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MORPHOLOGICAL DISPARITY AS A BIODIVERSITY METRIC IN LOWER BATHYAL AND ABYSSAL GASTROPOD ASSEMBLAGES

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Abstract.—Studies of deep-sea biodiversity focus almost exclusively on geographic patterns of α-diversity. Few include the morphological or ecological properties of species that indicate their actual roles in community assembly. Here, we explore morphological disparity of shell architecture in gastropods from lower bathyal and abyssal environments of the western North Atlantic as a new dimension of deep-sea biodiversity. The lower bathyal-abyssal transition parallels a gradient of decreasing species diversity with depth and distance from land. Morphological disparity measures how the variety of body plans in a taxon fills a morphospace. We examine disparity in shell form by constructing both empirical (eigenshape analysis) and theoretical (Schindel's modification of Raup's model) morphospaces. The two approaches provide very consistent results. The centroids of lower bathyal and abyssal morphospaces are statistically indistinguishable. The absolute volumes of lower bathyal morphospaces exceed those of the abyss; however, when the volumes are standardized to a common number of species they are not significantly different. The abyssal morphospaces are simply more sparsely occupied. In terms of the variety of basic shell types, abyssal species show the same disparity values as random subsets of the lower bathyal fauna. Abyssal species possess no evident evolutionary innovation. There are, however, conspicuous changes in the relative abundance of shell forms between the two assemblages. The lower bathyal fauna contains a fairly equable mix of species abundances, trophic modes, and shell types. The abyssal group is numerically dominated by species that are deposit feeders with compact unsculptured shells.

Key words.—Biodiversity, deep sea, gastropods, morphological disparity, shell form.

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The relationship between community assembly and the adaptive properties of constituent species is fundamental to ecology and evolution. It is central to such basic contemporary issues as whether communities are structured by biological interactions or represent loose aggregations maintained by a balance of dispersal and disturbance, the relative significance of local- and regional-scale processes, and how historical forces shape geographic variation in diversity (Ricklefs and Schluter 1993; Brown 1995; Bertness et al. 2001). Little is known about the connection between community structure and the lives of individual species in the deep sea. Most studies of deep-sea biodiversity at the community level focus on the simple number of coexisting species without regard to their natural history. Only a small number of studies attempt to relate taxonomic diversity to the potential adaptive properties of species such as dispersal ability (Stuart and Rex 1994), feeding types (Cosson-Sarradin et al. 1998), body size (Rex and Etter 1998), or morphological features (Thistle and Wilson 1987).

There is a growing interest in measures of diversity that incorporate biologically meaningful characteristics of species; for instance, resource dimensions (Alatalo and Alatalo 1977), taxonomic structure (Clarke and Warwick 2001), phylogenetic diversity (Faith 2002), trophic position (Cousins 1991), body size (Cousins 1991), and morphology (Roy and Foote 1997). These measures have the potential to reveal more about the specific causes of diversity than does the simple number of species and its general relationship to environmental gradients. In this paper, we examine morphological variation in gastropod shell form as an expression of biodiversity in the deep sea. Specifically, we explore the diversity of shell forms between lower bathyal and abyssal environments in the western North Atlantic. The transition between these two environments parallels both biological and physical gradients that could affect shell form.

Recently, paleontologists have introduced a way to examine diversity termed morphological disparity (Gould 1991; Foote 1992, 1995, 1996, 1997; Smith 1998). Morphological disparity is essentially the ''overall morphological variety within a taxon'' (Foote 1993, p. 404), or the ''range of design'' in body plans (Briggs et al. 1992, p. 1670). Disparity is assessed by how a group of organisms occupies a morphospace, which is the multidimensional space that encompasses a taxon's morphological variation. The power of morphological disparity lies in its ability to add a new dimension to understanding biodiversity—one based on a quantification of potential adaptive variation as opposed to merely enumerating taxa.

McGhee (1999) distinguishes two fundamental types of morphospace: those with axes that are measurement-dependent (empirical morphospaces), and those that are measurement-independent (theoretical morphospaces). In empirical morphospaces, axes are derived from multivariate statistical treatments of phenotypic measurements; therefore, the axes are defined a posteriori. Axes of theoretical morphospaces are defined a priori and are based on the variables of a geometric model of form. Both empirical and theoretical empirical morphospaces have limitations (Foote 1995; McGhee 1999). Empirical morphospaces are dimensionalized by the sample being analyzed. Changes in the number or kinds of forms represented and the descriptors used in the study can affect the morphospace, altering its dimensionality and the relative positions of individuals within the defined space.

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Since empirical morphospaces are completely controlled by the actual measured forms, they may provide little insight into how the theoretically possible range of form is realized by the species or individuals included in the analysis. However, empirical methods can capture complex morphology, including idiosyncratic features, with a very high degree of resolution. Theoretical morphospaces are mathematical constructs that include the full range of potential form, and are not subject to the limitations of form expressed in a particular sample, taxon, or fauna. This allows evolutionary questions to be posed about how the space is occupied. For example, why are some theoretically possible forms never expressed in nature, or why is only a subset of forms characteristic of a particular fauna? Theoretical morphospaces contain unambiguous axes that represent geometric parameters of form, rather than the multivariate statistical abstractions of empirical morphospaces. They seldom include irregularities in form. For example, allometry, shell ornamentation, and aperture shape, all biologically important features for many species, prove difficult to incorporate into theoretical models. Theoretical morphospaces typically provide only a basic picture of the possible variation in shell form.

Here we present an analysis of shell form in lower bathyal and abyssal assemblages of gastropods from the western North Atlantic by using a combination of empirical and theoretical morphospaces. Combination studies can provide additional insights that emerge from the differences or commonalities between theoretical and empirical treatments (Wagner 1995; Chapman et al. 1996; McGhee 1999). Similarly, using a variety of methods can help to identify biases inherent in any individual approach (Macleod 1999). Such studies have been highly successful in analyzing molluscan shell architecture (Williamson 1981; Saunders and Swan 1984; Swan and Saunders 1987; Saunders and Work 1996).

