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PAPER



Connecting species richness, abundance and body size in deep-sea gastropods

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ABSTRACT

Aim This paper examines species richness, abundance, and body size in deep-sea gastropods and how they vary over depth, which is a strong correlate of nutrient input. Previous studies have documented the empirical relationships among these properties in terrestrial and coastal ecosystems, but a full understanding of how these patterns arise has yet to be obtained. Examining the relationships among macroecological variables is a logical progression in deep-sea ecology, where patterns of body size, diversity, and abundance have been quantified separately but not linked together.

Location 196–5042 m depth in the western North Atlantic.

Method Individuals analysed represent all Vetigastropoda and Caenogastropoda (Class Gastropoda) with intact shells, excluding Ptenoglossa, collected by the Woods Hole Benthic Sampling Program (3424 individuals representing 80 species). Biovolume was measured for every individual separately (i.e. allowing the same species to occupy multiple size classes) and divided into \log_2 body size bins. Analyses were conducted for all gastropods together and separated into orders and depth regions (representing different nutrient inputs). A kernel smoothing technique, Kolmogorov-Smirnov test of fit, and OLS and RMA were used to characterize the patterns.

Results Overall, the relationship between the number of individuals and species is right skewed. There is also a positive linear relationship between the number of individuals and the number of species, which is independent of body size. Variation among these relationships is seen among the three depth regions. At depths inferred to correspond with intermediate nutrient input levels, species are accumulated faster given the number of individuals and shift from a right-skewed to a log-normal distribution.

Conclusion A strong link between body size, abundance, and species richness appears to be ubiquitous over a variety of taxa and environments, including the deep sea. However, the nature of these relationships is affected by the productivity regime and scale at which they are examined.

Keywords

Abundance, body size, deep sea, gastropods, macroecology, North Atlantic, productivity gradient, species richness.

INTRODUCTION

'Body size is one of the most important axes of biological diversity.' (Brown & Lomolino, 1998; p. 508)

Exploring how body size influences community structure in terms of species' abundances and species richness has pervaded the ecological literature. However, few studies have simultaneously documented the association between species richness,

abundances, and body size (terrestrial arthropods: Siemann *et al.*, 1996, 1999; marine gastropods: Fa & Fa, 2002). These findings have significant implications for how we assess global biodiversity. Yet the generality of these patterns and the mechanisms by which they arise have not been fully examined. Here, I focus on a deep-sea gastropod community over a depth gradient, which affords the opportunity to test both the ubiquity of these trends and how they vary over a productivity gradient.

Research in terrestrial habitats continues to establish the relationships between abundance, richness, and size trends. Previous studies support the idea that species richness and population abundance are related to body size (Warwick & Clarke, 1996; Blackburn *et al.*, 1997; Gaston *et al.*, 1997; Siemann *et al.*, 1999). In general, on coarse scales, the relationship between abundance and size is negative (Damuth, 1981; Cotgreave, 1993; Currie, 1993; Brown, 1995; Enquist *et al.*, 1998). On local scales, the relationship is log-normal or log-uniform (Brown & Nicoletto, 1991; Currie, 1993; Siemann *et al.*, 1996; Warwick & Clarke, 1996). The relationship between species richness and body size, although not as thoroughly researched, exhibits both negative (Morse *et al.*, 1985; May, 1988; Blackburn & Lawton, 1994) and unimodal trends (Brown, 1995; Siemann *et al.*, 1996; Navarette & Menge, 1997; Siemann *et al.*, 1999). Several theories exist to explain these relationships including: trade-offs between metabolic efficiency and reproductive success (Brown *et al.*, 1993), habitat heterogeneity (May, 1986), self-thinning (Stevens & Carson, 1999), density compensation (Marquet *et al.*, 1990), extinction and mobility (Ebenman *et al.*, 1995), fractal distribution of resources (Ritchie & Olff, 1999), and the energetic equivalence rule (Cotgreave, 1993).

