchia (P)	2.2	2.6 (10.2)	2.6 (13.5)	2.9 (14.3)
Glycera capitata (P)	2.1	2.4 (8.1)	2.4 (11.2)	2.7 (13.0)
Nemertea sp. 5 (N)	2.1	2.2 (5.4)	2.3 (11.4)	2.5 (13.5)

NOTE.—A, Aplacophora; N, Nemertea; O, Oligochaeta; and P, Polychaeta. Coefficients of variations are shown in parentheses.

polychaete *Aurospio dibranchiata*) comprised 7%–8% of the total individuals regardless of scale of sampling. The abundance of this and the other abundant species changed little regardless of station or sampling date (fig. 3).

About 20% of the species were found at all 10 2,100-m stations, and 34% occurred at only one station. For the entire soft-sediment fauna, 28% of the species occurred only once and 11% only twice. Peracarid crustacea have the narrowest distribution with only 15% (21 species) occurring at all 10 stations and 43% (60 species) occurring at a single station. The breadth of distribution of

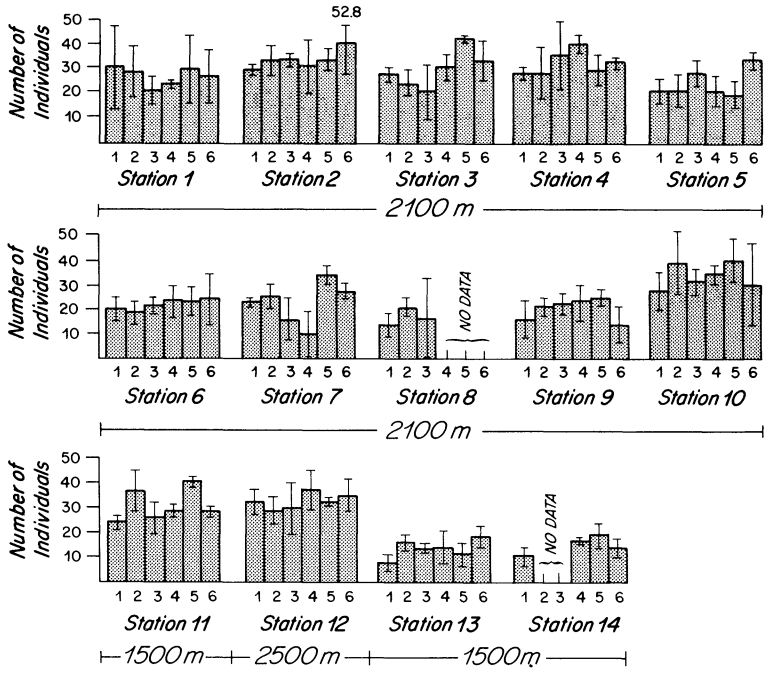

FIG. 3.—Temporal variation in abundance (no./900 cm^2 ± 1 SD) of *Aurospio dibranchiata* over a 2-yr period at each of 10 stations along the 2,100-m depth transect (stations 1–10), at depths of 1,500 m (stations 11, 13, 14) and 2,500 m (station 12). Each bar indicates the $\bar{X}$ and SD of three replicate samples from each sampling date.

polychaetes was near the mean for the entire fauna; 22% (65 species) occurred at all 10 stations and 36% (106 species) at one station. Bivalves, in addition to being better known (see above), had broader distributions with 37% (14 species) at all 10 stations and only 21% (8 species) at one station. Although variable in proportion, endemism was high both across and within all taxa.

Based on the six northernmost stations (stations 1–6), the normalized expected species shared (NESS) between samples of 50 individuals (m = 50 individuals) from adjacent pairs of stations was 83% ± 5% (95% confidence limits [CL]), and the mean NESS similarity for samples of the same size (m = 50) within each station was 92% ± 2%. The mean NESS similarity (m = 200 individuals) between samples from the most distant stations (6 and 10) was 79% ± 5% (within-station similarities were 93% ± 5% and 91% ± 4%, respectively).

The community at 2,100-m depth does not have sharp boundaries: a 500-m change in depth in either direction from station 1 produced a NESS similarity between stations of 68% ± 3% in the shallower direction and 64% ± 4% in the deeper direction (N. J. Maciolek and J. F. Grassle, unpublished manuscript). Clearly, although there are many endemic species and many are rare, the variation in the identity of relatively abundant species over a large scale (kilometers) is relatively small.

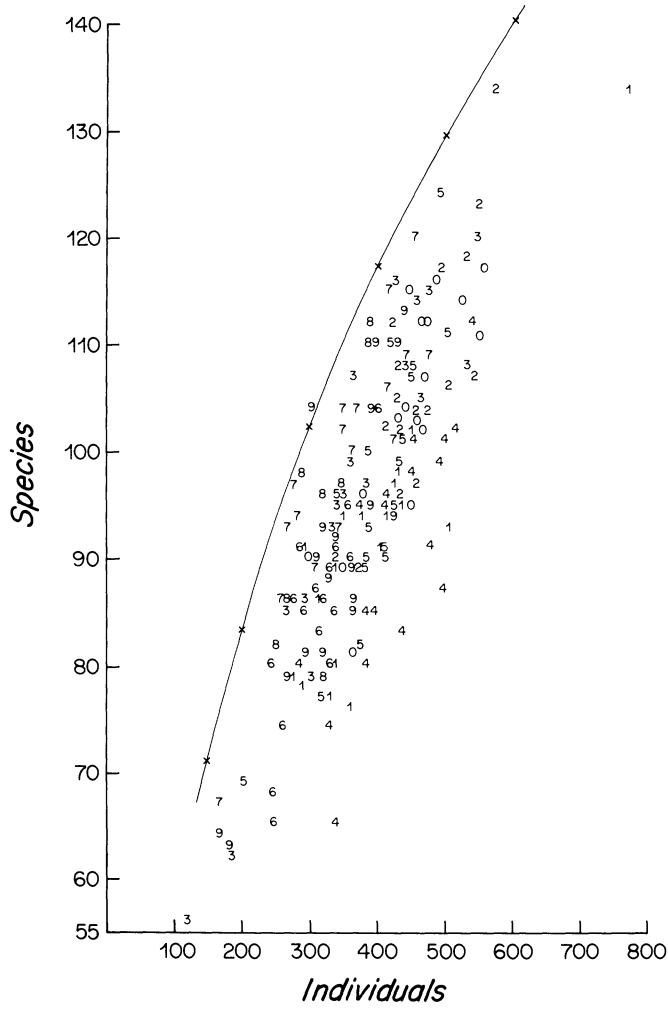

FIG. 4.—Number of species and individuals in each replicate 900-cm^2 sample from stations 1–10. The number indicates the station (1, station 1; 2, station 2; . . . ; 0, station 10). The line connecting the X's is a portion of the rarefaction curve calculated from a summation of all 168 individual samples.