MATERIALS AND METHODS

Biogeography

We chose gastropods for this analysis because their life history is retained in shell form and their hard carbonate shells allow precise measurements that are unaffected by artifacts of collection and preservation, as often occurs in soft-bodied taxa. Shell structure reflects a broad range of natural-history features including feeding type, predator defense mechanisms, physiology, locomotion, and calcium carbonate conservation (Raup and Graus 1972; Graus 1974; Vermeij 1978, 1993). As with any phenotype, it is affected by both the genotype and the environment and represents a compromise between phylogenetic inertia, recent selection, and presumably nonselective events. Still, morphological disparity as a biodiversity metric potentially reflects the ecology of constituent species, and community organization, in ways that simple α-diversity cannot.

We analyzed shell form in gastropods from five epibenthic sled samples taken at 3310–3834 m on the lower continental rise, and five at 4680–4853 m (Fig. 1; Table 1) on the abyssal plain in the western North Atlantic south of New England. These were collected as part of the Woods Hole Oceanographic Institution's Benthic Sampling Program (Sanders 1977). All available stations from the lower bathyal were used in the analysis (five stations total). We randomly chose five abyssal stations of 18 that were available to help standardize the comparison. The total sample sizes for the two assemblages are similar, 611 and 705 respectively for the lower bathyal and abyss.

The geographic transition between the lower continental rise and the abyssal plain is a particularly interesting region in which to explore patterns and causes of diversity in deep-sea mollusks. It is accompanied by a steep decline in gastropod species diversity, both richness and evenness, and by a shift from a trophically complex assemblage to one dominated by deposit feeders in terms of relative abundance (Rex 1973, 1976). These changes have been attributed, in a general way, to a severe reduction in the rate of nutrient input, and consequently, total animal abundance (Rex 1981).

This study centers on gastropods, excluding Heterobranchia and Ptenoglossa, with helicoid coiling, by far the most abundant and diverse group of deep-sea gastropods (a total of 37 species and 1316 individuals in this study; Table 2). For the sake of consistency in basic shell form, we excluded opisthobranchs (nine species, 117 individuals; Table 2), which are not abundant at these depths and exhibit a fundamentally different type of coiling and shell morphology. We also eliminated ectoparasitic ptenoglossates (Families Eulimidae, Epitoniidae, and Aclididae; six species, 31 individuals; Table 2) because of their equivocal taxonomic affinity (Fretter and Graham 1962; Ponder and Lindberg 1997). The remaining dataset still represents a morphologically diverse assemblage including representatives of the Family Trochidae and Seguenziidae in the Vetigastropoda and Families Buccinidae, Cerithiopsidae, Muricidae, Olividae, Rissoidae, and Turridae in the Caenogastropoda.

Empirical Morphospace

We constructed an empirical morphospace by performing an eigenshape analysis on shell form using a representative digitized image from each species. One image per species was used because previous studies have shown that geographic variation within species is negligible at these depths, and because shell morphologies of individual species are generally quite distinct (Etter and Rex 1990; Rex and Etter 1990; Rex et al. 2002). Eigenshape analysis describes shape and differences among shapes using net angular changes of outlines (Lohmann 1983; Rohlf 1986; Lohmann and Schweitzer

TABLE 1. Bathyal and abyssal stations in the western North Atlantic used in this analysis of morphological disparity in deep-sea gastropods. See Figure 1 for a map of the stations.

Region	Station number	Depth (m)	Latitude (N)	Longitude (W)
Lower bathyal	340	3310	38°16.0′	70°21.6′
	95	3753	38°33.0′	68°32.0′
	77	3806	38°00.7′	69°16.0′
	126	3806	39°37.3′	66°45.5′
	85	3834	37°59.2′	69°26.2′
Abyssal	175	4680	36°36.0′	68°30.0′
	84	4749	36°24.4′	67°56.0′
	121	4800	35°50.0′	65°11.0′
	125	4825	37°25.0′	65°52.0′
	123	4853	37°29.0′	64°14.0′