Despite the vast size of the deep sea, contemporary research has only quantified conspicuous macroecological trends in body size, abundance, and species diversity separately. These trends typically have been related to depth and correlated environmental variables. Several studies have described the unimodal trend

between species diversity and depth, in which diversity peaks at intermediate depths (Rex, 1973, 1981; Etter & Grassle, 1992). Abundance, however, declines exponentially with increasing depth (Rex *et al.*, 1990). Many early studies noted size extremes, gigantism and dwarfism, in deep-sea taxa. Thiel (1975) provided the first quantitative assessment, documenting that abundances of the smaller meiofauna decrease less rapidly with depth than abundances of the larger macrofauna. Additional studies have produced mixed results (reviewed in Rex & Etter, 1998), with many reporting increasing size with depth within and among species (Rex & Etter, 1998; Rex *et al.*, 1999; McClain & Rex, 2001).

METHODS

The individuals analysed in this study represent all vetigastropods and caenogastropods with intact shells, excluding Ptenoglossa, collected from the western North Atlantic by the Woods Hole Benthic Sampling Program (Sanders, 1977). Ectoparasitic ptenoglossates were eliminated because of their equivocal taxonomic affinity (Fretter & Graham, 1962; Ponder & Lindberg, 1997) and fundamentally different lifestyle. The remaining dataset still represents a diverse assemblage, including representatives of the families Trochidae and Seguenziidae in the Vetigastropoda and families Buccinidae, Cerithiopsidae, Muricidae, Olividae, Rissoidae, and Turridae in the Caenogastropoda.

Samples were taken from depths between 196 and 5042 m (Fig. 1) and contain 3424 individuals, representing 80 species. All

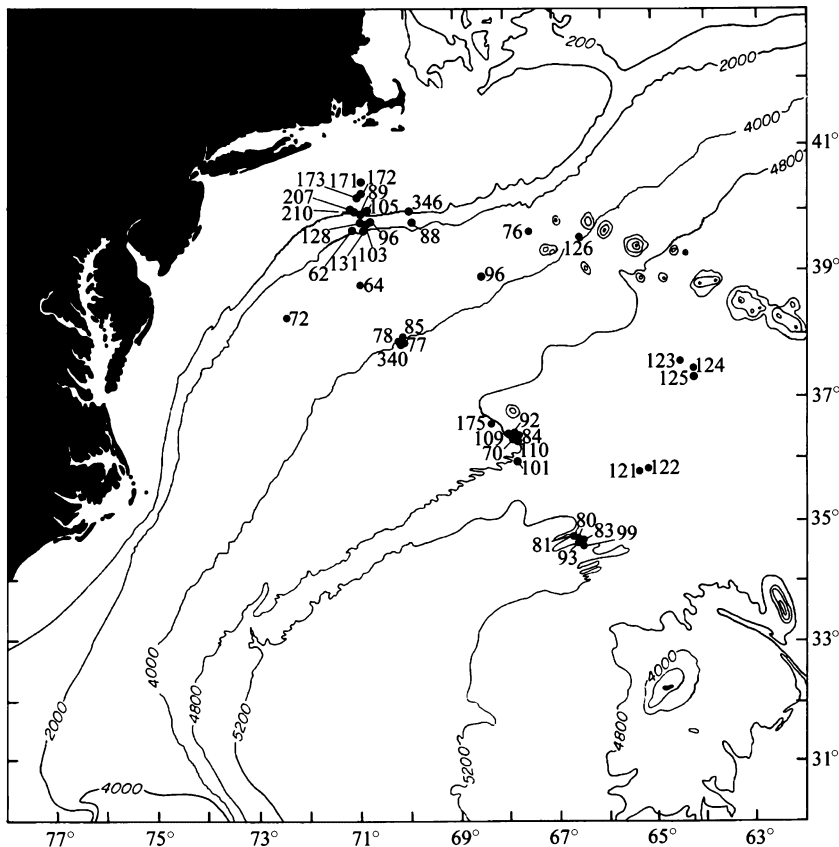


Figure 1 Map depicts positions of samples used in this study in the North-west Atlantic Ocean.