Species Diversity of Each Replicate from 2,100-m Stations Treated Separately

The diversity at the 2,100-m stations is shown in figure 4, in which the numbers of individuals and species in each 900-cm^2 sample are plotted. The number of species per 900-cm^2 core ranged from 55 to 135, with this measure of species richness varying according to faunal density. The rarefaction line indicated by the X's in figure 4 was calculated from a single sample obtained by summing the 168 2,100-m samples. With one exception, all of the numbers of species and

TABLE 4

MEAN AND 95% CONFIDENCE LIMITS PER 100 INDIVIDUALS FOR EACH SAMPLE TREATED SEPARATELY AT EACH STATION

Distance (km) and Station No.	Stations, Times, Replicates Separate (spp./900 cm^2)	Stations, Times, Replicates Separate (Shannon-Wiener index)	Stations, Times, Replicates Separate (spp./100)	Stations and Times Separate, Replicates Combined (spp./100)	Replicates and Times Combined, Stations Separate (spp./100)
0 (station 6)	84.7 ± 9.5	5.67 ± .19	48.5 ± 2.9	50.0	51.0
52 (station 5)	96.2 ± 13.2	5.70 ± .16	47.9 ± 2.6	49.0	50.3
68 (station 4)	90.5 ± 11.6	5.68 ± .14	47.1 ± 2.3	49.1	50.6
87 (station 3)	96.7 ± 17.9	5.86 ± .24	51.5 ± 2.9	53.4	55.3
91 (station 1)	91.6 ± 13.2	5.69 ± .18	48.0 ± 2.5	50.2	52.1
93 (station 2)	105.2 ± 11.6	5.91 ± .20	51.2 ± 3.0	53.1	54.7
133 (station 7)	100.6 ± 12.2	6.00 ± .15	54.2 ± 2.1	56.1	57.6
133 (station 8)	95.0 ± 12.2	5.99 ± .19	53.0 ± 4.0	55.1	56.4
139 (station 9)	89.5 ± 13.5	5.82 ± .23	51.0 ± 3.3	53.0	55.2
176 (station 10)	102.1 ± 12.9	5.85 ± .16	50.8 ± 2.6	52.4	53.8
Overall mean	95.2 ± 6.7	5.82 ± .13	50.4 ± 2.4	52.2 ± 2.5	53.7 ± 2.6

NOTE.—The 95% confidence interval is based on $N = 10$. The last two columns indicate change in the spp./100 individuals rarefaction estimate when replicates are summed within sampling periods and when sampling periods are combined as well. The stations are ordered from northeast to southwest on a 176-km, 2,100-m depth transect.

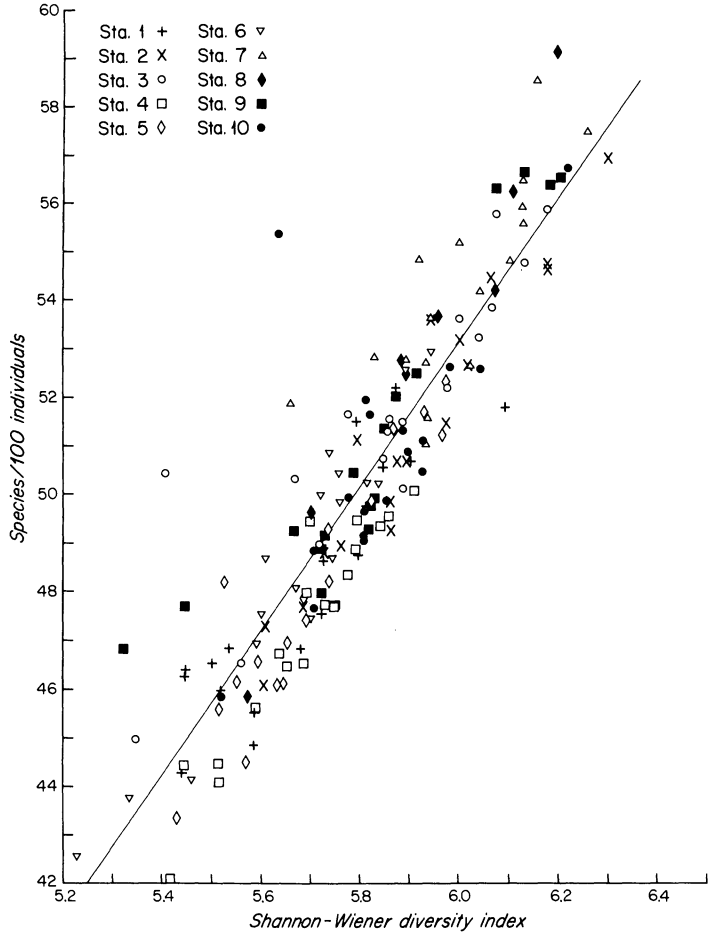

FIG. 5.—Relationship between the rarefaction estimate of species per 100 individuals and the Shannon-Wiener diversity index for each sample from the 2,100-m depth transect. The regression line for all points was $r^2 = 0.83$.

individuals per 900 cm^2 are to the right of the line, which indicates that the individuals of each species are not distributed randomly among the actual samples. This observation is not surprising in view of the obvious patchiness that was observed in bottom photographs (Grassle et al. 1975; Hecker in Maciolek et al. 1987*a*, 1987*b*). Numbers of species per 900 cm^2, Shannon-Wiener diversity indexes, and rarefaction estimates of species per 100 individuals are shown in table 4. At this scale of sampling, the Shannon-Wiener and species per 100 individuals estimates were correlated (fig. 5).

