



Bathymetric species-diversity patterns and boundary constraints on vertical range distributions

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Abstract

A system where a set of species is randomly distributed within two spatial boundaries produces parabolic species diversity patterns, where diversity is lowest in the vicinity of the boundaries, and highest in the mid-zone between the boundaries. We demonstrate this phenomenon using simulated data.

We tested whether parabolic depth trends in species diversity (Rex, 1981, 1983) can be explained by invoking only this phenomenon. We analyzed data sets for northwest-Atlantic gastropods and polychaetes previously used to document parabolic diversity patterns. Data sets are matrices of species' abundance where rows index depth, and columns species. Simulations where species vectors were randomly rearranged within the shallowest and deepest stations generally produced parabolic diversity patterns, with higher diversity at intermediate zones, and lowest diversity closest to the shallowest and deepest stations. For the gastropods, the location of the peaks for the observed and randomly rearranged taxa coincided at similar depths. Random rearrangements, however, did not match the original patterns in curvature (peakedness of the diversity curve) or in magnitude (height of the diversity peak). Highest values were for observed taxa, implying that the original distribution of species is highly non-random and that other factors not assumed in the simulation influence bathymetric species-diversity patterns. For the polychaetes, randomly rearranged data sets matched the magnitude of the observed data set. The original parabolic diversity curve, however, peaked at a shallower location than the random rearrangements, and the magnitude of the peak was higher for the observed taxa. Overall, we find that the random rearrangements cannot explain most characteristics of the parabolic diversity patterns of gastropods and polychaetes.

We also explored the influence of species with large vertical range in influencing parabolic species diversity patterns. Removal "experiments", where a portion of the species with the

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largest vertical range was removed, also removed parabolic bathymetric diversity patterns, for both observed and simulated taxa, suggesting that species with large vertical range are disproportionately important in determining such patterns. © 1998 Elsevier Science Ltd. All rights reserved.

1. Introduction

An important ecological phenomenon is the species diversity parabolic pattern with depth (e.g. Begon et al., 1986), where species diversity is relatively low on the continental shelf, increases at upper-continental rise depths, and then decreases again at abyssal depths (Rex, 1973, 1976, 1981, 1983, Figures 12 and 13; see also Vinogradova 1962). Rex analyzed data from the northwest Atlantic for protobranch bivalves, cumaceans, fish, gastropods, invertebrate megafauna and polychaetes, and found parabolic patterns in all taxa. Studies involving more intense sampling also have found parabolic diversity patterns with depth in the northwest Atlantic (Etter and Grassle, 1992). Paterson and Lamshead (1995) also found a parabolic pattern in polychaete species diversity in the eastern North Atlantic. This pattern, however, may not be universal. Hessler and Wilson (1983) discussed several crustacean taxa that do not appear to have parabolic patterns in the Gulf of Mexico, and Rex et al. (in press) discussed other similar cases for crustaceans and foraminiferans.

Parabolic patterns have been explained by invoking depth gradients in biological or physical properties. Rex (1973) first proposed that higher diversity in the upper-continental shelf could be accounted for by higher stability there, as explained by Sanders (1968), while lower diversity in the abyss could be explained by depressed productivity. Rex (1981, 1983) later suggested that parabolic diversity patterns could reflect a “balance between rates of competitive displacement and the frequency of population reduction by predation”, pointing out that Huston’s (1979) dynamic equilibrium model was the most parsimonious explanation (see also Huston, 1994, pp. 357–363). Paterson and Lamshead (1995) suggested that physical and biological disturbance in a portion of the bathymetric range could be partially responsible for the trend in polychaete diversity. Another explanation has been offered by Etter and Grassle (1992), who found that bathymetric patterns in species were correlated with depth changes in silt diversity.

A recent hypothesis for explaining large-scale species diversity patterns involves species distributional ranges (latitudinal, vertical, bathymetric, etc.). The latitudinal range of many species often decreases with decreasing latitude (Rapoport, 1982; but see Rohde et al., 1993; Roy et al., 1994; Rahbek, 1997). This pattern, the “Rapoport rule” (Stevens, 1989), parallels latitudinal diversity gradients in terrestrial environments, where species diversity increases at low latitudes. Stevens (1989) argued that diversity in the tropics is higher because species there are adapted to a narrow range of environmental conditions. Thus, more species co-occur, but they have narrower

geographical ranges. Diversity is also inflated because most of the populations at a given area might be marginal populations spilled from adjacent habitats. This hypothesis has been extended to altitudinal and bathymetric patterns in species diversity (Stevens, 1992, 1996), and it predicts that sites with highest diversity should contain species with the smallest ranges.

MacArthur (1972) recognized the importance of geographic ranges for understanding species diversity patterns and pointed that “... the range of single species would seem to be the basic unit of biogeography” (p. 127). Stevens’ (1989) work also highlighted the importance of distributional ranges for attacking diversity gradient problems. Pineda (1993) studied a system where species’ vertical (bathymetric) ranges were constrained by two boundaries, the sea surface and the abyss. It was found that vertical range and species position within the boundaries were inextricably associated; this phenomenon was called a *geometric constraint on species distribution*. Pineda (1993) found that Rapoport’s rule could not explain bathymetric diversity patterns because, contrary to prediction, most small-ranged deep-sea taxa were found close to the shallowest and deepest boundaries, where diversity was smallest. Colwell and Hurr (1994) created a model identical to that of Pineda (1993), consisting of two boundaries constraining a set of species. They simulated taxa whose midpoint of occurrence was drawn from a uniform distribution between the two boundaries, measured species richness between the two boundaries, and found that diversity was highest in the mid-zone. Rahbek (1997) found that the altitudinal trend in bird species richness was hump-shaped, and that a plausible hypothesis to explain this pattern was the geometric constraints model. These results suggest that when a set of species is constrained by two boundaries, parabolic species diversity patterns can arise without the necessity of invoking other ecological factors.