material was collected by using epibenthic sleds and anchor dredges with mesh sizes of 1 mm. The macrofaunal component was collected on a 0.420-mm sieve (Hessler & Sanders, 1967). There is considerable uncertainty about the effectiveness of deep-sea sampling, but the molluscs, in general, appear not to be affected by sampling inconsistencies as are other deep-sea fauna. The heavy fraction of material collected by the dredge, of which gastropods with their calcified shells are a part, are less likely to be excluded due to bow wave compression effects. They are also less subject to winnowing as the gear approaches the surface than other groups with lower densities. These observations are supported by evidence that different sampling gears provide consistent results for molluscs (Rex *et al.*, 1990). It is also important to note that although epibenthic sleds and anchor dredges provide only semiquantitative data, as long as relative abundances among size classes are accurate, the analyses presented herein are permissible.

Previous studies have used a single estimate of size for each species, whether it is an average or maximum size (e.g. Siemann *et al.*, 1996, 1999). Partly this reflects the difficulty of measuring body size for all individuals in an entire community. In addition, hypotheses of body size are often specific about constraints on maximum size (McClain & Rex, 2001). However, the choice of body size metric can have a drastic effect on the observed patterns (McClain & Rex, 2001). It is also important to consider that individuals of species within a community are not all the same size, and size distributions within a species can vary over environmental gradients, including in the deep sea (e.g. McClain & Rex, 2001). An individual of a species may actually never reach the maximum size or only spend a small percentage of its lifespan at this size. Moreover, indeterminate growers, such as some of the species considered herein, typically occupy a broad range of size classes, making a single-size approach inappropriate. Because the size changes over the lifespan of individual, size-dependent interactions also vary over the lifespan of animal. It is important to determine how the use of differing size metrics might influence the results. I undertook a preliminary analyses using first a single estimate of size for each species ($n = 80$) and second, including each individual separately ($n = 3424$), i.e. allowing the same species to occupy multiple size classes. Both methods gave similar results and so I only present and discuss the results using the second data set.

Images were obtained by using a Spot RT digital camera connected to a Nikon SMZ1000 dissection scope. Digital images were analysed and imaged on a Macintosh G4 using Spot Advanced software. Biovolume (B) was measured for every individual, such that $B = l \times w^2$ (Siemann *et al.*, 1996, 1999) where l is length and w is width. Although this calculation is a crude measure of volume, the error is minor relative to the differences in size among the specimens. Other methods of estimating shell volume exist (e.g. Raup & Graus, 1972), but were not used because they include measurements that require sectioning of shells, which is not feasible with the smaller species in a sample or with museum specimens. In addition, the range of shell forms here was not suitable for the measurement methodology.

The number of species and individuals in a sample were aggregated into \log_2 body size bins (size classes are: 1: -3 to -2, range

0.125–0.25 mm³; 2: -2 to -1, 0.25–0.5 mm³; 3: -1 to 0, 0.5–1 mm³; 4: 0–1, 1–2 mm³; 5: 1–2, 2–4 mm³; 6: 2–3, 4–8 mm³; 7: 3–4, 8–16 mm³; 8: 4–5, 16–32 mm³; 9: 5–6, 32–64 mm³; 10: 6–7, 64–128 mm³; 11: 7–8, 128–256 mm³; and 12: 8–9, 256–512 mm³). The individuals here range in size from 0.19 mm³ to 501.42 mm³. Separate analyses were conducted for both orders (Vetigastropoda and Caenogastropoda). I separated the dataset into three bathymetric regions (continental slope 200–2000 m, continental rise 2000–4000 m, and the abyssal plain > 4000 m) that represent high, medium, and low productivity regimes (Etter & Mullineaux, 2001). Although these regions do not contain equal depth coverage, they are generally considered to be biogeographic regions with differing benthic faunas and environmental variables (Gage & Tyler, 1991). A kernel smoothing technique was utilized to describe the relationship between species and individuals among \log_2 size classes. Deviation from a log-normal distribution was tested using a Kolmogorov-Smirnov test of fit. A nonparametric procedure was used because the arbitrary location and width of classes might influence the results. Previous studies (Siemann *et al.*, 1996, 1999; Fa & Fa, 2002) have demonstrated that the relationship between the number of species (S) and number of individuals (I) can be defined by the power function $S = cI^{0.5}$, derived from a broken-stick model, or $S = cI^{0.25}$ from a canonical log-normal distribution, where c is a constant. Both OLS and RMA regression have been used previously in the literature to characterize the power function. The two methods often give different slopes and intercepts (LaBarbera, 1989). Because of the ease of implementation, I use both to quantify a power function describing the relationship between number of species and number of individuals within a size class.

