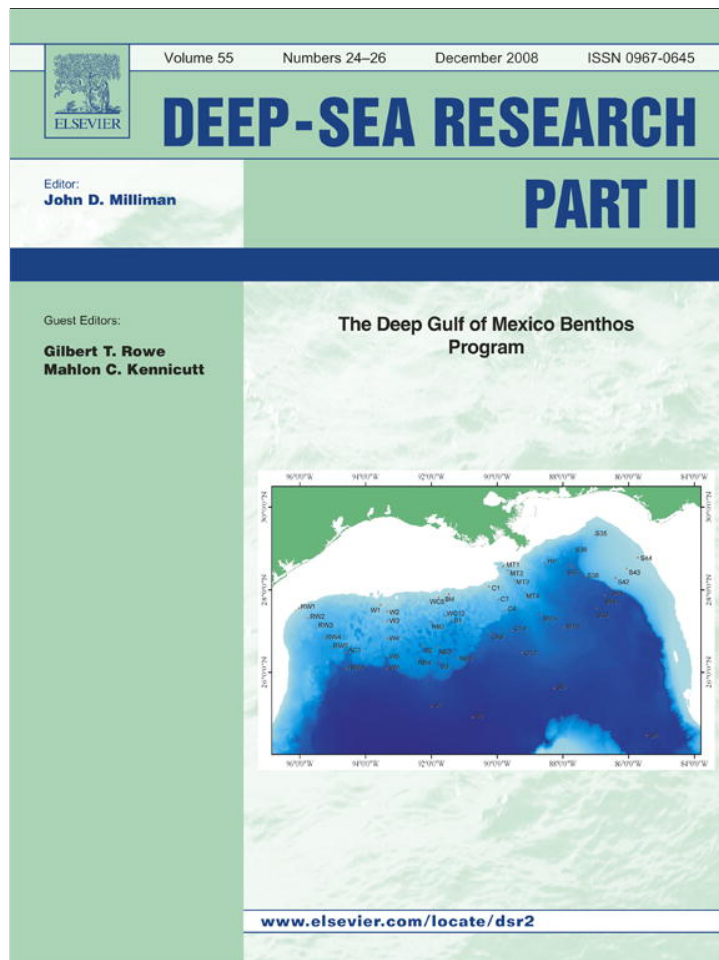


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Predictors of species richness in the deep-benthic fauna of the northern Gulf of Mexico

Richard L. Haedrich^a, Jennifer A. Devine^{b,*}, Valerie J. Kendall^a

^a Department of Biology, Memorial University, St. John's, NL, Canada A1B 5S7

^b National Institute of Water and Atmospheric Research, Wellington 6241, New Zealand

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ABSTRACT

Species richness in macrofauna and megafauna collected with box cores and trawls from 35 standard stations over a depth range of 175–3720 m in the northern Gulf of Mexico was examined in terms of two primary questions: (1) are observed patterns random? and (2) if not, what environmental factors might account for the patterns? A null model tested whether richness vs. depth distributions were random. Groups with species that had broad vertical depth ranges fit the null model better than groups with small ranges, but for almost all phyla a non-random pattern was indicated. With randomness as a proximal explanation ruled out, further examination of the relationship between richness and environmental factors was justified. A generalized linear model (GLM) showed that a suite of 18 factors categorized as food-related, habitat-related, pollution-related and location-related were significantly related to richness patterns, but that different mixes of factors applied to different phyla. No one factor accounted for any observed patterns. Thus, each taxonomic group needs to be examined individually, and no generally applicable explanation for the causes of richness patterns may exist. Nonetheless, mapping richness itself indicates valuable areas in the Mississippi Trough that must receive special consideration and possible protection.

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1. Introduction

Building on the original analysis of Vinogradova (1962), Rex (1981) presented the first general overview concerning the existence of a mid-depth biodiversity maximum in the benthic fauna of the deep sea. His empirical observations from the northwestern Atlantic showed that many diverse taxonomic groups, including polychaetes, gastropods, protobranch mollusks, cumaceans, megafaunal invertebrates generally and demersal fishes, displayed what he termed a parabolic pattern of richness. As a contribution to the then active debate around causes of diversity in the deep ocean, Rex (1983) discussed food availability, predation, competition and spatio-temporal heterogeneity as potential determinants to account for the pattern observed.

Pineda (1993) laid the foundation for a simpler explanation. He argued that a parabolic pattern could arise simply due to constraints imposed by the geometry of ranges. If ranges were large in relation to the full domain, i.e. the maximum and minimum depth boundaries of the region under study, then a mid-depth maximum could result from purely random distribution of the ranges. In such a case, no ecological explanations

would be needed. Pineda's (1993) idea was further developed by Pineda and Caswell (1998) and has become formalized into the notion of the mid-domain effect (MDE) with the suggestion that this null model could account for numerous observations of similar diversity maxima across latitude and altitude, as well as depth, gradients (Colwell and Lees, 2000).