Because parabolic patterns are emergent properties in a system where species are distributed between two boundaries, and because parabolic bathymetric patterns occur where species are constrained by the sea surface and the abyss, the obvious question is whether the parabolic patterns observed by Rex (1981, 1983) are just a reflection of this property, or whether other ecological factors contribute to the pattern.

In this paper, we use the approach and results of Pineda (1993) and Colwell and Hurr (1994) to explore the hypothesis that rearrangement of species between the surface and abyssal boundaries produces bathymetric patterns in species diversity. We first develop a simple model that contains only the basic elements of the hypothesis, a range with boundaries and a set of species, each with a vertical range. *The purpose of this model is to see if these mechanisms alone are capable of producing parabolic patterns*. In our second model, we take an observed set of species vertical ranges from situations that exhibit a parabolic pattern, and we quantitatively characterize the pattern by location, curvature, and magnitude of the peak. *The question here is whether the basic mechanism (random location of species ranges within a pair of boundaries) can generate the observed location, magnitude, and curvature*. We finally explore the influence of species with large vertical ranges on bathymetric species diversity patterns.

2. Methods and results

We used observed and simulated data. We analyzed two data sets originally used by Rex to describe parabolic species diversity patterns. A gastropod data set was taken from Rex (1972; pers. com.), where an epibenthic sled was used to sample 41 stations, where a total of 152 species were found. Polychaete data were taken from Hartman (1965), where 21 stations were sampled with an anchor dredge and a total of 212 species were found. Both data sets represent transects across the northwest Atlantic slope.

The vertical range of a species (= bathymetric range) VR is defined in terms of the *maximum depth of occurrence* (mx) and the *minimum depth of occurrence* (mn), $VR = mx - mn$, and the mean depth of occurrence as $Md = (mx + mn)/2$. The mean depth of occurrence describes the position of the species within the depth gradient (Pineda, 1993).

Diversity was calculated using Hurlbert's (1971) modification of Sanders (1968) rarefaction index:

$$E(S_n) = \sum_{i=1}^s \left[1 - \frac{\binom{N - N_i}{n}}{\binom{N}{n}} \right]$$

$E(S_n)$ is "the expected number of species in a sample of n individuals selected at random from a collection containing N individuals, S species, and N_i individuals in the i th species" (Hurlbert, 1971). Rarefaction is a technique that reduces each sample to a standard constant size, so that samples with different number of individuals can be compared (see Gotelli and Graves, 1996).

Simulations with artificial taxa were performed to test whether parabolic patterns arise in a system that only assumes two boundaries confining a set of species. Two types of simulations were performed, each generating 1000 artificial taxa between 0 and 1000 Md arbitrary depth units, and between 0 and 666 VR arbitrary units. (The selection of both the boundaries (0–1000) and maximum VR (666) was arbitrary.)

1. Md for each species was randomly drawn from a uniform distribution. VR was then obtained by randomly drawing it from a uniform distribution from 0 to 666, repeating this process until the taxon violated neither the upper nor the lower boundary constraints.

2. VR was randomly drawn from a uniform distribution between 0 and 666. Md was then randomly drawn from a uniform distribution from 0 to 1000, repeating this procedure until the taxon violated neither the upper or lower boundary constraints.

Each taxon was then assigned a triangular distribution of abundance over its range, with peak abundance of 100 individuals at Md and decreasing abundance to zero at mx and mn . This type of distribution was chosen because it is a parsimonious model for changes of abundance through environmental gradients (Brown, 1984) and some well-sampled deep-sea populations appear to follow this pattern (Thompson et al., 1987). All taxa were then re-sampled at 19 discrete depth stations: 50, 100, ..., 950

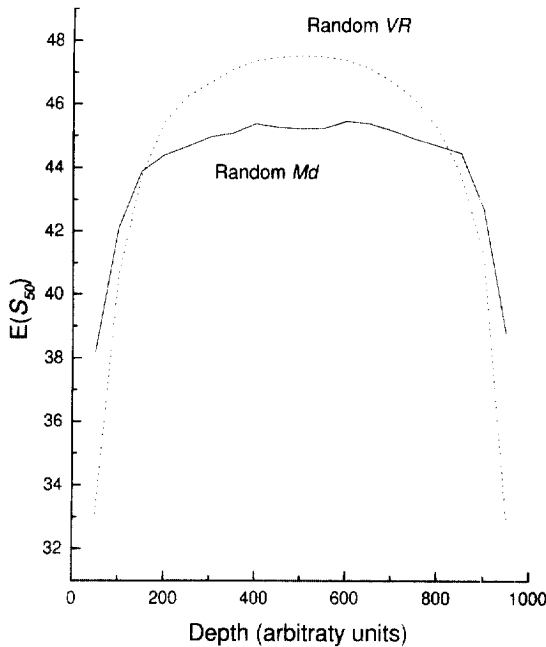


Fig. 1. Species diversity patterns with depth for artificial taxa. Artificial taxa were generated assuming a random uniform distribution in *mean depth of occurrence* and in *vertical range*.

arbitrary depth units, and $E(S_{50})$ was calculated at each station. Figure 1 shows that for both simulations diversity follows a parabolic pattern, with highest diversity at intermediate depths and lowest diversity close to the boundaries, with the curve corresponding to random *VR* shifted up with respect to the *Md* curve. Figure 2 shows distributions of *Md* and *VR* for simulations involving random *Md* and simulations involving random *VR*. Random distribution of *Md* produced a *VR* distribution skewed towards small ranges, while random *VR* produced an *Md* distribution peaking at intermediate depths.