Species Diversity at Each 2,100-m Station, When Replicates and Sampling Times Are Pooled

Species-accumulation curves for stations 1–7, 9, and 10 were calculated from the species means of every combination of each 1, 2, 3, . . . , *n* samples (fig. 6).

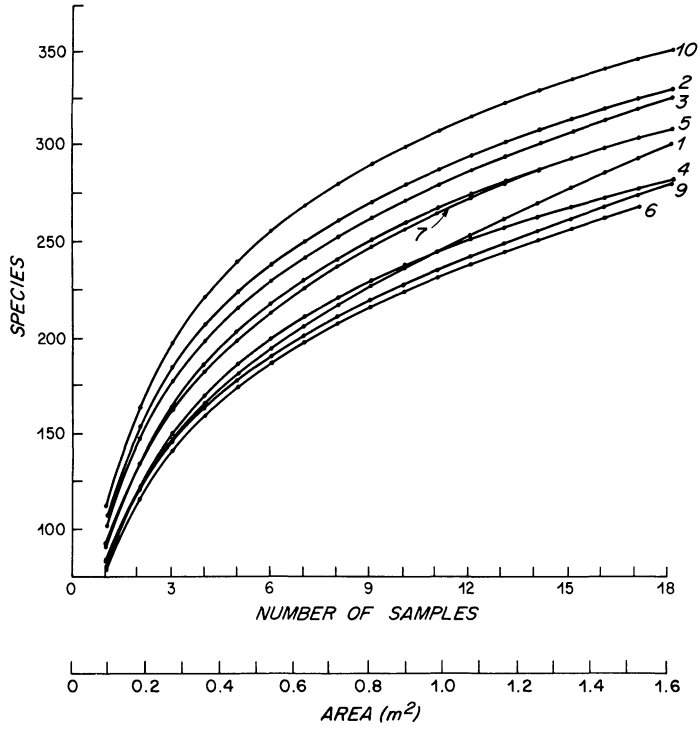

FIG. 6.—Species-area curves based on random addition of samples from each of the 2,100-m depth stations sampled six times over a 2-yr period. The area of 18 samples is 1.62 m^2.

Using this method, we found that diversity was greatest at the southernmost station, 10. The next most diverse stations—2, 3, and 5—did not represent any particular geographical pattern.

The rarefaction curves for these stations (fig. 7) indicated differences in diversity similar to those represented by the species-accumulation curves, with station 10 being the most diverse and station 4 the least diverse. The northernmost station, 6, was similar in species composition to the majority of stations, whereas the southernmost station, 10, showed the greatest dissimilarity to other 2,100-m stations. Forty-two species occurred only at station 10; in contrast, 17 species occurred only at station 6. The relatively high species richness at station 10 may reflect a contribution of species dispersing from denser populations to the south.

Rarefaction curves for the three major taxa—Polychaeta, Peracarida, and Mollusca—are shown in figure 7 as shaded areas delimited by the curves for the least and most diverse stations and include the actual end points of each of the nine curves for each taxa. Station 10 had the most diverse fauna in each of these taxa as well.

Fluctuations in diversity through time at each station are illustrated by the rarefaction number of species per 500 individuals on each sampling date (fig. 8).

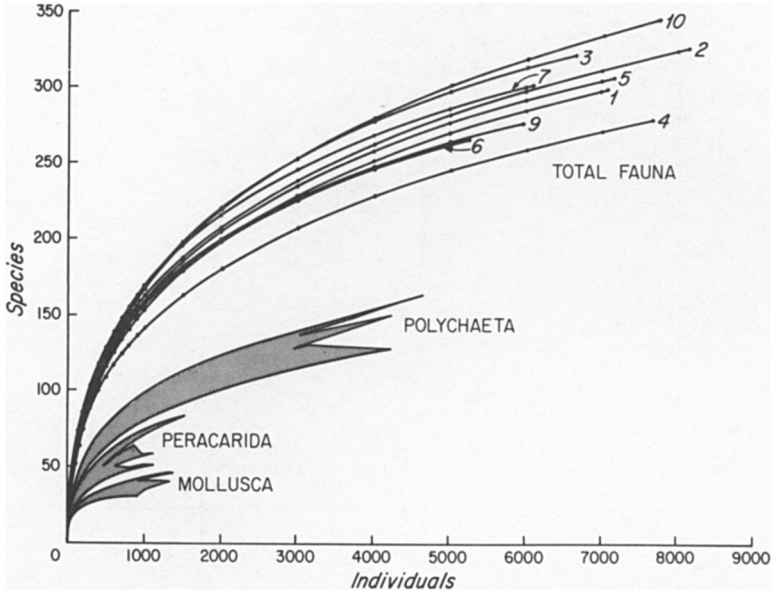

FIG. 7.—Rarefaction estimates of diversity of total fauna, Polychaeta, Peracarida, and Mollusca from each of the 2,100-m stations sampled six times.

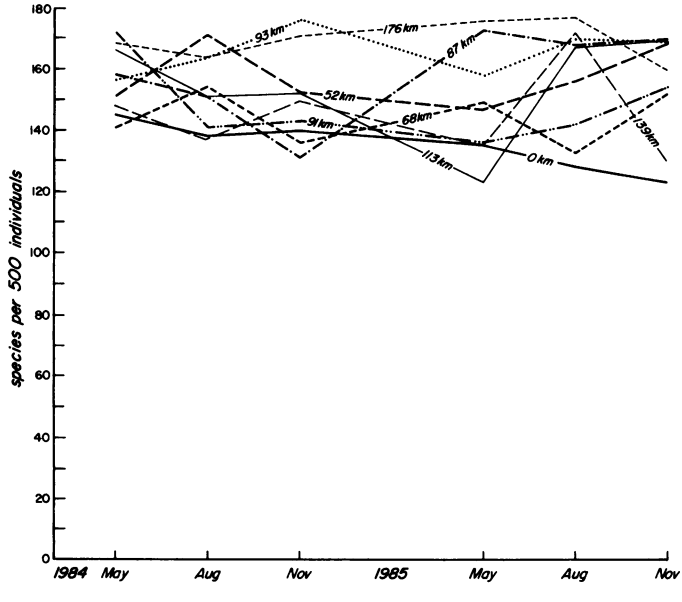

FIG. 8.—Temporal variation of species per 500 individuals over a 2-yr period at nine 2,100-m stations, identified by distance along the depth contour.