Some support for MDE has been found in terrestrial studies (e.g. McCain, 2004), but for the most part the results are at best ambiguous (Hawkins and Diniz-Filho, 2002; Connolly et al., 2003; Zapata et al., 2003). Studies to date on the MDE in the deep sea have relied on research that was conducted primarily to describe the deep-sea fauna. Most analyses are based on data from the northwestern Atlantic and focus primarily on macrofauna. Pineda and Caswell (1998) concluded that random re-arrangements of ranges did not explain the richness patterns for gastropods and polychaetes. McClain and Etter (2005) undertook a substantial review involving gastropods, bivalves and polychaetes from multiple locations, and found that empirical patterns in all cases differed greatly from those generated randomly. Kendall and Haedrich (2006) found no support from patterns in Atlantic fish distributions on both regional and basin scales.

The lack of evidence for a strong MDE in the ocean does not diminish the utility of null models as a first consideration in exploring diversity patterns. In any study of diversity patterns, it would be wise to first test for randomness. Veech (2000) offers a

* Corresponding author.

E-mail address: ja.devine@gmail.com (J.A. Devine).

simple yet powerful test that adopts an approach similar to that of Pineda and Caswell (1998). The method provides a statistical basis to test the degree to which an empirical distribution differs significantly from the distribution predicted by a null model that randomly distributes the observed ranges across a depth gradient.

If the null model does not apply (i.e., non-randomness is demonstrated), then further analysis to ascribe ecological explanations is justified. Levin et al. (2001) reviewed possible determinants, and offer a list that updates but mirrors in many respects that suggested by Rex (1981), including gradients of productivity, sediment heterogeneity, oxygen availability, hydrodynamic regimes and catastrophic physical disturbance. In the 20 years that separate the two papers, there have been a number of studies that add to a general understanding of deep-sea diversity patterns (Snelgrove and Smith, 2002) but there is still a lack of detailed observations across diverse taxa from the same sites within any region.

The comprehensive data from the DGoMB project (Rowe and Kennicutt, 2008; Powell et al., 2003), which uniformly assessed the benthic fauna and their environments at a series of standard stations across the depth gradient in the northern Gulf of Mexico, offer an opportunity to address a number of questions related to both the MDE and richness patterns: Do groups with large ranges fit the null model better than those with small ranges? Do different taxonomic groups respond differently? Is it justified to search associated environmental data for non-random (i.e. physical/biological) causes to fit the empirical patterns? If so, what factors seem to play the greatest role? This paper focuses a quantitative inquiry on two primary concerns: (1) the randomness of observed patterns and (2) environmental factors significantly associated with the observed pattern.

2. Methods

Data are found in and derived from the DGoMB data archive. Many people have contributed to these, and we especially appreciate the care taken by taxonomists in developing such an important data set. The information consists of taxonomic units and the number of individuals within each unit taken at a series of standard stations. The state of taxonomic knowledge varies from group to group; effort was made to resolve taxa to the species level but in some cases only family level was possible. Macrofauna were collected with box cores (Boland and Rowe, 1991) and megafauna were collected with bottom trawls (Powell et al., 2003).

An updated version of the computer program RangeModel, first presented by Colwell and Lees (2000), is available online (<http://viceroy.eeb.uconn.edu/RangeModel>). The model randomly places empirical ranges within the domain, thereby generating new mid-points for these ranges that can be used to construct a richness vs depth curve that is entirely random. RangeModel provides a graphic application and visualization of the earlier models of Pineda and Caswell (1998) and Lees et al. (1999).

RangeModel 4 was used to derive empirical and randomized distributions of species richness in 15 bins across the depth gradient from 175 to 3720 m (= the domain), i.e. 236 m/bin. Broad taxonomic groups were examined individually. Because richness in each bin is a count of the number of ranges that occur in that bin, no standardization by rarefaction could be applied. Data for individual species of amphipods, aplacophorans, cumaceans, fishes and polychaetes were divided into those with small ranges (species with ranges < within-group overall mean) and those with large ranges (> within-group overall mean). The relationship of empirical to randomized distributions across the domain was compared using Pearson's r^2 as the metric. The

same test was also applied to groups as a whole, i.e. no sub-division on the basis of small vs large within the group. The expectation was that large-range groups would have a higher r^2 than small-range groups. Because the binned data are not independent (Veech, 2000), r^2 is used as a metric only with no associated statistical meaning. The likelihood that the means of that metric are the same in the two groups being compared was assessed with an unpaired t -test.

