

Mid-domain models as predictors of species diversity patterns: bathymetric diversity gradients in the deep sea

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Geometric constraints represent a class of null models that describe how species diversity may vary between hard boundaries that limit geographic distributions. Recent studies have suggested that a number of large scale biogeographic patterns of diversity (e.g. latitude, altitude, depth) may reflect boundary constraints. However, few studies have rigorously tested the degree to which mid-domain null predictions match empirical patterns or how sensitive the null models are to various assumptions. We explore how variation in the assumptions of these models alter null depth ranges and consequently bathymetric variation in diversity, and test the extent to which bathymetric patterns of species diversity in deep sea gastropods, bivalves, and polychaetes match null predictions based on geometric constraints.

Range–size distributions and geographic patterns of diversity produced by these null models are sensitive to the relative position of the hard boundaries, the specific algorithms used to generate range sizes, and whether species are continuously or patchily distributed between range end points. How well empirical patterns support null expectations is highly dependent on these assumptions. Bathymetric patterns of species diversity for gastropods, bivalves and polychaetes differ substantially from null expectations suggesting that geometric constraints do not account for diversity–depth patterns in the deep sea benthos.

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Understanding the mechanisms that produce geographic patterns in species diversity is a fundamental goal of ecology and evolution. Species diversity often varies roughly parabolically with latitude (France 1992, Angel 1997, Roy et al. 1998), altitude (Shmida and Wilson 1985, Rahbek 1995, 1997, Flieshman et al. 1998, Grytnes and Vetaas 2002), and depth (Rex 1973, 1981, 1983). Explanations of these relationships invoke various processes that regulate species diversity such as speciation rates, climatic variability, productivity, variation in biotic interactions, and habitat heterogeneity (Ricklefs and Schluter 1993). However, recent work has suggested that null models based on geometric constraints produce

similar geographic patterns in diversity (Colwell and Hurtt 1994, Colwell and Lees 2000) raising questions about the validity of inferred mechanisms that potentially control these macroecological trends. It is important to explore how empirical trends differ from null models before invoking biological mechanisms (Gotelli and Graves 1996).

Mid-domain or boundary constraint models assume that hard boundaries constrain the size and placement of species' ranges which causes randomly distributed species' ranges to cluster near the center of the domain and produce unimodal diversity patterns (Colwell and Hurtt 1994, Colwell and Lees 2000). These null models are

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used to examine how species richness may vary along gradients under minimal biological assumptions. However, much controversy has surrounded mid-domain models and they have been criticized on multiple fronts (Koleff and Gaston 2001, Hawkins and Diniz-Filho 2002, Zapata et al. 2003, but see the response from Colwell et al. 2004). The most critical of these has been the logical validity of the model (Hawkins and Diniz-Filho 2002, Zapata et al. 2003). Mid-domain models assume a constant environment across the domain; however, under these conditions ranges would extend the entire domain and eliminate any mid-domain effect. Proponents have responded that mid-domain models are only concerned with resampling the spatial pattern of range location (Colwell et al. 2004). A variety of other concerns have been raised over mid-domain models including whether range size should be retained at the borders (Zapata et al. 2003), the treatment of endemics (Whittaker et al. 2001, Hawkins and Diniz-Filho 2002, Vetaas and Grytnes 2002), setting domain limits (Koleff and Gaston 2001, Laurie and Silander 2002, Vetaas and Grytnes 2002, Zapata et al. 2003), patchiness or incomplete sampling (Grytnes and Vetaas 2002), statistical tests (Zapata et al. 2003), and the dimensionality of the models (Jetz and Rahbek 2001, Zapata et al. 2003). Irrespective of the criticisms, increasing evidence suggests that they explain little variance in empirical data, and significant fits are only obtained when a substantial amount of biology is added to the model (Koleff and Gaston 2001, Hawkins and Diniz-Filho 2002, Grytnes and Vetaas 2002). Moreover, many studies allude to the sensitivity of these models to the starting assumptions, but few have rigorously tested them statistically. Here, we vary several mid-domain model assumptions to test the robustness of these models and their ability to predict bathymetric patterns of diversity in the deep sea.

In the deep sea, diversity varies on local, regional, and global scales (reviewed by Levin et al. 2001, Stuart et al. 2003). The best documented of these trends is the unimodal relationship between depth and species diversity (Rex 1981). A variety of biological explanations have been proposed for why species diversity peaks at intermediate depths (reviewed by Levin et al. 2001, Stuart et al. 2003) including competition, predation, patch dynamics, environmental heterogeneity, productivity and various combinations of these. Because species diversity peaks at mid depths, it is possible that bathymetric variation in diversity reflects boundary constraints. Recently, Pineda and Caswell (1998) found that bathymetric variation in species diversity of gastropods and polychaetes in the western North Atlantic differed from null patterns derived from geometric constraint models. However, it is unclear whether the lack of fit is due to the specific algorithm used to

generate species' ranges or various assumptions implicit in the model.

We build on previous work to test how sampling intensity, hard boundaries, abundance distributions, and range size/location algorithms influence the null curve and whether these more complex models accurately describe the unimodal relationship between depth and species diversity. We utilize the five models of Colwell and Lees (2000) that differ in how they generate species ranges and midpoints. We also present a sixth null model that constrains the size of species' ranges. Using the statistical procedures of Pineda and Caswell (1998), we test whether bathymetric patterns of species diversity predicted from null models differ from empirical estimates for gastropods, bivalves, and polychaetes, in the North American Basin. Both visually and statistically, the null models provide a poor fit for the empirical data. The differences between theoretical and empirical curves are partly based on the sensitivity of the null curves to spatial patchiness of the species, the ratio of large and small ranges, and the position of the hard boundaries.