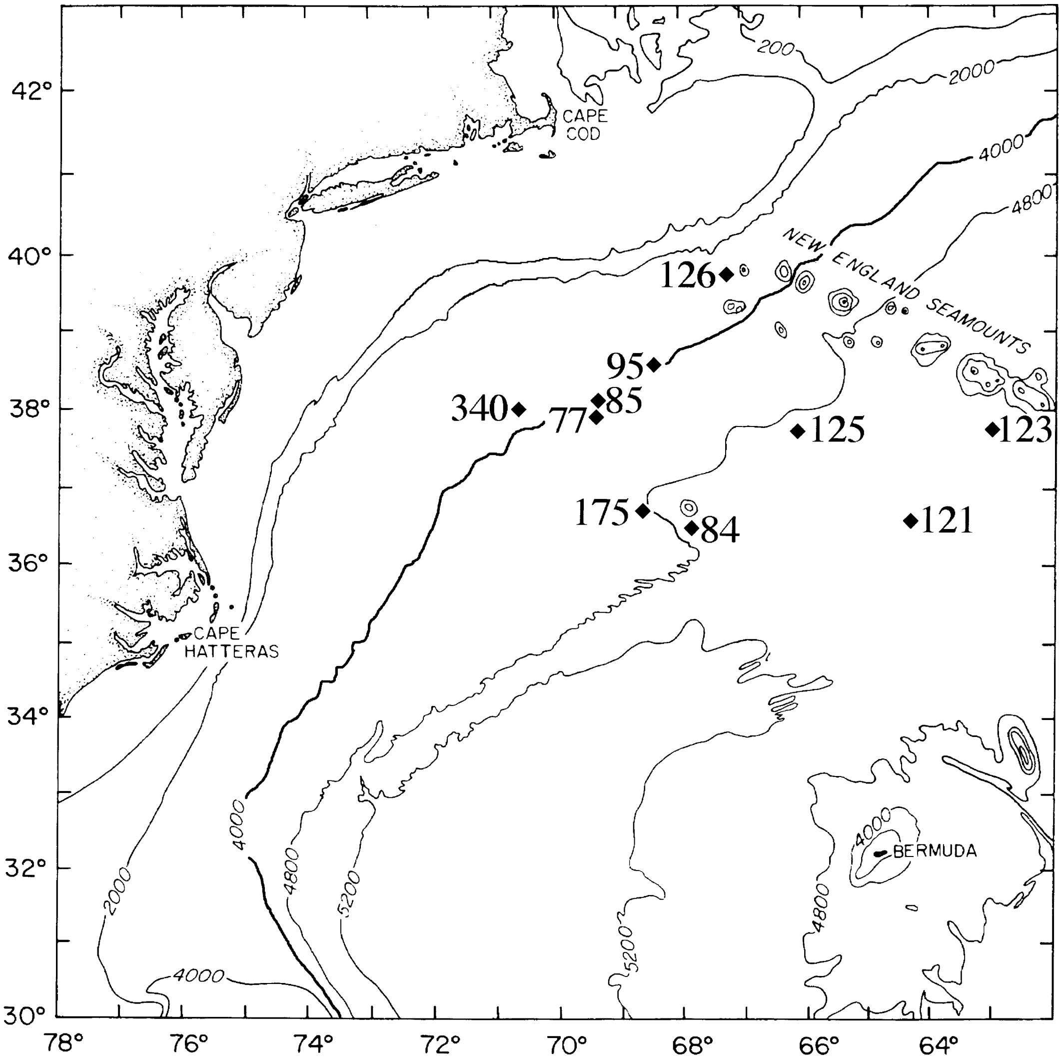

FIG. 1. Sampling stations used in this study on morphological disparity in lower bathyal and abyssal prosobranch assemblages in the western North Atlantic. The heavy depth contour corresponds to the 4000-m transition between the lower bathyal and abyssal zones. Station data are provided in Table 1.

1990). The goal of the procedure is to discern pattern within a collection of individuals whose shapes differ in complex and continuous ways. The first step in this procedure is to acquire outline data in the form of 100 x,y coordinate pairs spaced evenly around the outline, from individuals oriented in a standard position (Rex et al. 1988; Rex and Etter 1990). Shells were mounted on a clay disk so that the axis of coiling was parallel to the microscope stage in an aperture view (Fig. 2). Images were digitized into a Macintosh G4 and the program NIH Image (http://rsb.info.nih.gov/nih-image) was used to take measurements.

The x,y coordinates are then transformed into the $\phi(\lambda)$ function. This function is the net angular change in direction as a tangent to the outline is moved around the shape (such that $\phi(0) = 0$ and $\phi(\text{total}) = 2\pi$) in p equal-length steps (Fig. 2). Next, the $\phi(\lambda)$ function is transformed into $\phi(\lambda)^*$. This requires subtracting from the $\phi(\lambda)$ function of the outline, the $\phi(\lambda)$ function of a circle of the same circumference of points (0,0) to $(2\pi,\lambda)$. This new function $\phi(\lambda)^*$ is the exact description of how the shape differs from a circle, and it retains all the information necessary (except size) to reconstruct the original outline.

This representation is invariant to size, translation, and rotation of the object in the x,y plane, but is sensitive to location of the starting point and direction of tracing. Other advantages are that it does not require morphological land-

TABLE 2. Numbers of species and individuals retained and omitted in this analysis.

	Lower bathyal	Abyss	Total
Species in analysis	36	13	37
Individuals in analysis	611	705	1316
Species of opisthobranchs omitted	6	5	9
Individuals of opisthobranchs omitted	99	18	117
Species of ptenoglossates omitted	4	3	6
Individuals of ptenoglossates omitted	15	16	31

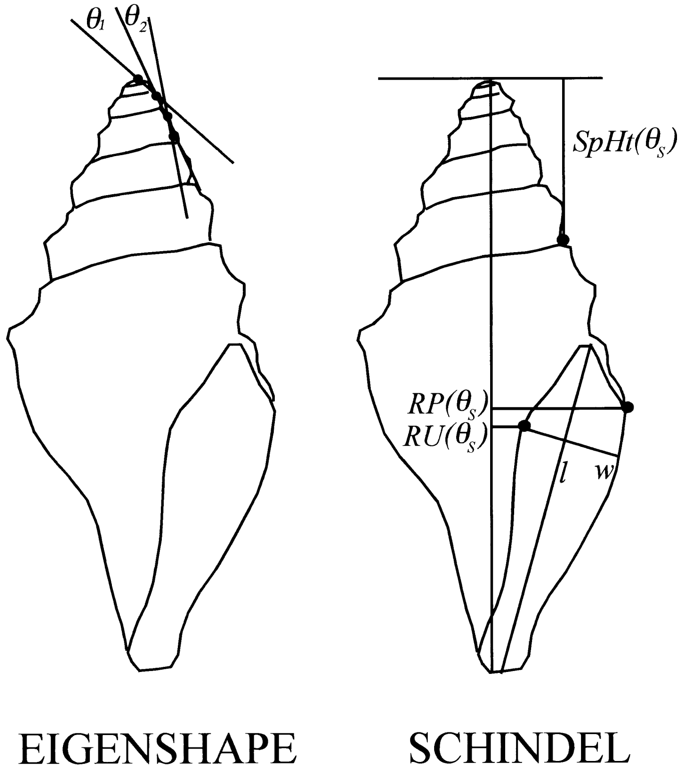

FIG. 2. Measurements taken for eigenshape analysis and Schindel's model. See text for explanations of measurements.

marks or a centroid (useful because shells lack bilateral symmetry), it can represent convoluted shapes, and it is easy to relate back to the original shape (it can be used to reconstruct actual shapes with high fidelity).

We conducted a principal components analysis (using species' $\phi(\lambda)^*$ functions as morphological descriptors) on the covariance/variance matrix obtained from eigenshape analysis. A principal components analysis was used so that the final morphospace would have orthogonal axes, and have reduced and more interpretable dimensions. Significant principal component axes, determined by the broken-stick method (Jackson 1993; Legendre and Legendre 1998), define the morphospace.

Theoretical Morphospace

To examine theoretical morphospaces, we used a variety of methods including those of Raup (1961, 1962, 1966, 1967), Schindel (1990), Harasewych (1982), and Cain (1977, 1978a,b, 1980). We also tried growth-based models (i.e., Ackerly 1989; Okamoto 1988a,b, 1993), but either the models provided no method for assessing parameters on real shells, or the range of shell forms studied here was not suitable for the measurement methodology. We have chosen to present Schindel's (1990) modification of Raup's (1961, 1962, 1966, 1967) classic model of gastropod coiling as our principal theoretical approach, but all theoretical models were in close agreement. Raup's model consists of four parameters: *W* measures the rate at which the generating curve expands, *T* is the rate at which the generating curve moves down the coiling axis, *S* is the shape of the growth frame (aperture), and *D* is the rate at which the generating curve moves away from the coiling axis.