The Veech (2000) program (<http://www.esapubs.org/archive/ecol/E081/010/default.htm>) tested for fit of the observed pattern within a group to a null model. The Veech approach uses displacement, D , as an index of how much the empirical curve differs from a simulated random one:

$$D = \sum |d_j| / n$$

with d the distance between observed and simulated null values at each sampling point $j = 1, 2, \dots, n$. Where $D_{\text{obs}} > D_{\text{sim}}$ there is no overlap. We used 1000 iterations to derive the simulated composite curve, and generated 500 null curves for each dataset to estimate the probability that $D_{\text{obs}} \leq \max D_{\text{sim}}$ for any individual run. Although there was no *a priori* expectation regarding which groups would best fit a null model, the general expectation was that the difference between observed and simulated might be more for smaller, less motile macrofauna than for larger, more motile megafauna. The argument is that the megafauna would have greater depth ranges and thus geometry alone would result in their mid-points falling necessarily more towards the center of the domain than would those for the probably smaller depth ranges of macrofauna.

Preliminary examination of the data using principal component analysis had indicated that three components could describe 51% of the variance and more than 10 components were needed to account for 90%. Because so many factors were needed to explain the variance, we felt using another technique to predict relationships between richness and external factors would be more appropriate. Backwards-stepwise regression was chosen as the most effective approach because of the suspected collinearity between environmental factors. We employed a generalized linear model (GLM) with a Poisson error structure and a log link to test for relationships between species richness and environmental factors:

$$S_i = \beta_0 + \beta_1 x_1 + \dots + \beta_j x_j + \varepsilon$$

where S_i is the species richness for phylum i and x the environmental factors 1 through j . The Poisson distribution was deemed appropriate for six phyla; overdispersion, however, was a problem for cumaceans, isopods, polychaetes, fishes, arthropods and echinoderms. Scaling the deviance of the model to the generalized chi-squared statistic divided by the residual degrees of freedom or using some other distribution, such as the negative binomial, can correct overdispersion. Analysis of the residuals, however, indicated that a negative binomial model was not appropriate for our data, and therefore we corrected for overdispersion by scaling the deviance. GLM identified the environmental factors significantly related to species richness for a given phylum by generating a final regression model iteratively. The reduction in residual deviance relative to the null deviance, denoted as R^2 , was calculated for each single term potentially added to the base model. A term was added to the model if it improved the residual deviance by at least 10% and remained in the model if its inclusion resulted in a reduction in residual deviance by 5% ($p \leq 0.05$). This approach produced a parsimonious model with moderate explanatory power.

Following analysis with GLM, Spearman rank correlation was performed on the factors that emerged as significant. Factors were

categorized as being predominately food-related, habitat-related, location-related or pollution-related.

3. Results

Table 1 compares the r^2 values of artificially constructed sets of small- and large-range species within six major taxonomic groups. The values for large-range species (mean = 0.47, s.d. = 0.24, range 0.22–0.85) are significantly higher (unpaired t -test, $p < 0.002$) than those for small-range species (mean = 0.06, s.d. = 0.06, range 0.002–0.16). Table 2 presents the empirical data for all groups considered, arranged in order of increasing mean range size. With fishes ($r^2 = 0.001$) considered separately, the r^2 's of megafaunal groups (mean = 0.38, s.d. = 0.20, range 0.15–0.67) are significantly higher (unpaired t -test, $p < 0.02$) than those for macrofaunal groups (mean = 0.12, s.d. = 0.13, range 0.023–0.36).

Although the individual richness patterns differ, none, with the possible exception of that for isopods, are particularly parabolic and many are skewed to the left and/or diminish sharply to the right (Fig. 1). Table 3 presents the results of the Veech analyses to test the null model against the observed distribution of richness in each group. In almost all cases the probability = 0 that the displacement value observed is less than that derived from null model simulations (i.e. $D_{obs} \leq \max D_{sim}$). For Aplacophora and Cnidaria the probability is very small ($p = 0.002$ and 0.008), but for Porifera $p = 0.43$. In the latter group, this could reflect the fact that the taxonomy is poorly resolved and identifications were not just to species but to higher categories as well. Aplacophora and Cnidaria had the fewest number of taxa recorded (both with 19) after Porifera, but these were mostly resolved to the species level. Veech (2000) indicates that the power of his test is low when richness is < 20 and the number of zones (bins) < 10 .

GLM was used to explore the environmental data associated with the DGoMB faunal collections for possible relationships with

Table 1
Artificially constructed sets comprising small and large ranges from real data

Group	N small	N large	r^2 Small	r^2 Large
Amphipods	69	31	0.16	0.53
Aplacophorans	10	9	0.04	0.59
Cumaceans	28	26	0.002	0.42
Fishes	77	40	0.09	0.23
Isopods	80	56	0.004	0.85
Polychaetes	116	86	0.08	0.22

N is the number of taxa in each set; r^2 is the Pearson correlation index comparing the empirical to the randomized richness distribution.