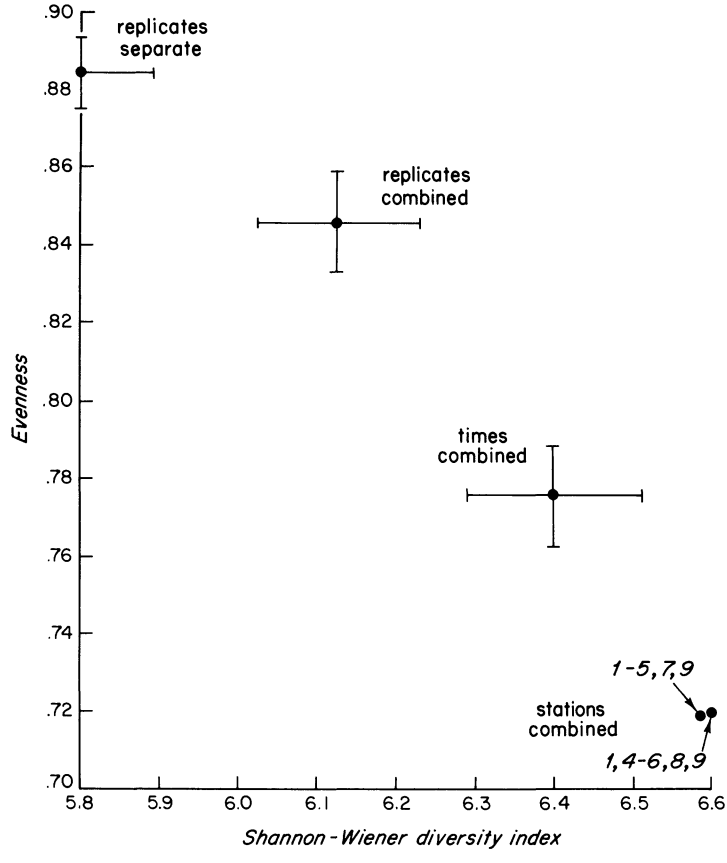

FIG. 9.—Mean and standard deviation of evenness (H'/H_{max}) and the Shannon-Wiener diversity index (H') of each 900-cm^2, 2,100-m depth sample separately, combined within sampling periods, combined over time within stations, and combined among stations (stations 1–5, 7, 9 and stations 1, 4–6, 8, 9).

Diversity fluctuated very little from station to station or from time to time. The abundance of the most common species, the polychaete *Aurospio dibranchiata,* also fluctuated surprisingly little with time and site along the depth contour (fig. 3). Similar histograms could be shown for most of the abundant species along the transect (Maciolek et al. 1987*a*).

Rarefaction estimates of species diversity did not change drastically when samples were combined (table 4). This was not the case with the Shannon-Wiener index (H') or evenness (H'/H_{max}) (fig. 9). For estimates of regional diversity, neither H' nor evenness are appropriate measures.

When the distributions of individuals among species at each station were fitted to a lognormal distribution (Gauch and Chase 1974; also see pros and cons of this approach in Nelson 1987), only the extreme right-hand tail of a lognormal distribution was observed (curves not shown). In six of the 10 fitted curves, the

mode of the curve was more than 1 SD unit to the left of the portion of the curve represented by our data. When the 2,100-m stations were combined to include more of the total pool of species in the region, the fit to the lognormal decreased (explaining 91% of the variance instead of 95%). The calculated mode of the curve, based on all 2,100-m samples, was 1.6 SD units to the left of the actual data. Assuming this distribution, we have collected only 5.5% of the species from the entire distribution, and there are 11,800 species in the community. Since only one extreme tail of the curve is present, the lognormal distribution may or may not be a good representation of the community. Because more complete lognormal plots have been fitted to other communities (Preston 1948; Patrick 1973; Sugihara 1980) with relatively few rare species, it seems unlikely to be a good approximation for deep-sea data. Hughes's community dynamics model of species abundance (Hughes 1984, 1986) provides a more complete approximation of the data than the lognormal or log series distributions. The Hughes model, however, does not provide a prediction of the total species pool.

Species Richness—Stations along the 2,100-m Contour Combined as a Single Assemblage

Faunal similarities were very high between stations along the 2,100-m depth contour sampled. Stations 6 and 10, the northernmost and southernmost stations, respectively, and station 8, which was sampled for only 1 yr, were eliminated, so that the length of the 2,100-m contour spanned by the remaining seven stations was 87 km. Faunal similarities were high between all pairs of these stations (NESS $> 85\%$), and the combined data provide a representation of regional species diversity (fig. 10). Both a rarefaction curve (+'s, based on combining the same samples into a single collection and calculating the number of species represented in successively smaller random draws of individuals from the combined collection) and a species-accumulation curve (based on the mean number of species in all combinations of 1, 2, 3, . . . , n samples) are illustrated (fig. 10). Because species distributions are not random, the mean number of species in combinations of samples accumulated species at a faster rate than chance combinations of individuals drawn from a single combined sample.

The individual points in figure 10 are the data from Hessler and Sanders's (1967) five epibenthic sled trawl samples that first showed the high diversity in the deep sea. The epibenthic sled inefficiently sampled a 0.81-m swath approximately 1–2 km long or 10^3 m^2. Although the sled samples were from the same general region as our study area, the diversity was much lower than our data show, especially when the much smaller surface area that we sampled is considered. Three reasons account for the difference. First, the box-core stations were spaced over a geographical area larger than that covered by a single trawl sample, so trawls miss many of the burrowing species (Gage 1975). Second, a finer sieve was used (0.3 mm instead of 0.42 mm). Finally, and most important, major advances have been made in deep-sea systematics in the intervening 2 decades, which has resulted in the recognition of many more species than were identified by Hessler and Sanders.