Materials and methods

Empirical data

We used the gastropod, polychaete, and bivalve fractions of epibenthic sled and anchor dredge samples taken in the western North Atlantic along a depth gradient from 97 m to 5042 m, as part of the Woods Hole Oceanographic Institutes Benthic Sampling Program (Sanders 1977). This transect extends from Gay Head, Massachusetts to Bermuda and is here after referred to as the Gay Head/Bermuda Transect (GBT). The samples contained 138 species of gastropods, 178 species of polychaetes and 39 species of bivalves. The data for polychaetes, bivalves, and gastropods were from Hartman (1965), Allen and Sanders (1997), and Rex (1981) respectively.

Null models

We used six null models to test whether boundary constraints could explain observed bathymetric patterns of diversity along the Gay-Head/Bermuda Transect. The first five are from Colwell and Lees (2000) and produce different diversity/depth curves. Because actual species' ranges rarely exceed 3500 m, we also created a sixth model, which is similar to null model one, but constrains the maximum range size to 3500 m. For each null model, species were randomly positioned along a depth gradient from 0–6500 m. This differs from the models created by Pineda and Caswell (1998) where the maximum depth was set to 5000 m. We increased the maximum depth

because the western North Atlantic reaches depths over 6500 m (GEBCO Chart produced by the Canadian Hydrographic Service 1987). However, sampling has only occurred to a maximum depth of 5042 m so we only compared null model expectations to empirical estimates over this narrower range. The number of species for each taxon in the null model was set to the number observed (178, 138, or 39 species for polychaetes, gastropods and bivalves respectively). After the generation of random species ranges and midpoints, we assigned species triangular abundance distributions with 100 individuals at its midpoint and decreasing linearly with distance from the midpoint. Although the choice of 100 individuals is arbitrary, the null models are largely insensitive to changes in the number of individuals except at extremely high and low numbers (less than 5 and more than 10000). Choices between these extremes retain relative abundances among species within a sample and do not affect the diversity curve with depth.

Null model 1

Null model one draws minimum and maximum depths of occurrence for each species randomly from a uniform distribution (Colwell and Lees 2000, Box 2). We generated range and midpoint data for each species from the minimum and maximum depths of occurrence. As Colwell and Lees (2000) point out, all midpoint/range pairs lie within an isosceles triangle defined by boundary constraints. Null model one produces a random distribution within this triangle (Fig. 1).

Null model 2

In null model two, we randomly selected the midpoints from a uniform distribution (Colwell and Lees 2000, Box 3). Ranges were then randomly chosen by using an algorithm that confines the uniform distribution to the allowed ranges for this midpoint, preventing species ranges from exceeding the hard boundaries. This produces a preponderance of species with small ranges located at the ends of the gradient (Fig. 1), because an

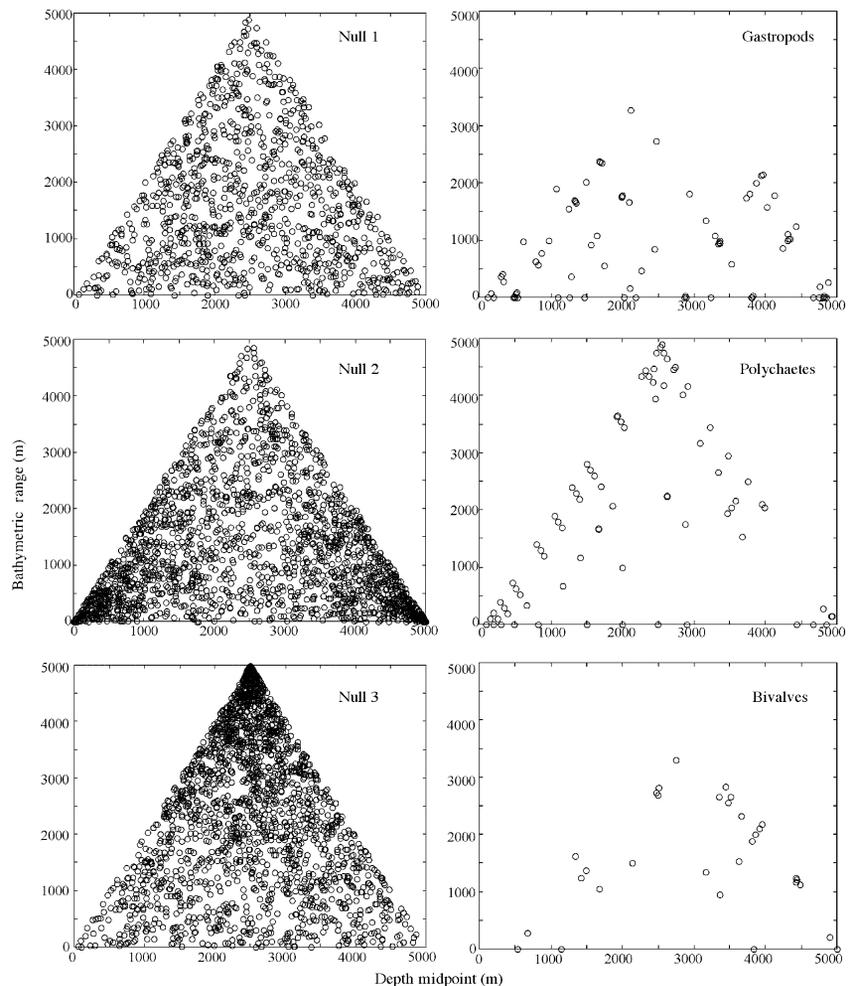


Fig. 1. Midpoint/range plots showing the isosceles triangle defined by boundary constraints for null 1–3, and empirical patterns for gastropods, polychaetes, and bivalves.

equal number of species are placed in each midpoint interval and ranges are truncated to remain within the boundaries.