Table 2
Minimum and maximum depths of occurrence (m), mean range size (m), number of taxa and r^2 as in Table 1 by group

Group	Min Z	Max Z	Mean range	Species	r^2
Porifera	175	3400	545	4	0.389
Amphipods	213	3670	657	100	0.047
Aplacophorans	213	3008	718	19	0.025
Fishes	213	3075	886	116	0.001
Isopods	213	3732	1042	136	0.363
Molluscs	175	3720	1121	39	0.154
Polychaetes	213	3732	1220	202	0.023
Cumaceans	213	3526	1275	54	0.190
Cnidarians	321	3675	1447	19	0.232
Arthropods	175	3720	1552	66	0.466
Bivalves	211	3732	1694	94	0.098
Echinoderms	175	3720	1770	44	0.666

Megafauna are indicated by boldface.

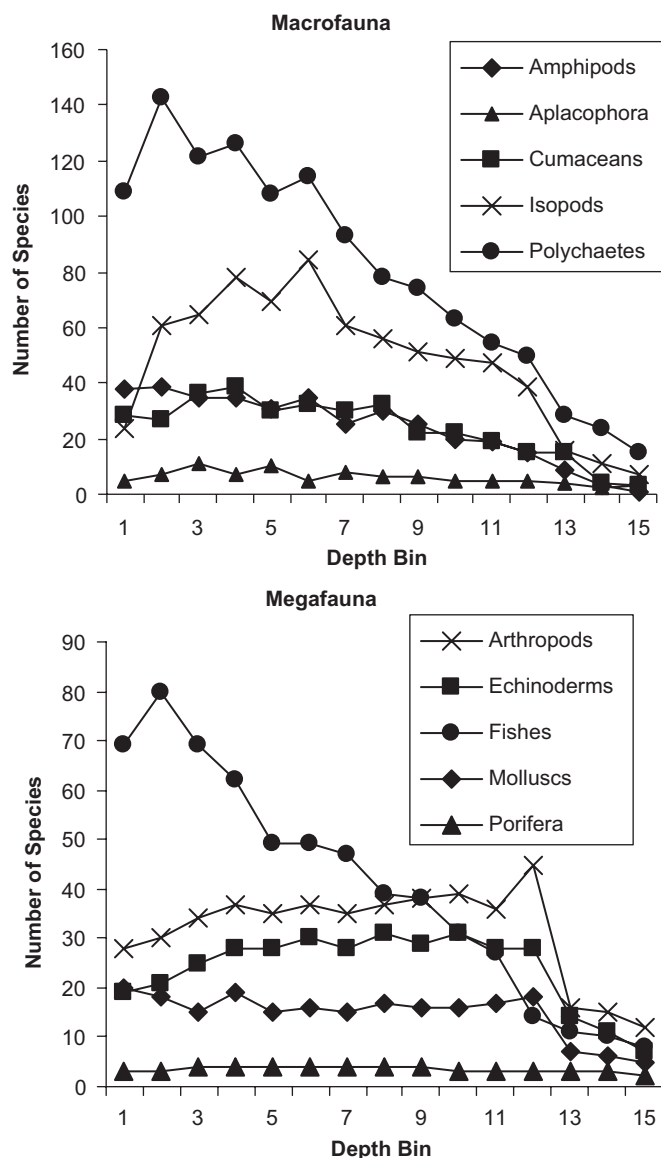


Fig. 1. Observed species richness of macrofaunal and megafaunal groups in 236-m depth bins across the depth gradient from shallow to deep, northern Gulf of Mexico.

Table 3
Results of Veech analysis

Group	D_{obs}	Max D_{sim}	Min D_{sim}	$p: D_{obs} \leq D_{sim}$
Amphipods	12.3	6.6	1.0	0
Aplacophorans	2.4	2.6	0.5	0.002
Arthropods	5.8	4.1	0.9	0
Bivalves	18.3	7.6	1.0	0
Cnidarians	2.5	2.8	0.5	0.008
Cumaceans	9.7	4.6	0.7	0
Echinoderms	3.6	3.4	0.7	0
Fishes	21.2	7.3	1.3	0
Isopods	18.7	7.3	1.3	0
Molluscs	4	2.9	0.5	0
Polychaetes	40.6	8.8	1.5	0
Porifera	0.5	0.7	0.3	0.43

D_{obs} is the actual displacement, D_{sim} is the displacement for a randomized distribution (1000 iterations) and p is the probability that D_{obs} is ever less than or equal to D_{sim} in 500 runs.