RESULTS

When all included species from the western North Atlantic are combined, there are strong relationships among $\log S$, $\log I$, and \log_2 size class (Fig. 2). The number of species and individuals peak in similar size classes ($\log S$: KS $P = 0.0012$, skewness (g_1) = 4.67; $\log I$: KS $P = 0.0324$, skewness (g_1) = 4.17). There is a significant, positive power function between $\log S$ and $\log I$.

These patterns exhibit slight variations among depth regions. Peak abundances and number of species shift among depth regions, with the modal size classes being larger on the rise (Fig. 3). All three depth regions display some evidence of a right-skewed distribution (Slope: KS $P = 0.0238$, skewness (g_1) = 2.97; Rise: KS $P = 0.3249$, skewness (g_1) = 2.21; Abyss: KS $P = 0.0021$, skewness (g_1) = 5.23) and individuals (Slope: KS $P = 0.0045$, skewness (g_1) = 3.25; Rise: KS $P = 0.4363$, skewness (g_1) = 1.97; Abyss: KS $P = 0.0001$, skewness (g_1) = 6.5833). An ANCOVA detects no differences among the slopes between $\log I$ and $\log S$ (Fig. 4, d.f. = 2.32, $F = 1.556$, $P = 0.2293$).

For both taxonomic orders, peak abundance occurs in approximately similar size classes (Fig. 5, Vetigastropoda: KS $P = 0.0217$, skewness = 3.13; Caenogastropoda: KS $P = 0.0013$, skewness = 3.85). However, the curve for $\log S$ peaks at a slightly smaller size class for vetigastropods (Fig. 5, Vetigastropoda: KS $P = 0.0014$,