We used the data from all nine stations sampled six times over a 2-yr period

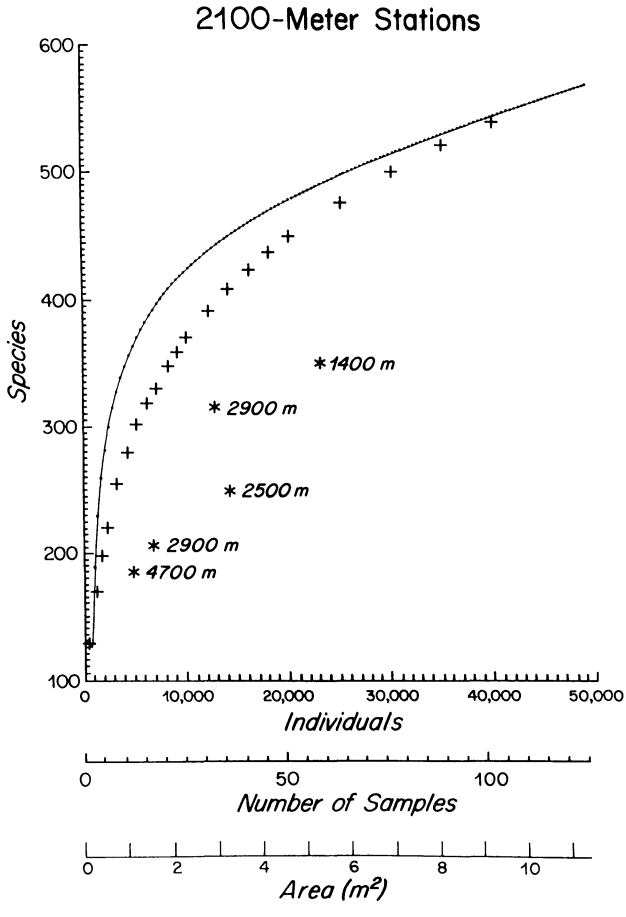

FIG. 10.—Upper curve is a computer-generated species-area plot of the mean number of species for each combination of samples from the 2,100-m stations 1–5, 7, and 9, regardless of sampling date. *Plus symbols* (+) mark the species-individuals relationship calculated by rarefaction from a single summation of the 125 separate samples. Trawl samples from Hessler and Sanders (1967) are indicated by *asterisks*.

to develop the species-accumulation curves by adding the samples together in order of time and order of distance along the transect (fig. 11). The rarefaction curve is also presented for reference. When the samples from separate stations were combined in an order proceeding from north to south within each sampling date and then according to time of sampling from the first to the last sampling date, the species-accumulation curve (*closed circles*) was very close to the rarefaction line. When samples within each station were ordered first by sampling date and then according to the order from north to south along the 2,100-m contour, the curve (*open circles*) fell below the rarefaction line and had a pronounced stepwise character. The horizontal part of the step consisted of individuals of species already represented in the cumulative collection. The vertical part

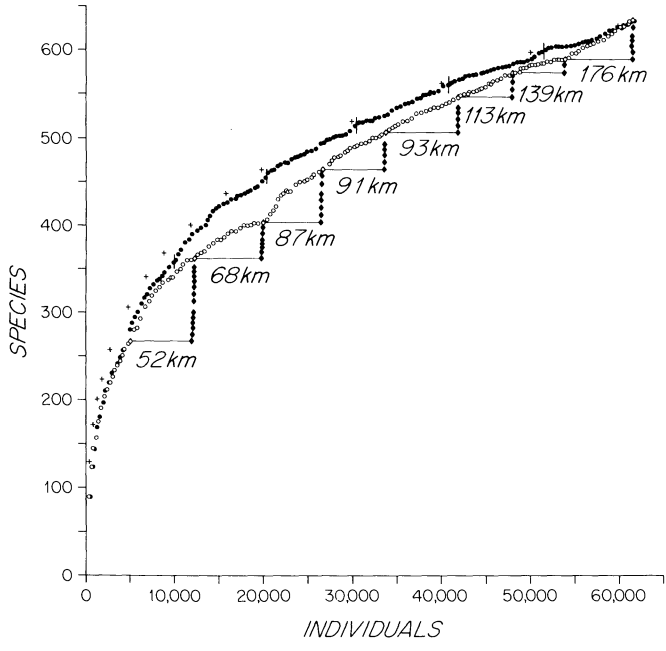

FIG. 11.—Individual samples combined in an ordered sequence by two different methods. The *open circles* are samples combined over time within stations and then combined according to station at the designated distances along a NE-to-SW transect. The staircase pattern is formed by horizontal lines representing individuals of species already represented in the samples accumulated at that point. The *closed diamond-shaped points* are rarefaction curves using individuals of the species added at that station. The *closed circles* are samples accumulated according to station within each time interval. This curve closely approximates the rarefaction curve represented by *plus symbols* (+). The rarefaction points are calculated from the combined collection of all samples.

of each step added very few individuals because species not previously collected were rare. This is as expected if the 2,100-m contour is all one assemblage. The steps became less steep with distance except for a marked addition of species from station 10 at the end of the transect. Station 10 may be at the start of a transition to a different 2,100-m community (see community homogeneity results). Because widely separated small patches are expected in the deep sea, we would predict a similar but somewhat lower curve if all the samples were from a single site. The data from the hundreds of samples needed to fully characterize a species-area curve at a single site are unlikely to be obtained in the near future because of the expense of processing a single deep-sea sample.

Rarefaction curves of the three major taxa, which used samples from stations 1–10 combined for all sampling periods, showed that polychaetes were the most diverse group, followed by the peracarid crustaceans and then the mollusks (fig. 12). Smaller groups such as tanaids, isopods, and bivalves (or the even less abundant gastropods and amphipods) gave an even less complete representation of the diversity (fig. 13).