We used a randomization procedure to test the null hypothesis that bathymetric species diversity patterns can be explained by such geometric constraints alone.

Each species in the data set is described by a vector giving its abundance at each of the depths where it was found.

A new distributional pattern was created, in which species distributions reflect only the geometric constraints on vertical range. The abundance vector for each species was moved to a new depth, chosen at random from a uniform distribution between the observed deepest and the shallowest stations. The location of the vector was adjusted so that it coincided with one of the sampling stations. The top of the range was used to line up with the sampling station (Fig. 3). This typically conserved *VR* size within very close range of its observed value. This process was repeated until the species violated neither the upper nor the lower boundary constraints.

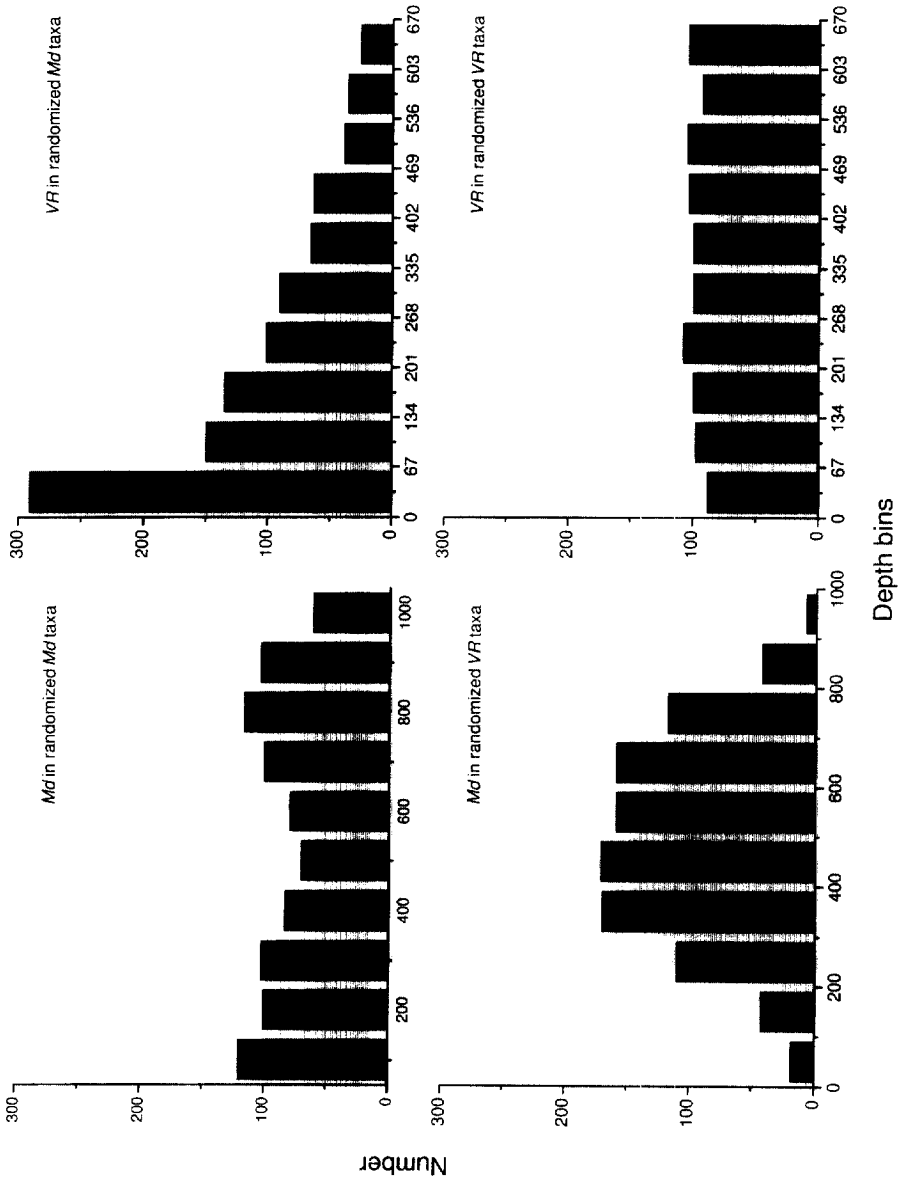


Fig. 2. Frequency distribution of *Md* and *VR* for artificial taxa used for calculating curves in Fig. 1.

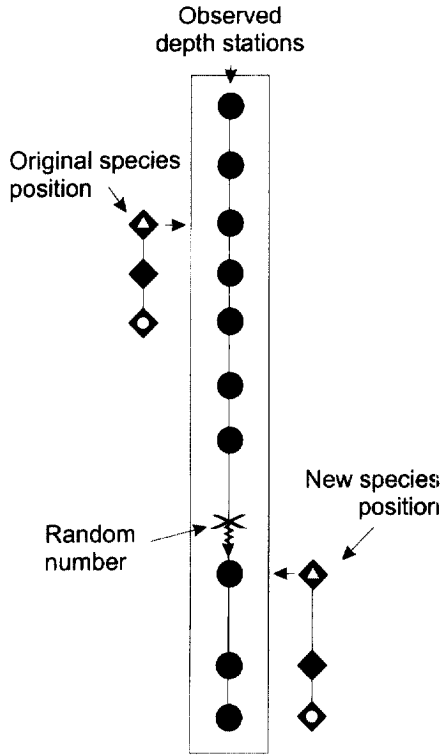


Fig. 3. Rearrangement protocol for gastropod and polychaete taxa.

