

## BATHYMETRIC PATTERNS OF MORPHOLOGICAL DISPARITY IN DEEP-SEA GASTROPODS FROM THE WESTERN NORTH ATLANTIC BASIN

CRAIG R. McCLAIN

*Department of Biology, University of New Mexico, Albuquerque, New Mexico 87131*

*E-mail: mcclainc@unm.edu*

**Abstract.**—Understanding patterns of species richness requires knowledge of the individual roles species play in community structure. Here, I use gastropod shells as a source of information about both their ecological and their evolutionary functions in generating bathymetric gradients of diversity. Specifically, morphological disparity of shell architecture in deep-sea gastropods is evaluated over a depth gradient in the western North Atlantic by constructing an empirical morphospace based on an eigenshape analysis. Morphological disparity is quantified by calculating the centroid, total range, and dispersion of the morphospace at each station along the depth gradient. The results indicate that local faunas are drawn from a regional pool with the same variance but that average dissimilarity in forms reflects the number of species in the sample. The range of the morphospace at local scales is also less than at regional scales, resulting from the variability of the morphospace centroid over depth. Although the position of the morphospace changes with depth, morphological disparity remains unaffected. Despite the lack of bathymetric patterns in variance, patterns in nearest neighbor distance persist. The findings suggest the importance of interacting ecological and evolutionary processes at varying spatiotemporal scales for both morphological disparity and species richness.

**Key words.**—Biodiversity, deep sea, diversity gradients, gastropods, morphological disparity.

Received November 30, 2004. Accepted April 26, 2005.

The exact mechanisms that lead to variation in diversity over spatial gradients continue to challenge ecologists. Many hypotheses about how these patterns are generated over specific environmental variables (e.g., temperature and energy) and over spatial correlates (i.e., altitude, depth, and latitude) are still heavily debated. These patterns may reflect not only the capacity of the environment to support species' coexistence but also the origins and diversification of clades (Ricklefs 2004). Much of the research into biodiversity over environmental gradients has concentrated on changes in species richness and evenness. However, discerning how the environment regulates species diversity requires an understanding of the variation in phenotypic properties of species in both ecological and evolutionary terms. For example, significant features of the deep-sea benthos include both an extreme wealth of species (Grassle 1989) and predictable patterns of species diversity over depth and latitude (Rex 1973; Rex et al. 1993). The exceptionally high and striking patterns in diversity of deep-sea communities may depend on an assortment of factors that interact on a variety of spatial and temporal scales (Levin et al. 2001). As for other systems, only a few studies have focused on the ecological or morphological characteristics of species that might generate these patterns (dispersal ability: Stuart and Rex 1994; body size: McClain 2004; feeding types: Cosson-Sarradin et al. 1998; morphological features: Thistle and Wilson 1987).

Morphological disparity represents a relatively new method used to explore biodiversity in terms other than standard species diversity estimates (Roy and Foote 1997). The expansion of this and other biodiversity metrics in part reflects increased efforts to conserve not only species richness "hot spots" but also genetic, morphological, and ecological variability in biological communities (Kareiva and Marvier 2003). Numerous measures of diversity have been developed that incorporate potential adaptive characteristics of community constituents including: resource dimensions (Alatalo and Alatalo 1977), phylogenetic diversity (Clarke and Warwick

2001; Faith 2002), trophic position (Cousins 1991), body size (Cousins 1991), and morphology (Roy and Foote 1997). The development of morphological disparity as a biodiversity metric can be traced to paleontology (reviewed in Foote 1995), although renewed interest in this metric arose out of the dialogue that developed to describe the wide range of morphological forms seen during the Cambrian Explosion. Morphological disparity has since solidified as a quantifiable attribute of biological communities, a hyperdimensional volume that encompasses the variety of forms in which a researcher is interested. Changes in the morphospace center, volume, and dispersion within the volume can be assessed across sites or along a gradient (McClain et al. 2004).

Morphological disparity has been an essential tool in understanding macroevolutionary patterns through the fossil record (Foote 1997). For crinoids (Foote 1994, 1995), arthropods (Foote and Gould 1992; McShea 1993; Wills et al. 1994), ammonoids (Swan and Saunders 1987; Saunders and Swan 1984), and gastropods (Wagner 1995), disparity analyses have indicated that morphological extremes are reached early in a clade's history despite continued increases in species richness over time. Analyses of this type have also been valuable in understanding the effects of extinction events on biological communities. After the end-Permian and end-Cretaceous mass extinctions, articulate brachiopods display a reduction in diversity related to a decrease in disparity toward an advantageous modal form (McGhee 1995). In addition, morphological disparity studies have shown a filling of previously occupied portions of the morphospace by new taxa after extinction events (Ward 1980; Roy 1996).

The value of exploring morphological disparity over spatial gradients has only recently been fully realized. A variety of contemporary assemblages have been examined including old world cuttlefish (Neige 2003), Indo-Pacific strombid gastropods (Roy et al. 2001), and western North Atlantic deep-sea gastropods (McClain et al. 2004). A surfacing idea from these analyses, reaffirming paleobiological findings, predicts

that diversity and disparity relationships are nonlinear and may lack any relationship at all. These metrics are independent and the differences between the two are potentially useful for a richer understanding of the mechanisms that pattern biodiversity. For example, McClain et al. (2004) found in their analysis of deep-sea gastropod communities that both species richness and evenness may largely be dictated by how environmental constraints such as calcium carbonate dissolution rates affect shell form.

The aim of this study is to explore the ecological and evolutionary processes that underlie depth gradients in species diversity in the deep sea. Specifically, I characterize the morphospace of deep-sea gastropods and explore which attributes both define and influence this morphospace over depth. I also examine the correspondence between morphological disparity and species diversity to determine whether it can be defined by a characteristic relationship.

#### MATERIALS AND METHODS

I analyzed the shell form of species in Vetigastropoda and Caenogastropoda from epibenthic sled samples taken from 196 m to 5042 m in the western North Atlantic. The samples are from the Gayhead-Bermuda Transect (GBT) and were collected as part of the Woods Hole Oceanographic Institution's Benthic Sampling Program (Sanders 1977). Ptenoglossate species were excluded because of their equivocal taxonomic affinity (Fretter and Graham 1962; Ponder and Lindberg 1997) and because their ectoparasitic lifestyle is likely subject to a different set of constraints on the diversity of shell forms than the other groups in the analysis. The remaining dataset represents 76 species from eight families with a correspondingly high diversity in shell variety.