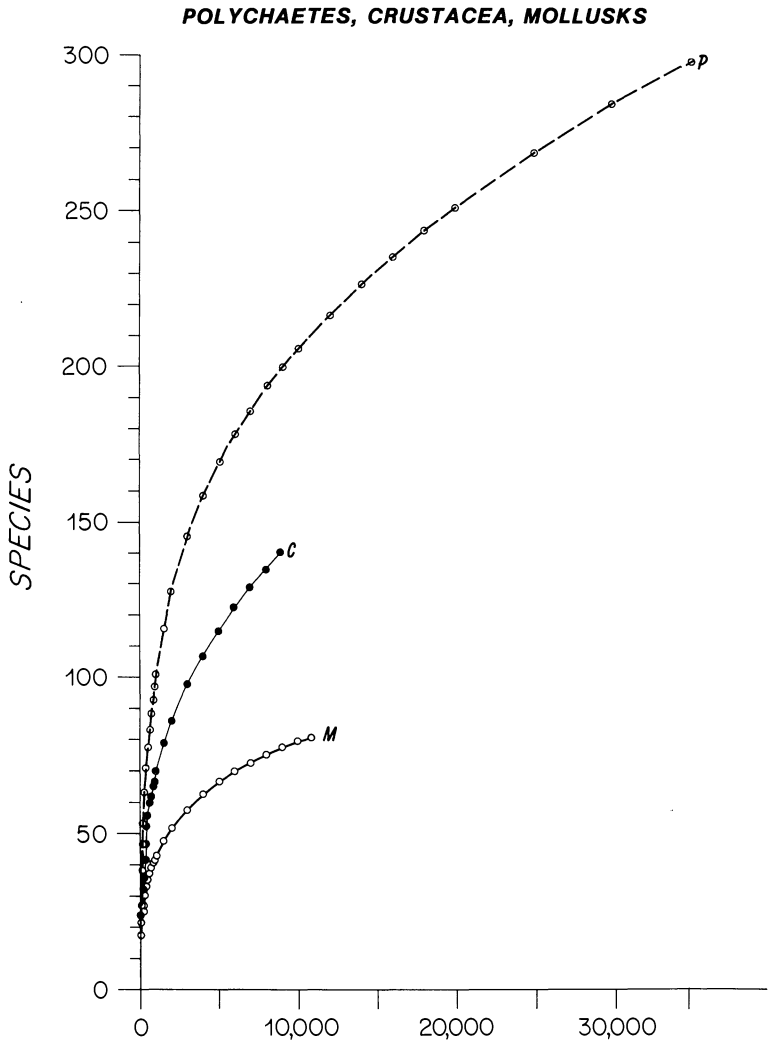

FIG. 12.—Rarefaction curves for polychaetes (*P*), peracarid crustaceans (*C*), and mollusks (*M*).

Diversity Including Stations off New England and the Carolinas

A combination of samples from 31 additional stations south of New England (Maciolek et al. 1987*b*) and off North and South Carolina (Blake et al. 1987) at depths from 255 to 3,494 m was used to extend the plot of species and individuals north and south beyond the region off New Jersey and Delaware (fig. symbols). The total number of species added was 799, which brought the total to 1,597 for 556 900-cm^2 samples (272,009 individuals). A plot of the number of species represented by single individuals against the total number of individuals collected showed that the rate of addition of rare species was undiminished with the addi-

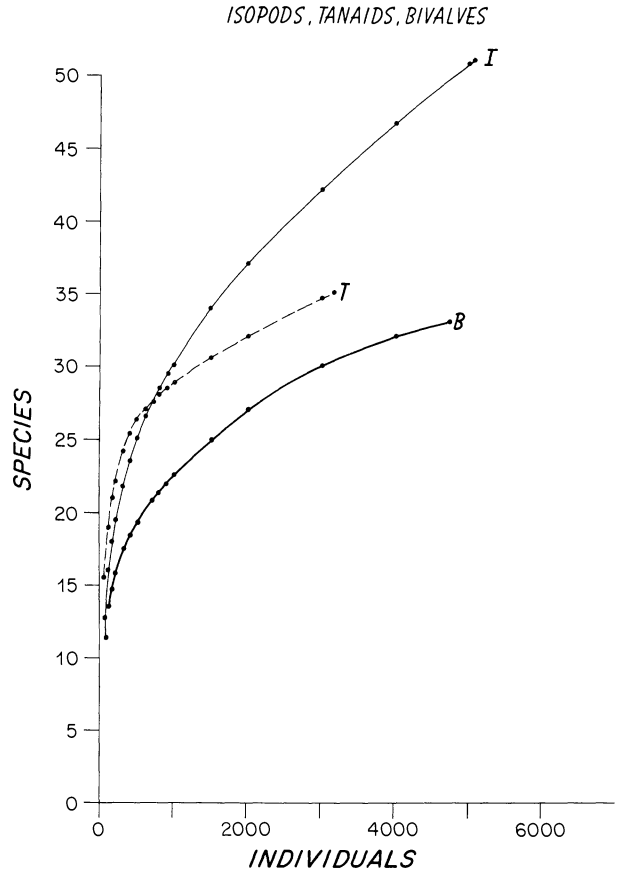

FIG. 13.—Rarefaction curves for isopods (*I*), tanaids (*T*), and bivalves (*B*)

tion of samples from other slope environments (fig. 14, other symbols). This is a critical point to consider in estimating where the species-abundance curve might eventually level off.

DISCUSSION

Faunal Homogeneity

The relative-abundance curves (fig. 2) show that the community structure was similar at each of the 2,100-m stations. The species listed in table 3 were consistently the most abundant at each of the 2,100-m stations, and the single most abundant species, the polychaete *Aurospio dibranchiata,* had a remarkably homogeneous abundance over the entire area sampled (fig. 3). Despite many rare species (90% of the species were represented by less than 1% of the individuals), about one-fifth of the species found at any of the 2,100-m stations occurred at all 10 stations. Mean similarity of samples within stations was slightly greater (NESS