Figure 4 shows the frequency distribution of the observed gastropods and polychaetes. As has been pointed before (Pineda, 1993), gastropods have a small portion of species with large VR , while this proportion is much higher for the polychaetes.

The upper and lower boundaries for the rearranged taxa were then equal to the shallowest and deepest observed stations, 69.5–5042 m for the gastropods, and 97–5001 m for the polychaetes. The shallow boundary is very close to the sea–air interface. For the deep boundaries, we choose to use the 5042 and 5001 m depths for two reasons. By using these boundaries, the parameters for our rearranged taxa can be directly compared with Rex’s original parabolic curves. This would not be the case if, for example, we had chosen a deeper boundary. Bathymetric charts show that in the geographic area of interest from which these data sets were obtained, the northwest Atlantic from 30° to 60°N latitude and from the coastline to about 45°W longitude, the deepest bottom is less than 6000 m (Anonymous, 1982).

From the set of randomized distribution, $E(S_{50})$ was calculated at each sampling station. A quadratic polynomial ($y = a + bx + cx^2$) was fit to the data to express the relationship between diversity and depth.

This randomization procedure was repeated 100 times, generating a distribution of depth regressions that reflect the geometric constraints. We can compare several aspects of this distribution with the observed data:

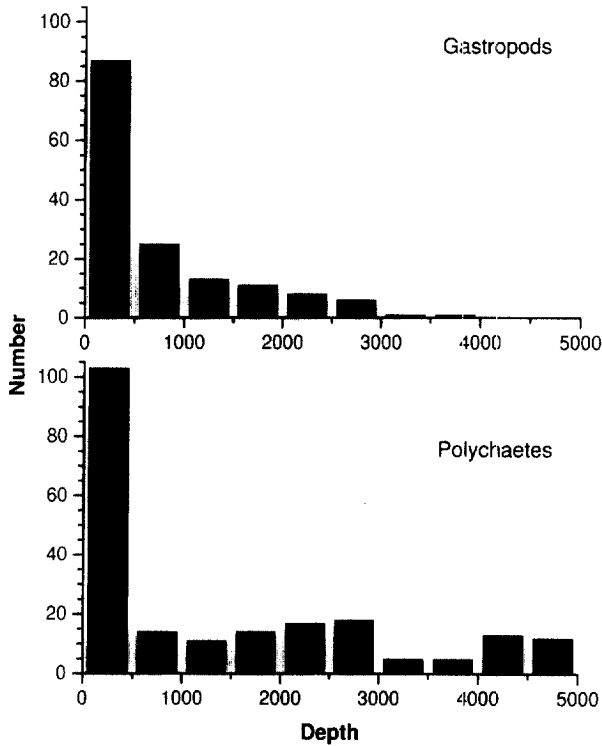


Fig. 4. Frequency distribution of vertical range for gastropod taxa in Rex (1972; pers. com.) and polychaete taxa in Hartman (1965).

1. Curvature (how peaked is the diversity curve?). The sharpness of the peak is given by the second derivative of diversity with respect to depth, evaluated at the peak; this is proportional to the coefficient c from the regression. The more negative c is, the sharper the peak in the diversity curve.
2. Location (at what depth does the peak in diversity occur?). This depth is given by

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

3. Magnitude (how high is the diversity peak?). This is given by

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

Figures 5 and 6 show the results of the regression analysis of the randomized data, compared with the observed fit. It is apparent that randomizing the data does not eliminate the peak in diversity at intermediate depths. The location of the diversity maximum in the randomized data agrees with the real data in the gastropod analysis, but not in the polychaete data. The magnitude of diversity at its peak is less in the randomized than in the real data.

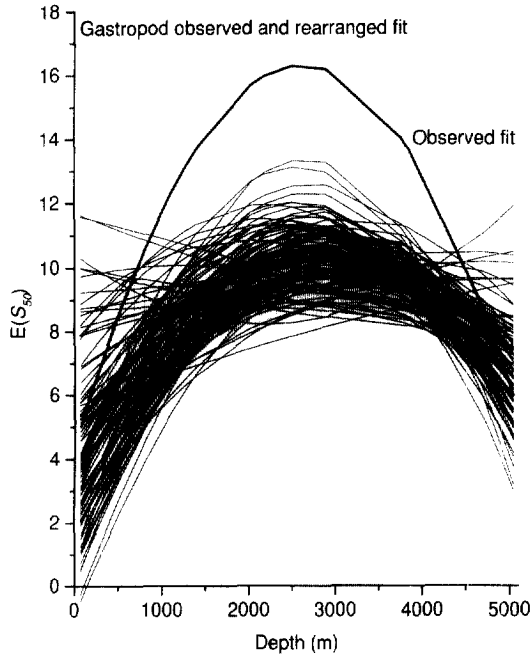


Fig. 5. Parabolic fit for $E(S_{50})$ values with depth for observed (heavy line) and rearranged gastropod taxa.