Two types of morphospace exist: those with axes that are measurement dependent (empirical morphospaces), and those that are measurement independent (theoretical morphospaces). In empirical morphospaces, axes are from a multivariate statistical analysis of morphological measurements; theoretical morphospaces are based on the variables of a geometric model of form (McGhee 1999). It should be noted that both methods encompass a mathematical description of form and have limitations (discussed in McClain et al. 2004), but differ in whether the axes are defined a priori or a posteriori. An empirical morphospace was chosen due to the lack of sensitivity of theoretical models to minor changes in shell shape among species (discussed in McClain et al. 2004). However, empirical (eigenshape analysis) and theoretical methods (Raup 1961; Schindel 1990; Harasewych 1982; Cain 1977) yield similar results for gastropods (McClain et al. 2004).

Shell form was analyzed using an eigenshape analysis on a representative digitized image from each species (Lohmann 1983; Rohlf 1986; Lohmann and Schweitzer 1990). In eigenshape analysis, outlines are represented by a series of tangential angles around the perimeter. This method assumes that individual outlines are homologous without assuming there are homologous points on the outlines. One hundred evenly spaced x,y coordinate pairs are taken from the shell outline. These coordinates are transformed into the  $\phi(\lambda)$  function, which represents the net angular change as a tangent line to the outline is moved around the shape. A new function

is obtained by subtracting from the  $\phi(\lambda)$  function the  $\phi(\lambda)$  function of a circle with the same circumference. This new function,  $\phi(\lambda)^*$  describes how the original outline differs from a circle. For a more detailed discussion of eigenshape analysis and its use with gastropods see McClain et al. (2004). A principal components analysis was conducted on the covariance/variance matrix from the species'  $\phi(\lambda)^*$  variables. For the morphological disparity analysis, I used only the significant axes as determined by the broken-stick method (Jackson 1993; Legendre and Legendre 1998).

I characterized the change in morphological diversity over depth by quantifying the centroid, total range, and dispersion of the morphospace of each station. Total range was taken as the sum of ranges of the significant principal component axes. The sum of ranges was used as opposed to the hypervolume (multiplied ranges) because it allows each axis to contribute to the total range in proportion to the amount of variance it explains (Wills 2001). Morphospace volume, taken as range, is known to be strongly influenced by the number of species in the sample (Foote 1992). To test the importance of this effect, I compared the total range of the empirical stations to the total range for a random sample taken from the combined stations. A random sample consisted of  $m$  species from the regional pool. For each  $m$ , 1000 samples were taken such that a mean and 95% confidence intervals could be calculated and compared to the empirical estimates. The change in the center of the morphospace over depth was quantified by taking the mean principal component score for each station for each significant axis.

I also assessed the dispersion of species within the morphospace total range using the methods outlined in Hertel and Lehman (1998). The Euclidean distance was calculated between all species in the principal component space for each station. Randomized hypothetical species are constructed by randomly drawing scores from a uniform distribution constrained by the empirical range for each principal component axis. From this hypothetical sample the mean first, second, third, and so on nearest-neighbor distances (NND) were obtained. A mean distribution and 95% confidence intervals were obtained from 5000 runs and compared to the empirical distribution. If the empirical NND distribution was significantly less than the randomized distribution, the empirical morphospace was considered underdispersed or clumped; if significantly higher, the morphospace was considered overdispersed; and if no difference exists, then species are considered randomly dispersed within the morphospace. The resulting distributions from the Monte Carlo simulations and empirical data are approximately parallel. The mean difference between these two distributions can then be used to estimate spatial dispersion. Positive values indicate overdispersion and negative values indicate underdispersion.

#### RESULTS

The principal components analysis yields six significant axes as determined by the broken-stick method. These six axes account for approximately 72.5% of the observed variance in shell outlines (PC1: 28.4%, PC2: 14.8%, PC3: 11.6%, PC4: 7.2%, PC5: 5.6%, and PC6: 4.9%). Principal component 1 corresponds to a shift in siphonate, elongated