Table 4

Maximum Spearman rank correlation (whether positive or negative) within the four categories food, habitat, pollution and location, and the associated factor (from GLM) for each group, Porifera excluded

Group	Food	Habitat	Pollution	Location
Amphipods	0.78 Meio-biomass	0.26 Silt	–	–0.79 Depth
Arthropods	0.20 Meio-biomass	–0.25 Clay	–0.12 Barium	–0.05 Depth
Bivalves	–0.09 Chl <i>a</i>	0.32 Silt	0.44 Barium	0.13 Latitude
Cnidarians	–0.10 Meio-biomass, no nematodes	–	0.25 PAH, no perylene	0.24 Depth
Cumaceans	0.57 Meio-biomass	0.12 Sand	0.21 Barium	0.64 Latitude
Echinoderms	0.21 Chl <i>a</i>	–	–	0.18 Depth
Fishes	0.61 Macro-biomass	–0.06 Clay	0.19 PAH, no perylene	0.26 Longitude
Isopods	–0.36 POC	0.16 Sand	–	–0.06 Longitude
Molluscs	–0.40 Chl <i>a</i>	–0.18 Clay	0.00 PAH, no perylene	0.13 Longitude
Polychaetes	0.80 Meio-biomass	0.15 Silt	0.09 PAH, no perylene	0.66 Latitude

Macrofauna

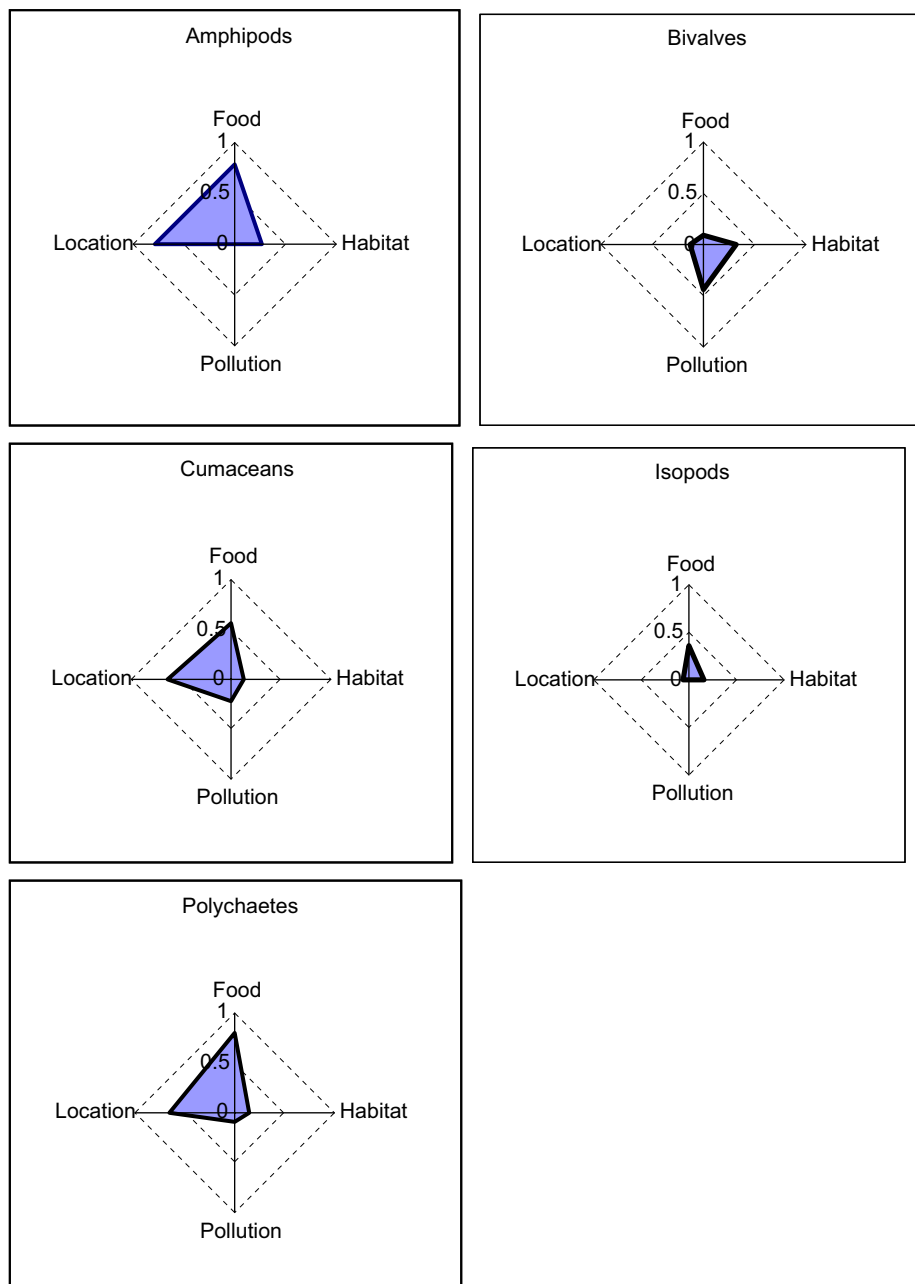


Fig. 2. Radar plots of maximum Spearman correlation within categories of food, habitat, pollution and location to species richness for macrofaunal groups. Data from Table 4.