Raup's original parameters of shell geometry were not algebraically independent. To correct this, Schindel (1990) developed a morphospace with a new variable *M* to represent translation of whorls down the axis of coiling, and redefined *W* (Fig. 2). *W*, the rate at which the whorl expands, is taken as the antilog of the regression slope between logRP (θ) and whorl number (θ). The antilog of the regression slope between logSpHt (θ) and whorl number (θ) gives a new variable *M*, the suture migration rate. *M* is inversely related to spire height. For example, Schindel (1990) showed that vetigastropods, which are typically more globular in shape, had on average higher *M* values compared to more turreted siphonate shells. Schindel also introduced another new variable *U*, the umbilical expansion rate that is conceptually similar to Raup's *D*. *U* is the antilog of the regression slope between whorl number θ, and logRU(θ). Schindel's variables have the added advantage of being more responsive to variation in form; that is, they display more variation than Raup's original parameters. Schindel's variables were measured on x-rays of shells for successive whorls using all whorls present. We constructed a theoretical morphospace by using Schindel's *W* and *M*, and Raup's *S*. *S* was measured (Fig. 2) as the aperture length (l) divided by the width (w). Neither Raup's *D* or Schindel's *U* were informative because few shells studied here are umbilicate.

Morphospace Analysis

We compared three basic features of bathyal and abyssal morphospaces, their centroids, volumes, and the dispersion of shells within the space. Centroids were compared by calculating the mean and 95% confidence limits for the species' scores on each significant principal component axis (empirical morphospace) or model parameter (theoretical morphospaces) for each sample. Dispersion was calculated as the mean and 95% confidence intervals for the nearest neighbor euclidean distance between species for each region. Because there is a lack of independence in the dataset (the same measurements were used for species with bathyal and abyssal representatives), a bootstrapping technique was implemented to test for a significant difference between samples. We illustrate shifts in the numerical representation of species between the lower bathyal and abyssal assemblages by indicating their relative abundances in the morphospaces.

We compared the morphospace volumes of bathyal and abyssal assemblages by using a rarefaction analysis of morphospace volumes (Foote 1992). The general analytical method of rarefaction is familiar to ecologists as a way to standardize species diversity to sample size by resampling the relative abundance distribution of species at successively smaller numbers of individuals (Sanders 1968; Hurlbert 1971). Here, it is used to standardize morphospace volume to the number of species. Volume is calculated by summing the ranges occupied on each significant principal component (or theoretical variable) in the morphospace. Rarefaction curves representing morphospace volumes were estimated from averages of 1000 random samples of the morphospace, from the actual number of species collected in each assemblage interpolated down to two species. This shows, essentially, how the morphospace accumulates (fills out) as species are added to the lower bathyal and abyssal faunas. Confidence limits were erected around the rarefaction curves to determine whether the volumes of lower bathyal and abyssal morphospaces differed significantly. Rarefaction permits a comparison of morphospace volumes at a common number of species. We illustrate how shells occupy the morphospaces by two- and three-dimensional perspective diagrams in which the sizes of points representing the shells are scaled to their relative abundances in the two regions.

The rarefaction of the morphospace volume provides the basis for a null model to determine whether the abyssal fauna is a random morphological subset of the lower bathyal fauna. In this case, we compare the two morphospaces at a faunal size of 13 species—the total number of species in the abyssal assemblage. This method tests whether the abyssal morphospace is consistent with a random draw of the same number of species from the lower bathyal morphospace, at least in terms of centroids, volumes, and density. We consider these three characteristics to be the most essential factors of the morphospace. It is possible that subtle differences in how the morphospace is occupied exist between the random draws and the lower bathyal. In others words, are different regions of the morphospace sampled evenly? However, it is unclear how to test and interpret spatial dispersion within a multidimensional morphospace. The extension of a two-dimensional analysis, such as spatial structure functions, trend surface analysis, connection networks, partial canonical test, or a partial Mantel test (Legendre and Legendre 1998) to a multidimensional morphospace may provide a possible analytical method to address questions about dispersion.

RESULTS

Empirical Models

The principal components analysis, based on the eigenshape variables, yielded five significant axes, which together account for 72.38% of the variance (axis I 43.41%, axis II 10.06%, axis III 8.26%, axis IV 5.62%, and axis V 5.02%). Figure 3 shows shells plotted against the first two principal components for bathyal and abyssal samples. Various other combinations of axes were generally uninformative (not shown), probably because they account for so little variance. Axis I, explaining most of the significant variance (43.41%), essentially represents a gradient in form from turreted-siphonate shells like *Benthomangelia antonia* (Fig. 3, left, negative values), through simple compact ventricose shells like *Benthonella tenella* (Fig. 3, middle), to globular trochiform shells like *Xyloskenea naticiformis* (Fig. 3, right, positive values). This gradient in form is one of decreased translation rate, increased whorl overlap, loss of sculpture and loss of the siphonal canal. In other words, a transition from sculptured high-spired shells to globular unadorned shells. The shift on axis I from siphonate (Fig. 3, negative values on the x-axis) to nonsiphonate morphotypes (Fig. 3, positive values), corresponds to a shift from predation to deposit feeding (Rex 1976). When the relative abundances of the different shell forms in the lower bathyal and abyssal zones are indicated an interesting pattern emerges (Fig. 3). The most abundant predator at lower bathyal depths, *B. antonia*, drops out completely in the abyss. The deposit feeders *B. tenella* and *X. naticiformis*, which are present in moderate abundance at lower bathyal depths, are the most numerically dominant species in the abyss. Significantly more individuals in the abyss have higher scores on principal component 1, indicating a predominance of compact shells (median test, $\chi^2 = 239.55$, $P < 0.0001$).

The centroids, or average scores, of the two regions show no significantly detectable shift in position in the morphospace (Fig. 4, $P > 0.50$). The abyss and lower bathyal do not appear to occupy distinct regions of the morphospace. However, nearest neighbor distances are significantly lower (bootstrap estimate, $P < 0.0001$) in the bathyal region, indicating that the morphospace of the abyss is more sparsely occupied than that of the lower bathyal.

