Patterns of species diversity in the deep sea as a function of sediment particle size diversity

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UNDERSTANDING the processes that generate and maintain patterns of species diversity is a major focus of contemporary ecological and evolutionary research. In the deep sea, species diversity varies geographically and bathymetrically[1–3], and may attain levels that rival tropical communities[4]. Many hypotheses have been proposed concerning the forces that shape patterns of species diversity in the deep sea[5], but so far it has not been possible to relate these patterns to potential causes in a direct quantitative way. The nature of sediments should be important in structuring deep-sea communities because deposit feeders rely on the sediments for nutrition and comprise most of the organisms in the deep sea[6]. The composition of soft sediment communities is influenced by sediment particle

TABLE 1 Correlations between species diversity and ten environmental variables (r1) for each geographic region and all regions combined

	North			Mid			South			Combined		
	r1	r2	r3	r1	r2	r3	r1	r2	r3	r1	r2	r3
Depth	0.653***	0.031	—	0.243***	0.169*	—	0.146	0.355***	—	0.430***	0.107*	—
Sediment and water	0.174*	0.119	0.279***	0.274***	—	0.214**	0.603***	0.480***	0.656***	0.015	0.088	0.099*
Sediment	0.323***	0.163*	0.345***	0.217***	0.141*	0.158*	0.657***	—	0.702***	0.149**	0.139**	0.207***
Silt	0.665***	—	0.398***	0.233***	0.134*	0.105	0.321**	0.292*	0.295*	0.545***	—	0.424***
Clay	0.626***	0.093	0.341***	0.229***	0.126	0.158*	0.368**	0.424**	0.358**	0.465***	0.012	0.387***
Mean ϕ	0.616***	0.023	0.316***				0.253*	0.434***	0.209	0.521***	0.137*	0.420***
Sorting coefficient	0.338***	0.248***	0.356***				0.390***	0.213	0.432***	0.311***	0.260***	0.375***
% C	0.516***	0.098	0.168*	0.244***	0.075	0.123	0.425***	0.235	0.488***	0.358***	0.099*	0.305***
% H	0.375***	0.166*	0.043	0.196**	0.076	0.136*	0.643***	0.544***	0.657***	0.359***	0.117*	0.303***
% N	0.514***	0.125	0.159*	0.25***	0.087	0.137*	0.212	0.361**	0.223	0.421***	0.019	0.292***

Columns r2 and r3 represent correlations after controlling for sediment diversity or depth, respectively. In each analysis we held constant the measure of sediment diversity that explained the maximum variance in species diversity. The actual variable controlled for in each analysis is indicated by a dash. All relationships are linear except depth, which is parabolic. Sediment and water, Sediment, Silt, and Clay refer to the particle size diversity of those sediment fractions; Mean ϕ, and Sorting coefficient are the standard measures of mean and variance of particle size; per cent C, H, and N refer to the content of these elements in the organic fraction of the sediments. Sediment and water diversity was calculated using the per cent by weight of water in the sample as one of the entries in the Shannon-Wiener diversity index. Silt diversity was based on four ϕ fractions between 4ϕ and $<8\phi$; clay diversity was based on three ϕ fractions between 8ϕ and $>10\phi$. Mean ϕ and the sorting coefficient were not available for Mid boxcores. * $P<0.05$, ** $P<0.01$; *** $P<0.001$.

size[7,8]. Shallow-water deposit feeders selectively ingest particular size fractions of the sediments[9,10] and there are interspecific differences in particle size preference[11–13]. Partitioning of sediments with respect to size may be more likely in the deep sea if there is strong selection for macrophagy as a result of reduced food supply and digestive constraints imposed by feeding on deposits[14]; macrophagy would permit species to ingest selectively the more labile components of the sediments. If deposit feeders in the deep sea partition the sediments with respect to size, species diversity may in part be a function of sediment particle size diversity. Also, sediment particle size diversity may reflect habitat complexity because the organisms live on or within the sediments[15–21]. Here we show that species diversity is a significant positive function of sediment particle size diversity. The relationship seems to be scale-invariant, accounting for a similar proportion of the variance at inter-regional, regional and local scales. Bathymetric patterns of species diversity also appear to be largely attributable to changes in sediment characteristics with depth. These results suggest that sediment diversity has an important role in determining the number of species within a community and identify a direct environmental factor that potentially influences species diversity in the deep sea.