species richness. Table A1 in Appendix A lists the 18 physical/biological factors that were identified by the GLM as having a significant relationship with richness in four categories—food, habitat, pollution and location; for all variables that emerged as significant, the strength of each relationship was measured by Spearman rank correlation. There are only 3–4 factors in total that emerged as significant for Cnidaria, Aplacophora and echinoderms, but for amphipods, mollusks and arthropods there are 10–12. The individual Spearman correlation and the associated factor within each category are listed in Table 4 and are plotted, as absolute values, in Figs. 2 and 3 by phylum. Table 4 shows, for example, that amphipod richness was related most positively to a food factor, most negatively to location, somewhat positively to habitat, and not at all to pollution. For amphipods, the individual factors with the strongest correlations were meiofaunal biomass

(food), percent silt (habitat) and depth (location, and no doubt a reflection of reduced amphipod richness with depth). Echinoderm richness, as another example, was only weakly related to two factors: chl *a* (food) and depth (location), both positively. In the radar (or star) plots of Figs. 2 and 3, the absolute values of the maximum Spearman correlation within each of the broad categories are plotted on the four axes and the points are connected to present an area.

4. Discussion

Pineda and Caswell (1998) suggested on intuitive grounds that groups of species with large ranges would fit the MDE model better than groups displaying small ranges. They showed this was