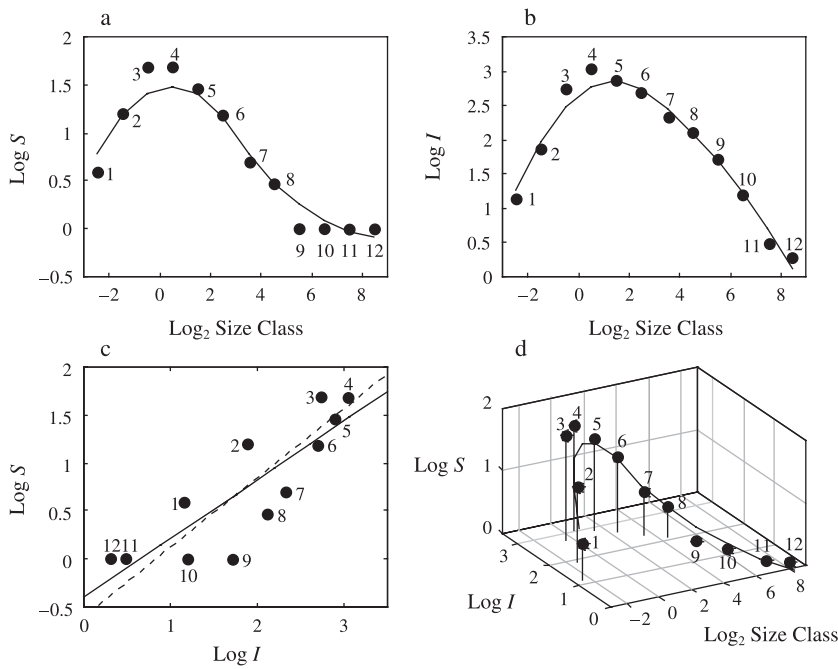


Figure 2 (a) Relationship of the log of species richness (S) per \log_2 size class where size = shell volume in mm^3 . The line represents a kernel smoothing curve fitted to the data. Numbers refer to the \log_2 size classes (see Methods for class size ranges). (b) Relationship of the log of number of individuals (I) per \log_2 size class. The line represents a kernel smoothing curve fitted to the data. (c) Relationship between log of species richness (S) and log of number of individuals (I) per \log_2 size class. The line represents a fitted regression (OLS: $S = -0.406I^{0.616}$, $R^2 = 0.719$, $P = 0.0005$; RMA: $S = -0.613I^{0.726}$, $R^2 = 0.848$, $P = 0.0500$). (d) Relationships between log of species richness (S), log of number of individuals (I), and \log_2 size class. The curve represents the fitted kernel smoothing curve from A and B.

skewness = 4.91; Caenogastropoda KS $P = 0.0001$, skewness = 3.35).

DISCUSSION

These results add to the growing evidence for a general relationship, despite differences in taxonomic groups and environments, between species richness, abundance, and body size. However, the relationship between the number of species and body size in North-west Atlantic gastropods in this study is right skewed as opposed to the log-normal relationships reported for terrestrial arthropods (Siemann *et al.*, 1996, 1999) and coastal gastropods (Fa & Fa, 2002). Here, the number of individuals and species are highest in the third to fifth size classes, similar to tropical molluscs in New Caledonia (Bouchet *et al.*, 2002), but in contrast to the intermediate and larger size classes (Roy *et al.*, 2000; Fa & Fa, 2002) reported for some coastal molluscs. The correspondence in modal size class for the number of individuals and species may arise because of the strong correlation between the number of individuals and number of species within a size class. The number of species scales to the number of individuals as $S = cI^{0.616}$, a finding similar to that of Siemann *et al.* (1996, 1999) for grassland arthropods. However, there is some variation, although not significant, in the exponent among the depth regions. This disparity in the scaling factor is also seen among taxonomic orders in the results of Siemann *et al.* (1996). The modal size class for number of individuals and number of species also displays some variation among depth regions.

The right-skewed relationship for the number of species among size classes at the regional level appears to be ubiquitous over an assortment of organisms and habitats (reviewed in Brown, 1995). Numerous models have attempted to explain this pattern (e.g. Hutchinson & MacArthur, 1959; Brown *et al.*, 1993;

Kozłowski & Gawelczyk, 2002). It is likely that that the right skew in body size distributions reflect multiple influences. Currently, the data do not exist to allow direct testing of any proposed mechanisms by which these relationships arise.

At smaller scales, decomposing the regional relationship into depth zones, the right-skewed trend begins to break down. In all three regions the curves represent an intermediate between a log-normal and a right-skewed distribution. These findings are consistent with those of Brown & Nicoletto (1991) for terrestrial mammals (see also Marquet & Cofre, 1999; Bakker & Kelt, 2000). Their findings demonstrate a movement from a right-skewed trend at the biome level to a uniform distribution at the patch level. Although, this study does not examine patch size scales, a trend away from the right-skewed regional relationship is observed. The breakdown of the trend at finer scales in other systems has been attributed to higher spatial turnover in species of the modal size classes (Brown & Nicoletto, 1991). This suggests that these modal-sized species occupy narrower ranges and may be more specialized than their larger or smaller counterparts (Brown, 1995). For the deep-sea gastropods here, depth range sizes show no distinctive pattern over body size classes, suggesting that modal-size species are not more specialized. Although depth may serve as the important geographic gradient for deep-sea species, it should be noted that depth represents only one axis of species distributions. Not accounting for latitudinal and longitudinal gradients, and limited deep-sea sampling, may account for the lack of a size/range trend.