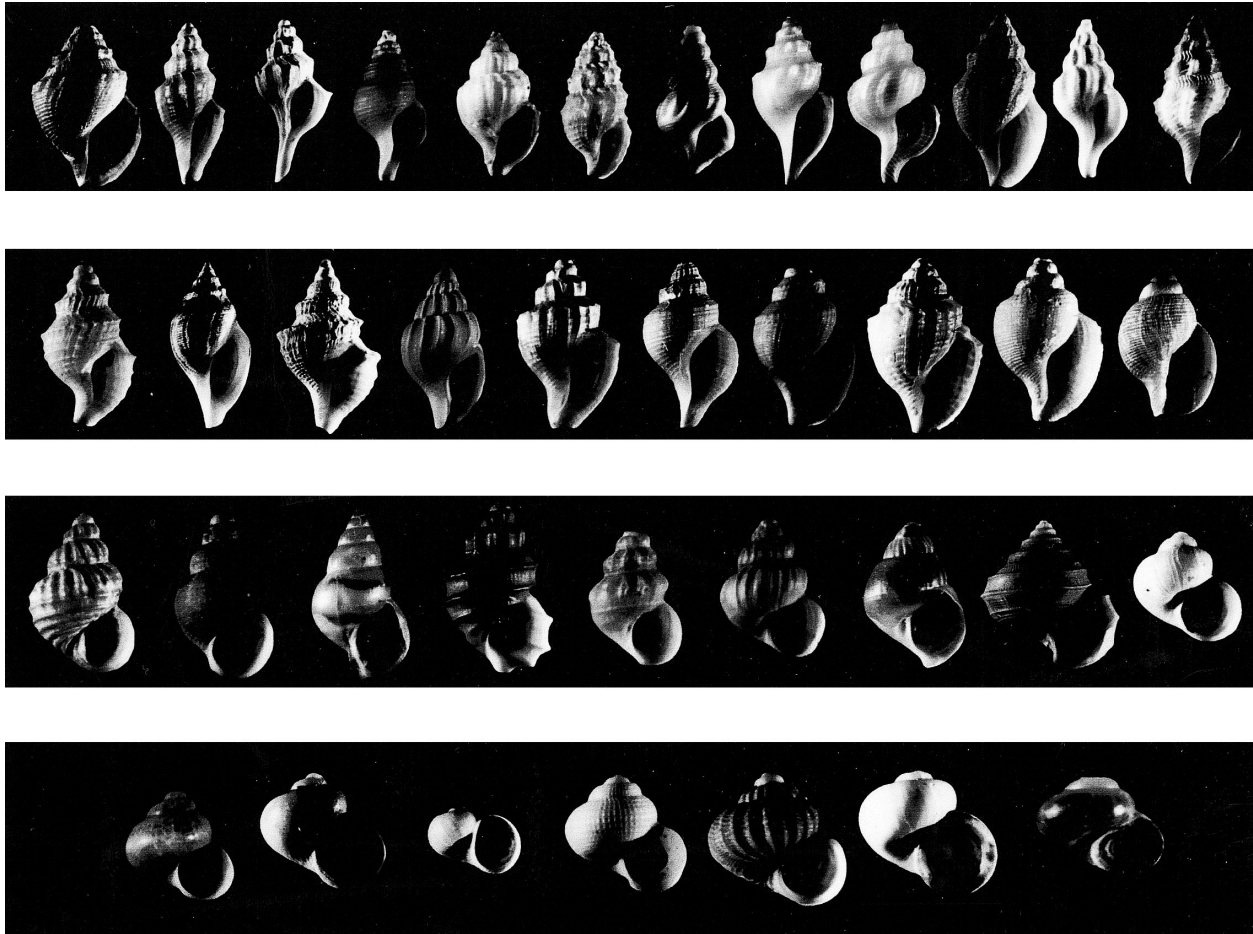


FIG. 1. Pictures of representative gastropods ordered along principal component axis 1 (left to right for each row). Shell values range from negative values (upper left) to positive values (lower right). Shell photographs are courtesy of M. A. Rex.

shell types to more globular forms (Fig. 1). This pattern has also been observed with a limited subset of gastropod species from bathyal and abyssal habitats along the GBT (McClain et al. 2004). Axis 1 also corresponds with shifts in taxonomy and feeding type. Those species with negative principal component values on axis 1 are predatory caenogastropods, and as values increase, species transition to deposit-feeding vetigastropods. No interpretable biological pattern is discernable over the remaining axes (Fig. 2).

The center of the morphospace volume shifts with depth (Fig. 3, Table 1). Species diversity ( $ES_{25}$ ) exhibits a parabolic relationship with depth, in which species diversity peaks at intermediate depths (Fig. 4A). This pattern is a well-documented trend among the gastropods of the GBT (Rex 1983). Morphospace total range, taken as summed range along the significant axes, displays a similar pattern with depth (Fig. 4B). The extent of the morphospace appears to be highest at intermediate depths. The average summed variance taken over the six significant axes does not change over depth (Fig. 4C). However, the range of values does increase markedly along the transect.

The similar relationships between species diversity and morphospace total range with depth may result from the sampling of more species in the morphospace. To test this,

summed range was taken for random samples of species from the regional pool (Fig. 5). The bootstrapped estimates (solid line) of total range and the empirical station estimates (open circles) show similar patterns. One interesting aspect of this analysis is that the morphospace total range for all of the stations is below the mean bootstrap estimate. Of the GBT stations, 23 (about 72%) have total ranges significantly lower than the bootstrapped estimate.

The spatial arrangement of species within the morphospace appears to be nonrandom. All stations have NNDs that are statistically higher than the randomized assemblages, indicating that the species are overdispersed. The mean difference between Monte Carlo and empirical distributions does change with depth. Assemblages at intermediate depths display increased overdispersion. There is also a strong pattern between species richness and hyperdimensional spatial dispersion, with high richness correlating with increased overdispersion (Fig. 6).

#### DISCUSSION

Despite the corresponding trends in species diversity and morphospace total range along the depth gradient (Fig. 4), the relationship between the two is nonlinear (Fig. 5). Both