Null model 3

In null model three, we selected random bathymetric ranges from a uniform distribution, and then generated midpoints such that ranges remained within the boundaries (Colwell and Lees 2000, Box 3). This forces the larger ranges to have midpoints in the middle of the gradient increasing the density of midpoints at intermediate depths (Fig. 1).

Null models 4 and 5

Null model four utilizes empirical midpoints for each species and assigns random ranges to them from a uniform distribution such that ranges do not exceed the hard boundaries (Colwell and Lees 2000, Box 5). Null model five uses the reverse method, randomly assigning a new midpoint to empirical ranges. This null is analogous to that of Pineda and Caswell (1998) and corresponds to shifting the ranges of species along the gradient. However, it differs in the method by which the null community is created. Pineda and Caswell (1998) shuffled columns of a species by station matrix, which retains the empirical abundances. In our null model, new midpoints from a uniform random distribution were assigned to empirical ranges and abundance distributions were created by assigning a triangular abundance distribution with 100 individuals at its midpoint. The models also differ in another fundamental way. In Pineda and Caswell (1998) midpoints were randomly drawn and those that cause ranges to extend outside the hard boundaries are excluded. This method differs from ours in that midpoints are randomly drawn from a distribution that is constrained to midpoints that do not force the range outside of the hard boundaries.

Null model 6

Null model six is similar to model one, but we constrained ranges to be less than 3500 m because observed bathymetric ranges of species rarely exceed 3500 m (Fig. 4). Allowing bathymetric ranges to span the entire 6500 m gradient is biologically unrealistic and produces null models that overestimate species diversity throughout the depth range.

Simulations

Species diversity was estimated at each sampling location along the GBT transect using Hurlbert's (1971) expected number of species (ES_n), such that n equals the normalized sample size. We fit a second order polynomial to diversity estimates across the depth gradient

for each iteration of the null model and the empirical data. To evaluate how well the null models predict empirical patterns, we compared curvature, location and magnitude of the fitted curves (Pineda and Caswell 1998). Curvature equals the second derivative of the diversity/depth relationship evaluated at the peak and is proportional to the coefficient c from the regression equation (Pineda and Caswell 1998). Diversity curves that peak more sharply give negative values. Location of the peak in diversity was evaluated by the equation

$$\hat{x} = \frac{-b}{2c}$$

Magnitude of the diversity peak was calculated by

$$y_{\max} = a - \frac{b^2}{4c}$$

We ran each null model 1000 times creating a distribution of values for curvature, location and magnitude. Empirical values were compared to these distributions to test the fit of the null models.

To determine the robustness of the models, we conducted simulations altering several assumptions. We increased the maximum depth of the bathymetric gradient from 4500 m to 6500 m by 500 m steps to determine how the lower boundary affects the depth gradient in diversity. Species rarely peak in abundance at exactly the midpoint of their range, and this may affect the relationship between diversity and depth because it will influence whether a particular species is sampled. Simulations were performed with the peak abundance occurring for all species in the first 25% of the species' range, the last 25% of the species' range, or randomly drawn from a uniform distribution. We also explored how the null models varied in response to a reduction in the maximum extent of species ranges.

All the null models assume that species are distributed continuously throughout their range. It is rare that all samples taken within a species' range yield individuals from that species, either because of patchiness in the environment or incomplete sampling. To incorporate this into the null models, we added a patchiness factor, similar to the incomplete sampling adjustments in the null models of Grytnes and Vetaas (2002). For each sample along the transect, we randomly deleted 20, 40, 60 and 80% of the species. The choice of percentages is arbitrary and meant only to explore how null predictions of species diversity respond to patchiness or incomplete sampling. Null models at 0% patchiness greatly overestimated diversity by a wide margin. Here, we only present the analyses for all taxonomic groups with a patchiness factor of 50%. This number represents the percentage of species missing from a typical sample when one assumes that a species is continuously distributed between the endpoints of its empirical bathymetric range.

Results

To demonstrate how altering the assumptions of the null models affect bathymetric patterns of diversity, we only present the results for null model one with an $ES_{(20)}$. Simulations from the other null models and normalized sample sizes produced similar results.