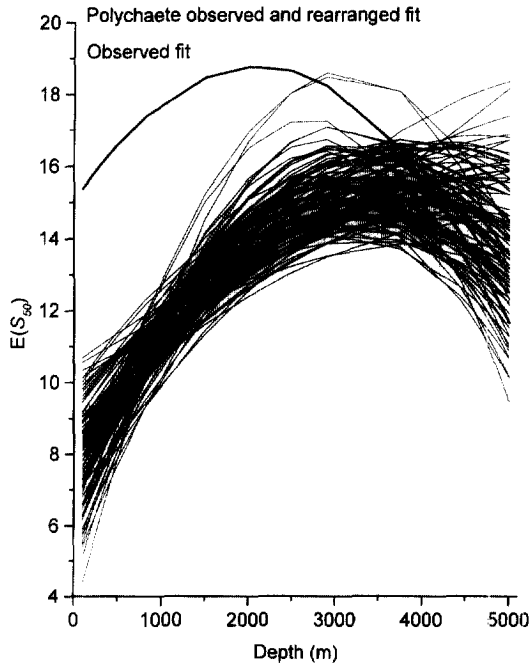


Fig. 6. Parabolic fit for $E(S_{50})$ values with depth for observed (heavy line) and rearranged polychaete taxa.

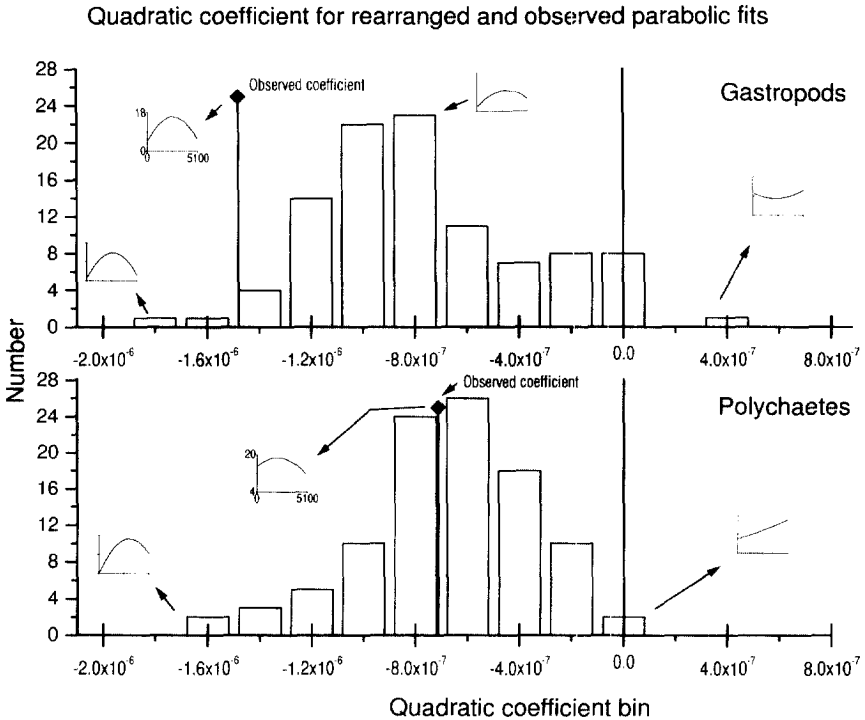


Fig. 7. Frequency distribution of quadratic coefficient c of the parabolic equations in observed (drop line) and rearranged fits. Small curves are samples of diversity patterns generated with the observed or rearranged fits.

These observations can be turned into hypothesis tests by comparing the observed curvature, location, and magnitude with the distribution obtained from the randomized data. Figure 7 shows the comparison for the curvature: only two of the randomized gastropod data sets produced a diversity curve as peaked as the observed data. We have to reject the null hypothesis that the curvature of the gastropod diversity curve can be explained by the geometric constraints. For polychaetes, however, the observed curvature falls in the middle of the distribution of the randomized data, and we cannot reject the null hypothesis. The observed gastropods location falls in the middle of the randomized-taxa distribution (Fig. 8). The null hypothesis that geometric constraints alone explain the position of the peak in diversity for the gastropods cannot be rejected. For the polychaetes, the observed location occurs to the left, with only one randomized value to the left of the curve (see Fig. 8 legend), and the null hypothesis that location is explained only by geometric constraints is rejected. The magnitude of the peak in diversity for both gastropods and polychaetes falls to the right (Fig. 9), with only one higher randomized in each case. In both gastropod and polychaetes, we then reject the hypothesis that geometric constraints alone explain the magnitude of the peak in diversity. Table 1 summarizes null hypotheses results for gastropods and polychaetes.

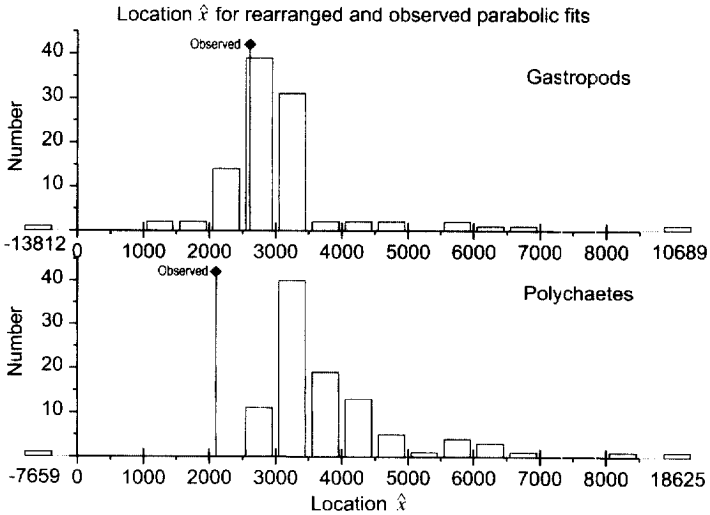


Fig. 8. Frequency distribution of location \hat{x} in observed (drop line) and rearranged fits. Very high and low off-scale values in the figure represent concave-up curves and curves with very low-curvature.