A comparison of morphospace volume is shown in Figure 5. The total abyssal morphospace (as indicated by the endpoints of the rarefaction curves) is smaller than the total bathyal morphospace. However, the rarefaction curves are similar over much of their shared range, and their confidence limits overlap extensively. This indicates that differences in the volumes between the two habitats are related simply to the difference in the number of species. If 13 species are randomly sampled out of the lower bathyal region, the volume is statistically indistinguishable from the volume of the actual 13 abyssal species ($P > 0.60$). When a similar null model was constructed for centroid and distance statistics, the randomly drawn assemblages from the lower bathyal have statistically indistinguishable values from the actual abyssal sample ($P > 0.30$ for both analyses).

An extended analysis was conducted that included the opistobranchs, ectoparasitic ptenoglossates, and all abyssal stations. Despite the lack of taxonomic control and unbalanced sampling design (five bathyal and 18 abyssal stations), the extended analysis produced a very similar outcome. This analysis helps to address Macleod's (1999) concern that averaging distance in an empirical morphospace through unoccupied and potentially biologically impossible regions can be unrealistic. In other words, it would not be meaningful to measure distance between existing shapes directly through intervening morphospace from which organisms are biologically excluded for some reason. In the extended analysis for deep-sea gastropods, relative distances and positions among species change very little. Unoccupied regions in the morphospace are reasonably filled in when species are added, suggesting that empty space in the original analysis is biologically feasible and realized. We obtained similar results with the theoretical models discussed below. ''Forbidden'' spaces in the theoretical space evidently lie beyond the occupied space.

Theoretical Model

The lower bathyal and abyssal morphospaces in the context of Schindel's model are shown in Figure 6 as three-dimensional perspective diagrams, the axes of which are M, W, and S. Again, *Benthomangelia antonia*, *Benthonella tenella*, and *Xyloskenea naticiformis* are shown in the diagrams to illustrate the relative positions of turreted-siphonate, simple ven-

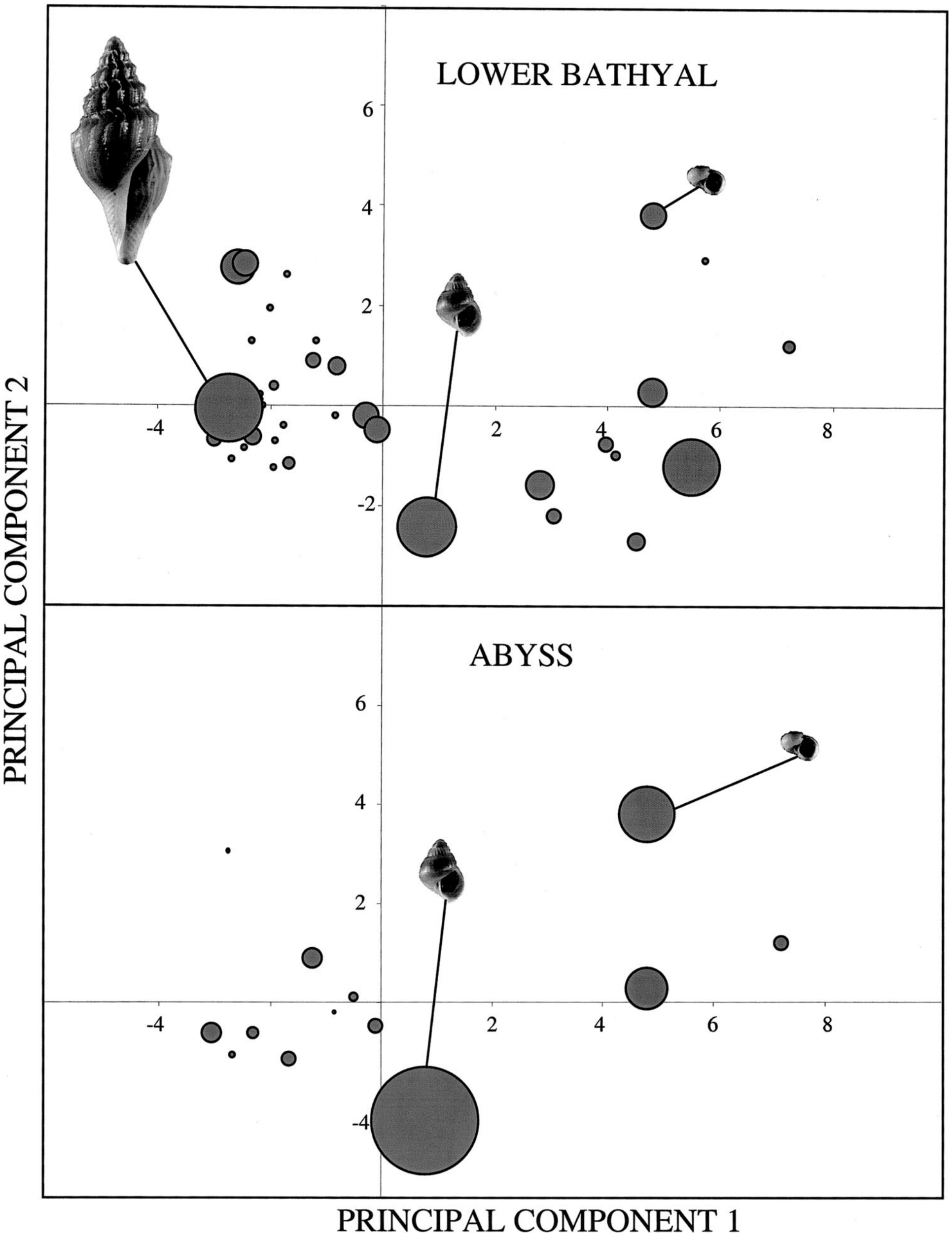

FIG. 3. Eigenshape analysis of shell architecture in bathyal and abyssal assemblages of prosobranch gastropods in the western North Atlantic on the first two principal component axes. Species' relative abundances in the two zones are indicated by the relative size of the circles. Actual shells are shown for *Benthomangelia antonia* (left), *Benthonella tenella* (middle), and *Xyloskenea naticiformis* (right) to emphasize the basic changes in shell architecture along the first principal component. The abyssal assemblage is dominated by deposit feeders with more compact shells (positive values of the first principal component).

tricose, and trochiform shells respectively. Results are very similar to those of the eigenshape analysis. In terms of the basic shell forms represented, the normalized dimensions (rarified volumes) and positions (centroids) of the lower bathyal and abyssal morphospaces do not differ statistically (Fig. 4). The nearest neighbor Euclidean distances are again significantly lower in the bathyal region ($P < 0.001$) indicating that the abyssal morphospace is less tightly packed than that of the lower bathyal—as is readily apparent in Figure 6. It appears that the abyssal species are a random morphological subset of the lower bathyal morphospace.