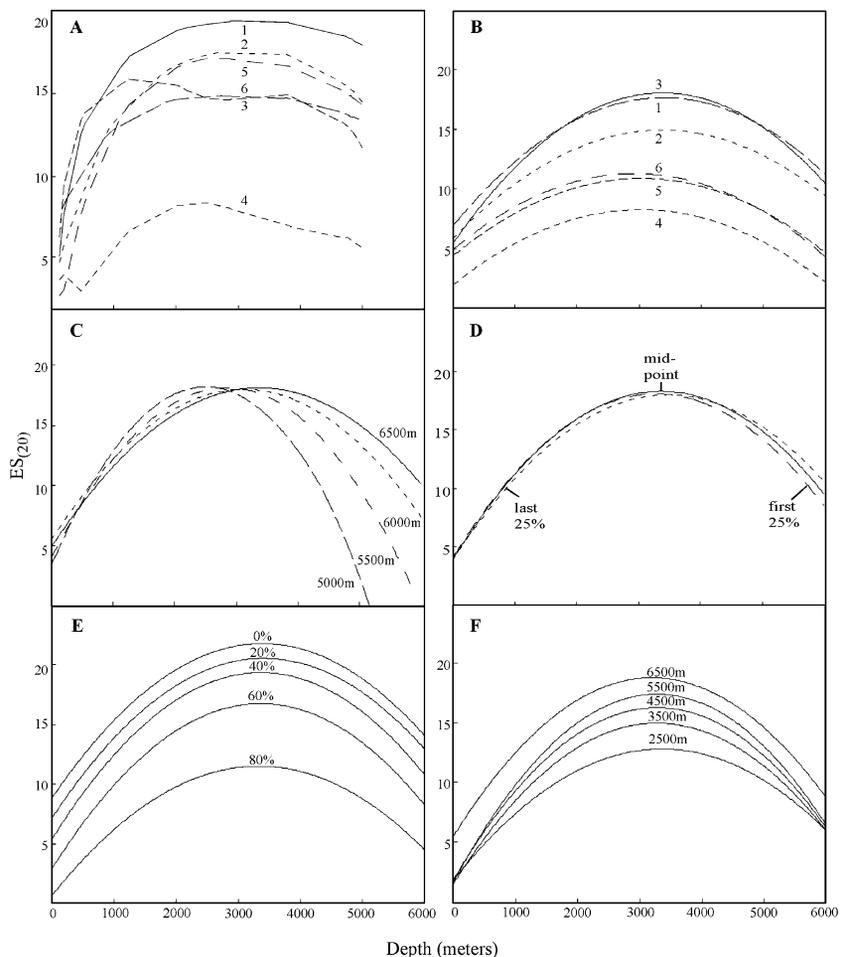
The algorithm used to generate null species distributions clearly affects the diversity patterns predicted by these models (Fig. 2A, B). Both the magnitude and the location of peak diversity differ among most of the models. Bathymetric patterns of diversity predicted by the null models were also sensitive to the depth of the lower boundary (Fig. 2C). Increasing the depth of the lower boundary increased the diversity of the samples below 4000 m, reducing the curvature. Making the lower boundary “soft” (sensu Colwell and Hurtt 1994) largely eliminated the parabolic pattern predicted by the typical decline in diversity at abyssal depths.

Altering the location of peak abundance had little influence on the bathymetric patterns produced by the null models (Fig. 2D). The peak of the diversity/depth curve varies slightly, but the basic curvature of the model remains the same.

An increase in patchiness, the percentage of species randomly removed from the sample, lowers the diversity curve (Fig. 2E). Curvature was unaffected until the number of species in a sample is reduced to 80%, at which point the sample size is inadequate to detect a trend in diversity (Fig. 3a). The location of the peak does not differ among patchiness levels (Fig. 3b), however, increasing the percentage of species removed from the sample reduces the magnitude of the diversity curve (Fig. 3c).

Constraining the maximum extent of species' ranges has a strong influence on the theoretical diversity estimates (Fig. 2F). As maximum range is reduced, the variance in diversity along the curve and the magnitude of the curve both decrease.

Fig. 2. The effect of varying starting assumptions on bathymetric variation in species diversity of a hypothetical assemblage. (A) Varying starting algorithms. See test for explanation of the null models. Lines in plot connect mean null estimates (1000 permutations) for empirical stations. (B) Varying starting algorithms. Lines are second-order polynomial regressions fitted to the same data. (C) The effects of increasing the depth of the lower boundary in null model one. Lines represent the mean parabolic regression fit for 1000 permutations of the model. (D) The effects of altering the peak abundance of species in their range to the first 25%, midpoint, or the last 25% of the species' depth range for a hypothetical assemblage for null model one. Lines represent the mean parabolic regression fit for 1000 permutations of the model. (E) The effect of increasing the patchiness factor on a hypothetical assemblage in null model one. Lines represent the mean parabolic regression fit for 1000 permutations of the model. (F) The effects of limiting species range sizes on hypothetical assemblage in null model one. Lines represent the mean parabolic regression fit for 1000 permutations of the model.



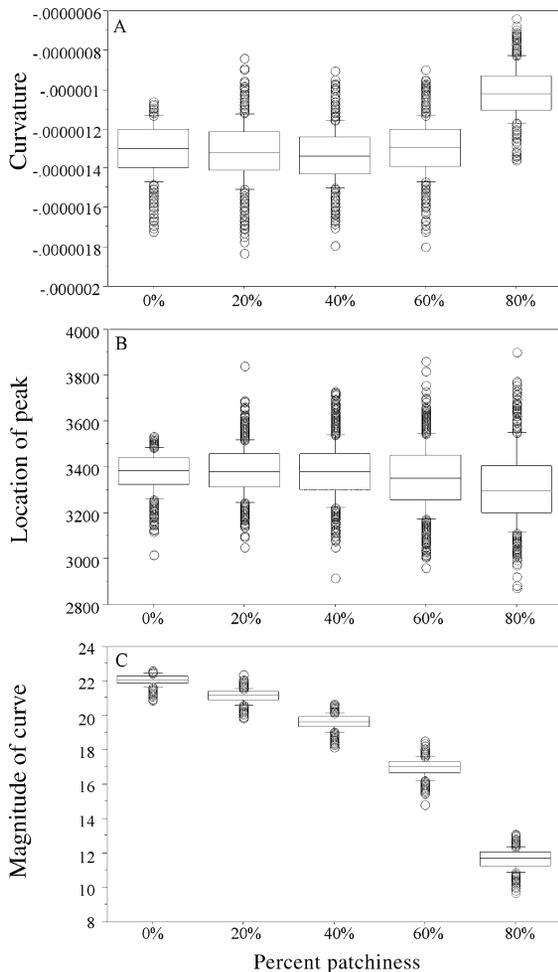


Fig. 3. Box plots showing how curvature, location, and magnitude of the curve vary with increasing patchiness in null model 1 in a hypothetical species.