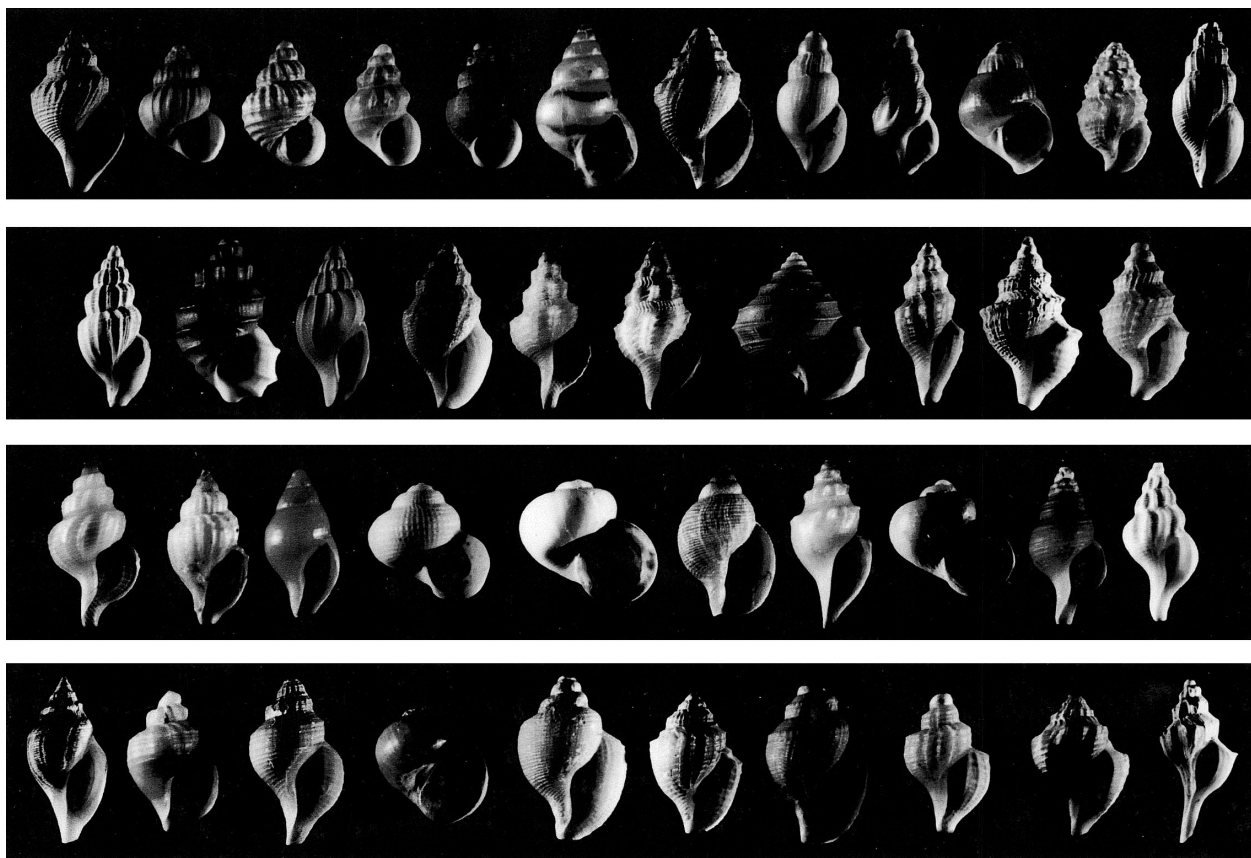


FIG. 2. Pictures of representative gastropods ordered along principal component axis 2 (left to right for each row). Shell values range from negative values (upper left) to positive values (lower right). Shell photographs are courtesy of M. A. Rex.

species diversity and morphospace total range are highest at intermediate depths. At high species richness, increased values are accompanied by only marginal increases in the morphospace total range. At low species richness, species are differentially added to the periphery of the morphospace, representing novel shell forms resulting in substantial increases in the total range. This follows Foote's (1996) argument that the "surface area" of the hypervolume is the most valuable for expanding disparity. Area increases slower than volume, and thus, if richness is proportional to hypervolume, only a small number of species can increase the size of the morphospace. These findings appear to be similar to Indo-Pacific strombid gastropods in which increases in species richness correspond to more drastic increases in the morphospace at low species numbers (Roy et al. 2001).

Previous studies have indicated that the relationship between morphospace total range and species richness may arise as a simple sampling artifact (Foote 1992, 1997; Roy et al. 2001). Here, the patterns are significantly different because of the differences in elevations but the shapes of the curves appear visually similar (Fig. 5). This is statistically supported by plotting the empirical ranges as a function of the theoretical predictions based on random sampling. The relationship between the two is highly linear and significant ( $y = 1.14 + 0.81x$ ,  $R^2 = 0.77$ ,  $P < 0.0001$ ). These findings imply that the changes in the total range with depth may

reflect changes in the number of species with depth; that is, the morphospace range is dictated by the number of species.

Despite the finding that total range varies with depth, total variance does not. To restate, despite the drastic changes in the number of species, the average dissimilarity among species does not vary. This pattern would arise if local fauna were all drawn from the same statistical population, in this case the regional pool, with the same variance. In contrast, the NND is greatest at intermediate depths. The above patterns in variance and NND would occur if species became more patchily distributed in the morphospace at these intermediate depths. Thus, species may live in clumps where the similarity within is high, but are quite distant from the next species clump. There is also support for nonrandom dispersion of species among all of the stations. The hyperdimensional spatial arrangement in all cases is greater than the Monte Carlo estimates. The discrepancy between empirical and random estimates is greatest at intermediate depths where species richness is also highest, lending further support to increased morphospace patchiness at these depths.

Hertel and Lehman (1998) note that if the hyperdimensional spatial arrangement is greater than the Monte Carlo estimates, then character displacement is occurring. If the results indicate an actual biological minimum distance between species within the morphospace, then deep-sea gastropod communities may be structured by competition. Char-

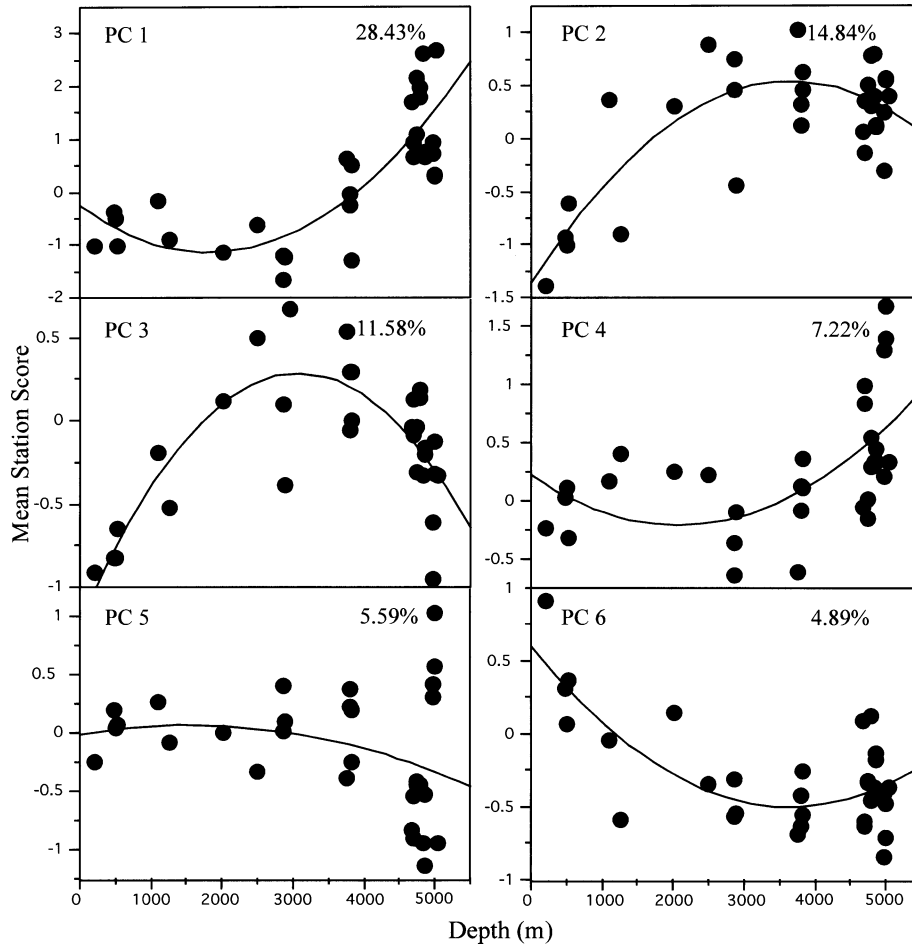


FIG. 3. Change of the morphospace centroid with depth along the first size principal component axes. Points represent the mean score for a station. Lines are quadratic regressions. Percentages in upper right corner are the percentage of the variance that each axis describes in shell form as measured here.