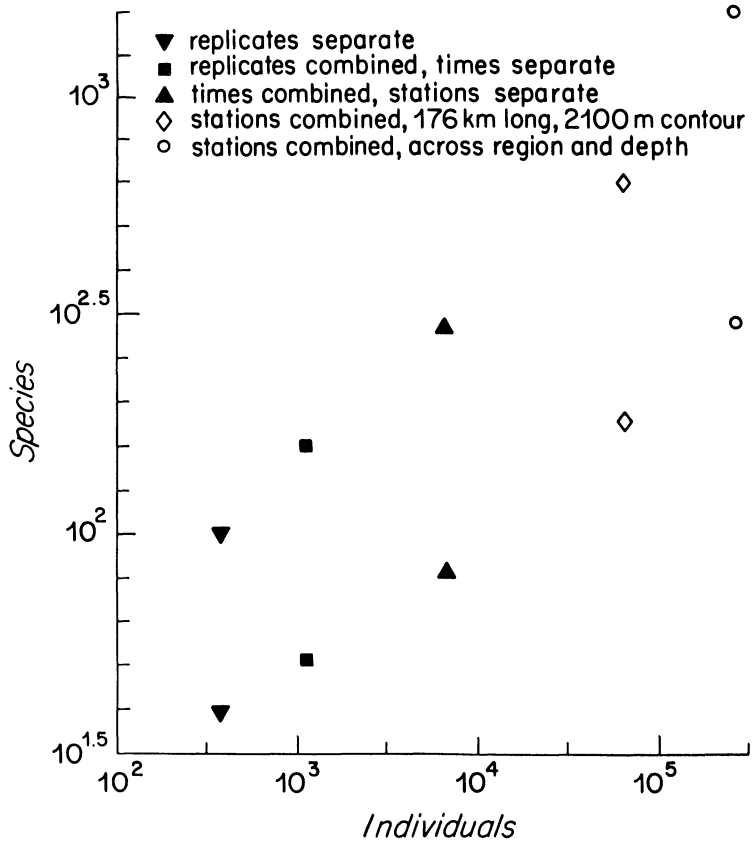

FIG. 14.—Relationship between species and individuals in successively larger combinations of samples. The lower set of points shows the relationship between number of species represented by a single individual and the total number of individuals. The *closed symbols* are within single 2,100-m stations. The *open circles* represent data from 45 stations taken from the continental slope off the east coast of the United States from depths of 255–3,494 m.

at 50 individuals = 92% ± 2%) than between adjacent 2,100-m stations (NESS at 50 individuals = 83% ± 5%) or between the two most distant 2,100-m stations (NESS at 50 individuals = 79% ± 5%). A change of 500 m in depth resulted in a drop in NESS similarity to 68% ± 3% in the shallower direction and to 64% ± 4% in the deeper direction.

Our results support evidence from other studies that species composition changes more rapidly across rather than along depth contours (Sanders and Hessler 1969; Grassle et al. 1979; Carney et al. 1983).

However, broad distributions of many of the abundant species both along and across depth contours (N. J. Maciolek and J. F. Grassle, unpublished manuscript) are evidence that boundaries between deep-sea communities are far less distinct than between communities in shallow water. This is shown by the small spatial

and temporal variation of faunal diversity in these samples compared with similar surveys for shallow-water communities (see figs. 4, 5, 8).

The three most abundant taxa differed similarly in breadth of distribution both across and along depth contours. Species of peracarid crustacea had the narrowest distribution, polychaete species had distributions similar to the mean for the whole fauna, and bivalves had the broadest depth distributions. A similar observation was made by Sanders and Grassle (1971) from epibenthic sled trawl data.

How Many Species Occur in the Deep Sea?

The discovery of 798 species from a total surface area of 21 m^2 clearly indicates a high species richness in a single area at a uniform depth. Even though other quantitative studies were based on very few samples, results from smaller sampling efforts can be compared with ours. The number of species (278–351 species at the 2,100-m stations and 324–363 species at the 1,500-m stations) present in the 1.62-m^2 surface area represented by the 18 samples from each single station was similar to the 315 species obtained in a slightly smaller sampling effort (1.25 m^2) at 1,230-m depth in the San Diego Trough off southern California (Jumars 1976). Gage (1979) obtained up to 146 species per 0.25-m^2 core at 1,800–2,900-m depths in the northeast Atlantic Rockall Trough. In clusters of four or five replicate 0.25-m^2 samples from the central Pacific (3,934–5,229-m depth), Hecker and Paul (1979) obtained approximately 60 species per 80 individuals even though densities were only about 120 individuals per square meter. Rowe et al. (1982) obtained about 130 species from eight 0.04-m^2 samples from approximately 2,800-m depth in the northwest Atlantic. Grassle and Morse-Porteous (1987) obtained 250 species in four box cores (two 0.25 m^2 and two 0.09 m^2) from 3,600-m depth in the same region.

Our data show that the number of species continued to rise steadily as more samples and more individuals were collected. At a single station, species were added at a rate of about 25 per 0.5 m^2 (fig. 6). Osman and Whitlatch (1978) have asked why there are not more species when one considers the surface area of the deep sea. One answer is that the number of deep-sea species has previously been greatly underestimated. After the initial rapid increase in species as samples are added along the 176-km transect, the data in figure 11 suggest a rate of increase in number of species with distance on the order of 100 species per 100 km. The rate of addition of species with distance across depth contours or in less homogeneous regions is even greater (this study; Blake et al. 1987). The deep sea at depths greater than 1,000 m occupies on the order of 3×10^8 km^2. If a linear rate of addition of one species per kilometer is conservatively generalized to one species per square kilometer, a deep-sea reservoir of undescribed species on the order of 10^8 is indicated. Since the deepest and most oligotrophic parts of the ocean have densities of life more than an order of magnitude lower (115/m^2; Hessler and Jumars 1974) than the depths considered here (4,597/m^2; Maciolek et al. 1987*a*), an estimate of 10^7 may be a better estimate. This estimate is probably conservative given that accumulation of species across depth contours appears to be much faster than within, and within-depth contour accumulation at a relatively homogeneous site is perhaps the slowest in the deep sea.

The projection we have made from a very small data set has severe limitations. The very high proportion of species represented by single individuals is a measure of the extreme inadequacy of sampling as well as some of the best evidence for a universe with orders of magnitude more species. Predictions concerning the number of species added as more sites are studied depend on the assumption that rare species that turn up at more distant sites will not be the same as the rare species already collected. In the more heterogeneous group of stations added from off New England and the Carolinas, different rare species were found, and the proportion of species represented by single individuals increased (fig. 14). As expected, the rate of addition of species also increases with the broadening of depths and habitats sampled.