To test for a relationship between species diversity and sediment particle size diversity (referred to as sediment diversity) we collected quantitative benthic samples from bathyal depths (250–3,029m) in the western North Atlantic. We used 0.25m^2 boxcores from the Atlantic Continental Slope and Rise study[22,23] because the sediment characteristics and the faunal diversities were quantified from each boxcore and because these data represent the most extensive quantitative samples of deep-sea community structure. The samples were collected from three bathyal regions along the east coast of the United States. The north Atlantic, southeast of Massachusetts; the mid-Atlantic, off the coasts of New Jersey and Delaware; and the south Atlantic, east of North and South Carolina. These regions will hereafter be referred to as the North, Mid, and South, respectively. A total of 558 boxcores were analysed and contained 272,009 individuals distributed among 1,597 species.

Details of the methods used in collecting and analysing the boxcores have been described[22,23]. Fauna were sieved from the central nine subcores (0.09 m^2) of each boxcore using a 0.3-mm sieve. Macrofaunal diversity for each boxcore was calculated using Hurlbert's[24] expected number of species, normalized to 100 individuals, and incorporates all taxa. For each boxcore, particle size diversity of disaggregated sediments was calculated from the per cent dry weight of each ϕ size class (12 size classes between -1 and >10 ϕ) using the Shannon-Wiener diversity index. Because deposit feeders generally consume the smaller (silt) size fractions[10,25], sediment diversity was calculated for the silt fraction, clay fraction, and for all fractions with and without water. The sorting coefficient, the standard measure for variance in grain size, was also used as an environmental variable.

We explored the relationship between species diversity and ten environmental variables using standard linear and nonlinear least-squares methods. Species diversity was highly correlated with most of the environmental variables (r1 in Table 1). For each region and for all data combined, species diversity is most strongly correlated with sediment diversity (or one of the sediment fractions), which generally accounted for more than 40% of the variance. Figure 1*a* and *b* depicts the relationship between species diversity and either depth or silt diversity for the North. Species diversity is a nonlinear function of depth with a peak in diversity at intermediate depths and is a linear function of silt diversity. The parabolic relationship between species diversity and depth is typical of previous studies of bathymetric variation in deep-sea community structure[2,3].

We used partial regression techniques to better characterize the relationship between species diversity and the two most important environmental variables, silt diversity and depth. If silt diversity is controlled statistically, the depth-related patterns in species diversity no longer exist (Fig. 1*c*). In contrast, if depth is held constant, there remains a significant relationship between the residuals, although it becomes nonlinear (Fig. 1*d*). This asymmetry suggests that the depth-related patterns of species diversity reflect the effects of silt diversity and are a consequence of changes in sediment characteristics with depth.

The Mid, South and combined data show similar patterns but the details are more complicated (Table 1). For the Mid and combined data, both depth and species diversity remain significant when the alternate variable is controlled, but the significance levels are asymmetric. If sediment diversity is held constant (r2), depth is only marginally significant; if depth is held constant (r3), sediment diversity remains highly significant. In the south, species diversity is initially uncorrelated with depth. But if sediment diversity is statistically controlled, depth becomes important in accounting for the variance in the residuals. When depth is held constant, the relationship between species diversity and sediment diversity actually improves. Similar analyses using species richness with variation in density factored out as the dependent variable gave similar patterns.