acter displacement also exhibits bathymetric variation, being greatest at intermediate depths and higher species numbers. These findings are similar to those for desert lizards (Pianka 1973, 1974, 1975, 1976) in which high species richness corresponded to a relatively low tolerance for niche overlap. This low tolerability of overlap is thought to ensue when there is some degree of environmental fluctuation (Rappoldt and Hogeweg 1980). However, it should be noted that it is unclear whether middepth communities have high character displacement because of high species diversity, or high character displacement has led to increased species diversity. Previous researchers have proposed competition as an important factor structuring deep-sea communities (Sanders 1968; Rex

1976, 1981, 1983). In addition, both experimental field tests and modeling suggest that intraspecific competition can lead to speciation through disruptive selection (Dieckmann and Doebeli 1999; Bolnick 2004). At this point any discussion of character displacement remains speculative because “character displacement is not compelling evidence of competition promoting species divergence” (Pfennig and Murphy 2002, p. 1217), and a variety of factors can instigate phenotypic variation. Thus, more research is needed to discern whether competition is highest at intermediate depths and the potential mechanisms by which this leads to an increase in species diversity.

As expected, regional disparity is much higher than local

TABLE 1. Quadratic regression estimates for principal components (PC) 1–6.

PC axis	Intercept	Depth	(Depth-3213) <sup>2</sup>	R <sup>2</sup>	P
1	-3.00 × 10 <sup>0</sup>	7.39 × 10 <sup>-4</sup>	2.65 × 10 <sup>-7</sup>	0.644	<0.0001
2	1.09 × 10 <sup>-1</sup>	1.25 × 10 <sup>-4</sup>	-1.42 × 10 <sup>-7</sup>	0.601	<0.0001
3	4.23 × 10 <sup>-1</sup>	-4.40 × 10 <sup>-5</sup>	-1.58 × 10 <sup>-7</sup>	0.623	<0.0001
4	-8.01 × 10 <sup>-1</sup>	2.24 × 10 <sup>-4</sup>	9.58 × 10 <sup>-8</sup>	0.335	0.0033
5	3.35 × 10 <sup>-1</sup>	-1.12 × 10 <sup>-4</sup>	-3.43 × 10 <sup>-8</sup>	0.092	0.2577
6	-2.52 × 10 <sup>-1</sup>	-7.30 × 10 <sup>-5</sup>	8.26 × 10 <sup>-8</sup>	0.536	<0.0001

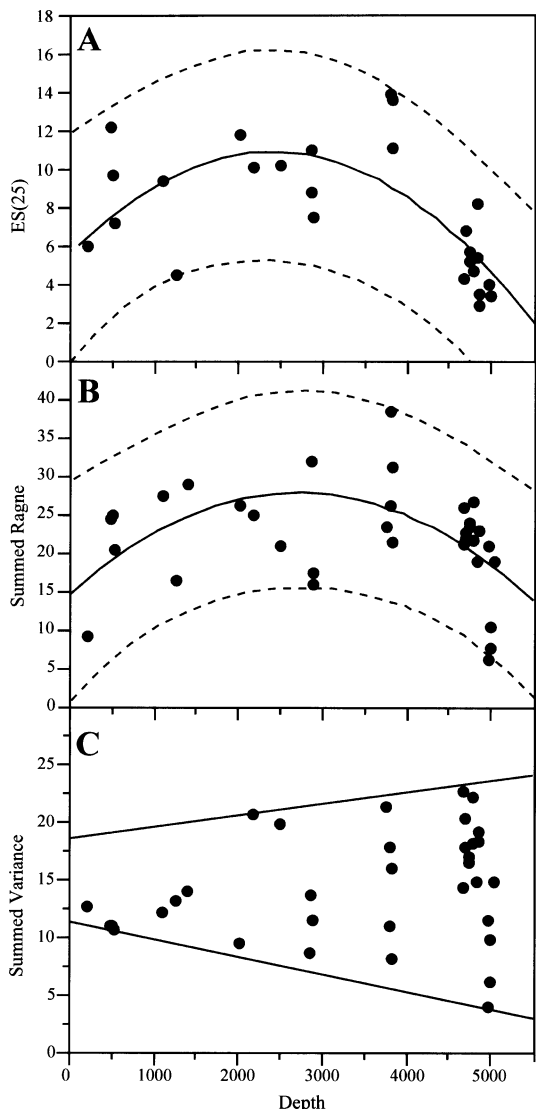


FIG. 4. Species diversity and morphological diversity with depth for western North Atlantic gastropods. (A) The relationship between depth and Hurlbert's expected number of species for 25 individuals ( $y = 15.28 - 0.0016x + 0.0029x^2$ ,  $R^2 = 0.463$ ,  $P = 0.0011$ ). (B) The relationship between depth and summed range along the first five principal component axes ( $y = 33.23 - 0.0018x + 0.0058x^2$ ,  $R^2 = 0.259$ ,  $P = 0.011$ ). (C) The relationship between depth and summed variance along the first five principal component axes. Lines represent the 95% and 5% quantile regression lines (95%:  $y = 18.99 + 0.00079x$ ,  $R_1 = 0.1841$ ,  $P = 0.0012$ ; 5%:  $y = 11.54 - 0.00153x$ ,  $R_1 = 0.2147$ ,  $P = 0.0042$ ).

disparity. The empirical samples typically have a lower morphospace total range than that of the randomly drawn samples from the regional pool. The regional morphological pool possesses a broader array of shell forms than any local community. In addition, Figure 1 shows that the morphospace centroid is highly variable with depth, and this variability is characterized by both the loss and addition of shells (i.e., high  $\beta$ -disparity). Several factors of both the abiotic and the biotic environment that influence shell form are known to vary with depth.