In contrast to the deep sea, shallow-water marine communities outside of tropical areas have relatively few species. Shallow tropical marine areas with the highest potential species richness are not well enough studied for an adequate comparison to be made. The best-studied soft-bottom communities are in intertidal areas or coastal embayments where the number of species per number of individuals collected usually reaches an asymptote at fewer than 100 species for collections larger than 1,000 individuals (see, e.g., Hessler and Sanders 1967). The continental shelf is more diverse; however, data from 70 0.04-m^2 grab samples, taken over a 3-yr period from a station at 80-m depth on Georges Bank and analyzed using the same methods, indicated that the number of species per number of individuals leveled off at just over 200 species for collections of greater than 100,000 individuals (N. J. Maciolek and J. F. Grassle, unpublished manuscript).

In general, deep-sea communities subjected to obvious, frequent physical disturbance have reduced species diversity (Grassle 1989). Since most deep-sea studies are based on very few samples, the comparison can only be made on the basis of relative abundance of species. Our results and other deep-sea studies show that the most abundant species is less than 10% of the fauna, and the majority of species in deep-sea communities are represented by less than 1% of the fauna. In shallow-water environments, the most common species generally makes up 30% or more of the fauna.

A few areas in the deep sea are known to be subjected to disturbance, and these are more like shallow-water communities in having species that are numerically dominant. For example, large-scale fluctuations in the environment such as those produced by widespread deep-sea currents or shallow-water storms are not favorable to the development of species-rich communities. In a deep-sea area where currents may be 20–25 cm/s for periods of several days, Thistle et al. (1985) found that the polychaete *Paedampharete acutiseries* (see Russell 1987 for synonomy of two species reported by Thistle et al.) made up 50%–64% of the fauna.

Features of the Deep-Sea Environment Favorable to Maintaining High Species Richness

The patchy input of food to the deep sea can be considered both as a disturbance and, in the sense of Atkinson and Shorrocks (1981), a patchy and ephemeral resource. Within a patch, single species may be abundant, and the diversity is

reduced on a microhabitat scale. Smith et al. (1986) reported abundances of 67% ± 1% of the polychaete *Levinsenia oculata* in background samples from a deep-sea area characterized by dense concentrations of megafaunal mounds. Artificial mounds also produced similar proportions (68% ± 2%) of the same species after 50 d. Grassle and Morse-Porteous (1987) found that the polychaete *Ophryotrocha* sp. A comprised 38% of the individuals in cores dominated by decomposing *Sargassum* weed from 3,600-m depth off New England; another member of this genus, *O. akessoni,* comprised more than 90% of the individuals in deep-sea sediments affected by hydrothermal venting (Grassle et al. 1985).

Although diversity may initially be reduced by disturbance on a microhabitat scale, high overall diversity appears to be maintained by the input of small patches of ephemeral resources and the disturbance that results from the activities of individual animals. Bottom mounds (Jumars 1976; Smith et al. 1986), vacant burrows (Aller and Aller 1986), activities of scavengers (Smith 1986), input of wood (Turner 1973, 1977), animals such as glass sponges (Jumars 1976) and xenophyophoreans (Levin et al. 1986) projecting above the sediment surface, and sunken patches of seaweed or salp blooms that have accumulated in topographic depressions (Grassle and Morse-Porteous 1987) are all important sources of small-scale spatial heterogeneity. Spatial patchiness is produced in part through disturbance of existing populations but, more importantly, through relatively high concentrations of food resources that result in long-lasting heterogeneity in the absence of widespread disturbance of the sediment or other large-scale catastrophic change. In most cases biogenic structures contribute to patchiness of organic input. Mechanisms by which patchy organic resources maintain high species diversity are reviewed by Hanski (1990) and Shorrocks (1990). As is true on coral reefs (Grassle 1973), patch structure relevant to individual species does not show up in quadrat sampling.

Pulses of food tend to arrive sporadically and to collect in depressions and burrows produced by the activities of animals on the deep-sea floor. Many of the rare species live only in association with these rare and ephemeral resources. Larvae or dispersing juveniles of deep-sea animals colonize these patches even though they are so rare as to be missed even by extensive sampling programs. The contribution of species that inhabit a variety of microhabitats (square centimeters to less than a few square meters in area) separated by hundreds to thousands of meters forms the species pool available to settle at any specific site. In this environment, local diversity depends less on species interactions and more on the total species pool and the rate of species recruitment to each area. The lack of barriers to dispersal allows distant migrants to contribute to local diversity. If competition among species is weak, as is suggested by low overall densities of macrofauna, then locally high species diversity can be explained solely on the basis of the regional species pool.

Cropping activities of megafaunal animals also play a role in maintaining deep-sea diversity (Dayton and Hessler 1972). Species with the highest potential rates of increase are prevented by predation from monopolizing resources (Grassle and Morse-Porteous 1987).

Temporal Variation in Deep-Sea Communities

Our results showed no detectable seasonal or annual variation in abundance or richness (figs. 3, 8). Most existing descriptions of deep-sea communities are inadequate to detect even truly drastic changes in community structure. Only counts of individual species will provide a sensitive measure of change. Without these data, climatic shifts or gradual increases in pollutant inputs over decades could result in undetected widespread extinctions. Casual observations of deep-sea communities are not possible. Even the simplest information on the state of these communities can only be obtained at considerable expense and involves a number of specialists working together. The continued quantitative study of deep-sea communities with appropriate taxonomic description of the faunas is particularly needed to determine whether the communities that characterize such a large area of the globe are changing.

SUMMARY

Extensive quantitative sampling of deep-sea macrofaunal communities from the continental slope and rise of the eastern United States shows that there are many more species in the deep sea than were indicated from qualitative sampling. In part because the surface area of the deep sea is so large and we have sampled so little of it, Thorson's (1971, p. 39) estimate of 160,000 marine species is certainly too low. Our results show a continual increase in the number of species along a depth contour and even greater rates of species addition or species accumulation across depth contours. Even very conservative extrapolations of these data to the enormous surface area of the deep ocean suggest that the number of species inhabiting the deep-sea floor has been greatly underestimated. As more of the deep sea is sampled, the number of species will certainly be greater than 1 million and may exceed 10 million.

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