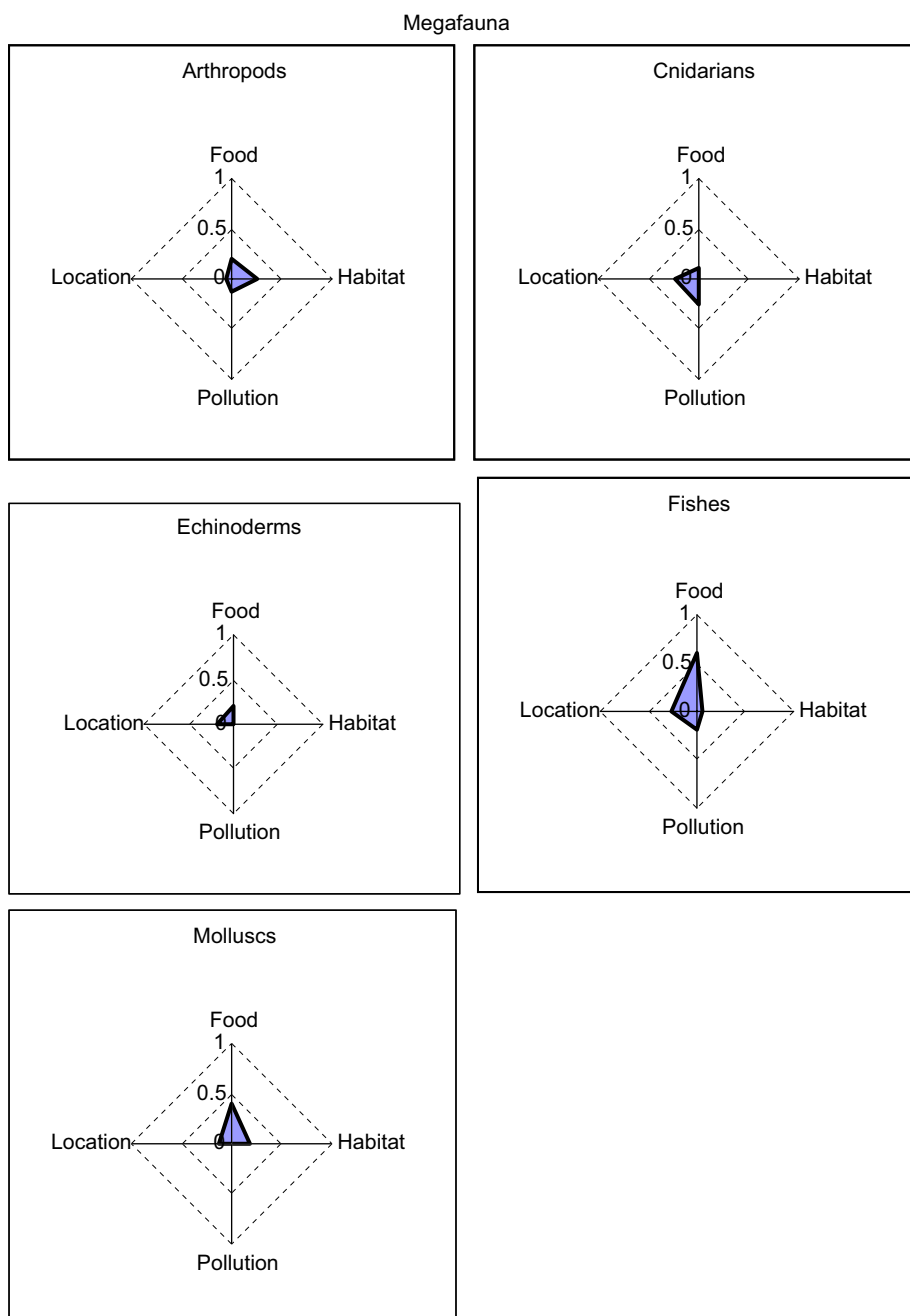


Fig. 3. Radar plots of maximum Spearman correlation within categories of food, habitat, pollution and location to species richness for megafaunal groups. Data from Table 4.

so for their data on gastropods and polychaetes by progressively removing species with large ranges and observing that the parabolic pattern was reduced. We compared artificial sets in a similar way by testing whether the small-range species within a group responded differently from the large-range ones within the same group. The differences (Table 1) are significant. The null model fits the richness distribution of species with large ranges better.

While the suggestion of Pineda and Caswell (1998) appears to hold for artificially constructed data sets, the picture derived from real data is less clear. We had assumed that the larger, more motile megafauna would have larger ranges than the smaller, less motile macrofauna, and therefore that megafaunal patterns of richness might better fit the null model. But there is no significant difference between the mean range size in macrofauna and megafauna. Porifera (megafauna) and amphipods (macrofauna) have the smallest ranges found in the Gulf of Mexico benthos and bivalves (macrofauna) and echinoderms (megafauna) have the largest (Table 2). On average, however, and with fishes considered on their own, megafauna do show a higher mean r^2 than do macrofauna. Thus, while large species do not necessarily have ranges greater than those of small ones, the null model does fit megafauna in general better than it does fit macrofauna. Nonetheless, as evidenced by the wide range of r^2 values, each major group relates differently to the null model. Fishes, for example, are usually considered as megafauna but have the lowest r^2 value obtained.

In all but the three groups with the lowest numbers of taxa (Aplousobranchia, Cnidaria and Porifera), the probability that a randomly generated model might fit the empirical distribution was 0 (Table 3). Thus, species richness patterns in virtually all benthic groups from the Gulf of Mexico are non-random, and further exploration for physical/biological factors to explain the patterns observed is justified. Furthermore, because of the wide range of phyla studied here, and the conclusions from other studies (Pineda and Caswell, 1998; McClain and Etter, 2005; Kendall and Haedrich, 2006), it seems apparent that non-random distributions of richness across the depth gradient are the rule in the deep-sea rather than the exception.

Etter and Grassle (1992) have shown that macrofaunal richness is higher in sediments with greater heterogeneity in grain size. Levin and Gage (1998) indicate no relationship with percent sand and clay, but found oxygen and sediment organic carbon concentrations to be negatively correlated with macrofaunal richness. Cosson-Sarradin et al. (1998) found a positive relationship of polychaete diversity with POC flux. Such results seem at odds with one another. Levin et al. (2001), from a rather broad-scale perspective, resolve the apparent conflict by offering a conceptual multivariate model of direct and indirect relationships among environmental factors and species richness, noting also that different groups and different situations might show varying responses. Snelgrove and Smith (2002), from a more fine-scale perspective, are even more emphatic in stating that “there is no single process that is responsible for the high diversity of deep-sea ecosystems”.

A graphical visualization (Figs. 2 and 3) helps to display the similarities and differences between phyla for the highest correlations in the four categories: food, habitat, pollution and location. If the factors identified were similar between phyla, the areas and shapes created by connecting the values on the four axes of the star plot would all tend to appear the same. This is scarcely the case. Amphipods, cumaceans and polychaetes display respectable areas of somewhat similar shape (Fig. 2), but the rest occupy only relatively small portions of the space in various orientations. Macrofauna (Fig. 2) appear to be more influenced than megafauna (Fig. 3) by the factors that comprise the four categories. But these visualizations are intended strictly as aids in

comparison and show only the maximum correlations. Considering all correlations that emerged as significant in the GLM (Appendix Table A1), the number of factors is independent of whether the phylum is macrofauna or megafauna.

While the strength and signs of the correlations of Appendix Table A1 and the individual factors involved invite speculation, the main message again is that the correlates of species richness vary a great deal from taxon to taxon. Levin et al. (2001) implied that this might prove to be the situation and Rex et al. (2000) characterized current explanations for latitudinal gradients as “stubbornly enigmatic”. The results of our quantitative, statistically based study support the more empirically based view that there is no common environmental factor to be invoked. Broad-scale reviews of sediment–animal relationships (Snelgrove and Butman, 1994) and productivity vs diversity (Mittelbach et al., 2001) come to a similar conclusion. Multiple factors clearly influence richness patterns (Snelgrove and Smith, 2002), and these can vary a great deal from group to group. Even at the level of the broad categories—food, habitat, pollution and location—the relationships by group are very different in their individual detail (Table 4, Figs. 2 and 3).