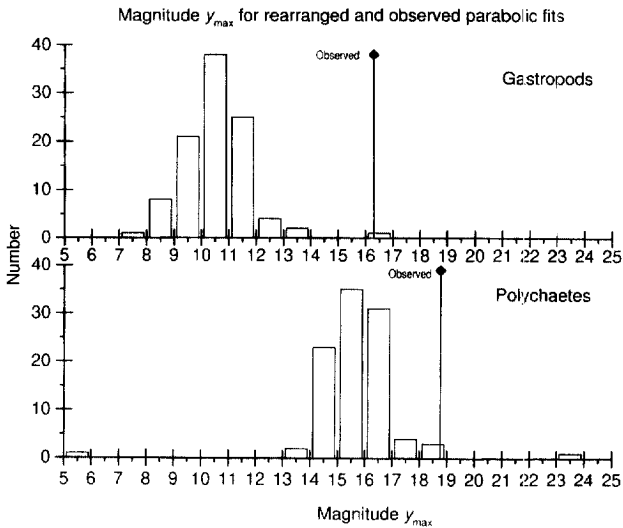


Fig. 9. Frequency distribution of magnitude y_{max} in observed (drop line) and rearranged fits. Very low and high values in the randomized taxa represent concave up curves, and curves with very low curvature, peaking at > 10000 m.

Our analysis so far has used the deepest stations reported by Rex and Hartman (5042 and 5001 m) as the lower boundaries. Other areas in the northwest Atlantic, although restricted, may be deeper, perhaps up to ~ 6500 m. In response to suggestions that our use of the deepest stations, rather than the maximum depth, as a lower

Table 1
Null-hypothesis tests for components of species-diversity parabolic trends

Component of diversity parabolic pattern	Gastropods	Polychaetes
Curvature	Reject	Cannot reject
Location	Cannot reject	Reject
Magnitude	Reject	Reject

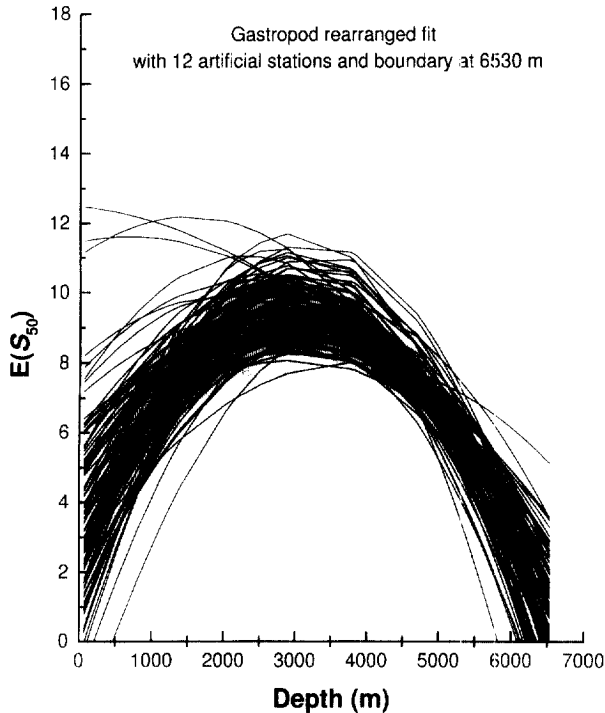


Fig. 10. Parabolic fit for $E(S_{50})$ values with depth for rearranged gastropod taxa using artificial stations with a deepest boundary of 6530 m.

boundary might be responsible for the persistence of parabolic patterns in our randomizations, we repeated the shuffling protocol described above, allowing species ranges as deep as 6500 m.

Of course, this procedure generates diversities and abundances in the depth range of 5000–6500 m that are based strictly on species shifted downward from shallower stations because there are no data on species that are actually present in that depth range. Artificial stations were created between 5042 and 6500 m and between 5001 and 6500 m. For both gastropods and polychaetes, the spacing of the new artificial

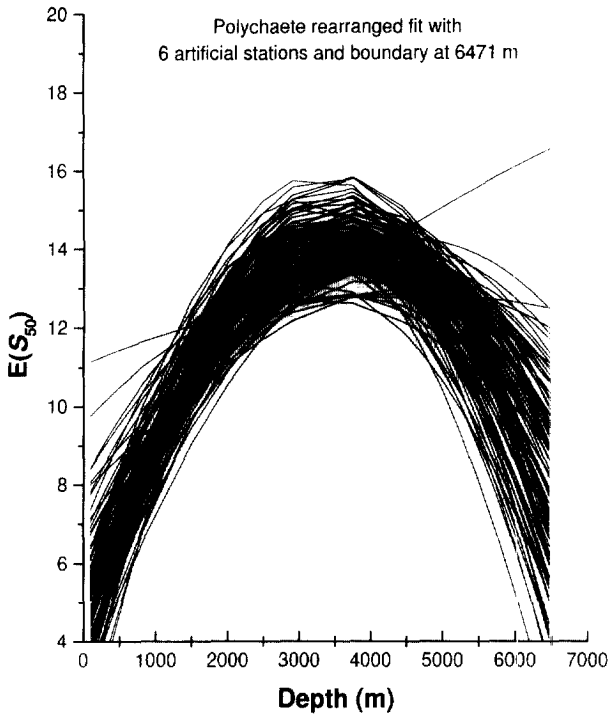


Fig. 11. Parabolic fit for $E(S_{50})$ values with depth for rearranged polychaete taxa using artificial stations with a deepest boundary of 6471 m.

stations was equal to the mean difference between observed stations rounded to the nearest integer, while the number of new artificial stations was determined as $(6500 - \text{observed depth})/\text{mean difference between observed stations}$, rounded to the nearest integer. This resulted in 12 new artificial stations separated by 124 m for the gastropods, with the deepest station at 6530 m, and six new artificial stations separated by 245 m for the polychaetes, with the deepest station at 6471 m. Figures 10 and 11 show that the parabolic patterns, especially over the observed range of 0–5000 m, persist with this new randomization, for both gastropods and polychaetes. These comparisons are only intended to be qualitative. We have not repeated the quantitative statistical analysis, because of the lack of samples below 5042 m.