Comparisons to empirical patterns

Gastropods

Gastropod diversity was greatly overestimated in part because empirical distributions have a high percentage of small ranges that most of the null models fail to produce (Fig. 4, 5). Null models 3, 5, and 6 provide better estimates, (Fig. 5), but all of the models differ significantly from the empirical values for curvature, peak location, and magnitude of the curve (Fig. 6).

Because the null models are dependent on the depth of the hard boundary (Fig. 2C), we compared empirical estimates for all three groups to null models with a lower boundary of 5042 m as in Pineda and Caswell (1998). Curvature, location of the peak, and magnitude of the peak still significantly differ from the empirical estimates for gastropods (Fig. 7). Similar results were obtained for polychaetes and bivalves but are not shown.

Polychaetes

Null models four, five, and six were most similar to the empirical data (Fig. 5). The other models produce diversity estimates considerably different from those observed, with the disparity greater for samples below 3000 m. Curvature, peak location, and magnitude were significantly different from empirical values for all null models (Fig. 8). As with gastropods, the lack of fit between empirical and theoretical values corresponds to differences in the distribution of range sizes between the null models and polychaetes (Fig. 4).

It should be noted there is some contention with the taxonomy of Hartman (1965). A few species in this dataset possess unusually large depth ranges for deep sea organisms. In other words, a few species in Hartman (1965) range from shallow coastal waters to the abyssal plain. It is more likely that these large ranges represent multiple closely related, small-ranged species. If this is the case, the lack of fit between polychaete diversity and the null model predictions would increase because of the addition of more smaller-ranged species.

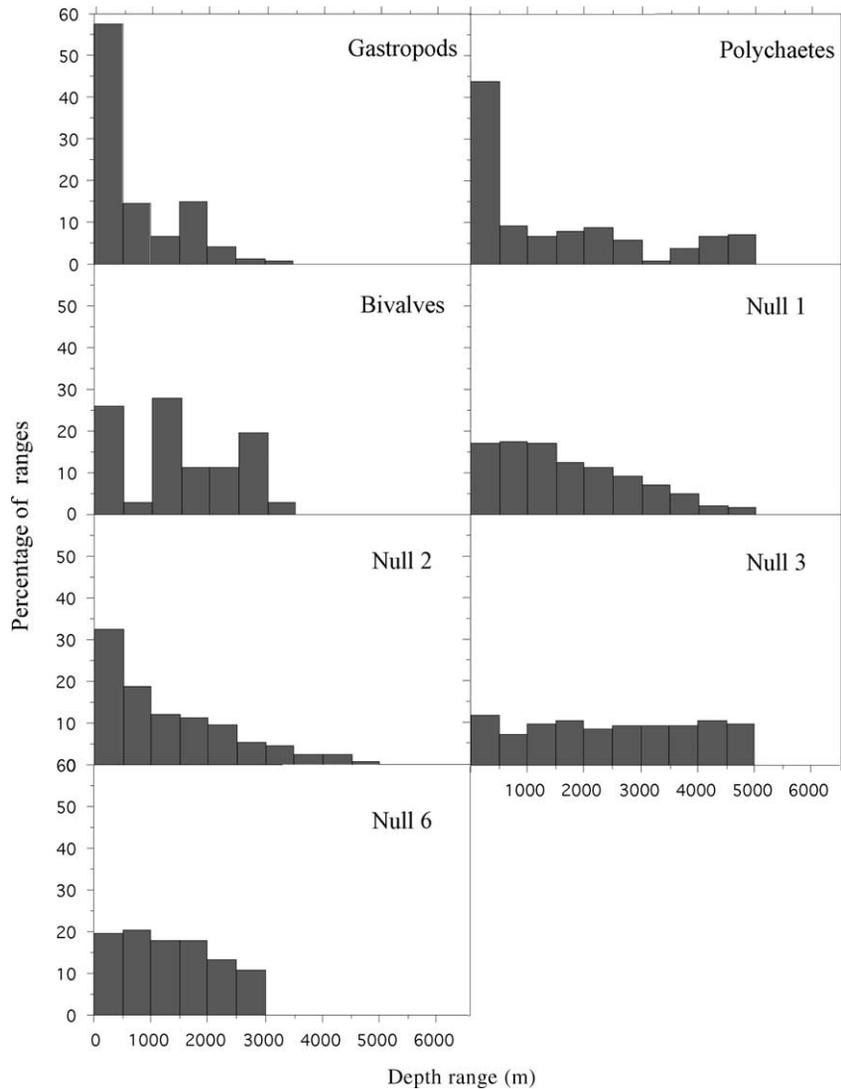
Bivalves

The bathymetric patterns produced by the null models for bivalves were more variable, probably because of the lower number of species ($S=39$, Fig. 5). The null models differ significantly from the empirical estimates of bivalve diversity for curvature, location, and magnitude (Fig. 9). The only exception was peak location in null model 2 which did not differ from the observed peak. This may reflect the large variance in results due to the low regional diversity and the relatively small bathymetric ranges of bivalves. Qualitatively, the best fit between null model predictions and empirical values comes from the null models that produce similar range frequency distributions to bivalves (Fig. 4).