The work of Etter and Grassle (1992) points to the influ-

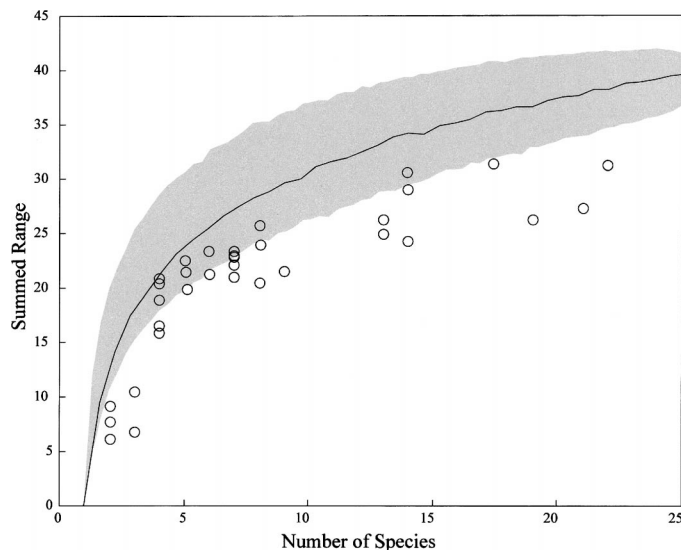


FIG. 5. The relationship between the number of species and summed range along the first five principal components axes. Open circles represent actual values for stations along the Gayhead-Bermuda Transect. Line represents the mean of summed ranges for random draws of species (see text for further explanation) with the 95% confidence intervals denoted by the shaded area.

ence of the size diversity of sediment particles in determining species diversity over bathymetric gradients. Although this relationship is attributed to partitioning of sediment size fractions among deposit feeders, it is possible that sediment characteristics may also affect shell diversity. For epifaunal gastropods, weight per unit area must be less than the sediment surface can withstand (Vermeij 1993). A reduction in sediment stress can occur by decreasing density, decreasing shell thickness, or increasing lip expansion. Deep-sea molluscs are known to possess very thin shells, and some deep-sea gastropods in this study do exhibit splaying of the aperture (Fig.

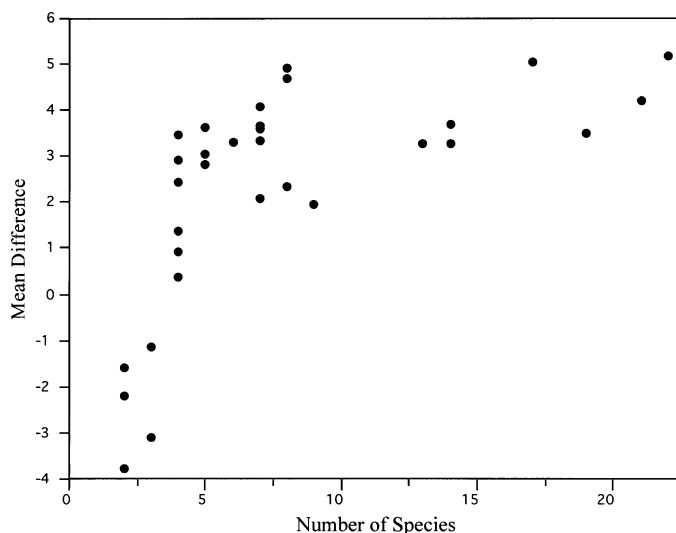


FIG. 6. Plot of mean difference between empirical nearest-neighbor distance and nearest neighbor for randomizations. All nearest neighbor distributions are significantly different from the Monte Carlo estimates.

2). However, how this changes over spatial gradients or whether this is an adaptation to minimize surface stress remains unclear. Infaunal gastropods must overcome another set of constraints that reflect a balance of stabilization of the sediment around the shell and rapid burrowing (Vermeij 1993). Strong secondary sculpture around the shell stabilizes sediment between subsequent ridges. The shell/sediment complex becomes less prone to being suspended and redistributed to other localities. Although much of the deep-sea floor experiences only very weak near-bottom currents, there are a number of areas that experience high current speeds of substantial duration (Levin et al. 2001). Research seems to suggest that the disturbance regime of the sediment decreases in duration and intensity onto the abyssal plain. This gradient matches the decrease in sculpture seen in this study and others (Rex et al. 1988; McClain et al. 2004).

Shell form in deep-sea gastropods may also be affected by the availability and dissolution rates of  $\text{CaCO}_3$  (McClain et al. 2004). The solubility of  $\text{CaCO}_3$  is related to temperature and pressure, both of which vary with depth (Morse and Mackenzie 1990). In regimes where solubility is high, shells that conserve material should predominate (Graus 1974). More conservative shell forms also require less energy for growth and maintenance of the shell. In lowered oxygen regimes and decreased nutrient input, both correlated with depth, one would expect less sculpture, globular shapes, circular apertures, and high degree of whorl overlap. There is some evidence that nutrient input, oxygen concentrations, and the  $\text{CaCO}_3$  availability may influence shell morphology (McClain and Rex 2001; McClain et al. 2004).

Vermeij (1993) also outlines several mechanisms in which predation pressure can influence shell type. Gastropod prey typically possess thicker shells, increased defensive sculpture, narrower apertures, and so on. Predation has been proposed as an important factor structuring deep benthic communities (Jumars and Eckman 1983; Rex 1983; Grassle 1989). Abundance of megafaunal predators is known to decrease with depth (Rex 1983) and presumably predation pressure also decreases with depth. Bathymetric variation in shell damage of deep-sea gastropods shows no clinal variation (Vale and Rex 1988, 1989). However, *Frigidoalvania brychia* does show increased variation in shell sculpture with depth (Vale and Rex 1988, 1989). Vale and Rex (1988) speculate that the addition of smoother forms at increased depths may represent a release from predation pressure.

Patterns of diversity, including those in the deep sea, have received much attention. Here, I add to other studies showing the value of exploring biodiversity in terms of morphological variety over extensive spatial scales. The results from this study indicate that for deep-sea gastropods in the western North Atlantic: (1) Local faunas are drawn from a regional pool with the same average dissimilarity. (2) The number of species in the sample dictates the morphological range. This contrasts sharply with other studies for molluscs in which species diversity is a poor predictor of morphological disparity (Roy et al. 2001; Neige 2003). (3) The range of the morphospace at local scales is less than at regional scales. Shifts in form occur over the gradient, but morphological disparity remains unaffected. To restate, the results imply that the environment directly dictates the types of species at

a locality (composition). However, the environment controls the overall variety of shell types only through its control of how many species can fit into the community (disparity). (4) Although the size of the morphospace does not change over the gradient, the distribution of individuals within the morphospace does.