To investigate the influence of large vertical range on species diversity patterns, we performed selective removal of species in observed and simulated taxa. Figures 12 and 13 (top panels) show $E(S_{35})$ with depth for the gastropod and polychaete taxa (originally calculated by Rex, 1981) and corresponding parabolic fits. Figures 12 and 13 (bottom panels) shows $E(S_{25})$ for the gastropod and polychaete taxa after removing 25% of the species with the largest vertical range, and least-squares linear regression lines. Lines were drawn for identifying dominant patterns, not for statistical purposes. For both groups, diversity increases at intermediate depths and then decreases at both

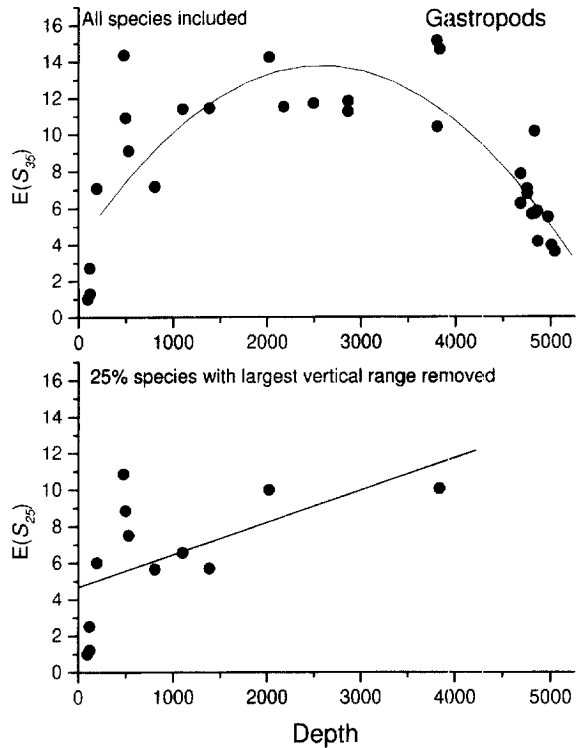


Fig. 12. Species diversity with depth for gastropod taxa in the northwest Atlantic. Originally shown and calculated by Rex (1981). Including all species (top), and after removing 25% species with the largest vertical range (bottom).

shallow and abyssal depths in the original plots (Rex, 1981), but this trend disappears in both cases after removing the species with the largest ranges. Fewer points are available for the curves corresponding to the data sets where 25% of the species was removed because it was algebraically impossible to calculate $E(S_{25})$ in missing points. Figure 14 shows $E(S_{50})$ with depth for simulated taxa in Fig. 1 (randomized Md) after having removed 0, 15, 30, and 45% of the species with the largest vertical range. The parabolic pattern disappears progressively as species with largest vertical ranges are removed.

3. Discussion

Osman and Whitlatch (1978) argued that diversity patterns could be artifacts emerging in open, dynamic systems, and pointed out that some diversity patterns had no ecological or biological basis. Colwell and Hurtt (1994) also found that species diversity patterns could arise without invoking ecological gradients. They simulated

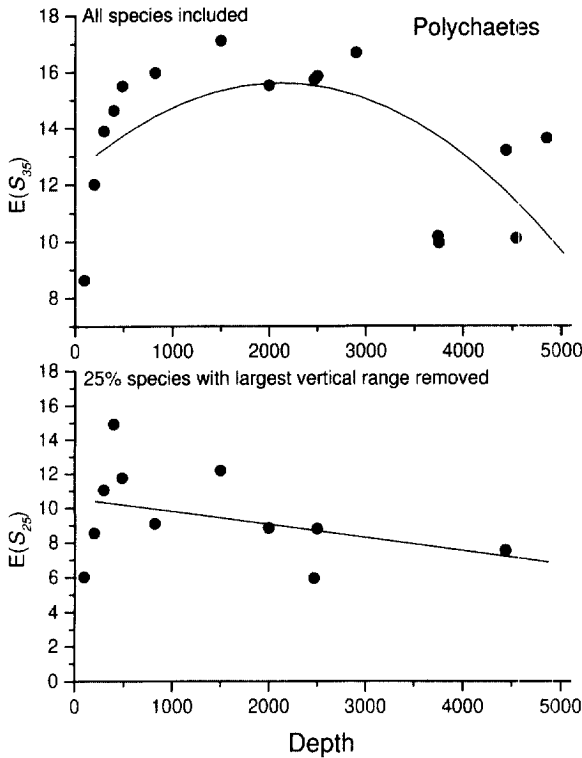


Fig. 13. Species diversity with depth for polychaete taxa in the northwest Atlantic. Originally shown and calculated by Rex (1981). Including all species (top), and after removing 25% species with the largest vertical range (bottom).

a system where a set of species was constrained within two boundaries, and found that species richness increased in the mid-zone between the boundaries. They randomized medium depth of occurrence *Md*. Our simulation results corroborate their results for *Md* and also show parabolic patterns for randomized vertical range *VR*. These results suggest that parabolic diversity patterns are an emergent property of a system consisting of two boundaries constraining a set of species. It appears that *VR* distribution and the ecological factors determining it may be of major importance for understanding parabolic diversity patterns.