Discussion

Mounting evidence from a variety of taxa indicates that mid-domain models fail to accurately predict variation in species diversity across latitudinal, altitudinal, or depth gradients (e.g. bats and marsupials: Willig and Lyons 1998; New World mammals: Bokma et al. 2001; Amazonian flora: Ter Steege et al. 2000; Afrotropical birds: Jetz and Rahbek 2001; South American raptors: Diniz-Filho et al. 2002; Nearctic birds: Hawkins and Diniz-Filho 2002; and Norwegian plants: Grytnes 2003). We find that although these models qualitatively predict a mid-domain peak in diversity, they differ significantly from empirical distributions of gastropods, polychaetes and bivalves. The poor conformity with empirical patterns probably reflects a variety of factors including: the generating algorithms, the distribution of range sizes, patchiness of the species, and the identification of hard boundaries.

Fig. 4. Frequency distributions of range lengths for gastropods, polychaetes, bivalves, null models 1–3, and null model 6. Simulated ranges represent averages of 1000 simulations.



The generating algorithm profoundly affects the null curve by controlling how species are distributed within the midpoint/range triangle (Fig. 1, 2A, B). The null and empirical curves are more similar when ranges are distributed similarly within the triangle. The best fits are produced by null models using empirical ranges or midpoints (null models 4 and 5), a finding similar to that of Koleff and Gaston (2001). When the algorithm generates species with ranges that span the entire domain, an unrealistic assumption in both the deep sea (Fig. 4) and terrestrial systems (Koleff and Gaston 2001), the null model overestimates diversity. Although empirical ranges are limited to the triangle, their location in this space appears to be nonrandom (Jetz and Rahbek 2001, Laurie and Silander Jr. 2002, Mora et al. 2003).

Many tests of the mid-domain model have assumed that a species occurs everywhere along its range. It is

unlikely that every species whose range includes a particular site actually resides there because many species have patchy distributions even when their ranges are continuous (Kaspari et al. 2003), and sampling will rarely capture all the species in a given area (Grytnes and Vetaas 2002). When patchiness is ignored, null models overestimate diversity. Grytnes and Vetaas (2002) controlled for this by removing 20% of the species from a null sample. Pineda and Caswell (1998) column shifted the original species by station matrix, which retains empirical levels of patchiness, but cannot be used with all the algorithms. Here, we reduce the species in a null sample by the mean percentage of species absent from all empirical samples if ranges were continuous between range endpoints. Our findings indicate that null model predictions are closer to the empirical curves when spatial patchiness is included.

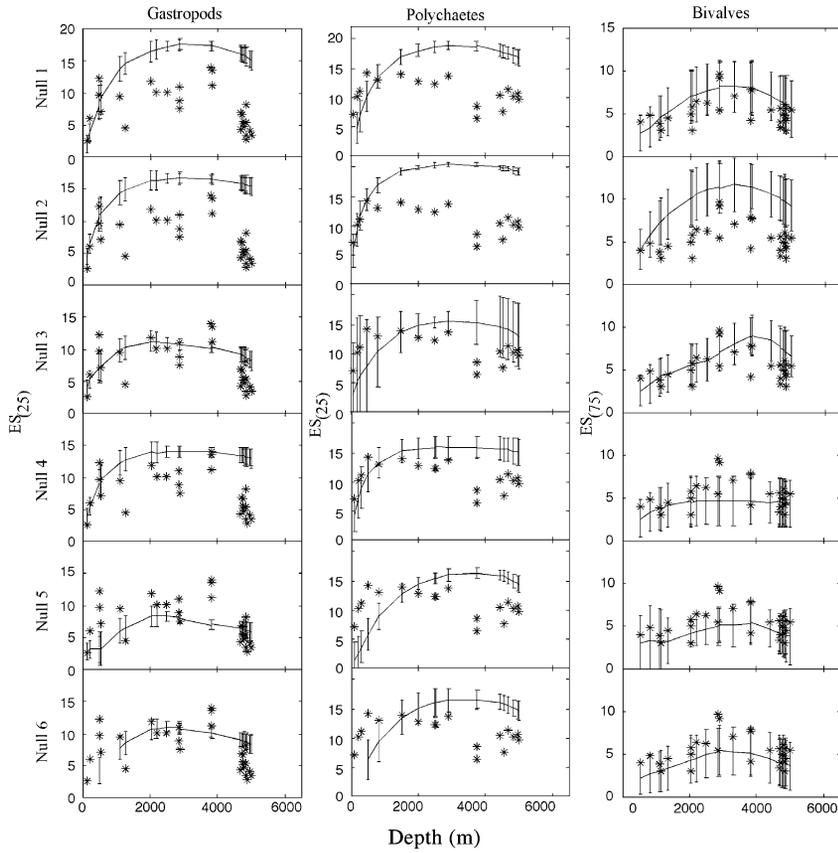


Fig. 5. Results for null models one through six (lines and 95% confidence intervals) plotted with empirical data (*) for gastropods, polychaetes, and bivalves. Lines in plot connect null estimates for empirical stations. Lines and confidence intervals are based on 5000 runs of the null model.