These findings begin to reveal the links between the environment, morphological disparity, and species richness at both local and regional spatial scales and the interplay between ecological and evolutionary processes. Both the similarities and discrepancies between these results and previous studies beg for further research about the generalities of disparity/diversity relationships and their evolutionary and ecological consequences.

#### ACKNOWLEDGMENTS

I thank M. G. McClain for helping to improve this manuscript. M. Rex, R. Stevens, and E. White provided valuable comments and insights into this project. I also thank M. Foote and P. Wagner who provided insightful and valuable reviews on this manuscript. This research was funded by National Science Foundation grants GER-9552836 and OCE-0135949 to M. Rex.

#### LITERATURE CITED

- Alatalo, R., and R. Alatalo. 1977. Components of diversity: multivariate analysis with interaction. *Ecology* 58:900–906.
- Bolnick, D. I. 2004. Can intraspecific competition drive disruptive selection? An experimental test in natural populations of sticklebacks. *Evolution* 58:608–618.
- Cain, A. J. 1977. Variation in the spire index of some coiled gastropod shells, and its evolutionary significance. *Philos. Trans. R. Soc. Lond. B* 277:377–428.
- Clarke, K. R., and R. M. Warwick. 2001. A further biodiversity index applicable to species lists: variation in taxonomic distinctness. *Mar. Ecol. Prog. Ser.* 216:265–278.
- Cosson-Sarradin, N., M. Sibuet, G. L. J. Paterson, and A. Van-griesheim. 1998. Polychaete diversity at tropical Atlantic deep-sea sites: environmental effects. *Mar. Ecol. Prog. Ser.* 165:173–185.
- Cousins, S. H. 1991. Species diversity measurement—choosing the right index. *Trends Ecol. Evol.* 6:190–192.
- Dieckmann, U., and M. Doebeli. 1999. On the origin of species by sympatric speciation. *Nature* 400:354–357.
- Etter, R. J., and J. F. Grassle. 1992. Patterns of species diversity in the deep sea as a function of sediment particle size diversity. *Nature* 360:576–578.
- Faith, D. P. 2002. Quantifying biodiversity: a phylogenetic perspective. *Conserv. Biol.* 16:248–252.
- Foote, M. 1992. Rarefaction analysis of morphological and taxonomic diversity. *Paleobiology* 18:1–16.
- . 1994. Morphological disparity in Ordovician-Devonian crinoids and the early saturation of morphological space. *Paleobiology* 20:320–344.
- . 1995. Morphological diversification of Paleozoic crinoids. *Paleobiology* 21:273–299.
- . 1996. Perspective: Evolutionary patterns in the fossil record. *Evolution* 50:1–11.
- . 1997. The evolution of morphological diversity. *Annu. Rev. Ecol. Syst.* 28:129–152.
- Foote, M., and S. J. Gould. 1992. Cambrian and recent morphological disparity. *Science* 258:1816.
- Fretter, V., and A. Graham. 1962. British prosobranch mollusks. *Ray Soc. Publ.* 144:1–755.
- Grassle, J. F. 1989. Species diversity in deep-sea communities. *Trends. Ecol. Evol.* 4:12–15.