Again, when the actual relative abundances of species are added to the picture, important differences in predominant shell architecture between the two assemblages become evident (Fig. 6). Species with low S values (elongate apertures with siphons) become uncommon in the abyss. Abundant abyssal forms also tend to have higher rates of whorl expansion (W) and higher suture migration rates (M). These

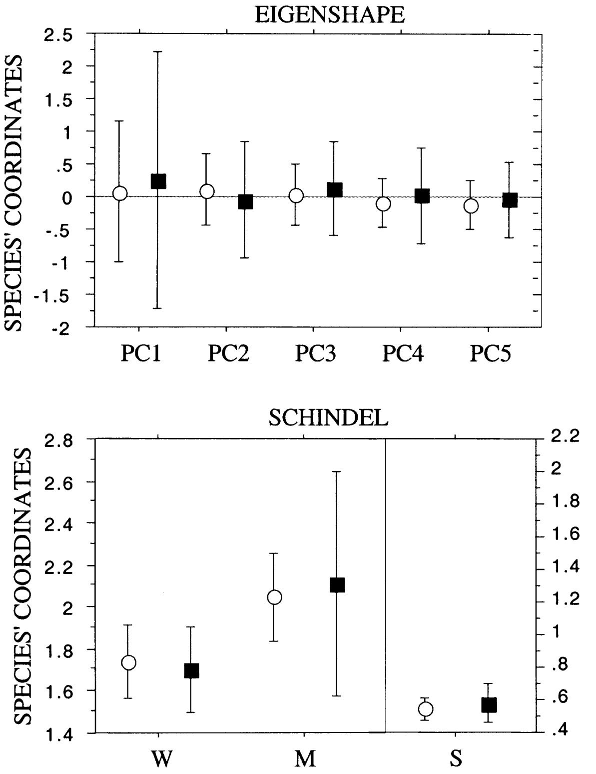

FIG. 4. Means and confidence limits (95%) of bathyal (open circles) and abyssal (closed squares) species' coordinates for all five significant principal components in the eigenshape analysis (see Fig. 3), and for the variables of shell geometry (*W*, *M*, and *S*) in Schindel's model (see Fig. 6). The centroids of abyssal and bathyal morphospaces do not differ significantly for any of the five analyses.

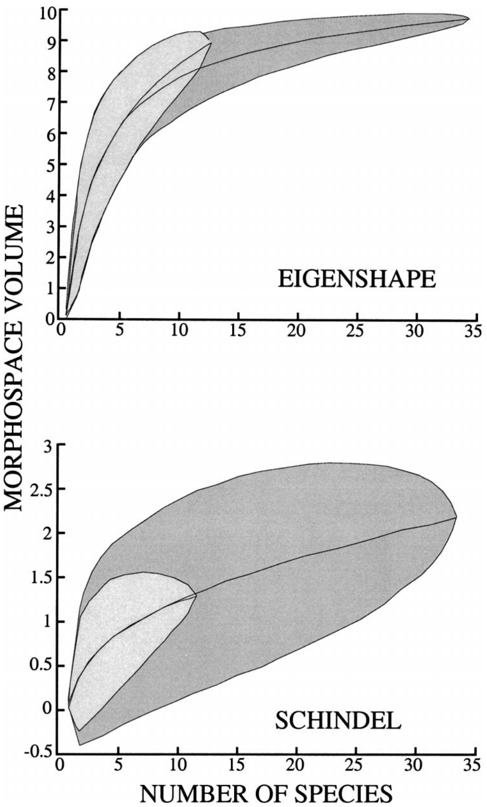

FIG. 5. Rarefactions of morphological volume for abyssal and bathyal gastropod assemblages for the eigenshape analysis and Schindel's morphospaces. These plots show how the morphospaces accumulate (fill out) as the number of species increases. Confidence limits (95%) for the two morphospaces overlap broadly indicating that the normalized volumes of the bathyal and abyssal morphospaces are not significantly different. Morphological volume represents the combined ranges of shape variables on all axes for a given morphospace.

values of W and M represent shells with high whorl overlap resulting in globular form. Median tests show that more abyssal individuals have higher values of S ($\chi^2 = 226.59$, $P < 0.0001$), W ($\chi^2 = 268.85$, $P < 0.0001$), and M ($\chi^2 = 227.26$, $P < 0.0001$).

DISCUSSION

The abyssal gastropod fauna of the western North Atlantic is largely an attenuation of the lower bathyal fauna. Species diversity decreases in the abyss in terms of both number of species and lower equability of the relative abundance distribution. For example, in this study, 36 species were collected in the lower bathyal and only 13 species in the abyss from five epibenthic samples and a comparable number of individuals in each environment (Table 2). Species diversity indices (Shannon-Wiener information function, Hurlbert's normalized expected number of species) and species evenness (Pielou's J) all decrease in the abyss (Rex 1973, 1976, 1981). This decline has long been attributed, in a general way, to the decrease in nutrient input to the abyss (Rex 1973).

The patterns observed in our analysis of morphological disparity convey more than just a simple decrease in α-diversity associated with low food availability. Results from empirical and theoretical approaches are very similar. In terms of the range of basic shell types represented, the lower bathyal and abyssal morphospaces are remarkably alike. Their centroids are statistically indistinguishable, indicating no alteration in the spatial concentration of shell types. When standardized morphospace volumes are compared in the two faunas, no significant differences emerge. The abyssal morphospace is simply more sparsely occupied because of lower diversity. Basic shell forms found in the lower bathyal region are not excluded from the abyss. The range of shell forms present in the abyss is consistent with random draws of lower bathyal shells. What is different is that species with simple ventricose and trochiform shells, which are more compact like *B. tenella* and *X. naticiformis*, become much more relatively abundant in the abyss at the expense of more highly sculptured turreted forms. Thus, differences in shell form between lower bathyal and abyssal regions are manifested more at the level of changes in population size within species, than strong shifts in species makeup. Put another way, the diversity of shell morphology does not decrease from the lower bathyal to the abyss in terms of the number of forms present. However, there is a dramatic decrease in diversity in terms of the equability of forms represented.