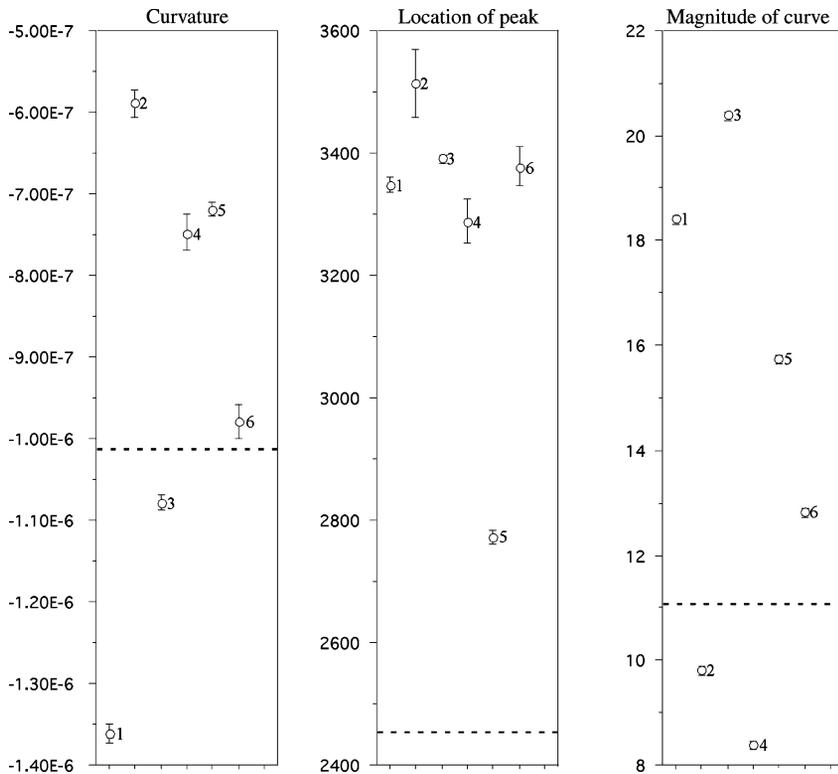
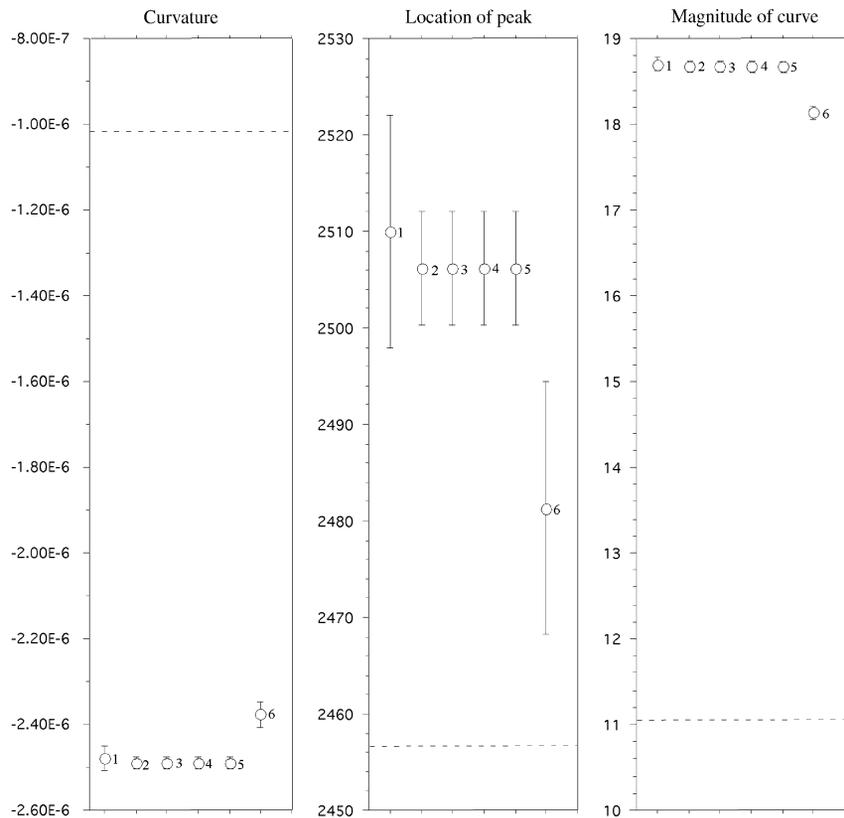


Fig. 6. Means and 95% confidence intervals for curvature, location, and magnitude for all six null models with maximum depth set to 6500 m. Dashed lines are the empirical values for gastropods.

Fig. 7. Means and 95% confidence intervals for curvature, location, and magnitude for all six null models with maximum depth set to 5042 m. Dashed lines are the empirical values for gastropods.



The definition of a hard boundary is simple – a point beyond which species ranges cannot extend (Colwell and Hurtt 1994). Mid-domain models are contingent on defining these hard boundaries, and the diversity curves are sensitive to their placement (Fig. 2C). In practice, identifying hard boundaries is often difficult. For example, Pineda and Caswell (1998) use 5042 m, the maximum depth of the samples, as a lower hard boundary. In this study, we use the hard boundary of 6500 m, the maximum depth of the basin. Vetaas and Grytnes (2002) discuss the difficulty inherent in determining hard boundaries for vascular plants along an elevational gradient where the permanent snow line, the timberline, and past glaciation limits might influence position of the boundary. When either ecological or physiological processes set boundaries, they are likely to differ among species (Koleff and Gaston 2001). Despite difficulties in defining the lower boundary in the North American Basin, neither 6500 m nor 5042 m provided a good fit to the empirical data.

Our findings suggest that deep sea communities are not random configurations of species but are probably structured by both biological interactions and abiotic environmental conditions (reviewed by Levin et al.