Nonetheless, the highest correlations are found in the food column (Table 4). The idea of a relationship between productivity and species richness has been around for a long time (Mittelbach et al., 2001), and is re-cast recently by Rex et al. (2005) with the suggestion that productivity and history together contribute to observed patterns. This view could explain our findings for the northern Gulf of Mexico. None of these various faunas have co-evolved in situ and the total fauna is only a local mixture of species that have very different evolutionary histories, including radiations in and dispersal from centers that span the oceans. Such a situation is evident in the deep-benthic fauna of Newfoundland where the fishes have the strongest links to the fauna of the east coast of North America to the southwest, and the echinoderms have their strongest link across the Atlantic to the faunas of northern Europe (Haedrich and Maunder, 1985). With respect to pelagic mid-water fishes, it can as well be argued that the Gulf of Mexico is an ecotone between well-defined tropical and sub-tropical faunas (J.L. Bangma, Hopkins Marine Station, personal communication).

One aim of the DGoMB study was to determine whether there were a few over-arching parameters that could be measured to give some sense of the status of the deep-sea ecosystem. Because the study was done prior to expanding oil and gas exploration in the region, for which an environmental assessment would be required, there was a very practical reason behind this. Our results suggest that, at least from a faunal perspective, a few simple measurements will probably not suffice.

On the other hand, biodiversity itself reflects a number of valued ecosystem services (Worm et al., 2006), so mapping richness on its own can be a worthwhile exercise. In the northern Gulf of Mexico, the shallow portion of the Mississippi Trough is a center of maximum richness. There were 269 macrofaunal species including 34 cumaceans and 153 polychaetes reported from Sta. MT3 (983 m), and 87 megafaunal species including 29 fishes, 21 arthropods and 18 echinoderms from Sta. MT1 (483 m). Slightly west of the Trough, maxima of 34 cumaceans and 37 isopods were recorded at Sta. C4 (1450 m). As commercial development proceeds, these are areas that should receive special consideration and possible protection.

Acknowledgements

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Table A1

Summary data: significant factors (from GLM, $p \leq 0.05$), the category to which each was assigned and Spearman rank correlation with richness for each group

Factor	Category	APLAC	AMPH	BIV	CUMAC	ISOP	POLY	FISHES	ARTHRO	ECHINO	MOLL	CNID	PORIF
POC	Food	-0.33	-0.02	-0.06	-	-0.36	-0.14	-	-	-	0.09	-	-
PON	Food	-	-	-	-	-	-	-	0.06	-	0.05	-	-0.03
Meiobiomass	Food	-	0.78	-	0.57	-	0.80	-	0.20	-	-	-	-
Biomass, no nematodes	Food	-	0.67	-	-	-	-	0.59	-	-	-0.17	-0.10	-
Chl α	Food	-	-	-0.09	-	-	-	-	0.01	0.21	-0.40	-	0.14
Macrobioass	Food	-	-	-	-	-	-	0.61	0.04	-	-0.02	-	0.01
Silt	Habitat	-	0.26	0.32	-	0.10	0.15	-	0.05	-	-	-	-
Sand	Habitat	-	0.09	-0.04	0.12	0.16	0.03	-	0.15	-	-	-	-
Clay	Habitat	-	-0.22	0.01	-	-0.03	-0.15	-0.06	-0.25	-	-0.18	-	-
O ₂	Habitat	-0.44	-	-	-	-	-	-	-0.17	-	-0.01	-	-
NH ₄	Habitat	-	-	-	-	-	-	-	-	-0.14	-	-	-
Latitude	Location	-	0.56	0.13	0.64	0.01	0.66	-	-	0.13	-	-	-
Longitude	Location	-	0.06	-0.09	-	-0.06	0.22	0.26	-	-	0.13	-	-
Depth	Location	-0.52	-0.79	-	-	-	-	-	-0.05	0.18	-0.03	0.24	-
Region	Location	-	0.03	-	-	-	-	-	0.04	-	-0.03	-	-
Perylene	Pollution	-	-	-0.26	-	-	-	-	-	-	-	-	0.04
Barium	Pollution	-	-	0.44	0.21	-	-	-	-0.12	-	-	-	-0.16
tPAH, no perylene	Pollution	0.06	-	-	-0.06	-	0.09	0.19	0.01	-	-0.0003	0.25	-
Fauna		Macro	Macro	Macro	Macro	Macro	Macro	Mega	Mega	Mega	Mega	Mega	Mega
Number of factors	18	4	10	9	5	6	8	5	12	4	11	3	5

Dashed lines indicate non-significant correlations.

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Appendix A

See Table A1.

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