What environmental factors might favor relatively larger populations of species with simple globular shells in the abyss? In coastal environments, a great many factors includ-

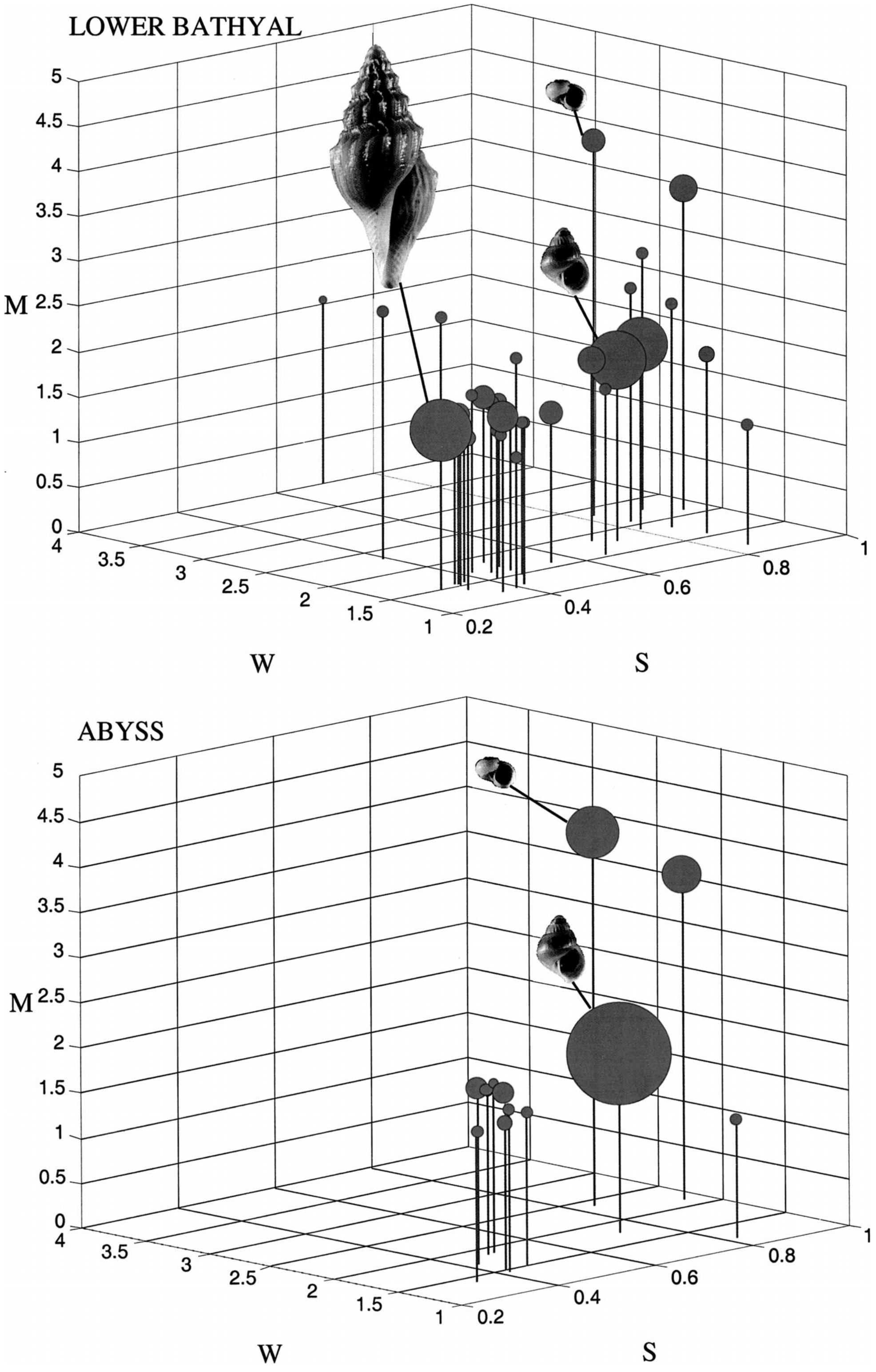

FIG. 6. Three-dimensional plots of bathyal and abyssal assemblages with species plotted against three of Schindel's parameters of shell geometry *M*, *W*, and *S*. Species' relative abundances in the two zones are indicated by the sizes of the circles. The abyssal assemblage is dominated by deposit feeders with more compact shells (higher values of *M*, *W*, and *S*).

ing biological interactions, locomotion, $CaCO_3$ conservation, and physical forces can affect molluscan shell form (Vermeij 1978, 1993). We lack specific knowledge about the energetic costs and benefits afforded by different shell types, and the trade-offs between shell design and other functional requirements in deep-sea snails. However, several lines of evidence suggest that the numerical dominance of more globular shells at abyssal depths may be related, directly or indirectly, to severe energy depletion at great depths.

Raup's basic model makes specific predictions about shell morphologies that are economical to construct and maintain (Raup and Graus 1972). Efficient shells have lower translation rates (*T*), higher rates of whorl expansion (*W*), and circular growth frames (*S*). In Schindel's modification of Raup's model, which we use here as a theoretical morphospace (Fig. 6), this corresponds to higher values of *M*, *W* and *S*. These shifts in geometry conspire to make shells more compact. They optimize the amount of living space contained within the shell—the maximum living space afforded by the least amount of shell. The resulting high whorl overlap also means that shell material can be conserved by more resorption of interior partitions between successive whorls. The lack of ornate sculpture in *Benthonella tenella* and *Xyloskenea naticiformis* also reduces the cost of calcification (Graus 1974). By contrast, high-spired shells with low whorl overlap, pronounced sculpture, and elongated apertures with siphonal canals are more costly to construct and maintain. The shift from the prevalence of species with elongate sculptured shells to those with more globular featureless shells is precisely what we observe across the bathyal-abyssal transition.