2001). The parabolic pattern of diversity with depth in the western North Atlantic is shaped by a variety of biotic and abiotic processes that vary along the depth gradient (Stuart et al. 2003). The putative processes are similar to what has been invoked in other ecosystems and include competition, predation, disturbance, productivity and habitat heterogeneity, but the exact mechanisms are unclear because the manipulative experiments that are needed to arbitrate among the various hypotheses have not been done.

Here, we show that a variety of null mid-domain curves can be generated, even under minimal biological assumptions. Although Colwell and Lees (2000) state the general null predictions are insensitive to details of the model, we find that the nature of the null curve is sensitive to the starting assumptions. Despite this variability in curves, the empirical patterns differed significantly from the null models. The best fits were obtained after incorporating more realistic biology into the null models, yet still failed to accurately predict the observed bathymetric diversity patterns in the western North Atlantic. Many studies have accepted geometric constraints as an explanation for geographic patterns of diversity (Falster et al. 2001, Summerville et al. 2001, Beaugrand et al. 2002, Ellison 2002, Krystufek and

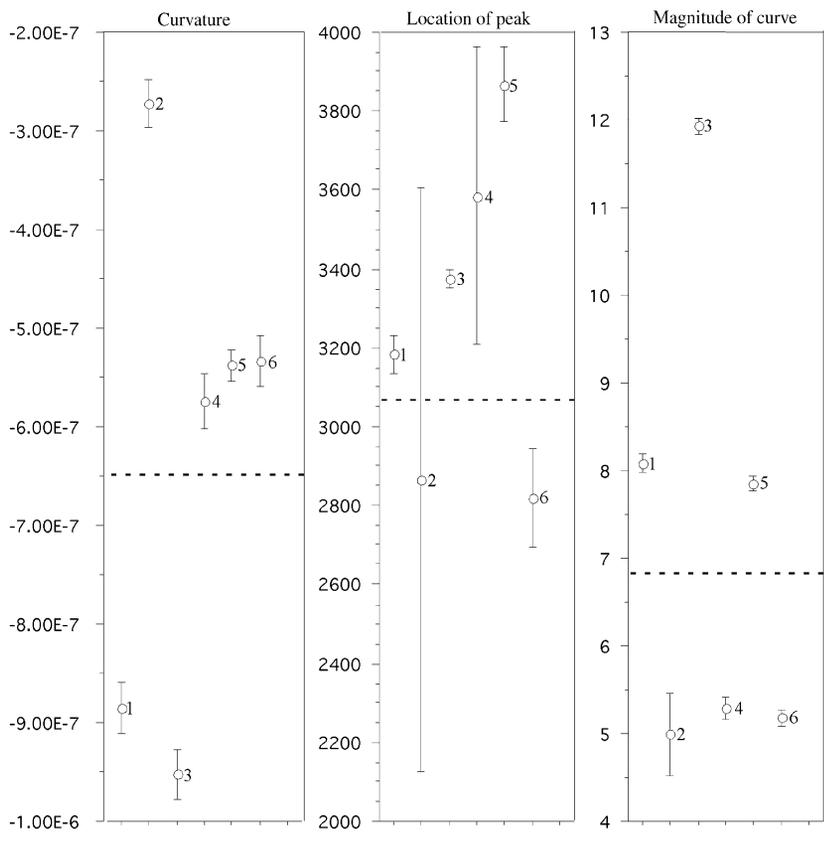


Fig. 8. Means and 95% confidence intervals for curvature, location, and magnitude for all six null models. Dashed lines are the empirical values for polychaetes.

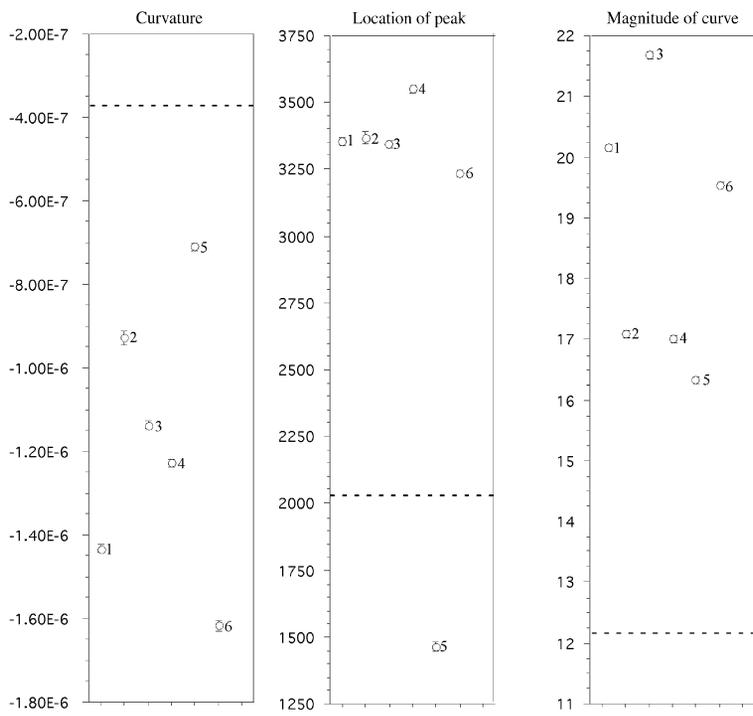


Fig. 9. Means and 95% confidence intervals for curvature, location, and magnitude for all six null models. Dashed lines are the empirical values for bivalves.

Griffiths 2002). Although it is important to compare empirical patterns to null expectations, this should be with rigorous statistical tests of fit and not qualitative assessments.

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