Our randomized tests on polychaetes and gastropods identified three aspects of the parabolic diversity pattern: curvature, location, and magnitude. Randomization tests give mixed results. Only one of three features can be explained on the basis of random rearrangements of species within geometric constraints. Furthermore, gastropod and polychaete randomization results differ in different aspects of the parabolic pattern. For gastropods, we reject the null hypothesis that geometric constraints alone could explain curvature and magnitude, while we could not reject for location. For polychaetes, the null hypothesis of geometric constraints alone explaining location and

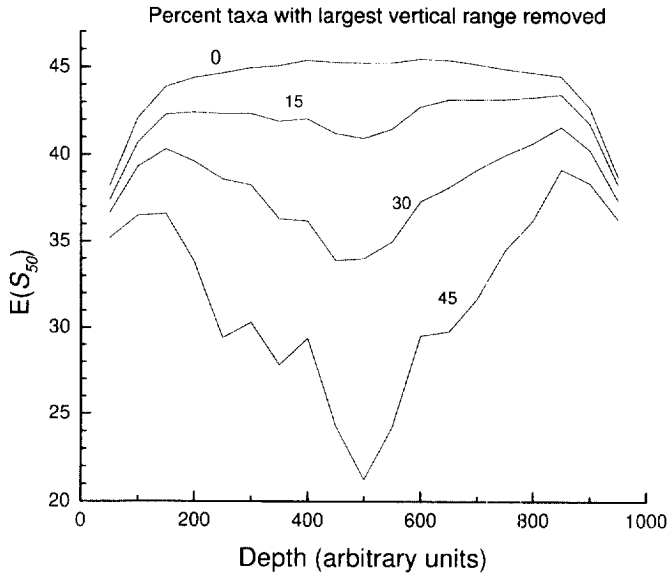


Fig. 14. Species diversity patterns with depth for artificial taxa with removal of 0 (= Fig. 1), 15, 30 and 45% of the species with the largest vertical range. Artificial taxa were generated assuming a random uniform distribution in *mean depth of occurrence*.

magnitude was rejected, but we were unable to reject the null hypothesis for curvature. These differences between taxa may have implications for originally observed patterns. If original gastropod and polychaete diversity patterns were similar, one would expect that null-hypothesis tests for the different aspects of the diversity pattern would produce consistent results across taxa. This was not the case, however, and these differences suggest that the original patterns for gastropods and polychaetes observed by Rex (1981, 1983) differ, and that these differences are related to two different aspects of the parabolic pattern, curvature and location. In summary, while random rearrangement of observed taxa generally produced parabolic diversity patterns, our randomizations did not account for most parameters of the observed patterns. We conclude then that while geometric constraints can contribute to parabolic patterns, observed patterns (Rex, 1981, 1983) result from a non-random distribution of species along the depth gradient.

Ideally, a data set to be analyzed in this way would extend all the way to the deepest depths in the region. The data that we used extended only to ~ 5000 m, although there may be depths as great as ~ 6500 m in the Northwest Atlantic. Our randomizations distributing species vertical ranges over this extended range showed that the parabolic patterns are not an artifact of the restricted depth range of the samples. However, because these randomizations distribute the data over a range $\sim 30\%$ greater than that over which they were observed, we cannot reliably conduct statistical tests on the quantitative details of the parabolic patterns.

We found that the parabolic pattern is also sensitive to removal of species with large vertical range in both observed and artificial taxa. (A 25% removal “experiment” of species with the smallest vertical ranges fails to remove the patterns; results not presented.) Species with large vertical ranges may overlap in more mid-depth regions along the depth gradient, and then produce a more peaked diversity pattern. The proportion of large-ranged species varies in different taxa. For example, polychaetes have a large proportion of species with large ranges, while this proportion is notably smaller in gastropods or desmosomatid isopods (Fig. 4; Pineda, 1993). Given that parabolic patterns in species diversity are sensitive to the removal of species with large ranges, and given that there is variation in the proportion of species with large ranges across taxa, variation in diversity patterns possibly may correlate with variation in the proportion of species with large ranges.

Stevens (1996) recently suggested the extension of the Rapoport-rule species-diversity hypothesis to bathymetric patterns. A single data set for coastal fish from Baja California to Alaska showed that as diversity decreased with depth, vertical range increased. Unfortunately, because the data set is for coastal fish, the evaluation is incomplete because it ignores the largest portion of the bathymetric gradient, where parabolic trends in several taxa, including fish, have been previously found (Rex, 1981, 1983). In fact, there is no reference to the well-known phenomenon of parabolic diversity patterns. Pineda (1993) also argued previously that the Rapoport rule transported to the depth gradient domain cannot explain parabolic diversity patterns, because observed phenomena in the benthic deep-sea refuted Stevens (1989) prediction that the zone within the depth gradient with highest species diversity would include species with the smallest vertical ranges. Observations in the deep sea show that smallest vertical ranges tend to aggregate in the vicinity of the boundaries, corresponding to the zones of lowest diversity (Pineda, 1993). This is opposite to the prediction of Stevens' hypothesis. Other marine studies also contradict Stevens' hypothesis (Rohde *et al.*, 1993; Roy *et al.*, 1994). In summary, while our results demonstrate that vertical range is important for understanding diversity patterns, the best-known hypothesis linking distributional ranges with species-diversity gradients (Stevens, 1989) fails to explain observed patterns in the benthic deep sea.

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