These results demonstrate that much of the variability in species diversity, geographically and bathymetrically, seems to

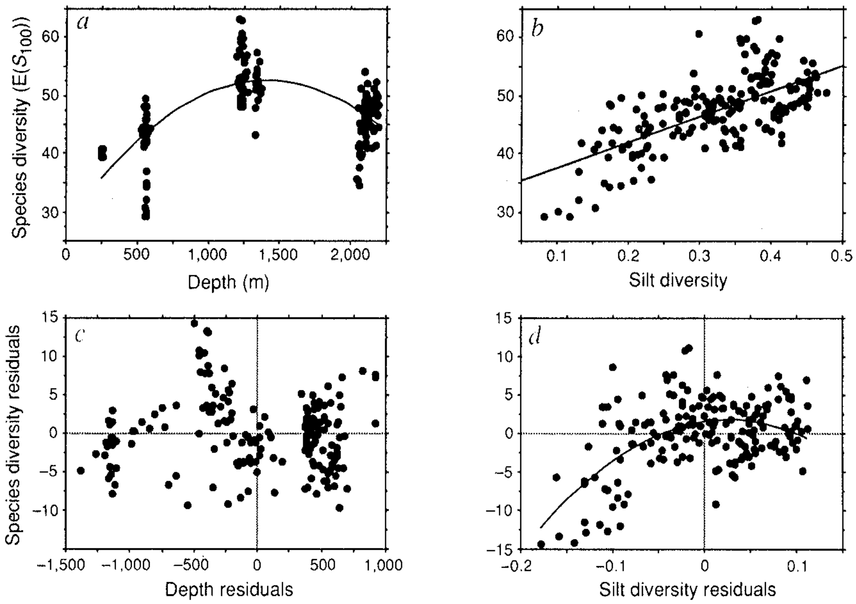

FIG. 1 The relationship between species diversity and *a*, depth or *b*, silt diversity for the North samples. Species diversity was normalized to 100 individuals. Silt diversity refers to the particle size diversity of the silt fraction of the sediments. The relationship between the residuals after the effects of silt diversity (*c*) or depth (*d*) are statistically removed. Regression lines were fitted to the data using typical least-squares procedures and are all highly significant ($P \leq 0.0001$). No line is shown in (*c*) because the relationship was not significant ($P = 0.67$). $E(S_{100})$ is the expected number of species in each sample when normalized to 100 individuals[24].

be related to changes in sediment characteristics. Moreover, this explanation of species diversity appears to be just as effective at inter-regional (combined analysis), regional (within North and South) and local (Mid samples with little depth variability) scales. Although the correlation is highly significant, sediment diversity is least successful in accounting for the variance in species diversity at the Mid site. This can probably be attributed to the fact that the Mid samples were also the most homogeneous with respect to sediment diversity and species diversity.

Species diversity in intertidal soft-sediment communities also seems to be strongly correlated with variability in particle and food diversity[25]. The similarity in the relationship between species diversity and sediment diversity in shallow- and deep-water communities suggests that this phenomenon may be a general feature of soft-sediment communities.

Regardless of the strength of a relationship or how universal it seems, correlations do not imply causality. Indeed, one could argue that highly diverse communities create more diverse sediment characteristics. For example, many of the particles have a biological origin, burrowing organisms may redistribute sediments of particular size classes, and biogenic structures create more variable hydrodynamic regimes that may induce the deposition of a greater range of particle sizes[26-28]. It is also possible that the correlation reflects more important proximal factors such as nutrient availability, hydrodynamics, microtopography or bioturbation.

The exact nature of the relationship between sediment diversity and species diversity and the mechanisms that underlie it can only be determined through direct experimentation. Experimental testing of this putative relationship should be straightforward, and in this sense alone offers advantages over previous plausible but untestable hypotheses. These results are sufficiently compelling to warrant a more detailed investigation of the role of sediment diversity in controlling the spatiotemporal variability in deep-sea species diversity.

The deep sea covers nearly two-thirds of the Earth's surface, yet the processes that generate and maintain species diversity in this vast and complex environment are poorly understood. Our work now identifies a direct environmental factor that is potentially responsible for generating spatiotemporal patterns of species diversity in the deep sea. Because similar findings have been documented in shallow water, the effects of sediment diversity on species diversity may be a ubiquitous feature of soft-sediment communities. □

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