- Graus, R. R. 1974. Latitudinal trends in the shell characteristics of marine gastropods. *Lethaia* 7:303–314.
- Harasewych, M. G. 1982. Mathematical modeling of the shells of higher prosobranchs. *Bull. Am. Malacol. Union* 1981:6–10.
- Hertel, F., and N. Lehman. 1998. A randomized nearest-neighbor approach for assessment of character displacement: the vulture guild as a model. *J. Theor. Biol.* 190:51–61.
- Jackson, D. A. 1993. Stopping rule in principal components analysis: a comparison of heuristical and statistical approaches. *Ecol. Monogr.* 63:477–587.
- Jumars, P. A., and J. Eckman. 1983. Spatial structure within deep-sea benthic communities. Pp. 399–452 in G. T. Rowe, ed. *The sea*. Wiley, New York.
- Kareiva, P., and M. Marvier. 2003. Conserving biodiversity coldspots. *Am. Sci.* 91:344–351.
- Legendre, P., and L. Legendre. 1998. *Numerical ecology*. Elsevier, Amsterdam.
- Levin, L. A., R. J. Etter, M. A. Rex, A. J. Gooday, C. R. Smith, J. Pineda, and C. T. Stuart. 2001. Environmental influences on regional deep-sea species diversity. *Annu. Rev. Ecol. Syst.* 32: 51–93.
- Lohmann, G. P. 1983. Eigenshape analysis of microfossils: a general morphometric method for describing changes in shape. *Math. Geol.* 15:659–672.
- Lohmann, G. P., and P. N. Schweitzer. 1990. On eigenshape analysis. Pp. 145–166 in F. J. Rohlf and F. L. Bookstein, eds. *Proceedings of the Michigan morphometrics workshop*. Univ. of Michigan Museum of Zoology, Ann Arbor, MI.
- McClain, C. R. 2004. Connecting species richness, abundance, and body size in deep-sea gastropods. *Global Ecol. Biogeogr.* 13: 327–334.
- McClain, C. R., and M. A. Rex. 2001. The relationship between dissolved oxygen concentration and maximum size in deep-sea turrid gastropods: an application of quantile regression. *Mar. Biol.* 139:681–685.
- McClain, C. R., N. A. Johnson, and M. A. Rex. 2004. Morphological disparity as a biodiversity metric in lower bathyal and abyssal gastropod assemblages. *Evolution* 58:338–348.
- McGhee, Jr., G. R. 1995. Geometry of evolution in the biconvex Brachiopoda: morphological effects after a mass extinction. *Neues Jahrb. Geol. Palaeontol. Abh. B.* 197:356–382.
- . 1999. *Theoretical morphology: the concept and its applications*. Columbia Univ. Press, New York.
- McShea, D. W. 1993. Arguments, tests, and the Burgess Shale: a commentary on the debate. *Paleobiology* 19:399–402.
- Morse, J. W., and F. T. Mackenzie. 1990. *Geochemistry of sedimentary carbonates*. Elsevier, Amsterdam.
- Neige, P. 2003. Spatial patterns of disparity and diversity of the Recent cuttlefishes (Cephalopoda) across the Old World. *J. Biogeogr.* 30:1125–1137.
- Pfennig, D. W., and P. J. Murphy. 2002. How fluctuating competition and phenotypic plasticity mediate species divergence. *Evolution* 56:1217–1228.
- Pianka, E. R. 1973. The structure of lizard communities. *Annu. Rev. Ecol. Syst.* 4:53–74.
- . 1974. Niche overlap and diffuse competition. *Proc. Natl. Acad. Sci. USA* 71:2141–2145.
- . 1975. Niche relations of desert lizards. Pp. 292–314 in M. L. Cody and J. M. Diamond, eds. *Ecology and evolution of communities*. Harvard Univ. Press, Cambridge, MA.
- . 1976. Competition and niche theory. Pp. 114–141 in R. M. May, ed. *Theoretical ecology*. Blackwell Scientific, Oxford, U.K.
- Ponder, W. F., and D. R. Lindberg. 1997. Towards a phylogeny of gastropod molluscs: an analysis using morphological characters. *Zool. J. Linn. Soc. Lond.* 119:83–265.
- Rappoldt, C., and P. Hogeweg. 1980. Niche packing and number of species. *Am. Nat.* 116:480–492.
- Raup, D. M. 1961. The geometry of coiling in gastropods. *Proc. Natl. Acad. Sci. USA* 47:602–609.
- Rex, M. A. 1973. Deep-sea species diversity: decreased gastropod diversity at abyssal depths. *Science* 181:1051–1053.
- . 1976. Biological accommodation in the deep-sea benthos: comparative evidence on the importance of predation and productivity. *Deep-Sea Res.* 23:957–987.
- . 1981. Community structure in the deep-sea benthos. *Annu. Rev. Ecol. Syst.* 12:331.
- . 1983. Geographic patterns of species diversity in the deep-sea benthos. Pp. 453–472 in G. T. Rowe, ed. *The sea*. Wiley, New York.
- Rex, M. A., C. T. Stuart, R. R. Hessler, J. A. Allen, H. L. Sanders, and G. D. F. Wilson. 1993. Global-scale latitudinal patterns of species diversity in the deep-sea benthos. *Nature* 365:636–639.
- Rex, M. A., M. C. Watts, R. J. Etter, and S. Oneill. 1988. Character variation in a complex of rissoid gastropods from the upper continental slope of the western North Atlantic. *Malacologia* 29: 325–340.
- Ricklefs, R. E. 2004. A comprehensive framework for global patterns in biodiversity. *Ecol. Lett.* 7:1–15.
- Rohlf, F. J. 1986. Relationships among eigenshape analysis, Fourier analysis and analysis of coordinates. *Geology* 18:845–857.
- Roy, K. 1996. The roles of mass extinction and biotic interaction in large-scale replacements: a reexamination using the fossil record of stromboidean gastropods. *Paleobiology* 22:436–452.
- Roy, K., D. P. Balch, and M. E. Hellberg. 2001. Spatial patterns of morphological diversity across the Indo-Pacific: analyses using stromboid gastropods. *Proc. R. Soc. Lond. B* 268:1–6.
- Roy, K., and M. Foote. 1997. Morphological approaches to measuring biodiversity. *Trends Ecol. Evol.* 12:277–281.
- Sanders, H. L. 1968. Marine benthic diversity: a comparative study. *Am. Nat.* 102:243–282.
- Sanders, H. L. 1977. *Evolutionary ecology of the deep-sea benthos. The changing scenes in natural sciences: 1776–1976*. Academy of Natural Sciences, Philadelphia.
- Saunders, W. B., and A. R. H. Swan. 1984. Morphology and morphologic diversity of mid-Carboniferous (Namurian) ammonoids in time and space. *Paleobiology* 10:195–228.
- Schindel, D. E. 1990. Unoccupied morphospace and the coiled geometry of gastropods: architectural constraint or geometric covariation? Pp. 270–304 in R. A. Ross and W. D. Allmon, eds. *Causes of evolution*. Univ. of Chicago Press, Chicago.
- Stuart, C. T., and M. A. Rex. 1994. The relationship between development pattern and species diversity in deep-sea prosobranch snails. Pp. 118–136 in C. M. Young and K. J. Eckelbarger, eds. *Reproduction, larval biology, and recruitment of the deep-sea benthos*. Columbia Univ. Press, New York.
- Swan, A. R. H., and W. B. Saunders. 1987. Function and shape in late Paleozoic (mid-Carboniferous) ammonoids. *Paleobiology* 37:409–423.
- Thistle, D., and G. D. F. Wilson. 1987. A hydrodynamically modified abyssal isopoda fauna. *Deep-Sea Res.* 34:73–87.
- Vale, F. K., and M. A. Rex. 1988. Repaired shell damage in deep-sea prosobranch gastropods from the western North Atlantic. *Malacologia* 28:65–79.
- Vale, F. K., and M. A. Rex. 1989. Repaired shell damage in a complex of rissoid gastropods from the upper continental slope south of New England. *Nautilus* 103:105–108.
- Vermeij, G. J. 1993. *A natural history of shells*. Princeton Univ. Press, Princeton, NJ.
- Wagner, P. J. 1995. Testing evolutionary constraint hypotheses with early Paleozoic gastropods. *Paleobiology* 21:248–272.
- Ward, P. D. 1980. Comparative shell shape distributions in Jurassic-Cretaceous ammonites and Jurassic-Tertiary nautilids. *Paleobiology* 6:32–43.
- Wills, M. A. 2001. *Morphological disparity: a primer*. Pp. 55–143 in J. M. Adrain, G. D. Edgecombe, and B. S. Lieberman, eds. *Fossils, phylogeny, and form: an analytical approach*. Kluwer Academic/Plenum Publishers, New York.
- Wills, M. A., D. E. G. Briggs, and R. A. Fortey. 1994. Disparity as an evolutionary index: comparison between Cambrian and Recent arthropods. *Paleobiology* 20:93–130.