The problem of building and maintaining turreted sculptured shells in deep-sea gastropods may be exacerbated by $CaCO_3$ dissolution. The solubility of $CaCO_3$ increases with increased pressure and decreased temperature (Morse and Mackenzie 1990). In coastal environments, where $CaCO_3$ availability is largely a function of temperature, Graus (1974) demonstrated a latitudinal gradient of gastropod shell morphology with more efficient forms predominating at higher, cooler latitudes where the solubility of $CaCO_3$ is higher. In the deep sea, $CaCO_3$ conservation is likely to be more costly in general because of both extremely low temperatures and tremendous pressures.

The accumulation of $CaCO_3$ in deep-sea sediments represents an equilibrium between the rate of dissolution and the sedimentation rate of biogenic carbonate from surface waters. Dissolution of sinking carbonate begins at several hundred meters and increases only gradually to the lysocline, a zone rapid dissolution (Berger 1968). Below the lysocline the calcium carbonate compensation depth (CCD) is reached where the rate of carbonate flux equals the rate of dissolution. Sediments below the CCD are severely depleted of carbonate. Also, the principal mineral forms of calcium carbonate in marine organisms, calcite and aragonite, have different solubilities in seawater. Molluscan shells of benthic species typically have both aragonite and calcite (Lutz et al. 1994; Kennish et al. 1998). In the western North Atlantic at the latitudes of our study (Fig. 1), the lysocline of calcite is theoretically predicted to occur at roughly 4600–5000 m, and the compensation depth at around 5500 m (Morse and Mackenzie 1990). Since aragonite is more soluble, its lysocline and compensation depth are shallower.

However, carbonate dissolution is not a simple monotonic function of depth. The lysocline and CCD vary geographically and temporally depending on the complex interactions of overhead production, current patterns, and water chemistry (Morse and Mackenzie 1990; Broecker and Clark 2001). Depth transects of $CaCO_3$ content in sediments in the western North Atlantic show that the percentage of carbonate increases with depth and remains high at abyssal depths (Balsam 1982). Moveover, dissolution rates are actually higher and $CaCO_3$ content of sediments correspondingly lower between 3000 and 4400 m, than below 4400 m. This surprising pattern appears to be caused by the existence of less corrosive near-bottom currents at abyssal depths in this region of the North American Basin. Bathyal sites (3310–3834 m, Table 1) in our study should experience more dissolution than abyssal sites (4680–4853 m). Thus, the occurrence of more individuals with compact shells in the abyss would not seem to be attributable to calcium carbonate conservation as a response to lower carbonate availability. In the western North Atlantic, it seems more likely that, if the shift to more efficient shell forms is adaptive, then it is selected for by the overall decrease in energy for shell construction and maintenance.

Another possible explanation for the shift in relative abundance of shell form is that it is linked to feeding type. The two most abundant species in abyssal samples, *Benthonella tenella* and *Xyloskenea naticiformis*, are deposit feeders. Deposit feeders make up 90% of the individuals in the combined abyssal samples, in contrast to the nearly one-to-one ratio of deposit feeders and predators in the combined lower bathyal samples. In a system with extremely low nutrient input, food chain length should shorten (Post 2002). Deposit feeding may predominate because there is simply not enough energy for upper consumer levels to develop and diversify. Elsewhere, we propose that populations of gastropods in the abyss, which are very sparsely distributed, may be maintained largely by dispersal from the adjacent continental margin. *Benthonella tenella* and *X. naticiformis* belong to the families Rissoidae and Trochidae respectively. These two families are the most common deposit-feeding taxa among deep-sea caenogastropods. Shells of *B. tenella* and *X. naticiformis* are quite characteristic of deep-sea rissoids and trochids. Neighboring deposit-feeding species on the continental margin that are available to colonize the abyssal plain already possess compact shells as a taxon-specific trait that may be of no particular adaptive relevance to life in the abyss. In other words, they may be successful in the abyss principally because they are deposit feeders.

Although it is unclear whether the increase in abundance of species with compact shells represents an adaptation to abyssal conditions or is a nonadaptive feature linked to deposit feeding, both potential explanations ultimately relate to extremely low energy availability at abyssal depths. The relative importance of adaptive and nonadaptive aspects might be determined by conducting a comparative analysis of a single deep-sea taxon in different nutrient and dissolution regimes. It is important to point out that numerous other environmental causes of shell form may be implicated (Vermeij 1978, 1993), but are difficult to detect given our present understanding of life in this remote and only recently explored habitat. We also stress that although low energy may account for some conspicuous changes in the representation of feeding types and shell architectures, it does not explain the distribution of all species across the lower bathyal-abyssal transition, as evinced by the presence of rare species with turreted shells in the abyss. Another notable exception is *Eccliseogyra nitida,* one of the ptenoglossate species excluded from the present analyses, as explained earlier. *Eccliseogyra nitida* has an open-coiled shell (Rex and Boss 1976) in which successive whorls are not in contact. This is one of the least energetically efficient shell forms; yet *E. nitida* has both bathyal and abyssal populations in the western North Atlantic (Rex and Boss 1976). It is uncommon in both environments, particularly so in the abyss.

Our observation of no evolutionary innovation of shell form in the abyssal fauna tends to support, in a general way, the depth-differentiation model of evolution in the deep sea proposed by Etter and Rex (1990). Species in the bathyal zone show strong phenotypic and genetic depth clines (Etter and Rex 1990; Rex and Etter 1998; Chase et al. 1998; Quattro et al. 2001). The continental margin of the western North Atlantic appears to be a site of active population differentiation and speciation associated with steep selection gradients and topographic complexity. The abyssal plain seems less conducive to population divergence and offers less ecological opportunity for species coexistence.

Our study indicates that morphological disparity, as a new dimension of deep-sea biodiversity, can provide a richer understanding of biogeographic patterns and their causes. Theoretical (Fig. 6) and empirical (Fig. 3) morphospaces independently show the same trend. In this case, the results of the theoretical approach are more easily interpreted because the model predicts specifically how the morphospace should change as a response to lower energy availability. The empirical morphospace provides a consistent outcome based on a highly accurate and more comprehensive description of form. Adding relative abundance information to the analysis can improve resolution beyond the basic dimensions of a morphospace and how species occupy it. Although used largely so far as an analytical method to study the temporal evolutionary development of taxa in the fossil record, morphological disparity may also have potential to help explain spatial variation in contemporary communities.

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