In most of the deep sea, apart from chemosynthetic communities (Van Dover, 2000), organisms rely on the import of organic material from surface production to the sea floor for food. Energy flux to the benthos displays both latitudinal, depth, and offshore gradients (Rowe & Pariente, 1992). This nutrient input controls a species' density, body size, growth, life history, and

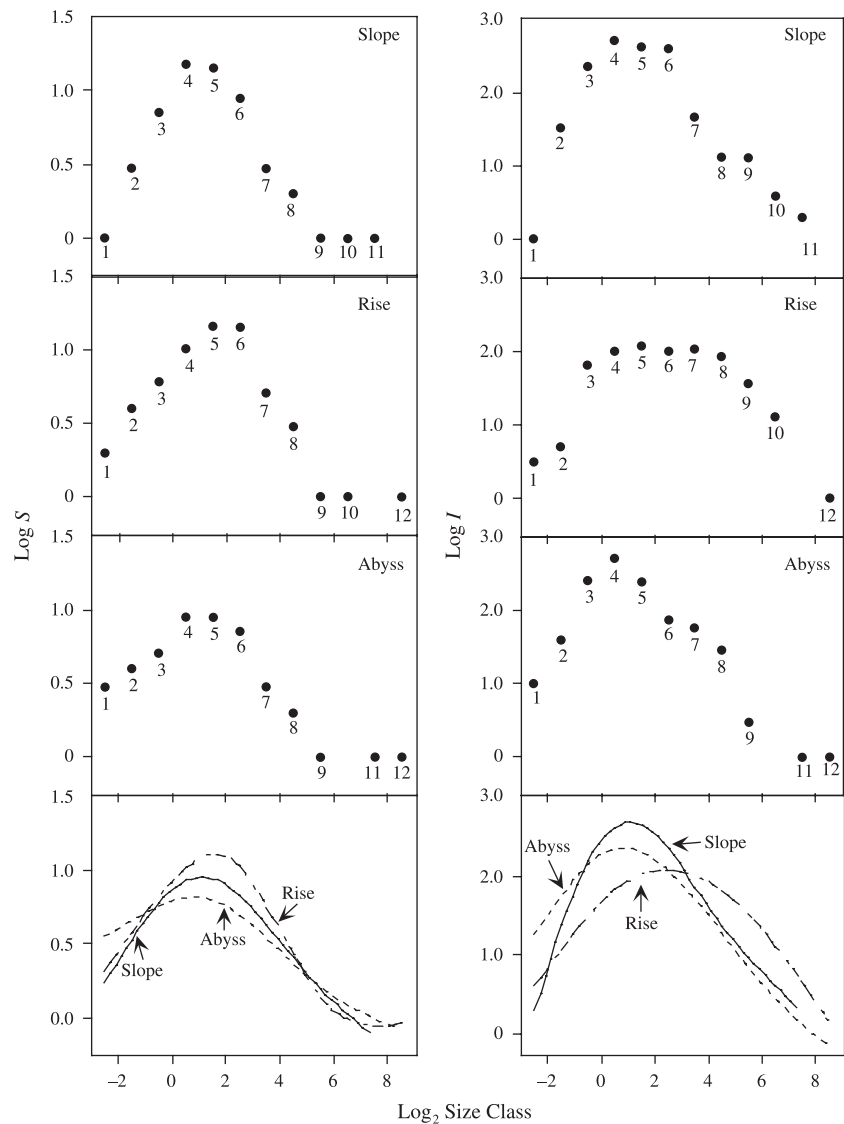


Figure 3 Relationship of the log of number of species (S) and individuals (I) per \log_2 size class (mm^3) for slope (200–2000 m), rise (2000–4000 m), and abyss (> 4000 m). Numbers refer to the \log_2 size classes (see Methods for class size ranges). The lines represent kernel smoothing curves fitted to the data.

physiology (Gage & Tyler, 1991). Through the regulation of these energetic factors, it is feasible that organic input could direct the equitability of relative abundances among species, species makeup, and the number of species. Some differences in the distribution of species and individuals among size classes do exist among the slope, rise, and abyss, indicating that depth and possibly the rate of carbon flux to the benthos (Etter & Mullineaux, 2001) is related to how body size, abundance, and species richness interrelate. At the slope and rise (high and low nutrient input), a right-skewed trend is observed, but at intermediate levels, the relationship is log normal. The exact mechanism by which energy flux into a system could dictate these relationships is still not completely understood and would be speculative at this time. However, recent advances in spatial scaling theory have inter-related the availability of niches, productivity, area, body size, and species diversity (Ritchie & Olff, 1999; Haskell *et al.*, 2002).

Sampling procedure may have an influence on the distribution of individuals and species among size classes. It has been suggested in previous studies (e.g. Currie, 1993) that the

right-skewed relationship exists because of the undersampling of smaller species. This is especially relevant in the deep-sea where remote and limited sampling raises questions about the reliability of detected trends. In most deep sea studies a mesh size of 300–420 μm is used to separate the macrofaunal component, which includes the gastropods in this study. This sieve size often retains individuals smaller than 300 μm mesh. The results of this study indicate that most individuals are larger than 2.5 mm. This sieve size aperture adequately samples extremely rare and small species such as *Palazzia planorbis* (Rex, 2002). This suggests that the patterns observed herein are not likely to be an artifact of too coarse a mesh size.

This is the first time the association between body size, abundance, and number of species has been characterized in the deep sea or over a presumed productivity gradient. This work corroborates the observation, by Siemann *et al.* (1996), that the relationship between the number of species and the number of individuals may be independent of body size. However, it should be acknowledged that there is some variation in this relationship

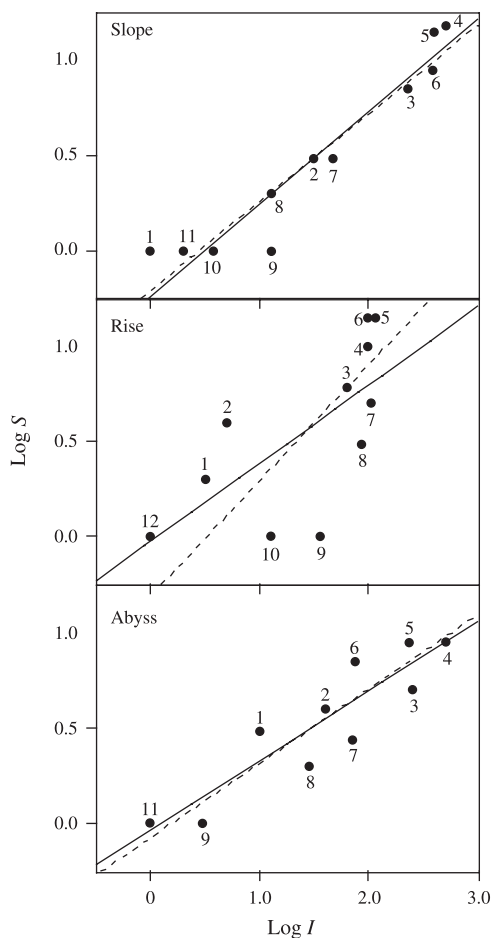


Figure 4 Relationship between log of species richness (*S*) and log of number of individuals (*I*) per \log_2 size class. Numbers refer to the \log_2 size classes (see Methods for class size ranges). The solid lines are the fitted OLS regressions (Slope: $S = -0.210I^{0.465}$, $R^2 = 0.9130$, $P > 0.0001$. Rise: $S = -0.027I^{0.411}$, $R^2 = 0.460$, $P = 0.0218$. Abyss: $S = -0.035I^{0.364}$, $R^2 = 0.870$ $P < 0.0001$) and dashed lines are the fitted RMA regressions (Slope: $S = -0.242I^{0.487}$, $R^2 = 0.956$, $P > 0.0050$. Rise: $S = -0.305I^{0.605}$, $R^2 = 0.678$, $P = 0.0050$. Abyss: $S = 0.072I^{0.390}$, $R^2 = 0.933$, $P = 0.0050$).

between taxa and depth; and it is unclear how body size relates to this. Although numerous studies have found unimodal trends between number of species and individuals across size classes (Siemann *et al.*, 1996 and references within), the present work adds to the growing body of evidence of a right-skewed relationship. I tentatively suggest that the variation in the form of this relationship may in part reflect differences in scales of the studies or productivity input into the community. Because there are differences among habitats and taxa, it is interesting that a similar right-skewed trend in the number of species among size classes is seen in groups as different as deep-sea invertebrates presented here and terrestrial mammals (Brown & Nicoletto, 1991). Hypotheses about how size, abundance, and diversity interact should, if they are to be general, include factors that apply to deep-sea assemblages. Numerous studies suggest that one common underlying factor among all these environments is the strong

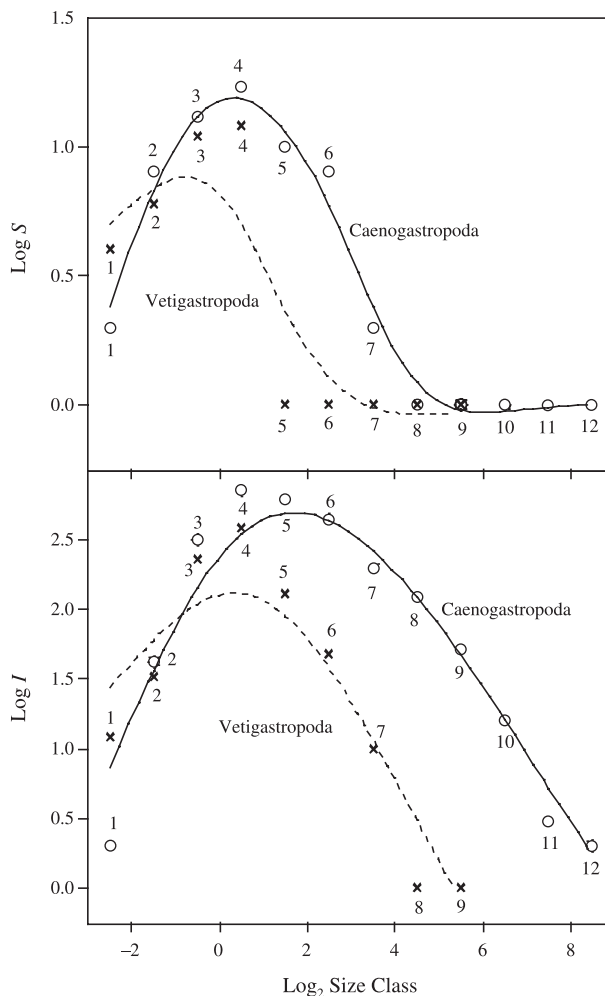


Figure 5 Relationship of the log of number of individuals (*I*) and the log of species richness (*S*) per \log_2 size class (mm^3) for vetigastropods and caenogastropods. Numbers refer to the \log_2 size classes (see Methods for class size ranges). The lines represent kernel smoothing curves fitted to the data.

influence of nutrient input on community structure (Ricklefs & Schluter, 1993). The results presented herein indicate that depth, a correlate of productivity, may affect body size, abundance, and species diversity. It is likely that the relationship between these three variables is affected by the overall amount of and variance in energy flow into the assemblage.

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BIOSKETCH

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